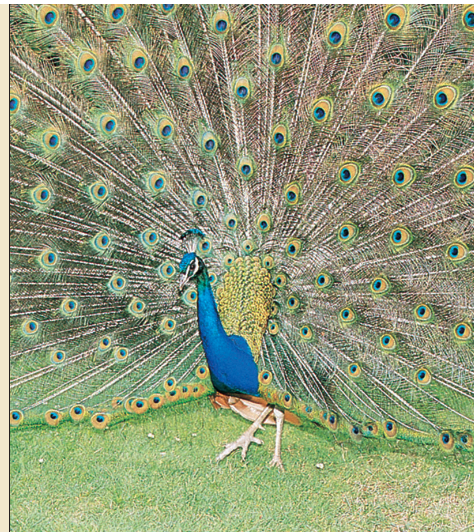
12 Natural Selection and Evolution



CHAPTER 12

Chapter Outline

Key Concepts	Applications
Recognize that evolutionary change is the result of natural selection.	• Describe how the concepts of evolution and natural selection are related.
Understand how natural selection works.	• Recognize common misunderstandings about the nature of natural selection. • Recognize that genetic variety is essential for natural selection to occur. • Understand the various ways in which an organism can be "fit" for survival. • Understand the importance of excess reproduction and gene expression in natural selection.
Understand that evolution is the process of changing gene frequencies.	• Understand how natural selection can change the nature of a species. • Understand how scientists can observe that evolution is occurring. • Recognize why genetic diversity is important to the survival of species.
Recognize the conditions under which the Hardy-Weinberg concept applies.	• Describe whether anything besides natural selection can result in evolution. • Recognize that genetic drift is possible under some conditions.

12.1 The Role of Natural Selection in Evolution

In many cultural contexts, the word *evolution* means progressive change. We talk about the evolution of economies, fashion, or musical tastes. From a biological perspective, the word has a more specific meaning. **Evolution** is the continuous genetic adaptation of a population of organisms to its environment over time. Evolution results when there are changes in genes present in a population. Individual organisms can not evolve—only populations can. Although evolution is a population process, the mechanisms that bring it about operate at the level of the individual.

There are three factors that interact to determine how a species changes over time: environmental factors that affect organisms, sexual reproduction among the individuals in the gene pool, and the generation of genetic variety within the gene pool. The success of an individual is determined by how well its characteristics match the demands of the environment in which it lives. There is a fit between the characteristics displayed by a species of organism and the surroundings the species typically encounters. Biologists refer to this match between characteristics displayed, the demands of the environment, and reproductive success as the **fitness** of the organism. Those individuals whose characteristics best fit their environment will be likely to live and reproduce. Since the various processes that encourage the passage of beneficial genes to future generations and discourage the passage of harmful or less valuable genes are natural processes, they are collectively known as **natural selection.**

The idea that some individuals whose gene combinations favor life in their surroundings will be most likely to survive, reproduce, and pass their genes on to the next generation is known as the **theory of natural selection.** The *theory of evolution,* however, states that populations of organisms become genetically adapted to their surroundings over time. Natural selection is the process that brings about evolution by "selecting" which genes will be passed to the next generation. The processes of natural selection do not affect genes directly but do so indirectly by selecting individuals for success based on the phenotype displayed. Recall that the characteristics displayed by an organism (phenotype) are related to the genes possessed by the organisms (genotype).

It is also important to recognize that when we talk about the characteristics of an organism that we are not just talking about structural characteristics. Behavioral, biochemical, or metabolic characteristics are also important. However, when looking at evidence of the past evolution of species of organisms it is difficult to assess these kinds of characteristics, so we tend to rely on structural differences.

Recall that a theory is a well-established generalization supported by many different kinds of evidence. The theory of natural selection was first proposed by Charles Darwin and Alfred Wallace and was clearly set forth in 1859 by Darwin in his book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life* (How Science Works 12.1). Since the time it was first proposed, the theory of natural selection has been subjected to countless tests and remains the core concept for explaining how evolution occurs.

12.2 What Influences Natural Selection?

Now that we have a basic understanding of how natural selection works, we can look in more detail at factors that influence it. Genetic variety within a species, genetic recombination as a result of sexual reproduction, the degree to which genes are expressed, and the ability of most species to reproduce excess offspring all exert an influence on the process of natural selection.

In order for natural selection to occur, there must be genetic differences among the many individuals of an interbreeding population of organisms. If all individuals are identical genetically, it does not matter which ones reproduce—the same genes will be passed on to the next generation and natural selection cannot occur. Genetic variety is generated in two ways. First of all, mutations may alter existing genes, resulting in the introduction of entirely new genetic information into a species' gene pool.

Mutations Produce New Genes

Spontaneous mutations are changes in DNA that cannot be tied to a particular causative agent. It is suspected that cosmic radiation or naturally occurring mutagenic chemicals might be the cause of many of these mutations. It is known that subjecting organisms to high levels of radiation or to certain chemicals increases the rate at which mutations occur. It is for this reason that people who work with radioactive materials or other mutagenic agents take special safety precautions.

Naturally occurring mutation rates are low (perhaps 1 chance in 100,000 that a gene will be altered), and mutations usually result in an allele that is harmful. However, in populations of millions of individuals, each of whom has thousands of genes, over thousands of generations it is quite possible that a new beneficial piece of genetic information could come about as a result of mutation. When we look at the various alleles that exist in humans or in any other organism, we should remember that every allele originated as a modification of a previously existing gene. For example, the allele for blue eyes may be a mutated brown-eye allele, or blond hair may have originated as a mutated brown-hair allele. When we look at a species such as corn (*Zea mays*), we can see that there are many different alleles for seed color. Each probably originated as a mutation (figure 12.1). Thus, mutations have been very important for introducing new genetic material into species over time.

In order for mutations to be important in the evolution of organisms, they must be in cells that will become gametes. Mutations to the cells of the skin or liver will only affect those specific cells and will not be passed on to the next generation.

