CHAPTER 16

Population Genetics and Speciation

Sexual selection, which is one variation of natural selection, influences the development of extreme phenotypic traits in some species. The vibrant red stripe on the blue muzzle of this male mandrill baboon, *Mandrillus sphinx,* does not appear in females.

GENETIC EQUILIBRIUM

By the time of Darwin's death, in 1882, the idea of evolution by natural selection had gained wide acceptance among scientists. Within the next century, an increasing scientific understanding of genetics became strongly linked with theories of evolution and natural selection.

SECTION 1

OBJECTIVES

- **Identify** traits that vary in populations and that may be studied.
- **Explain** the importance of the bell curve to population genetics.
- **Compare** three causes of genetic variation in a population.
- **Calculate** allele frequency and phenotype frequency.
- **Explain** Hardy-Weinberg genetic equilibrium.

VOCABULARY

population genetics
microevolution
bell curve
gene pool
allele frequency
phenotype frequency
Hardy-Weinberg genetic equilibrium

VARIATION OF TRAITS WITHIN A POPULATION

Population genetics is the study of evolution from a genetic point of view. Evolution at the genetic level is sometimes called **microevolution,** defined as a change in the collective genetic material of a population. Recall that the genetic material of organisms consists of many alleles—or variations—of many genes that code for various traits. Recall that a population consists of a group of individuals of the same species that routinely interbreed. Populations are important to the study of evolution because a population is the smallest unit in which evolution occurs.

Within a population, individuals may vary in observable traits. For example, fish of a single species in a pond may vary in size. Biologists often study variation in a trait by measuring that trait in a large sample. Figure 16-1 shows a graph of the frequency of lengths in a population of mature fish. Because the shape of the curve looks like a bell, it is called a **bell curve.** The bell curve shows that whereas a few fish in this population are very short and a few are very long, most are of average length. In nature, many quantitative traits in a population—such as height and weight—tend to show variation that follows a bell curve pattern.

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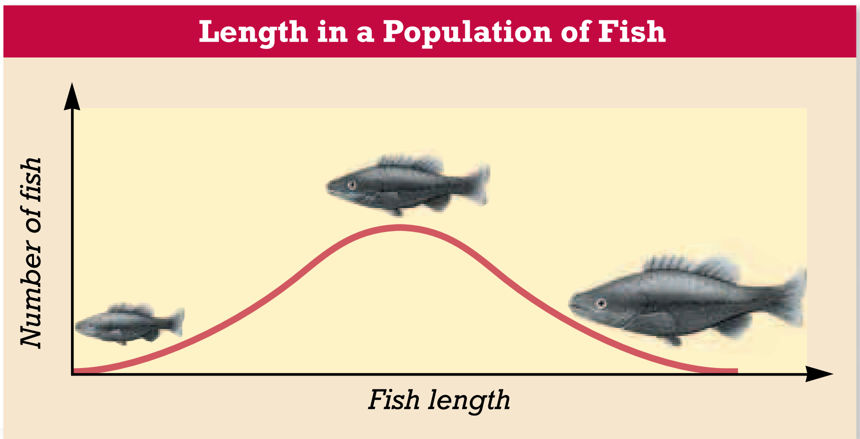


FIGURE 16-1

A bell curve illustrates that most members of a population have similar values for a given, measurable trait. Only a few individuals display extreme variations of the trait.

FIGURE 16-2

Many varied but similar phenotypes occur within families because members of a family share some alleles but not others.

Causes of Variation

What causes variation in traits? Some variations are influenced by environmental factors, such as the amount or quality of food available to an organism. Variation is also influenced by heredity. Some variations occur as a range of phenotypic possibilities (such as a range of body sizes), whereas others occur as a set of specific phenotypes (such as two possible flower colors).

To consider variability, think about phenotypes within a single human family. Two parents, each with a distinct genotype, may produce several children. In the picture of the family in Figure 16-2, the two young-adult brothers are not identical to each other, even though their genotypes are combinations of the genotypes of the same two parents. Both young men resemble their father, though in different traits. The baby resembles his young father, his grandfather, and his uncle. Thus, these males representing three generations look similar but not identical.

What causes genes to vary? Variations in genotype arise in three main ways. (1) *Mutation* is a random change in a gene that is passed on to offspring. (2) *Recombination* is the reshuffling of genes in a diploid individual. Recall that recombination occurs during meiosis by independent assortment and crossing-over of genes on chromosomes. (3) The *random pairing of gametes* occurs because each organism produces large numbers of gametes. So, the union of a particular pair of gametes is partly a matter of chance.

Scientists are still exploring other causes of variation in traits. For example, the expression of some genes depends upon the presence or absence of other genes or factors in the environment. The net result of having many alleles of many genes is the variety of unique genotypes and phenotypes that we see in populations.

THE GENE POOL

Population geneticists use the term **gene pool** to describe the total genetic information available in a population. It is easy to imagine genes for the next generation as existing in an imaginary pool. If you could inventory this pool and know all of the alleles that are present, then you could apply a simple set of rules based on probability theory to predict expected genotypes and their frequencies for the next generation.

Suppose, for example, that there are two alleles of a hypothetical gene, *A* and *a*, in a set of 10 gametes. If half the gametes in the set (5 gametes) carry the allele A, we would say that the allele frequency of the *A* allele is 0.5, or 50 percent. **Allele frequency** is determined by dividing the number of a certain allele (five instances of the *A* allele) by the total number of alleles of all types in the population (10 gametes, each with either an *A* or an *a* allele). Remember that a gamete is haploid and therefore carries only one allele for each gene.

Predicting Phenotype

The population of four o'clock flowers, shown in Figure 16-3, illustrates how phenotype can change from generation to generation. Homozygous *RR* flowers are red. Homozygous *rr* flowers are white. Heterozygous *Rr* flowers are pink rather than red, as you might expect. These flowers show incomplete dominance for color, meaning heterozygotes show a trait that falls between the dominant trait and the recessive trait. Thus, homozygotes and heterozygotes can be easily identified by observing the phenotype.

Compare the parent generation with the offspring generation of the four o'clock flowers shown in Figure 16-3. There are equal numbers of plants with the *RR* genotype and the *Rr* genotype in the first generation. You can compute the phenotype frequencies from the figure. A **phenotype frequency** is equal to the number of individuals with a particular phenotype divided by the total number of individuals in the population. Phenotype frequencies in the first generation are 0.5 pink (4 pink plants out of a total of 8 plants), 0.5 red (4 red plants out of a total of 8 plants), and 0.0 white. Recall that allele frequencies are computed using the same principle: the allele frequencies in the first-generation plants are 0.75 *R* (12 *R* alleles out of a total of 16 alleles) and 0.25 *r* (4 *r* alleles out of a total of 16 alleles).

