The Modern Theory of Evolution

29

A noisy toucan displays its bill and plumage. Its colors are extravagant, its bill oversized. Each, however, has a function. Its colors attract mates; its large bill discourages predators. Species survive or die out in accordance with how effective their adaptations are for survival. All living things struggle for existence. They compete for food, for territory, for warmth, for the chance to reproduce. Some species blend into their environment, others stand out. Some species change, some stay the same, some disappear. In this chapter you will learn what causes the changes that help species survive.

Guide for Reading

Key words: natural selection, variation, adaptation, population, gene pool, evolution, genetic equilibrium, speciation

Questions to think about:

How did Lamarck's theory of evolution differ from Darwin's theory?

What is the synthetic theory of evolution?

What role does natural selection play in the evolution of species?

29-1 Early Theories of Evolution

Section Objectives:

- *Outline* Lamarck's theory of evolution and describe Weissman's experiment that showed that acquired characteristics are not passed from generation to generation.
- *Explain* the principle of natural selection.
- *List* the six main points of Darwin's theory of evolution and state the chief weakness of Darwin's theory.
- *Distinguish* between gradualism and the theory of punctuated equilibrium.

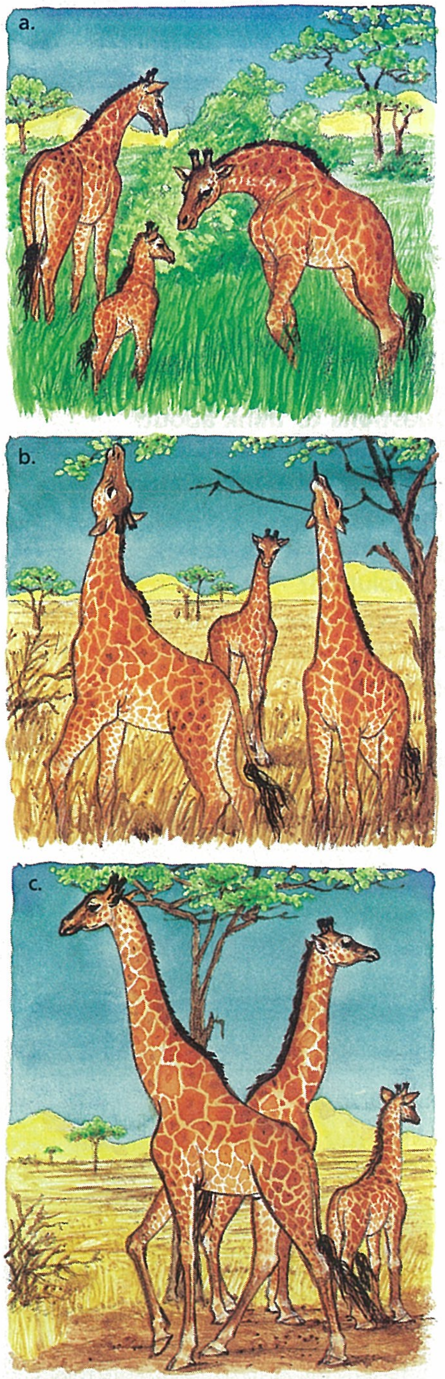
In the previous chapter, you read some of the scientific evidence for organic evolution. But, the evidence for evolution does not explain how or why it occurs. This chapter deals with theories about how evolutionary change occurs.

Lamarck's Theory of Evolution

One of the first theories of evolution was presented by the French biologist Jean Baptiste de Lamarck in 1809. From his studies of animals, Lamarck became convinced that species were not constant. Instead, he believed they evolved from preexisting species.

▲ **Figure 29–1**
Evolution of Species. The theory of evolution accounts for how this Alaskan walrus and all other species have arisen.

◀ A keel-billed toucan is adapted for life in the rain forests of South America.



▲ **Figure 29–2**
Lamarck's Theory of Evolution. (a) Early giraffes had short necks. (b) When low-growing plants became scarce, giraffes stretched their necks to reach food. (c) The giraffes with stretched necks passed on their long-neck trait to their offspring.

He thought that these evolutionary changes in animals were caused by their need to adapt to changes in the environment.

According to Lamarck's theory, evolution involved two principles. He called his first principle *the law of use and disuse.* According to this principle, the more an animal uses a particular part of its body, the stronger and better developed that part becomes. At the same time, the less a part is used, the weaker and less developed it becomes. An athlete, for example, develops the strength of certain muscles by constant use. Muscles that are not used tend to become smaller and weaker. The second part of Lamarck's theory was *the inheritance of acquired characteristics.* Lamarck assumed that the characteristics an organism developed through use and disuse could be passed on to its offspring.