HOW SCIENCE WORKS 12.1

The Voyage of HMS *Beagle,* 1831–1836

Young Charles Darwin examining specimens on the Galápagos Islands

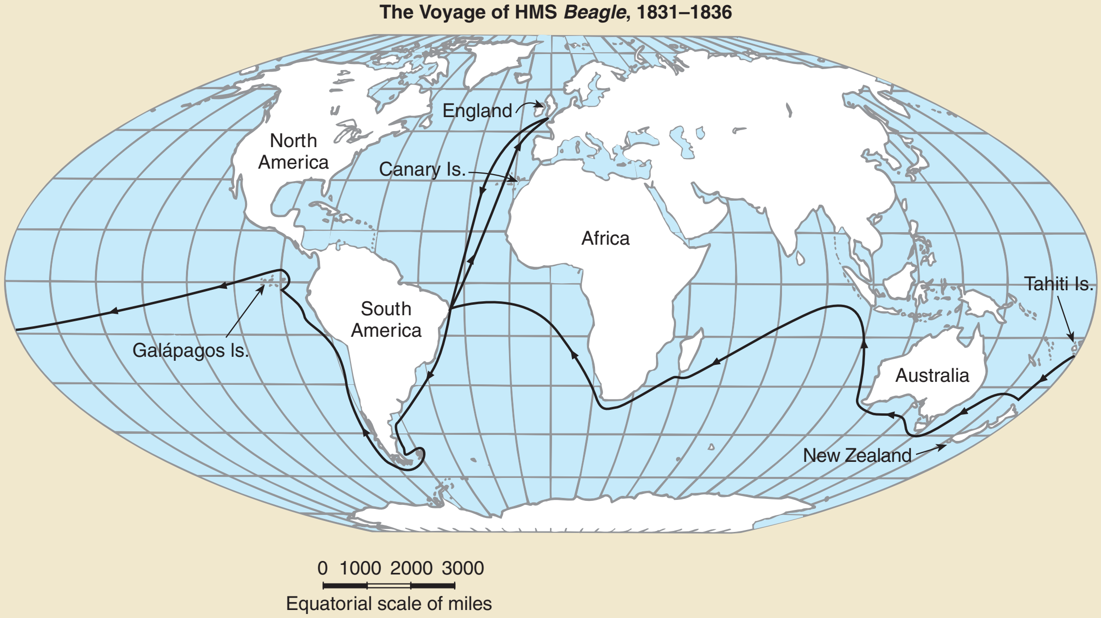
Probably the most significant event in Charles Darwin's life was his opportunity to sail on the British survey ship HMS *Beagle.* Surveys were common at this time; they helped refine maps and chart hazards to shipping. Darwin was 22 years old and probably would not have gotten the opportunity had his uncle not persuaded Darwin's father to allow him to go. Darwin was to be a gentleman naturalist and companion to the ship's captain Robert Fitzroy. When the official naturalist left the ship and returned to England, Darwin became the official naturalist for the voyage. The appointment was not a paid position.

The voyage of the *Beagle* lasted nearly five years. During the trip, the ship visited South America, the Galápagos Islands, Australia, and many Pacific Islands (the entire route is shown on the accompanying map). Darwin suffered greatly from seasickness and, perhaps because of it, he made extensive journeys by mule and on foot some distance inland from wherever the *Beagle* happened to be at anchor. His experience was unique for a man so young and very difficult to duplicate because of the slow methods of travel used at that time.

Although many people had seen the places that Darwin visited, never before had a student of nature collected volumes of information on them. Also, most other people who had visited these faraway places were not trained to recognize the significance of what they saw. Darwin's notebooks included information on plants, animals, rocks, geography, climate, and the native peoples he encountered. The natural history notes he took during the voyage served as a vast storehouse of information that he used in his writings for the rest of his life.

Because Darwin was wealthy, he did not need to work to earn a living and could devote a good deal of his time to the further study of natural history and the analysis of his notes. He was a semi-invalid during much of his later life. Many people think his ill health was caused by a tropical disease he contracted during the voyage of the *Beagle.* As a result of his experiences, he wrote several volumes detailing the events of the voyage, which were first published in 1839 in conjunction with other information related to the voyage of the *Beagle.* His volumes were revised several times and eventually were entitled *The Voyage of the Beagle.* He also wrote books on barnacles, the formation of coral reefs, how volcanos might have been involved in reef formation, and, finally, the *Origin of Species.* This last book, written 23 years after his return from the voyage, changed biological thinking for all time.

The Voyage of HMS *Beagle*, 1831–1836



Sexual Reproduction Produces New Combinations of Genes

A second very important process involved in generating genetic variety is sexual reproduction. Although sexual reproduction does not generate new genetic information the way mutations do, it allows for the recombination of genes into mixtures that did not occur previously. Each individual entering a population by sexual reproduction carries a unique combination of genes; approximately half donated by the mother and half donated by the father. During meiosis, variety is generated in the gametes through crossing-over between homologous chromosomes and independent assortment of nonhomologous chromosomes. This results in millions of possible combinations of genes in the gametes of any individual. When fertilization occurs, one of the millions of possible sperm unites with one of the millions of possible eggs, resulting in a genetically unique individual. The gene mixing that occurs during sexual reproduction is known as **genetic recombination.** The new individual has a complete set of genes that is different from that of any other organism that ever existed.

There are many kinds of organisms that reproduce primarily asexually and, therefore, do not benefit from genetic recombination. In most cases, however, when their life history is studied closely, it is apparent that they also have the ability to reproduce sexually at certain times. Organisms that reproduce exclusively by asexual methods are not able to generate new gene combinations but still experience mutations and acquire new genes through mutations.

Figure 12.1

Genetic Diversity in Corn (*Zea mays*)
There are many characteristics of corn that vary considerably. The ears of corn shown here illustrate the genetic diversity in color of the seeds. Although this is only one small part of the genetic makeup of the plant, the diversity is quite large.

The Role of Gene Expression

The importance of generating new gene combinations is particularly important because the way genes express themselves in an individual can depend on the other genes present. Genes don't always express themselves in the same way. In order for genes to be selected for or against, they must be expressed in the phenotype of the individuals possessing them.

There are many cases of genes expressing themselves to different degrees in different individuals. Often the reason for this difference is unknown. **Penetrance** is a term used to describe how often an allele expresses itself when present. Some alleles have 100% penetrance, others may only express themselves 80% of the time. There is a dominant allele that causes people to have a stiff little finger. The tendons are attached to the bones of the finger in such a way that the finger does not flex properly. This dominant allele does not express itself in every person that contains it; occasionally parents without the characteristic have children that show the characteristic. **Expressivity** is a term used to describe situations in which the gene expresses itself but not equally in all individuals that have it. An example of expressivity involves a dominant allele for six fingers. Some people with this allele have an extra finger on each hand, some have an extra finger on only one hand. Furthermore some sixth fingers are well-formed with normal bones, whereas others are fleshy structures that lack bones.

Genes may not express themselves for a number of different reasons. Some genes express themselves only during specific periods in the life of an organism. If the organism dies before the gene has had a chance to express itself, the gene never had the opportunity to contribute to the fitness of the organism. Say, for example, a tree has genes for producing very attractive fruit. The attractive fruit is important as a dispersal mechanism because animals select the fruit for food and distribute the seeds as they travel. However, if the tree dies before it can reproduce, the characteristic may never be expressed. By contrast genes such as those that contribute to heart disease or cancer late in a person's life were not expressed during the person's reproductive years and, therefore, were not selected against because the person reproduced before the effects of the gene were apparent.

In addition, many genes require an environmental trigger to initiate their expression. If the trigger is not encountered, the gene never expresses itself. It is becoming clear that many kinds of human cancers are caused by the presence of genes that require an environmental trigger. Therefore, we seek to identify the triggers and prevent these negative genes from being turned on and causing disease.