We now can predict the genotypes and phenotypes of the second generation. If a male gamete encounters a female gamete, they will produce a new four o'clock plant whose genotype is the combination of both parental gametes. Thus, an *R* male gamete combined with an *R* female gamete will produce a plant with the *RR* genotype, which has red flowers. According to the laws of probability, the chance of an *R* gamete (a single allele) meeting with another *R* gamete is the arithmetic product of their allele frequencies in the gene pool:

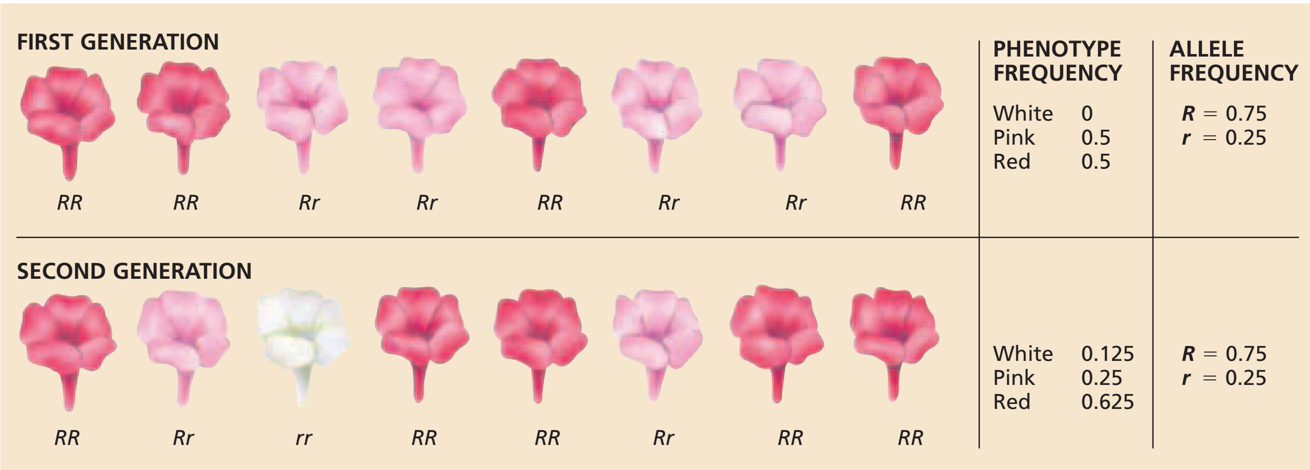
$$\text{frequency of } R \times \text{frequency of } R = \text{frequency of } RR \text{ pair}$$
$$0.75 \times 0.75 = 0.5625$$

The expected frequency of the *rr* genotype is then

$$\text{frequency of } r \times \text{frequency of } r = \text{frequency of } rr \text{ pair}$$
$$0.25 \times 0.25 = 0.0625$$

FIGURE 16-3

Although the four o'clock flowers differ phenotypically from generation to generation, the allele frequencies tend to remain the same.



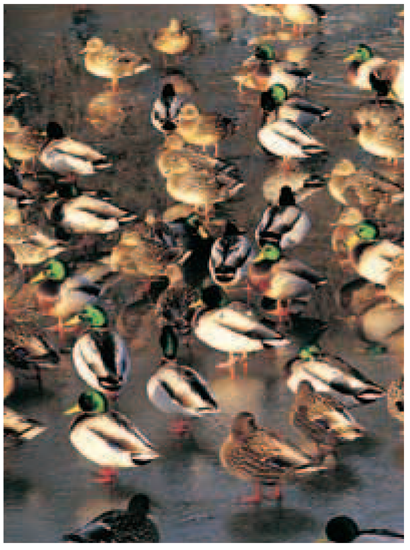


FIGURE 16-4

This flock of mallards, *Anas platyrhynchos*, likely violates some or all of the conditions necessary for Hardy-Weinberg genetic equilibrium.

The frequencies of all genotypes expected in the second generation must add up to 1.0, just as fractions of a whole must add up to 1. Having established the probabilities of getting an *RR* and an *rr* plant, we can compute the expected frequency of the *Rr* plants. All those plants that are neither *RR* nor *rr* will be *Rr*, so

$$1.0 - \text{frequency of } RR - \text{frequency of } rr = \text{frequency of } Rr$$
$$1.0 - 0.5625 - 0.0625 = 0.375$$

HARDY-WEINBERG GENETIC EQUILIBRIUM

It is clear from the example of the four o'clock flowers that phenotype frequencies can change dramatically from generation to generation. But what happens to allele frequencies over generations? A German physician, Wilhelm Weinberg (1862–1937), and a British mathematician, Godfrey Hardy (1877–1947), independently showed that genotype frequencies in a population tend to remain the same from generation to generation unless acted on by outside influences. This principle is referred to as **Hardy-Weinberg genetic equilibrium,** and it is based on a set of assumptions about an ideal hypothetical population that is not evolving:

1. No net mutations occur; that is, the alleles remain the same.
2. Individuals neither enter nor leave the population.
3. The population is large (ideally, infinitely large).
4. Individuals mate randomly.
5. Selection does not occur.

Bear in mind that true genetic equilibrium is a theoretical state. Real populations, such as the flock of mallards in Figure 16-4, may not meet all of the conditions necessary for genetic equilibrium. By providing a model of how genetic equilibrium is maintained, the Hardy-Weinberg principle allows us to consider what forces disrupt genetic equilibrium.

Word Roots and Origins

equilibrium

from the Latin *aequilibris*, meaning "equal balance"

SECTION 1 REVIEW

1. How does the distribution of traits in a population look when displayed as a graph?
2. Describe three causes of genetic variation in a population.
3. What is meant by the term *human gene pool*?
4. How is phenotype frequency computed?
5. What are the conditions that a population must meet in order to have genetic equilibrium?

CRITICAL THINKING

6. **Evaluating Methods** By observation only, is it easier to deduce the genotype of organisms for an allele that has complete dominance or incomplete dominance?
7. **Making Calculations** Half of a population of four o'clocks has red flowers, and half has white flowers. What is the frequency of the *r* allele?
8. **Relating Concepts** How does the pairing of gametes produce genotypic variation?

SECTION 2

DISRUPTION OF GENETIC EQUILIBRIUM

Evolution is the change in a population's genetic material over generations, that is, a change of the population's allele frequencies or genotype frequencies. Any exception to the five conditions necessary for Hardy-Weinberg equilibrium can result in evolution.

OBJECTIVES

- **List** five conditions under which evolution may take place.
- **Explain** how migration can affect the genetics of populations.
- **Explain** how genetic drift can affect populations of different sizes.
- **Contrast** the effects of stabilizing selection, directional selection, and disruptive selection on populations over time.
- **Identify** examples of nonrandom mating.

VOCABULARY

immigration
emigration
gene flow
genetic drift
sexual selection
stabilizing selection
disruptive selection
directional selection

MUTATION

The first requirement for genetic equilibrium is that allele frequencies not change overall because of mutations. Spontaneous mutations occur constantly, at very low rates under normal conditions. But if an organism is exposed to mutagens—mutation-causing agents such as radiation and certain chemicals—mutation rates can increase significantly. Mutations can affect genetic equilibrium by producing totally new alleles for a trait. Many mutations are harmful, although some have no effect. Because natural selection operates only on genes that are expressed, it is very slow to eliminate harmful recessive mutations. In the long run, however, beneficial mutations are a vital part of evolution.