Using his theory, Lamarck offered the following explanation for the long neck of the giraffe. See Figure 29–2. The ancestors of modern giraffes had short necks and fed on grasses and shrubs close to the ground. As the supply of food near the ground decreased, the giraffes had to stretch their necks to reach leaves farther from the ground. Their necks became longer from stretching, and this trait was passed on to their offspring. In the course of generations, the giraffe's neck became longer and longer, thus giving rise to the modern giraffe.

Modern genetics has shown that traits are passed from one generation to the next by genes in an individual's gametes. As far as we can tell, however, these genes are not affected by an individual's life experiences or activities. Although there have been many experiments looking for evidence of such an effect, all have failed. The most well known of these experiments was performed in the 1870s by the German biologist August Weismann. Weismann cut the tails off mice for 22 generations. In each generation, the mice were born with tails of normal length. The acquired characteristic of shortened tails was not inherited.

Darwin's Observations

The name most closely connected with the theory of evolution is that of Charles Darwin. Darwin was the son of a well-to-do physician. At his father's urging, Darwin began to study medicine, but he did not enjoy the subject and gave it up. He then began to prepare for a career as a minister, but his real interest was in nature study—in observing the natural environment and collecting specimens.

In 1831, the British naval vessel HMS *Beagle* was about to set out on a scientific expedition to chart the coastline of South America and some of the islands of the Pacific Ocean. The expedition also planned to collect specimens of wildlife from the lesser-known regions of this part of the world. Darwin applied for the position of ship's naturalist and was accepted. He was 22 years old when he sailed from England on a voyage that was expected to take 2 years but actually lasted 5 years.

During those years, Darwin collected hundreds of specimens and made detailed observations of the regions through which he traveled. He left the ship several times to make inland journeys, rejoining the *Beagle* later. Darwin had plenty of time for thinking about what he saw. He also read the first volume of *The Principles of Geology* by Charles Lyell, which had been published shortly before Darwin left England. Lyell proposed that the earth was very old, that it had been slowly changing for millions of years, and that it was still changing. His ideas led Darwin to think that perhaps living things also changed slowly over long periods of time.

On his trip, Darwin made several types of observations that supported his idea. He noticed that there was a gradual change in each species as he traveled down the coast of South America. For example, the ostrichlike rheas that live in the latitudes around Buenos Aires are different from those found at the tip of South America. Darwin also observed fossils that were different from the living animals he saw in the same region. At the same time, the fossils had many similarities that suggested they might be related to modern forms.

The most significant of Darwin's observations were those he made on the Galapagos Islands, which lie about 1000 kilometers from the coast of Ecuador in the Pacific Ocean. He found many different species of finches living on these islands. The birds were alike, yet each species was slightly different from those on the next island or in another part of the same island. See Figure 29-3.

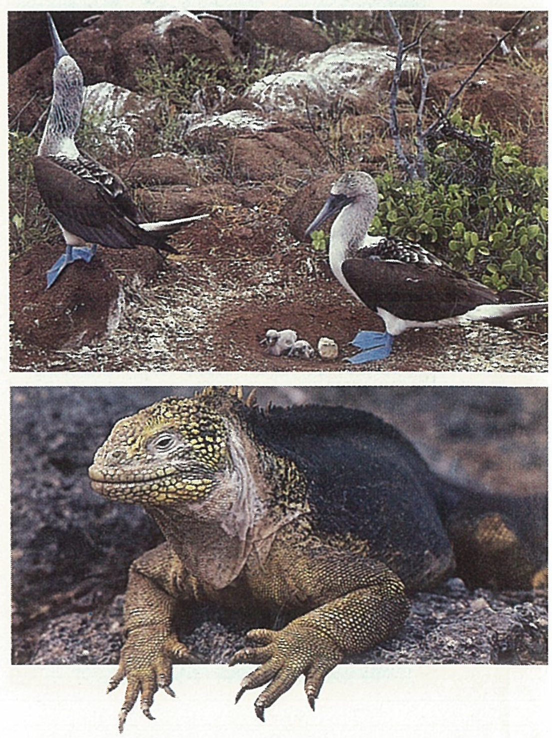
▲ **Figure 29–3**

Darwin's Finches. Two of the finch species native to the Galapagos Islands are shown above.