When both dominant and recessive alleles are present for a characteristic, the recessive alleles must be present in a homozygous condition before they have an opportunity to express themselves. For example, the allele for albinism is recessive. There are people who carry this recessive allele but never express it because it is masked by the dominant gene for normal pigmentation (figure 12.2).

Some genes may have their expression hidden because the action of a completely unrelated gene is required before they can express themselves. The albino individual in figure 12.2 has genes for dark skin and hair which will never have a chance to express themselves because of the presence of two alleles for albinism. The genes for dark skin and hair can express themselves only if the person has the ability to produce pigment and albinos lack that ability. Just because an individual organism has a "good" gene does not guarantee that that gene will be passed on. The organism may also have "bad" genes in combination with the good, and the "good" characteristics may be overshadowed by the "bad" characteristics. All individuals produced by sexual reproduction probably have certain genes that are extremely valuable for survival and others that are less valuable or harmful. However, natural selection operates on the total phenotype of the organism. Therefore, it is the combination of characteristics that is evaluated—not each characteristic individually. For example, fruit flies may show resistance to insecticides or lack of it, may have well-formed or shriveled wings, and may exhibit normal vision or blindness. An individual with insecticide resistance, shriveled wings, and normal vision has two good characteristics and one negative one, but it would not be as successful as an individual with insecticide resistance, normal wings, and normal vision.

Figure 12.2

Gene Expression

Genes must be expressed to allow the environment to select for or against them. The recessive gene *c* for albinism shows itself only in individuals who are homozygous for the recessive characteristic. The man in this photo is an albino who has the genotype *cc*. The characteristic is absent in those who are homozygous dominant and is hidden in those who are heterozygous. The dark-skinned individuals could be either *Cc* or *CC*.

The Importance of Excess Reproduction

Whenever a successful organism is examined, it can be shown that it reproduces at a rate in excess of that necessary to merely replace the parents when they die (figure 12.3). For example, geese have a life span of about 10 years and, on the average, a single pair can raise a brood of about eight young each year. If these two parent birds and all their offspring were to survive and reproduce at this same rate for a 10-year period, there would be a total of 19,531,250 birds in the family.

However, the size of goose populations and most other populations remains relatively constant over time. Minor changes in number may occur, but if the species is living in

Figure 12.3

Reproductive Potential

The ability of a population to reproduce greatly exceeds the number necessary to replace those who die. Here are some examples of the prodigious reproductive abilities of some species.

harmony with its environment, it does not experience dramatic increases in population size. A high death rate tends to offset the high reproductive rate and population size remains stable. But don't think of this as a "static population." Although the total number of organisms in the species may remain constant, the individuals that make up the population change. It is this extravagant reproduction that provides the large surplus of genetically different individuals that allows natural selection to take place. In fact, to maintain itself in an ever-changing environment, each species must change in ways that enhance its ability to adapt to its new environment. For this to occur, members of the population must be eliminated in a non-random manner. Those individuals that survive are those that are, for the most part, better suited to the environment than other individuals. They reproduce more of their kind and transmit more of their genes to the next generation than do individuals with genes that do not allow them to be well adapted to the environment in which they live.

12.3 Common Misunderstandings About Natural Selection

There are several common misinterpretations associated with the process of natural selection. The first involves the phrase "survival of the fittest." Individual survival is certainly important because those that do not survive will not reproduce. But the more important factor is the number of descendants an organism leaves. An organism that has survived for hundreds of years but has not reproduced has not contributed any of its genes to the next generation and so has been selected against. The key, therefore, is not survival alone but survival and reproduction of the more fit organisms.

Second, the phrase "struggle for life" does not necessarily refer to open conflict and fighting. It is usually much more subtle than that. When a resource such as nesting material, water, sunlight, or food is in short supply, some individuals survive and reproduce more effectively than others. For example, many kinds of birds require holes in trees as nesting places (figure 12.4). If these are in short supply, some birds will be fortunate and find a top-quality nesting site, others will occupy less suitable holes, and some many not find any. There may or may not be fighting for possession of a site. If a site is already occupied, a bird may not necessarily try to dislodge its occupant but may just continue to search for suitable but less valuable sites. Those that successfully occupy good nesting sites will be much more successful in raising young than will those that must occupy poor sites or those that do not find any.

Similarly, on a forest floor where there is little sunlight, some small plants may grow fast and obtain light while shading out plants that grow more slowly. The struggle for life in this instance involves a subtle difference in the rate at which the plants grow. But the plants are indeed engaged in a struggle, and a superior growth rate is the weapon for survival.

Figure 12.4

Tree Holes as Nesting Sites
Many kinds of birds, like this red-bellied woodpecker, nest in holes in trees. If old and dead trees are not available they may not be able to breed. Many people build birdhouses that provide artificial "tree holes" to encourage such birds to nest near their homes.

A third common misunderstanding involves significance of phenotypic characteristics that are not caused by genes. Many organisms survive because they have characteristics that are not genetically determined. The **acquired characteristics** are gained during the life of the organism; they are not genetically determined and, therefore, cannot be passed on to future generations through sexual reproduction. Therefore, acquired characteristics are not important to the processes of natural selection. Consider an excellent tennis player's skill. Although this person may have inherited characteristics that are beneficial to a tennis player, the ability to play a good game of tennis is acquired through practice, not through genes. An excellent tennis player's offspring will not automatically be excellent tennis players. They may inherit some of the genetically determined physical characteristics necessary to become excellent tennis players, but the skills are still acquired through practice (figure 12.5).

We often desire a specific set of characteristics in our domesticated animals. For example, the breed of dog known as boxers is "supposed" to have short tails. However, the alleles for short tails are rare in this breed. Consequently, the tails of these dogs are amputated—a procedure called docking. Similarly, the tails of lambs are also usually amputated. These acquired characteristics are not passed on to the next generation. Removing the tails of these animals does not remove the genes for tail production from their genomes and each generation of puppies and lambs is born with tails.

Figure 12.5

Acquired Characteristics
The ability to play an outstanding game of tennis is learned through long hours of practice. The tennis skills this person acquired by practice cannot be passed on to her offspring.

Figure 12.6

The Peppered Moth
This photo of the two variations of the peppered moth shows that the light-colored moth is much more conspicuous against the dark tree trunk. (The two dark moths are indicated by arrows.) The trees are dark because of an accumulation of pollutants from the burning of coal. The more conspicuous light-colored moths are more likely to be eaten by bird predators, and the genes for light color should become more rare in the population.

12.4 Processes That Drive Natural Selection

Several mechanisms allow for selection of certain individuals for successful reproduction. The specific environmental factors that favor certain characteristics are called **selecting agents.** If predators must pursue swift prey organisms, then the faster predators will be selected for, and the selecting agent is the swiftness of available prey. If predators must find prey that are slow but hard to see, then the selecting agent is the camouflage coloration of the prey, and keen eyesight is selected for. If plants are eaten by insects, then the production of toxic materials in the leaves is selected for. All selecting agents influence the likelihood that certain characteristics will be passed on to subsequent generations.