GENE FLOW

The second requirement for genetic equilibrium is that the size of the population remains constant. If individuals move, genes move with them. **Immigration** is the movement of individuals into a population, and **emigration** is the movement of individuals out of a population.

The behavioral ecology of some animal species encourages immigration and emigration. Common baboons live on the savannas of eastern Africa in social and breeding groups called *troops.* A troop is dominated by a few adult males, and it may have from 10 to 200 members. Females tend to remain with the troop they are born into; however, younger or less dominant males leave their birth troop, eventually joining another troop. This constant movement of male animals ensures gene flow. **Gene flow** is the process of genes moving from one population to another. Gene flow can occur through various mechanisms, such as the migration of individuals or the dispersal of seeds or spores.

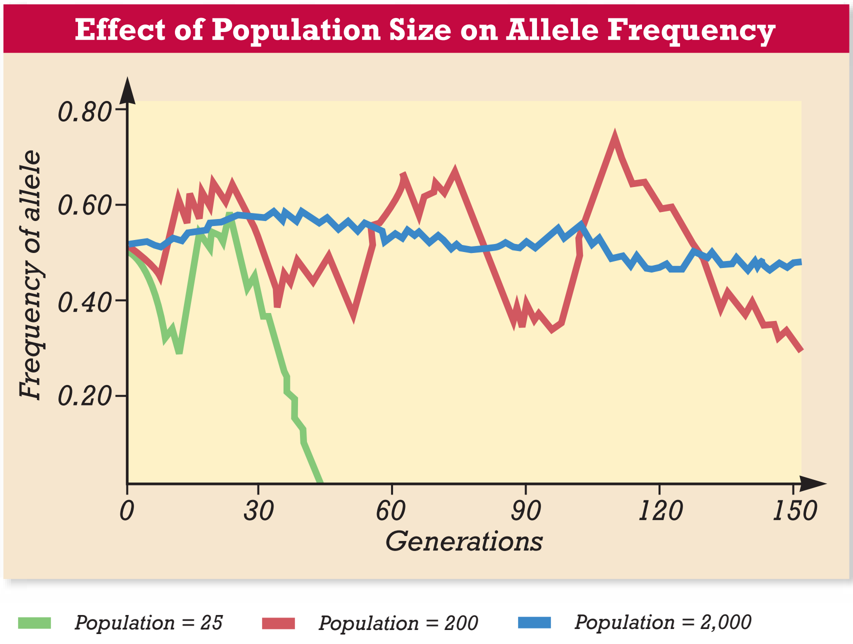
Word Roots and Origins

immigration

from the Latin *immigrare*, meaning "to go into"

FIGURE 16-5

Genetic drift is significant only in small and medium-sized populations. In a small population, a particular allele may disappear completely over a few generations. In a larger population, a particular allele may vary widely in frequency due to chance but still be present in enough individuals to be maintained in the population. In a much larger population, the frequency of a particular allele may vary slightly by chance but remain relatively stable over generations.



GENETIC DRIFT

The third requirement of genetic equilibrium is the presence of a large population. The Hardy-Weinberg principle is based on the laws of probability, which are less applicable to smaller populations. **Genetic drift** is the phenomenon by which allele frequencies in a population change as a result of random events, or chance. In small populations, the failure of even a single organism to reproduce can significantly disrupt the allele frequency of the population, as can greater-than-normal reproduction by an individual, resulting in genetic drift. Because it can result in significant changes within a population, genetic drift is thought to be another possible mechanism for the evolution of new species.

Figure 16-5 shows a graph of genetic drift in populations of three differing sizes. Small populations can undergo abrupt changes in allele frequencies, exhibiting a large degree of genetic drift, whereas large populations retain fairly stable allele frequencies, maintaining a small degree of genetic drift. In the smallest population shown in the graph, the frequency of the example allele reaches zero at about the 45th generation. If we assume that the population started with two alleles for a trait, then only one allele is left, and every individual is homozygous for that trait. Once this change happens, the population is in danger of becoming extinct because there is no variation for natural selection to act on. For example, a natural disaster or a new disease could wipe out the entire population. For this reason, endangered species, such as the northern elephant seal, as shown in Figure 16-6, remain in peril of extinction even as their numbers increase.

FIGURE 16-6

Populations of the once nearly extinct northern elephant seal, *Mirounga angustirostris*, have lost genetic variability—individuals are homozygous for all of their genes that have been tested. This result of genetic drift could make the species vulnerable to extinction.

NONRANDOM MATING

The fourth requirement of genetic equilibrium is random matings, without regard to genetic makeup. However, many species do not mate randomly. Mate selection is often influenced by geographic proximity, which can result in mates with some degree of kinship. Matings of related individuals can amplify certain traits and can result in offspring with disorders caused by recessive genes, which, although rare, may be present in the genomes of related individuals.

In another example of nonrandom mating, individuals may select a mate that has traits similar to their own traits. This mate would probably have some similar genes. The selection of a mate based on similarity of traits is called *assortative mating.* Nonrandom mating affects which alleles will be combined within individuals, but it does not affect overall allele frequencies within a population.

Sexual Selection

In many species of birds, the males are brightly colored and often heavily plumed, such as the peacock shown in Figure 16-7. These elaborately decorated males are easy for predators to see. Why would natural selection work in favor of an organism being conspicuous to a predator? Females tend to choose the males they mate with based on certain traits. This tendency is referred to as **sexual selection.** In order to leave offspring, a male must be selected by the female. The peacock's gaudy plumage increases his chances of being selected. Extreme traits, such as heavy, brightly colored plumage, may give the female an indication of the quality of the male's genes or his fitness in his environment. Remember that natural selection acts upon differences in survival *and* reproduction. Natural selection favors an increase in the genes of successful *reproducers,* rather than merely those of successful *survivors*.

FIGURE 16-7

Males sometimes display extreme traits, such as the large tail of this peacock, *Pavo cristatus.* This trait is favorable if it attracts females and increases the reproductive fitness of the male.

Quick Lab

Evaluating Selection

Materials unlined paper, colored pencils, 25 colored candies

Procedure

1. Fold a sheet of unlined paper in half, top over bottom. Using colored pencils, decorate half the paper with different colored circles. Make each colored circle about the size of a quarter.
2. Scatter your "population" of candies over the undecorated half of the sheet of paper. Count and record how many candies match the background color.
3. Now, scatter the candies over the decorated half of the sheet of paper. Count and record how many candies match the background color.
4. Candies that match the background color are camouflaged. Calculate the ratio of camouflaged candies to uncamouflaged candies in steps 2 and 3.
5. Repeat steps 2–4 two times, and average your results.
6. Exchange paper with another group, and repeat steps 2–5.

Analysis Was your population more successfully camouflaged on the white background or on the colored background? How did color diversity affect your population's success on the colored background? Based on your results, predict which type of selection might increase your population's fitness in a multicolored environment.

NATURAL SELECTION

The fifth requirement of genetic equilibrium is the absence of natural selection. Natural selection is an ongoing process in nature, so it often disrupts genetic equilibrium. As you have learned, natural selection means that some members of a population are more likely than other members to survive and reproduce and thus contribute their genes to the next generation.