Darwin made similar observations about many plants, insects, and other organisms. While species on the Galapagos Islands resembled species on the mainland, they were always different in certain characteristics. See Figure 29-4. Darwin came to believe that these organisms originally had reached the islands from the mainland. Because of their isolation on the islands, the species had opportunities to develop special adaptations to each different region.

Figure 29–4

Species Unique to the Galapagos Islands. The blue-footed booby (top) and the land iguana (bottom) are two species unique to the Galapagos Islands. ▼



Darwin returned to England in 1836 convinced that species evolve. Although he had recorded many observations that supported such a hypothesis, he could offer no explanation of how evolution occurred. Because he could not, he did not publish his ideas at once. Instead, he continued to collect and organize his data and to search for a reasonable theory of how evolution occurs.

Darwin's Theory of Evolution

Shortly after he returned to England, Darwin read *An Essay on the Principle of Population* by Thomas Malthus. This essay greatly influenced Darwin's thinking and became the basis for his theory of evolution. Malthus, a minister, mathematician, and economist, was concerned about the social problems of an increasing human population. Malthus reasoned that the human population tends to increase geometrically (2, 4, 8, 16, . . .). For example, if each pair of parents produced four children, the new generation would have 4 individuals to replace the two that had produced them. The next generation would have 8, the next 16, and so on. On the other hand, food production could increase only arithmetically (1, 2, 3, 4, . . .) by gradually increasing the amount of land under cultivation. According to this reasoning, the food supply could not keep up with the increase in population. Therefore, to keep a balance between the need for food and the supply of food, millions of individuals had to die by disease, starvation, or war.

Darwin realized that all organisms face the same danger of overpopulation. He was also familiar with the competition and struggle for existence that occurs in nature. In 1838, the idea came to him that organisms with favorable variations would be better able to survive and to reproduce than organisms with unfavorable variations. He called this process **natural selection,** because nature "selects" the survivors. The result of natural selection would be evolution.

Darwin now had an explanation for how evolution occurred. Although many of his friends urged him to publish a book on the subject, Darwin would not be rushed. He insisted on building a strong case for his theory first. Then, in 1858, Darwin received an essay written by Alfred Russel Wallace, an English naturalist working in Indonesia. Wallace had arrived at the same conclusions as Darwin. Not knowing that Darwin had been thinking along the same lines, Wallace had sent the paper to Darwin for his opinion.

Darwin and Wallace agreed that Wallace's essay should be published along with a summary of Darwin's theory. A year later, in 1859, Darwin published his book under the title, *On the Origin of Species by Means of Natural Selection.* Darwin's book was fully supported by examples. His theory of evolution was eventually accepted by most of the leading scientists of his time.

The six main points of Darwin's theory are summarized below.

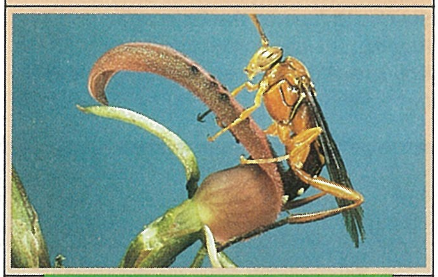
Overproduction Most species produce far more offspring than are needed to maintain the population. Species populations remain more or less constant because only a small fraction of offspring live long enough to reproduce.

Competition Since living space and food are limited, offspring in each generation must compete among themselves and with other species for the necessities of life. Only a small fraction can possibly survive long enough to reproduce.

Variation The characteristics of the individuals in any species are not exactly alike. They may differ in the exact size or shape of a body, in strength or running speed, in resistance to a particular disease, and so on. These differences are called **variations.** Some variations may not be important. Others may affect the individual's ability to get food, to escape enemies, or to find a mate. These are of vital importance.

Adaptations Because of variations, some individuals will be better adapted to survive and reproduce than others. In the competition for existence, the individuals that have favorable

Can You Explain This?



Several species of orchid emit a fragrance that is similar to the odor of female insects. Male insects are fooled by the scent and attempt to mate with the orchid's flowers. When the male lands on a flower, it makes contact with the orchid's pollen. Unsuccessful in its mating attempt, the insect flies off in search of a more appropriate mate, carrying the pollen to another orchid flower.

■ ***Suggest an explanation for how this ability to deceive insects developed in orchids.***

adaptations to their environment will have a greater chance of living long enough to reproduce. An **adaptation** is any kind of inherited trait that improves an organism's chances of survival and reproduction in a given environment.