Differential Survival

As stated previously, the phrase "survival of the fittest" is often associated with the theory of natural selection. Although this is recognized as an oversimplification of the concept, survival is an important factor in influencing the flow of genes to subsequent generations. If a population consists of a large number of genetically and phenotypically different individuals it is likely that some of them will possess characteristics that make their survival difficult. Therefore, they are likely to die early in life and not have an opportunity to pass their genes on to the next generation.

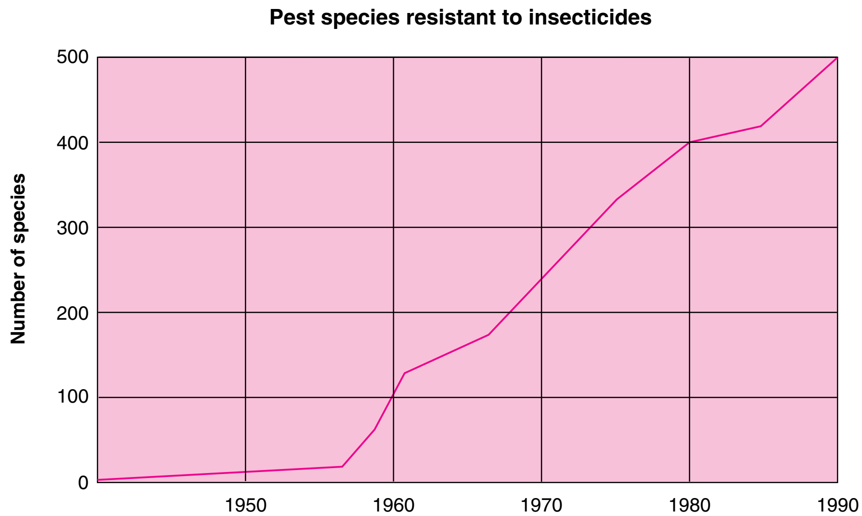
The English peppered moth provides a classic example. Two color types are found in the species: One form is light-colored and one is dark-colored. These moths rest on the bark of trees during the day, where they may be spotted and eaten by birds. The birds are the selecting agents. About 150 years ago, the light-colored moths were most common. However, with the advance of the Industrial Revolution in England, which involved an increase in the use of coal, air pollution increased. The fly ash in the air settled on the trees, changing the bark to a darker color. Because the light moths were more easily seen against a dark background, the birds ate them (figure 12.6). The darker ones were less conspicuous; therefore, they were less frequently eaten and more likely to reproduce successfully. The light-colored moth, which was originally the more common type, became much less common. This change in the frequency of light- and dark-colored forms occurred within the short span of 50 years. Scientists who have studied this situation have estimated that the dark-colored moths had a 20% better chance of reproducing than did the light-colored moths. This study is continuing today. As England has reduced its air pollution and tree bark has become lighter in color, the light-colored form of the moth has increased in frequency again.

As another example of how differential survival can lead to changed gene frequencies, consider what has happened to many insect populations as we have subjected them to a variety of insecticides. Because there is genetic

Figure 12.7

Resistance to Insecticides
The continued use of insecticides has constantly selected for the genes that give resistance to a particular insecticide. As a result, many species of insects and other arthropods are now resistant to many kinds of insecticides, and the number continues to increase.

Source: Data from Georghiou, University of California at Riverside.



variety within all species of insects, an insecticide that is used for the first time on a particular species kills all those that are genetically susceptible. However, individuals with slightly different genetic compositions may not be killed by the insecticide.

Suppose that, in a population of a particular species of insect, 5% of the individuals have genes that make them resistant to a specific insecticide. The first application of the insecticide could, therefore, kill 95% of the population. However, tolerant individuals would then constitute the majority of the breeding population that survived. This would mean that many insects in the second generation would be tolerant. The second use of the insecticide on this population would not be as effective as the first. With continued use of the same insecticide, each generation would become more tolerant, because the individuals that are not tolerant are being eliminated and those that can tolerate the toxin pass their genes for tolerance on to their offspring.

Many species of insects produce a new generation each month. In organisms with a short generation time, 99% of the population could become resistant to the insecticide in just five years. As a result, the insecticide would no longer be useful in controlling the species. As a new factor (the insecticide) was introduced into the environment of the insect, natural selection resulted in a population that was tolerant of the insecticide. Figure 12.7 indicates that more than 500 species of insects have populations that are resistant to many kinds of insecticides.

Differential Reproductive Rates

Survival alone does not always ensure reproductive success. For a variety of reasons, some organisms may be better able to utilize available resources to produce offspring. If one individual leaves 100 offspring and another leaves only 2, the first organism has passed more copies of its genetic information on to the next generation than has the second. If we assume that all 102 individual offspring have similar survival rates, the first organism has been selected for and its genes have become more common in the subsequent population.

Scientists have conducted studies of the frequencies of genes for the height of clover plants (figure 12.8). Two identical fields of clover were planted and cows were allowed to graze in one of them. Cows acted as a selecting agent by eating the taller plants first. These tall plants rarely got a chance to reproduce. Only the shorter plants flowered and produced seeds. After some time, seeds were collected from both the grazed and ungrazed fields and grown in a greenhouse under identical conditions. The average height of the plants from the ungrazed field was compared to that of the plants from the grazed field. The seeds from the ungrazed field produced some tall, some short, but mostly medium-sized plants. However, the seeds from the grazed field produced many more shorter plants than medium or tall ones. The cows had selectively eaten the plants that had the genes for tallness. Because the flowers are at the tip of the plant, tall plants were less likely to successfully reproduce, even though they might have been able to survive grazing by cows.

Differential Mate Selection

Within animal populations, some individuals may be chosen as mates more frequently than others. This is called "sexual selection." Obviously, those that are frequently chosen have an opportunity to pass on more copies of their genes than those that are rarely chosen. Characteristics of the more frequently chosen individuals may involve general characteristics, such as body size or aggressiveness, or specific conspicuous characteristics attractive to the opposite sex.