Recall that natural selection operates on variations of traits within a population, such as body size or color. When natural selection is at work over time, the distribution of traits in a population may change. In a graph, this kind of change would appear as a shift away from the normal bell curve. Scientists observe three general patterns of natural selection: stabilizing selection, disruptive selection, and directional selection.

Stabilizing Selection

In **stabilizing selection,** individuals with the average form of a trait have the highest fitness. The average represents the optimum for most traits; extreme forms of most traits confer lower fitness on the individuals that have them. Consider a hypothetical species of lizard in which larger-than-average individuals might be more easily spotted, captured, and eaten by predators. On the other hand, lizards that are smaller than average might not be able to run fast enough to escape.

Figure 16-8a shows the effect of stabilizing selection on body size in these lizards. The red curve shows the initial variation in lizard size as a standard bell curve. The blue curve represents the variation in body size several generations after a new predator was introduced. This predator easily captured the large, visible lizards and the small, slower lizards. Thus, selection against these extreme body types reduced the size range of the lizards. Stabilizing selection is the most common kind of selection. It operates on most traits and results in very similar morphology between most members of a species.

Disruptive Selection

In **disruptive selection,** individuals with either extreme variation of a trait have greater fitness than individuals with the average form of the trait. Figure 16-8b shows the effect of disruptive selection on shell color in limpets, which are marine animals. The shell color of limpets varies from pure white to dark tan. White-shelled limpets that are on rocks covered with goose barnacles, which are also white, are at an advantage. Birds that prey on limpets have a hard time distinguishing the white-shelled limpets from the goose barnacles. On bare, dark-colored rocks, dark-shelled limpets are at an advantage. Again, the limpet-eating birds have a hard time locating the dark shells against the dark background. However, the birds easily spot limpets with shells of intermediate color, which are visible against both the white and dark backgrounds.

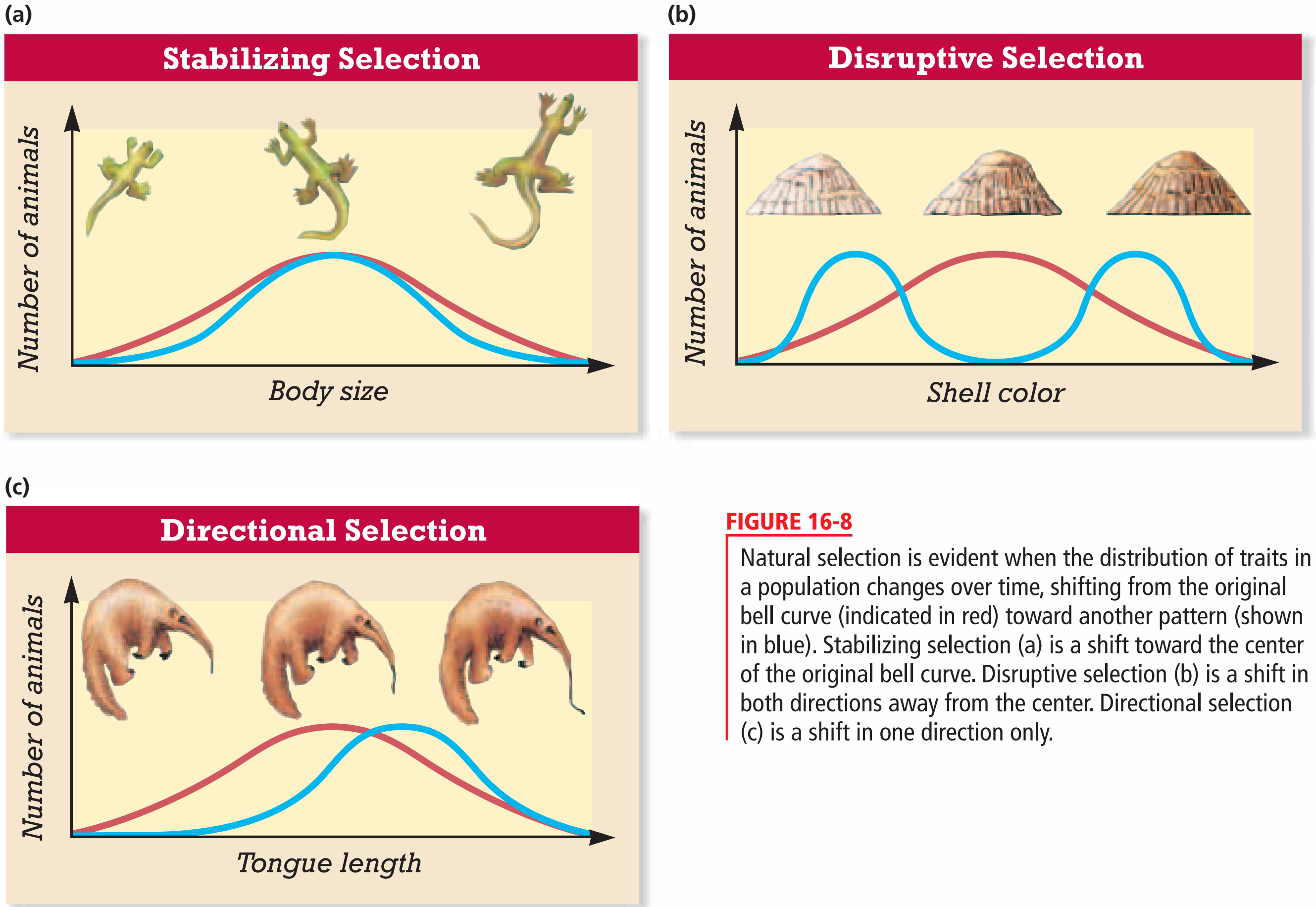


FIGURE 16-8
Natural selection is evident when the distribution of traits in a population changes over time, shifting from the original bell curve (indicated in red) toward another pattern (shown in blue). Stabilizing selection (a) is a shift toward the center of the original bell curve. Disruptive selection (b) is a shift in both directions away from the center. Directional selection (c) is a shift in one direction only.

Directional Selection

In **directional selection,** individuals that display a more extreme form of a trait have greater fitness than individuals with an average form of the trait. Figure 16-8c shows the effects of directional selection on tongue length in anteaters. Anteaters feed by breaking open termite nests, pushing their sticky tongue into the nest, and lapping up termites. Suppose that the termites in an area began to build deeper nests. Anteaters with long tongues could more effectively prey on these termites than could anteaters with short or average tongues. Thus, directional selection would act to direct the trait of tongue length away from the average and toward one extreme.

SECTION 2 REVIEW

1. List five conditions that can disrupt genetic equilibrium and cause evolution to occur.
2. Explain the role of mutations in evolution.
3. Contrast gene flow with genetic drift.
4. Explain why genetic drift is more significant in smaller populations.
5. Contrast stabilizing selection, disruptive selection, and directional selection.

CRITICAL THINKING

6. **Making Inferences** Why might a harmful allele persist in a population for many generations?
7. **Relating Concepts** Give an example of a species that exhibits the effects of sexual selection.
8. **Applying Concepts** For each of the three patterns of natural selection, give an example of a species that exhibits the effects of that selection.

SECTION 3

FORMATION OF SPECIES

OBJECTIVES

- **Relate** the biological species concept to the modern definition of species.
- **Explain** how the isolation of populations can lead to speciation.
- **Compare** two kinds of isolation and the pattern of speciation associated with each.
- **Contrast** the model of punctuated equilibrium with the model of gradual change.

VOCABULARY

speciation
morphology
biological species concept
geographic isolation
allopatric speciation
reproductive isolation
prezygotic isolation
postzygotic isolation
sympatric speciation
gradualism
punctuated equilibrium

How many species of organisms exist on Earth today? Undiscovered species may be so numerous that we have no accurate answer. For example, even small areas of tropical rain forests can contain thousands of species of plants, animals, and microorganisms. New species are discovered and others become extinct at an increasing rate. In this section, you will learn how one species can become two through a process called speciation.

THE CONCEPT OF SPECIES

You have learned that existing species are essentially changed versions of older species. The process of species formation, **speciation** (SPEE-shee-AY-shun), results in closely related species. Some are very similar to their shared ancestral species, whereas other descendant species become quite different over time.

Morphological Concept of Species

For many years, scientists used the internal and external structure and appearance of an organism—its **morphology** (mawr-FAHL-uh-jee)—as the chief criterion for classifying it as a species. Using the morphological concept of species, scientists defined species primarily according to structure and appearance. Because morphological characteristics are easy to observe, making species designations based on morphology proved convenient.

The morphological concept of species has limitations, however. There can be phenotypic differences among individuals in a single population. Notice, for example, the variation between the two red-tailed monkeys shown in Figure 16-9. To further complicate the matter, some organisms that appear different enough to belong to different species interbreed in the wild and produce fertile offspring. In response to the capacity of dissimilar organisms to reproduce, the biological species concept arose.

FIGURE 16-9
The facial features of red-tailed monkeys, *Cercopithecus ascianus,* can differ from individual to individual.

The Biological Species Concept

According to the **biological species concept,** as proposed by German-born, American biologist Ernst Mayr (1904–2005), a species is a population of organisms that can successfully interbreed but cannot breed with other groups. Although this definition is useful for living animals, the biological species concept does not provide a satisfactory definition for species of extinct organisms, whose reproductive compatibility cannot be tested. Nor is it useful for organisms that do not reproduce sexually. Thus, our modern definition of species includes components of both the morphological and biological species concepts. A species is a single kind of organism. Members of a species are morphologically similar and can interbreed to produce fully fertile offspring. The many species alive today diverged from a smaller number of earlier species.

ISOLATION AND SPECIATION

How do species give rise to other, different species? Speciation begins with isolation. In isolation, two parts of a formerly interbreeding population stop interbreeding. Two important types of isolation frequently drive speciation.

Geographic Isolation

Geographic isolation is the physical separation of members of a population. Populations may be physically separated when their original habitat becomes divided. A deep canyon could develop, a river could change course, or a drying climate in a valley could force surviving fragments of an original population into separate mountain ranges. Once the subpopulations become isolated, gene flow between them stops. Natural selection and genetic drift cause the two subpopulations to diverge, eventually making them incompatible for mating.

In pupfish, small freshwater fish shown in Figure 16-10, speciation following geographic isolation apparently took place in parts of the western United States, including the desert of Death Valley. Death Valley has a number of isolated ponds formed by springs. Each pond contains a species of fish that lives only in that one pond, but the fish species of various ponds in the area are quite similar.

How did these different populations of fish become isolated in Death Valley? Geologic evidence indicates that most of Death Valley was covered by a lake during the last ice age. When the ice age ended, the region became dry, and only small, spring-fed ponds remained. Members of a fish species that previously formed a single population in the lake may have become isolated in different ponds. The environments of the isolated ponds differ enough that the separate populations of fish diverged. Eventually, the fishes in the different ponds diverged enough to be considered separate species.

FIGURE 16-10

These two types of pupfish live in isolated water sources in the western United States. Both types appear to have evolved from a common ancestor after undergoing geographic isolation.

(a) desert pupfish, *Cyprinodon macularius*

(b) Amargosa pupfish, *Cyprinodon nevadensis*

(a) white-tailed antelope squirrel, *Ammospermophilis leucurus*

(b) Harris's antelope squirrel, *Ammospermophilis harrisi*

FIGURE 16-11

These two closely related squirrels are probably the result of allopatric speciation. The white-tailed antelope squirrel (a) is found on the north rim of the Grand Canyon, and Harris's antelope squirrel (b) is found on the south rim.

Geographic barriers can be formed by canyons, mountain ranges, bodies of water, deserts, or other geographic features that organisms cannot cross. In addition, parts of a population may be accidentally transported to new islands or slowly drift apart on separate continents. On the geologic time scale, the processes of geology frequently rearrange populations.

Whether or not a geographic barrier will isolate a particular group of organisms depends on the organisms' ability to move around. Birds, for example, can easily fly back and forth across a deep canyon. However, a canyon might be a major barrier to a small, crawling mammal. An example of such a barrier is the Grand Canyon in Arizona. The ever-deepening canyon separates the habitats of two closely related populations of squirrels, shown in Figure 16-11. These two populations are different enough to be considered separate species, but similar enough that scientists debate whether they might simply be subspecies. Because their ranges do not overlap, the two populations do not interbreed.

Allopatric Speciation

Allopatric speciation happens when species arise as a result of geographic isolation. *Allopatric* means "different homelands." Populations separated by a geographic barrier no longer experience gene flow between them. So, the gene pools of each separate population may begin to differ due to genetic drift, mutations, and natural selection.

Allopatric speciation is more likely to occur in small populations because a smaller gene pool will be changed more significantly by genetic drift and natural selection. The key question in this type of speciation is whether or not the separated populations become different enough to be reproductively isolated from one another. In other words, if the geographic barrier is removed, could the two groups interbreed and produce fertile offspring?

Reproductive Isolation

Sometimes, groups of organisms within a population become genetically isolated without being geographically isolated. **Reproductive isolation** results from barriers to successful breeding between population groups in the same area. Reproductive isolation and the species formation that follows it may sometimes arise through disruptive selection. Remember that in disruptive selection, the two extremes of a trait in a given population are selected for and the organisms begin to diverge. Once successful mating is prevented between members of the two subpopulations, the effect is the same as what would have occurred if the two subpopulations had been geographically isolated. There are two general types of reproductive isolation: prezygotic (pree-zie-GAHT-ik) isolation and postzygotic isolation. **Prezygotic isolation,** or *premating isolation,* occurs before fertilization, and **postzygotic isolation,** or *postmating isolation,* occurs after fertilization.