For example, male red-winged blackbirds establish territories in cattail marshes where females build their nests. A male will chase out all other males but not females. Some

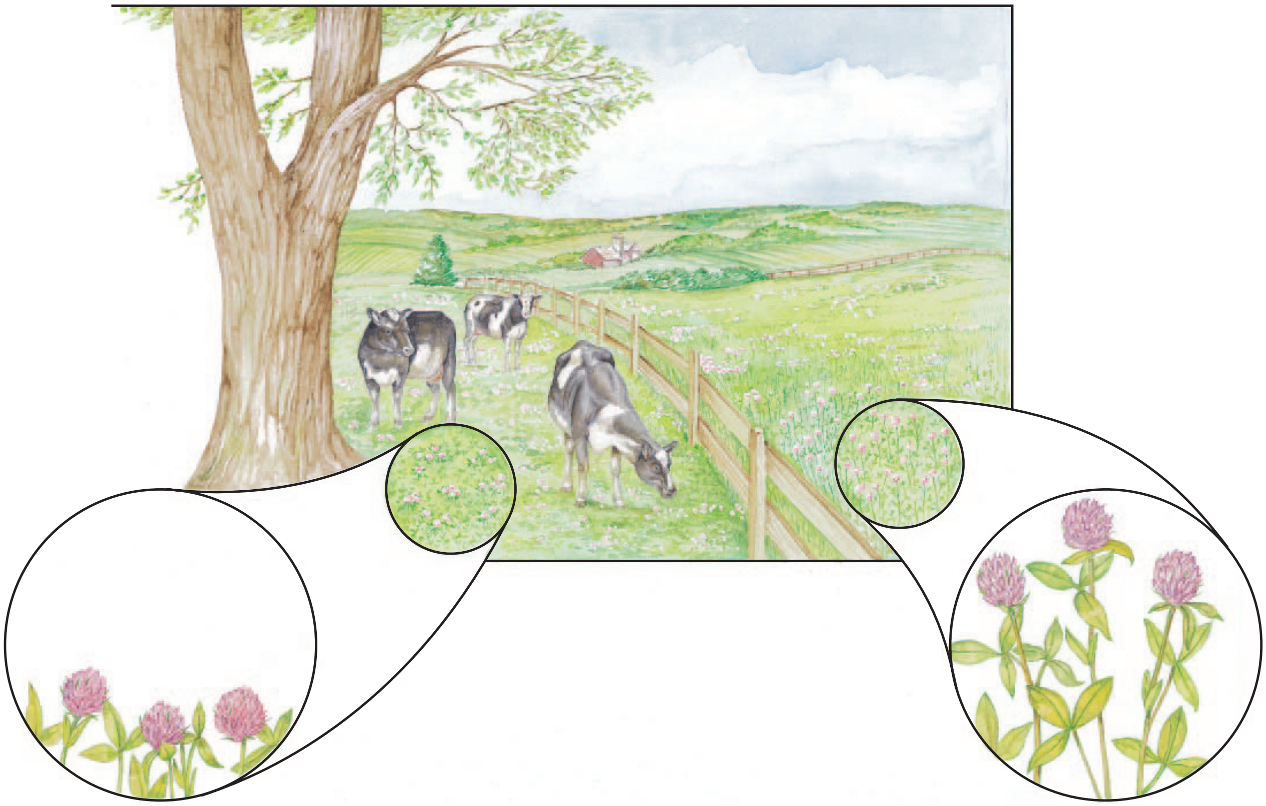


Figure 12.8

Selection for Shortness in Clover
The clover field to the left of the fence is undergoing natural selection: the grazing cattle are eating the tall plants and causing them to reproduce less than do the short plants. The other field is not subjected to this selection pressure, so its clover population has more genes for tallness.

males have large territories, some have small territories, and some are unable to establish territories. Although it is possible for any male to mate, it has been demonstrated that those that have no territory are least likely to mate. Those that defend large territories may have two or more females nesting in their territories and are very likely to mate with those females. It is unclear exactly why females choose one male's territory over another, but the fact is that some males are chosen as mates and others are not.

In other cases, it appears that the females select males that display conspicuous characteristics. Male peacocks have very conspicuous tail feathers. Those with spectacular tails are more likely to mate and have offspring (figure 12.9). Darwin was puzzled by such cases as the peacock in which the large and conspicuous tail should have been a disadvantage to the bird. Long tails require energy to produce, make it more difficult to fly, and make it more likely that predators will capture the individual. The current theory that seeks to explain this paradox involves female choice. If the females have an innate (genetic) tendency to choose the most elaborately decorated males, genes that favor such plumage will be regularly passed on to the next generation. Such special cases in which females choose males with specific characteristics has been called sexual selection.

12.5 Gene-Frequency Studies and Hardy-Weinberg Equilibrium

Throughout this chapter we have made frequent references to changing gene frequencies. (*Mutations introduce new genes into a species, causing gene frequencies to change. Successful organisms pass on more of their genes to the next generation, causing gene frequencies to change.*) In the early 1900s an English mathematician, G. H. Hardy, and a German physician, Wilhelm Weinberg, recognized that it was possible to apply a simple mathematical relationship to the study of gene frequencies. Their basic idea was that if certain conditions existed, gene frequencies would remain constant, and that the distribution of genotypes could be described by

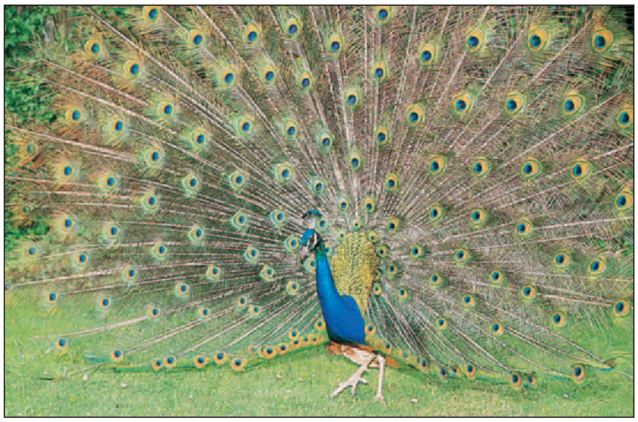


Figure 12.9

Mate Selection
In many animal species the males display very conspicuous characteristics that are attractive to females. Because the females choose the males they will mate with, those males with the most attractive characteristics will have more offspring and, in future generations, there will be a tendency to enhance the characteristic. With peacocks, those individuals with large colorful displays are more likely to mate.

the relationship $A^2 + 2Aa + a^2 = 1$, where A^2 represents the frequency of the homozygous dominant genotype, $2Aa$ represents the frequency of the heterozygous genotype, and a^2 represents the frequency of the homozygous recessive genotype. Constant gene frequencies over several generations would imply that evolution is *not* taking place. Changing gene frequencies would indicate that evolution is taking place.

The conditions necessary for gene frequencies to remain constant are:

1. Mating must be completely random.
2. Mutations must not occur.
3. Migration of individual organisms into and out of the population must not occur.
4. The population must be very large.
5. All genes must have an equal chance of being passed on to the next generation. (Natural selection is not occurring.)

The concept that gene frequencies will remain constant if these five conditions are met has become known as the **Hardy-Weinberg concept.**

Determining Genotype Frequencies

It is possible to apply the Punnett square method from chapter 10 to an entire gene pool to illustrate how the Hardy-Weinberg concept works. Consider a gene pool composed of only two alleles, *A* and *a*. Of the alleles in the population 60% (0.6) are *A* and 40% (0.4) are *a*. In this hypothetical gene pool, we do not know which individuals are male or female and we do not know their genotypes. With these gene frequencies, how many of the individuals would be homozygous dominant (*AA*), homozygous recessive (*aa*), and heterozygous (*Aa*)? To find the answer, we treat these genes and their frequencies as if they were individual genes being distributed into sperm and eggs. The sperm produced by the males of the population will be 60% (0.6) *A* and 40% (0.4) *a*. The females will produce eggs with the same relative frequencies. We can now set up a Punnett square as follows:

		Possible female gametes	
		A = 0.6	*a* = 0.4
Possible male gametes	*A* = 0.6	Genotype of offspring *AA* = 0.6 x 0.6 = 0.36 = 36%	Genotype of offspring *Aa* = 0.6 x 0.4 = 0.24 = 24%
	a = 0.4	Genotype of offspring *Aa* = 0.4 x 0.6 = 0.24 = 24%	Genotype of offspring *aa* = 0.4 x 0.4 = 0.16 = 16%

The Punnett square gives the frequency of occurrence of the three possible genotypes in this population: *AA* = 36%, *Aa* = 48%, and *aa* = 16%.