Word Roots and Origins

prezygotic

from the Latin *prae*, meaning "before," and the Greek *zygotos*, meaning "yoked"

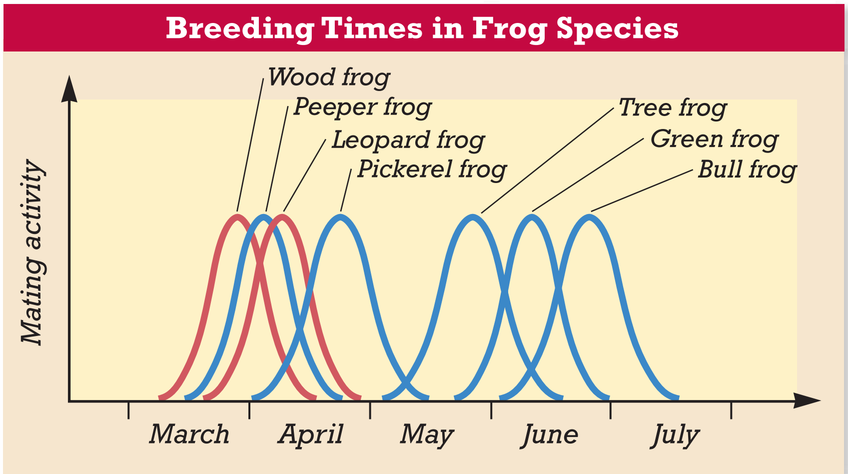


FIGURE 16-12

As the graph shows, frogs that share habitats may be reproductively isolated by differences in timing of mating activity.

If two potentially interbreeding species mate and fertilization occurs, success is measured by the production of healthy, fully fertile offspring. But this may be prevented by one of several types of postzygotic isolation. The offspring of interbreeding species may not develop completely and may die early, or, if healthy, they may not be fertile. From an evolutionary standpoint, if death or sterility of offspring occurs, the parent organisms have wasted their gametes producing offspring that cannot, in turn, reproduce.

In contrast, prezygotic isolating mechanisms can reduce the chance of hybrid formation. For example, a mating call that is not recognized as such by a potential mate can contribute to isolation. Differences in mating times are another type of prezygotic isolation. Both mechanisms are in effect for the frogs shown in Figure 16-12. The time of peak mating activity differs for each frog, reducing the chance of interbreeding. As a result, the wood frog and the leopard frog, shown in Figure 16-13, are reproductively isolated. Though these two frogs interbreed in captivity, they do not interbreed where their ranges overlap in the wild. The wood frog usually breeds in late March, and the leopard frog usually breeds in mid-April.

FIGURE 16-13

Differences in peak mating times and in mating calls appear to have led to reproductive isolation of the wood frog (a) from its close relative, the leopard frog (b).

(a) wood frog, *Rana sylvatica*

(b) leopard frog, *Rana pipiens*

Sympatric Speciation

Sympatric speciation occurs when two subpopulations become reproductively isolated within the same geographic area. Charles Darwin proposed this model of speciation in the 1850s. He hypothesized that competing individuals within a population could gain an adaptive advantage by using slightly different niches. This specialization could lead each group to become reproductively isolated from the other.

For example, a population of insects might live on a single type of plant. If some of the individuals from this population began to live on another type of plant, they might no longer interbreed with the original population. The two groups of insects would then be able to evolve independently and could eventually become two different species.

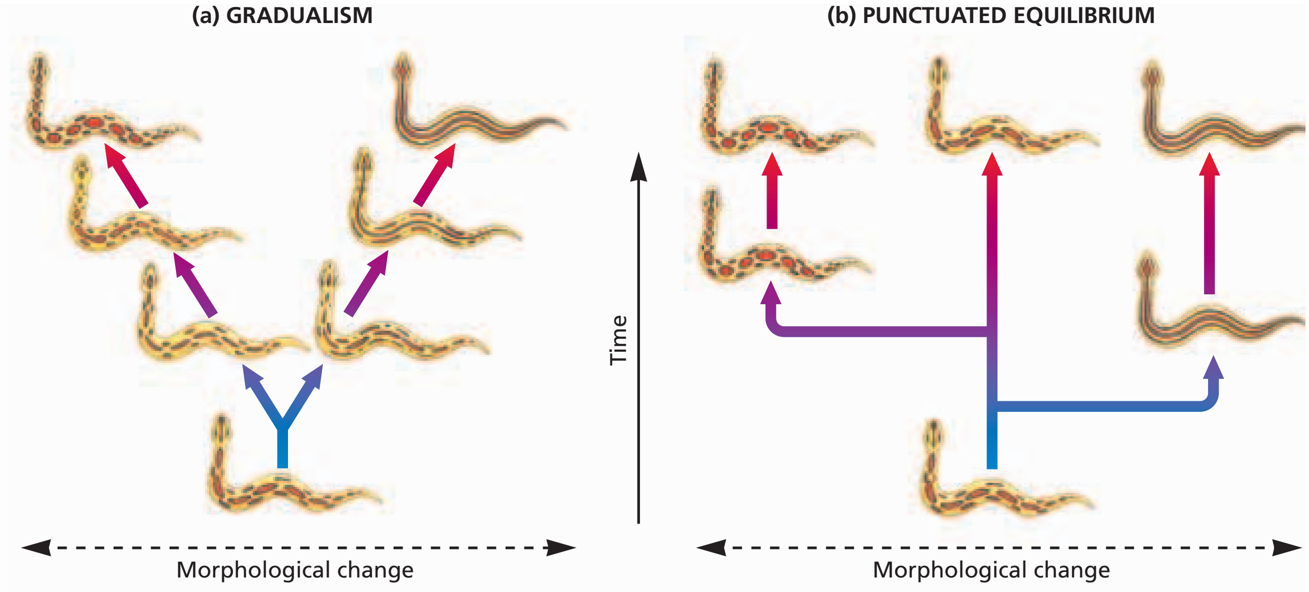


FIGURE 16-14

In the model of speciation shown on the left, species evolve gradually, at a stable rate. In the model of speciation shown on the right, species arise abruptly and differ noticeably from the root species. These species then change little over time.

RATES OF SPECIATION

Speciation sometimes requires millions of years. But apparently some species can form more rapidly. For example, Polynesians introduced banana trees to the Hawaiian Islands about a thousand years ago. Today, there are several species of moths that are unique to the Hawaiian Islands and that feed only on bananas. These species likely descended from ancestral moths during the past thousand years, since bananas were introduced to Hawaii.

The idea that speciation occurs at a regular, gradual rate is called **gradualism.** However, some scientists think that speciation happens in "bursts" relative to the geologic time scale. The fossil record holds evidence that many species existed without change for long periods of time, whereas in some cases a great diversity of new forms seems to have evolved rapidly. That is, change occurred in a few thousand, rather than a few million, years. Scientists call this pattern of species formation **punctuated equilibrium.** The term *punctuated* refers to sudden, rapid change, and *equilibrium* refers to periods of little change. Figure 16-14 illustrates these two contrasting models as they might apply to the evolution of snakes.

SECTION 3 REVIEW

1. What role did Ernst Mayr play in the development of the modern biological species concept?
2. Explain how geographic isolation can lead to allopatric speciation.
3. Explain how reproductive isolation can lead to sympatric speciation.
4. Contrast the model of punctuated equilibrium with the model of gradualism.

CRITICAL THINKING

5. **Critiquing Explanations** What are two shortcomings of the biological species concept?
6. **Analyzing Concepts** Describe one possible scenario of postzygotic reproductive isolation in an animal species.
7. **Drawing Conclusions** How might the generation time of a population affect future speciation?

CHAPTER HIGHLIGHTS

SECTION 1 Genetic Equilibrium

- Population biologists study many different traits in populations, such as size and color.
- Traits vary and can be mapped along a bell curve, which shows that most individuals have average traits, whereas a few individuals have extreme traits.
- Variations in genotype arise by mutation, recombination, and the random fusion of gametes.
- The total genetic information available in a population is called the gene pool.
- Allele frequencies in the gene pool do not change unless acted upon by certain forces.
- The principle of Hardy-Weinberg genetic equilibrium is a theoretical model of a population in which no evolution occurs and the gene pool of the population is stable.

Vocabulary

microevolution (p. 317)
population genetics (p. 317)
bell curve (p. 317)
gene pool (p. 318)
allele frequency (p. 318)
phenotype frequency (p. 319)
Hardy-Weinberg genetic equilibrium (p. 320)

SECTION 2 Disruption of Genetic Equilibrium

- Evolution can take place when a population is not in a state of genetic equilibrium. Thus, evolution may take place when populations are subject to genetic mutations, gene flow, genetic drift, nonrandom mating, or natural selection.
- Emigration and immigration cause gene flow between populations and can thus affect gene frequencies.
- Genetic drift is a change in allele frequencies due to random events. Genetic drift operates most strongly in small populations.
- Mating is nonrandom whenever individuals may choose partners. Sexual selection occurs when certain traits increase an individual's success at mating. Sexual selection explains the development of traits that improve reproductive success but that may harm the individual.
- Natural selection can influence evolution in one of three general patterns. Stabilizing selection favors the formation of average traits. Disruptive selection favors extreme traits rather than average traits. Directional selection favors the formation of more-extreme traits.

Vocabulary

immigration (p. 321)
emigration (p. 321)
gene flow (p. 321)
genetic drift (p. 322)
sexual selection (p. 323)
stabilizing selection (p. 324)
disruptive selection (p. 324)
directional selection (p. 325)

SECTION 3 Formation of Species

- According to the biological species concept, a species is a population of organisms that can successfully interbreed but cannot breed with other groups.
- Geographic isolation results from the separation of population subgroups by geographic barriers. Geographic isolation may lead to allopatric speciation.
- Reproductive isolation results from the separation of population subgroups by barriers to successful breeding. Reproductive isolation may lead to sympatric speciation.
- In the gradual model of speciation, species undergo small changes at a constant rate. In the punctuated equilibrium model, new species arise abruptly, differ greatly from their ancestors, and then change little over long periods.

Vocabulary

speciation (p. 326)
morphology (p. 326)
biological species concept (p. 327)
geographic isolation (p. 327)
allopatric speciation (p. 328)
reproductive isolation (p. 328)
prezygotic isolation (p. 328)
postzygotic isolation (p. 328)
sympatric speciation (p. 329)
gradualism (p. 330)
punctuated equilibrium (p. 330)

CHAPTER REVIEW

Using Vocabulary

1. Use each of the following terms in a separate sentence: *bell curve* and *gene flow*.
2. For each pair of terms, explain how the meanings of the terms differ.
   a. *allele frequency* and *phenotype frequency*
   b. *stabilizing selection* and *disruptive selection*
   c. *immigration* and *emigration*
   d. *geographic isolation* and *reproductive isolation*
   e. *allopatric speciation* and *sympatric speciation*
   f. *punctuated equilibrium* and *gradualism*
3. Use the following terms in the same sentence: *nonrandom mating, assortative mating,* and *sexual selection*.
4. Use the following terms in the same sentence: *genetic equilibrium, gene pool,* and *speciation*.
5. **Word Roots and Origins** The word *disrupt* is derived from the Latin *disruptus,* which means "to break apart." Using this information, explain the term *disruptive selection.*

Understanding Key Concepts

6. **Compare** the three main causes of variation in the genotypes of organisms.
7. **Identify** the five conditions that are necessary for Hardy-Weinberg genetic equilibrium.
8. **Identify** the five conditions that may cause evolution to occur in a population.
9. **Describe** how immigration and emigration can alter allele frequencies in a population.
10. **List** examples of how mating could be nonrandom in a population.
11. **Contrast** natural selection with sexual selection.
12. **Identify** which type of selection is happening when a population's bell curve narrows over time.
13. **Explain** why prezygotic isolating mechanisms have an advantage over postzygotic isolating mechanisms.
14. **Relate** the size of a population to the influence of genetic drift on the population's gene pool.
15. **Compare** the effects of stabilizing selection, disruptive selection, and directional selection.
16. **Model** a situation that might cause the geographic isolation of a subgroup of a population of fish living in a large river.
17. **Explain** why the biological species concept cannot be used to identify fossil organisms.
18. **Identify** the type of isolating mechanism in the following scenario: Where populations of two related species of frogs overlap geographically, their mating calls differ more than they do where the species don't overlap.
19. **Summarize** the hypothesis of punctuated equilibrium as it relates to the rate of speciation.
20. **CONCEPT MAPPING** Use the following terms to create a concept map of how new species can form: *natural selection, allele frequency, geographic isolation, reproductive isolation,* and *speciation.*

Critical Thinking

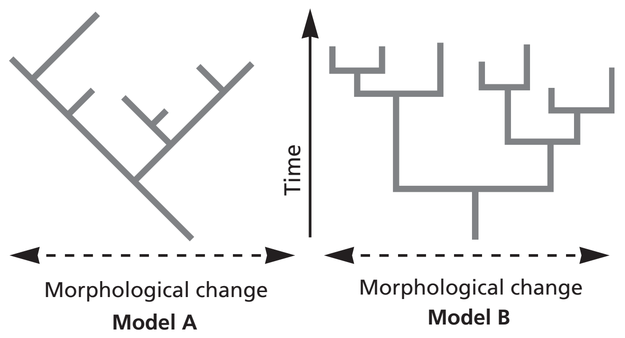
21. **Relating Concepts** Explain the relationship between evolution and natural selection.
22. **Forming Hypotheses** Propose a hypothesis about how pollutants in the environment could influence the evolution of its inhabitants.
23. **Drawing Conclusions** Freeways may provide an effective geographic isolating mechanism for some slow-moving animals. Are such artificial barriers likely to result in complete speciation?
24. **Applying Information** The common biological definition of *species* states that a species is a group of organisms that can interbreed and produce fertile offspring in nature. A mule is the offspring of a horse and a donkey. Mules are always sterile. By the definition above, do a horse and a donkey belong to the same species? Explain your answer.
25. **Interpreting Graphics** From the illustration of four o'clock flowers shown below, calculate the frequency of the *R* and *r* alleles, and state the phenotype frequency.

Standardized Test Preparation

DIRECTIONS: Choose the letter of the answer choice that best answers the question.