If we use the relationship $A^2 + 2Aa + a^2 = 1$, you can see that if $A^2 = 0.36$ then *A* would be the square root of 0.36, which is equal to 0.6—our original frequency for the *A* allele. Similarly, $a^2 = 0.16$ and *a* would be the square root of 0.16, which is equal to 0.4. In addition, $2Aa$ would equal $2 \times 0.6 \times 0.4 = 0.48$. If this population were to reproduce randomly, it would maintain a gene frequency of 60% *A* and 40% *a* alleles.

The Hardy-Weinberg concept is important because it allows a simple comparison of allele frequency to indicate if genetic changes are occurring. Two different populations of the same organism can be compared to see if they have the same allele frequencies, or populations can be examined at different times to see if allele frequencies are changing. It is important to understand that Hardy-Weinberg equilibrium conditions rarely exist; therefore, we usually see changes in gene frequency over time or genetic differences in separate populations of the same species. If gene frequencies are changing, evolution is taking place. Let's now examine why this is the case.

Why Hardy-Weinberg Conditions Rarely Exist

First of all, random mating does not occur for a variety of reasons. Many species are divided into segments that are isolated from one another to some degree so that no mating with other segments occurs during the lifetime of the individuals. In human populations, these isolations may be geographic, political, or social. In addition, some individuals may be chosen as mates more frequently than others because of the characteristics they display. Therefore, the Hardy-Weinberg conditions often are not met because non-random mating is a factor that leads to changing gene frequencies.

Second, you will recall that DNA is constantly being changed (mutated) spontaneously. Totally new kinds of genes are being introduced into a population, or one allele is converted into another currently existing allele. Whenever an allele is changed, one allele is subtracted from the population and a different one is added, thus changing the frequency of genes in the gene pool.

Third, immigration or emigration of individual organisms is common. When organisms move from one population to another they carry their genes with them. Their genes are subtracted from the population they left and added to the population they enter, thus changing the frequency of genes in both populations. It is important to understand that migration is common for plants as well as animals. In many parts of the world, severe weather disturbances have lifted animals and plants (or their seeds) and moved them over great distances, isolating them from their original gene pool. In other instances, organisms have been distributed by floating on debris on the surface of the ocean. As an example of how important these mechanisms are, consider the tiny island of Surtsey (3 km^2) which emerged from the sea as a volcano near Iceland in 1963. It continued to erupt until 1967. The new island was declared a nature preserve and has been surveyed regularly to record the kinds of organisms present. The nearest possible source of new organisms was about 20 kilometers away. The first living thing observed on the island was a fly seen less than a year after the initial eruption. By 1965 the first flowering plant was found and by 1996 fifty different species of flowering plants had been recorded on the island. In addition, several kinds of sea birds nest on the island.

The fourth assumption of the Hardy-Weinberg concept is that the population is infinitely large. If numbers are small, random events to a few individual organisms might alter gene frequencies from what was expected. Take coin flipping as an analogy. Coins have two surfaces, so if you flip a coin once, there is a 50:50 chance that the coin will turn up heads. If you flip two coins, you may come up with two heads, two tails, or one head and one tail. Only one of these possibilities gives us the theoretical 50:50 ratio. To come closer to the statistical probability of flipping 50% heads and 50% tails, you would need to flip many coins at the same time. The more coins you flip, the more likely it is that you will end up with 50% of all coins showing heads and the other 50% showing tails. The number of coins flipped is important. The same is true of gene frequencies.

Gene-frequency differences that result from chance are more likely to occur in small populations than in large populations. A population of 10 organisms of which 20% have curly hair and 80% have straight hair is significantly changed by the death of 1 curly-haired individual. Such situations in which the frequency of a gene changes significantly but the change in gene frequency is not the result of natural selection are called **genetic drift.** Often the characteristic does not appear to have any particular adaptive value to the individuals in the population, but in extremely small populations vital genes may be lost. Perhaps a population has unusual colors or shapes or behaviors compared to others of the same species. When trying to account for how such unusual occurrences come about, they are typically associated with populations that are small, or passed through a genetic bottleneck in the past. In large populations any unusual shifts in gene frequency in one part of the population usually would be counteracted by reciprocal changes in other parts of the population. However, in small populations the random distribution of genes to gametes may not reflect the percentages present in the population. For example, consider a situation in which there are 100 plants in a population and 10 have dominant genes for patches of red color while others do not. If in those 10 plants the random formation of gametes resulted in no red genes present in the gametes that were fertilized, then the gene could be eliminated. Similarly if those plants happened to be in a hollow that was subjected to low temperatures, they might be killed by a late frost and would not pass their genes on to the next generation. Therefore the gene would be lost but the loss would not be the result of natural selection.

Consider the example of cougars in North America. Cougars require a wilderness setting for success. As Europeans settled the land over the past 200 years, the cougars were divided into small populations in those places where relatively undisturbed habitat still existed. The Florida panther is an isolated population of cougars found in the Everglades. The next nearest population of cougars is in Texas. Because the Florida panther is on the endangered species list, efforts have been made to ensure its continued existence in the Everglades. However, the population is small and studies show that it has little genetic variety. A long period of isolation and a small population created conditions that led to this reduced genetic diversity. The accidental death of a few key individuals could have resulted in the loss of certain genes from the population. The general health of individuals in the population is poor and reproductive success is low.

In 1995, wildlife biologists began a program of introducing individuals from the Texas population into the Florida population. The purpose of the program is to reintroduce genetic variety that has been lost during the long period of isolation (figure 12.10).

Many zoos around the world cooperate in captive breeding programs designed to maintain genetic diversity in the gene pool of endangered species. Some of these species no longer exist in the wild but there are hopes that they may sometime be reintroduced to the wild. For example, at one time the entire California condor population consisted of a few individuals in zoos. Although most individuals of the species still reside in zoos, attempts are being made to reintroduce them to the wild in California and Arizona. Maintaining genetic diversity in the population can be very difficult when the species consists of few individuals. Often the DNA of the animals is characterized and records are kept to assure that the animals that breed are not close relatives. To accomplish their goals zoos often exchange or loan animals for breeding purposes.

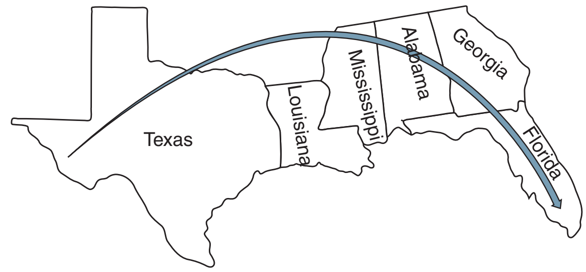


Figure 12.10

The Florida Panther
The Florida panther (cougar) is confined to the Everglades at the southern tip of Florida. The population is small, isolated from other populations of cougars, and shows little genetic diversity. Individual cougars from Texas were introduced into the Everglades to increase the genetic diversity of the Florida panther population.

Finally, it is important to understand that genes differ in their value to the species. Some genes result in characteristics that are important to survival and reproductive success. Other genes may reduce the likelihood of survival and reproduction. Many animals have cryptic color patterns that make them difficult to see. The genes that determine the cryptic color pattern would be selected for (favored) because animals that are difficult to see are not going to be killed and eaten as often as those that are easy to see. Albinism is the inability to produce pigment so that the individual's color is white. White animals are conspicuous and so we might expect them to be discovered more easily by predators (figure 12.11). Because not all genes have equal value, natural selection will operate and some genes will be more likely to be passed on to the next generation than will others.

Figure 12.11

Albino Animal in the Wild
Predators are more likely to spot an albino than a member of the species with normal coloration. Albinism prevents the prey from blending in with its surroundings.

Using the Hardy-Weinberg Concept to Show Allele-Frequency Change

Now we can return to our original example of genes *A* and *a* to show how natural selection based on differences in survival can result in allele-frequency changes in only one generation. Again, assume that the parent generation has the following genotype frequencies: *AA* = 36%, *Aa* = 48%, and *aa* = 16%, with a total population of 100,000 individuals. Suppose that 50% of all the individuals having at least one *A* gene do not reproduce because they are more susceptible to disease. The parent population of 100,000 would have 36,000 individuals with the *AA* genotype, 48,000 with the *Aa* genotype, and 16,000 with the *aa* genotype. Because only 50% of those with an *A* allele reproduce, only 18,000 *AA* individuals and 24,000 *Aa* individuals will reproduce. All 16,000 of the *aa* individuals will reproduce, however. Thus, there is a total reproducing population of only 58,000 individuals out of the entire original population of 100,000. What percentage of *A* and *a* will go into the gametes produced by these 58,000 individuals?

The percentage of *A*-containing gametes produced by the reproducing population will be 31% from the *AA* parents and 20.7% from the *Aa* parents (table 12.1). The frequency of the *A* gene in the gametes is 51.7% (31% + 20.7%). The percentage of *a*-containing gametes is 48.3% (20.7% from the *Aa* parents plus 27.6% from the *aa* parents). The original parental gene frequencies were *A* = 60% and *a* = 40%. These have changed to *A* = 51.7% and *a* = 48.3%. More individuals in the population will have the *aa* genotype, and fewer will have the *AA* and *Aa* genotypes.

If this process continued for several generations, the gene frequency would continue to shift until the *A* gene

Table 12.1

DIFFERENTIAL REPRODUCTION

The percentage of each genotype in the offspring differs from the percentage of each genotype in the original population as a result of differential reproduction.

Original Frequency of Genotypes	Total Number of Individuals Within a Population of 100,000 with Each Genotype	Number of Each Genotype Not Reproducing Subtracted from the Total	Total of Each Genotype in the Reproducing Population of 58,000 Following Selection	New Percentage of Each Genotype in the Reproducing Population
AA = 36%	36,000	36,000 −18,000 18,000	18,000	18,000/58,000 = 31.0%
Aa = 48%	48,000	48,000 −24,000 24,000	24,000	24,000/58,000 = 41.4%
aa = 16%	16,000	16,000 − 0 16,000	16,000	16,000/58,000 = 27.6%
100%	100,000		58,000	100.0%

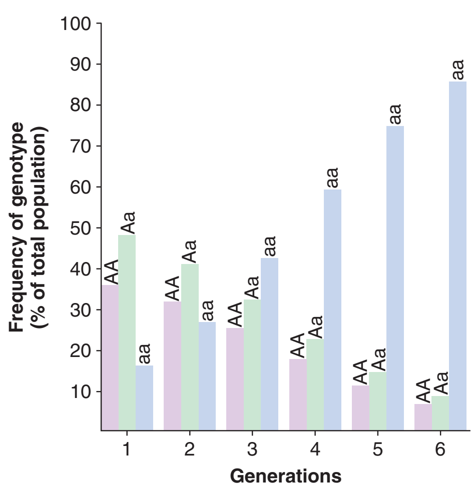


Figure 12.12

Changing Gene Frequency

If 50% of all individuals with the genotypes *AA* and *Aa* do not reproduce in each generation, the frequency of the *aa* genotype will increase as the other two genotypes decrease in frequency.

became rare in the population (figure 12.12). This is natural selection in action. Differential reproduction rates have changed the frequency of the *A* and *a* alleles in this population.

12.6 A Summary of the Causes of Evolutionary Change

At the beginning of this chapter, evolution was described as the change in gene frequency over time. We can now see that several different mechanisms operate to bring about this change. Mutations can either change one allele into another or introduce an entirely new piece of genetic information into the population. Immigration can introduce new genetic information if the entering organisms have unique genes. Emigration and death remove genes from the gene pool. Natural selection systematically filters some genes from the population, allowing other genes to remain and become more common. The primary mechanisms involved in natural selection are differences in deathrates, reproductive rates, and the rate at which individuals are selected as mates (figure 12.13). In addition, gene frequencies are more easily changed in small populations because events such as death, immigration, emigration, and mutation can have a greater impact on a small population than on a large population.

Now that you have an understanding of the mechanisms of natural selection and how natural selection brings about evolution, examine some common myths and misunderstandings about evolution in Outlooks 12.1.

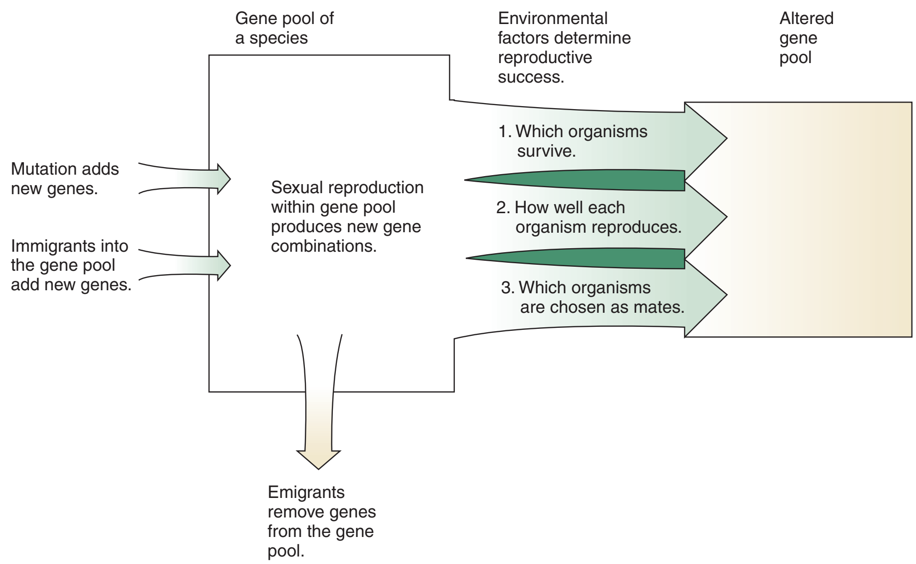


Figure 12.13

Processes That Influence Evolution
Several different processes cause gene frequencies to change. Genes enter populations through immigration and mutation. Genes leave populations through death and emigration. Natural selection operates within populations through death and rates of reproduction.