1. What is the term for the total genetic information in a population?
   A. gene pool
   B. allele frequency
   C. distribution of traits
   D. phenotype frequency
2. Saint Bernards and Chihuahuas (two breeds of domestic dogs) cannot normally mate because they differ so much in size. Thus, they are reproductively isolated to some extent. What type of isolating mechanism is operating in this case?
   F. artificial
   G. prezygotic
   H. postzygotic
   J. geographic
3. How do mutations affect genetic equilibrium?
   A. Mutations cause emigration.
   B. Mutations cause immigration.
   C. Mutations introduce new alleles.
   D. Mutations maintain genotype frequency.

INTERPRETING GRAPHICS: The illustration below shows two contrasting models for rates of speciation. Use the illustration to answer the questions that follow.

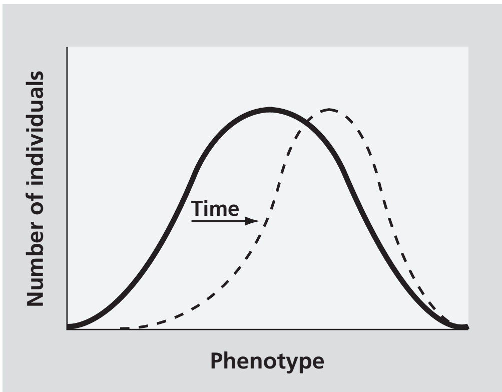


4. Which model of speciation rates is illustrated by model A in the graph?
   F. gradualism
   G. sexual selection
   H. disruptive selection
   J. punctuated equilibrium
5. Which model of speciation rates is illustrated by model B in the graph?
   A. gradualism
   B. sexual selection
   C. disruptive selection
   D. punctuated equilibrium

DIRECTIONS: Complete the following analogy:

6. genotype : allele :: phenotype :
   F. trait
   G. mutation
   H. gene pool
   J. population

INTERPRETING GRAPHICS: The illustration below shows the occurrence of variations in a particular characteristic within a population. The dark line represents an earlier point in time than the dashed line. Use the illustration to answer the question that follows.



7. Which type of selection is modeled in the illustration above?
   A. sexual selection
   B. disruptive selection
   C. stabilizing selection
   D. directional selection

SHORT RESPONSE

Explain the difference between reproductive isolation and geographic isolation.

EXTENDED RESPONSE

The phrase *Hardy-Weinberg genetic equilibrium* refers to the frequency of genotypes in populations from generation to generation.

Part A Briefly describe what this model predicts about genotype frequencies.

Part B What are the set of assumptions that must be met for the Hardy-Weinberg genetic equilibrium to be valid?

Test TIP For multiple-choice questions, try to eliminate any answer choices that are obviously incorrect, and then consider the remaining answer choices.

EXPLORATION LAB

Predicting Allele Frequency

OBJECTIVES

- Demonstrate the effect of natural selection on genotype frequencies.

PROCESS SKILLS

- modeling
- predicting
- calculating
- analyzing

MATERIALS

- 300 black beads
- 300 white beads
- 3 containers
- labeling tape
- marking pen

Background

1. What is natural selection?
2. What is the result of natural selection?

PART A Random Mating

1. Obtain three containers, and label them "Parental," "Offspring," and "Dead."
2. Place 200 black beads and 200 white beads in the "Parental" container. Assume that each black bead represents a dominant allele for black coat *(B)* and that each white bead represents a recessive allele for white coat *(b)* in a hypothetical animal. Assume that the container holds gametes from a population of 200 of these hypothetical animals: 50 *BB*, 100 *Bb*, and 50 *bb*.
3. In your lab report, make a data table like Table A.
4. Without looking, remove two beads from the "Parental" container. What does this simulate?
5. Record the genotype and phenotype of the resulting offspring in your data table. Then, put the alleles into the "Offspring" container. Replace the beads that you removed from the "Parental" container with new beads of the same color.
6. Repeat steps 4 and 5 forty-nine times. Record the genotype and phenotype of each offspring in your data table.
7. Calculate the frequencies of alleles in the offspring. First, make a table in your lab report like Table B. Then, count and record the number of black beads in the "Offspring" container. This number divided by the total number of beads (100) and multiplied by 100% is the frequency of *B* alleles. Then, count and record the number of white beads in the "Offspring" container. Determine the frequency of *b* alleles as you did with the *B* alleles.

TABLE A *MATING*

Trial	Random mating		Nonrandom mating	
	Offspring genotype	Offspring phenotype	Offspring genotype	Offspring phenotype
1				
2				
3				
4				
5				

TABLE B *ALLELE FREQUENCIES*

Generation	Number of *B* alleles	*B* alleles/ total alleles	*B* allele frequency	Number of *b* alleles	*b* alleles/ total alleles	*b* allele frequency
Parental	200	200/400	50%	200	200/400	50%
Offspring						

TABLE C *PHENOTYPE FREQUENCIES*

Generation	Number of black animals	Black animals/ total animals	Frequency of black animals	Number of white animals	White animals/ total animals	Frequency of white animals
Parental	100	150/200	75%	50	50/200	25%
Offspring						

8. Calculate the frequencies of phenotypes in the offspring. First, make a table in your lab report like Table C. Then, count and record the number of offspring with black coat color. Divide this number by the total number of offspring (50), and multiply by 100% to determine the frequency of black phenotype. Repeat this calculation to determine the frequency of white coat color among the offspring.

PART B Nonrandom Mating

9. Return the beads in the "Offspring" container to the container labeled "Parental."
10. Assume that animals with white-coat phenotype are incapable of reproducing. What is the genotype of animals with a white coat? To simulate this situation, remove 100 white beads from the container labeled "Parental," and set them aside.
11. Start by removing two beads from the container labeled "Parental," and record the results in your Table A. If the offspring has a white-coat phenotype, put its alleles in the container labeled "Dead." If the offspring has a black-coat phenotype, put its alleles in the container labeled "Offspring."
12. If animals with a white-coat phenotype cannot reproduce, predict what would happen to allele frequency if step 11 were repeated until the parental gene pool was empty. Write your prediction in your lab report.
13. Repeat step 11 until the parental gene pool is empty. Record the results of each pairing in your lab report in Table A. Compare your results with your prediction.
14. Transfer the beads from the "Offspring" container to the "Parental" container. Leave the beads that you have placed in the "Dead" container in that container. Do not return those beads to the parental container.
15. Repeat step 11 again until the parental pool is empty. Record your results in your data table.
16. Repeat steps 14 and 15 two more times.
17. Calculate the frequencies of the final genotypes produced, as you did in Part A. Compare the results with your prediction from step 12.
18. Clean up your materials before leaving the lab.

Analysis and Conclusions

1. Compare the frequency of recessive alleles produced in Part A with that produced in Part B. Did you correctly predict the frequencies?
2. Did the frequency of the *b* allele change uniformly through all generations? If not, what happened?
3. Why did you remove 100 white beads from the "Parental" container in step 10?
4. How did this change the phenotype frequency of white animals in the parental generation from the original ratio of 50/200?

Further Inquiry

If you continued Part B, would you eventually eliminate the *b* allele? Form a hypothesis and test it.