OUTLOOKS 12.1

Common Misconceptions About the Theory of Evolution

1. *Evolution happened only in the past and is not occurring today.* In fact we see lots of evidence that changes in the frequency of alleles is occurring in the populations of current species (antibiotic resistance, pesticide resistance, and moth color).
2. *Evolution has a specific goal.* Natural selection selects those organisms that best fit the current environment. As the environment changes so do the characteristics that have value. Random events such as changes in sea level, major changes in climate such as ice ages, or collisions with asteroids have had major influences on the subsequent natural selection and evolution. Evolution results in organisms that "fit" the current environment.
3. *Changes in the environment cause mutations that are needed to survive under the new environmental conditions.* Mutations are random events and are not necessarily adaptive. However, when the environment changes, mutations that were originally detrimental may have greater value. The gene did not change but the environmental conditions did. In some cases the mutation rate may increase or there may be more frequent exchanges of genes between individuals when the environment changes, but the mutations are still random. They are not directed to a particular goal.
4. *Individual organisms evolve.* Individuals are stuck with the genes they inherited from their parents. Although individuals may adapt by changing their behavior or physiology they cannot evolve; only populations can change gene frequencies.
5. *Today's species can frequently be shown to be derived from other present-day species (apes gave rise to humans).* There are few examples in which it can be demonstrated that one current species gave rise to another. Apes did not become humans but apes and humans had a common ancestor several million years ago.
6. *Genes that are valuable to an organism's survival become dominant.* A gene that is valuable may be either dominant or recessive. However, if it has a high value for survival it will become *common* (more frequent). Commonness has nothing to do with dominance and recessiveness.

SUMMARY

All sexually reproducing organisms naturally exhibit genetic variety among the individuals in the population as a result of mutations and the genetic recombination resulting from meiosis and fertilization. The genetic differences are reflected in phenotypic differences among individuals. These genetic differences are important for the survival of the species because natural selection must have genetic variety to select from. Natural selection by the environment results in better-suited individual organisms having greater numbers of offspring than those that are less well off genetically. Not all genes are equally expressed. Some express themselves only during specific periods in the life of an organism and some may be recessive genes that show themselves only when in the homozygous state. Characteristics that are acquired during the life of the individual and are not determined by genes cannot be raw material for natural selection.

Selecting agents act to change the gene frequencies of the population if the conditions of the Hardy-Weinberg concept are violated. The conditions required for Hardy-Weinberg equilibrium are random mating, no mutations, no migration, large population size, and no selection for genes. These conditions are met only rarely, however, so that typically, after generations of time, the genes of the more favored individuals will make up a greater proportion of the gene pool. The process of natural selection allows the maintenance of a species in its environment, even as the environment changes.

THINKING CRITICALLY

Penicillin was first introduced as an antibiotic in the early 1940s. Since that time, it has been found to be effective against the bacteria that cause gonorrhea, a sexually transmitted disease. The drug acts on dividing bacterial cells by preventing the formation of a new protective cell wall. Without the wall, the bacteria can be killed by normal body defenses. Recently, a new strain of this disease-causing bacterium has been found. This particular bacterium produces an enzyme that metabolizes penicillin. How can gonorrhea be controlled now that this organism is resistant to penicillin? How did a resistant strain develop? Include the following in your consideration: DNA, enzymes, selecting agents, and gene-frequency changes.

CONCEPT MAP TERMINOLOGY

Construct a concept map to show relationships among the following concepts.

differential reproductive success
evolution
gene frequency
natural selection
selecting agent
"survival of the fittest"

KEY TERMS

acquired characteristics
evolution
expressivity
fitness
genetic drift
genetic recombination
Hardy-Weinberg concept
natural selection
penetrance
selecting agent
spontaneous mutation
theory of natural selection

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Topics	Questions	Media Resources
12.1 The Role of Natural Selection in Evolution		**Quick Overview** • An engine to drive the process **Animation and Review** • Natural selection • Adaptation **Key Points** • The role of natural selection in evolution
12.2 What Influences Natural Selection?	1. Why are acquired characteristics of little interest to evolutionary biologists? 2. What factors can contribute to variety in the gene pool? 3. Why is over-reproduction necessary for evolution? 4. Why is sexual reproduction important to the process of natural selection?	**Quick Overview** • Assumptions behind natural selection **Key Points** • What influences natural selection **Interactive Concept Maps** • Natural selection **Experience This!** • Genetic variation in the human population
12.3 Common Misunderstandings About Natural Selection		**Quick Overview** • But I thought that . . . **Key Points** • Common misunderstandings about natural selection

(*continued*)

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Topics	Questions	Media Resources
12.4 Processes That Drive Natural Selection	5. A gene pool has equal numbers of genes *B* and *b*. Half of the *B* genes mutate to *b* genes in the original generation. What will the gene frequencies be in the next generation? 6. List three factors that can lead to changed gene frequencies from one generation to the next. 7. Give two examples of selecting agents and explain how they operate.	**Quick Overview** • Differences in survival rates, reproduction rates, and mate selection **Key Points** • Processes that drive natural selection **Animations and Review** • Other processes • Concept quiz **Interactive Concept Maps** • Text concept map
12.5 Gene-Frequency Studies and Hardy-Weinberg Equilibrium	8. The Hardy-Weinberg concept is only theoretical. What factors do not allow it to operate in a natural gene pool? 9. How might a harmful gene remain in a gene pool for generations without being eliminated by natural selection? 10. The smaller the population, the more likely it is that random changes will influence gene frequencies. Why is this true? 11. What is natural selection? How does it work?	**Quick Overview** • When allele frequencies stay the same **Key Points** • Gene-frequency studies and Hardy-Weinberg equilibrium **Interactive Concept Maps** • Hardy-Weinberg assumptions
12.6 A Summary of the Causes of Evolutionary Change		**Quick Overview** • Many factors influence evolution **Key Points** • A summary of the causes of evolutionary change **Interactive Concept Maps** • Influences on evolutionary change **Food for Thought** • Creationism **Review Questions** • Natural selection and evolution