Natural Selection In effect, the environment selects plants and animals with optimal traits to be the parents of the next generation. Individuals with variations that make them better adapted to their environment survive and reproduce in greater numbers than those without such adaptations. Experience has shown that the offspring of better adapted individuals usually inherit these favorable variations.

Speciation Over many generations, favorable adaptations gradually accumulate in the species and unfavorable ones disappear. Eventually, the accumulated changes become so great that the net result is a new species. The formation of new species is called **speciation** (spee shee AY shun).

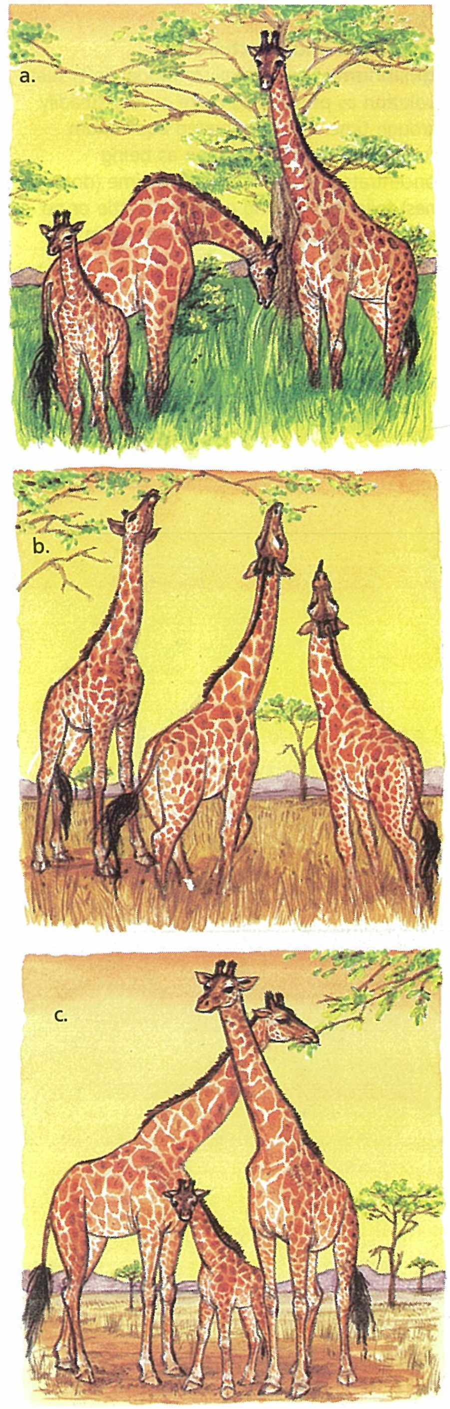
Applying Darwin's Theory

Figure 29–5 shows how Darwin's theory would account for the evolution of the modern giraffe. The original giraffe population had short necks and ate grass. However, unlike Lamarck's theory, Darwin's theory assumes some giraffes had longer necks than others. Those with longer necks could eat the lower leaves of trees as well as grass. In times when grass was scarce, the longer-necked animals could obtain more food than the others and, therefore, would be more likely to survive and reproduce. Their offspring would inherit the favorable variation of a longer neck. The longer the neck of a giraffe, the higher it could reach for leaves on the trees and the greater its chances for survival. As a result of natural selection, giraffe necks were slightly longer on the average in each succeeding generation. The modern long-necked animal is the result of this gradual process of evolution.

Overall, Darwin's theory of natural selection gives a satisfactory explanation of evolution. However, there are weaknesses in his theory. For one thing, it does not explain how variations originate and are passed on to the next generation. Also, it does not distinguish between variations caused by hereditary differences and variations caused by the environment, which are not inherited. For example, a plant growing in poor soil may be smaller than a plant of the same species growing in rich, fertile soil. Here, the differences in height are caused by the environment and cannot be inherited.

The Rate of Evolution

At present, scientists do not agree on the rate at which evolution or species formation occurs. According to Darwin's theory, new species arise through the gradual accumulation of small variations. In other words, evolution occurs slowly and continuously over



▲ **Figure 29–5**
Darwin's Theory of Natural Selection. (a) Adult giraffes' necks varied in length. (b) When the environment changed, only the long-necked giraffes could reach food. (c) The short-necked giraffes died, leaving only the long-necked giraffes to reproduce.

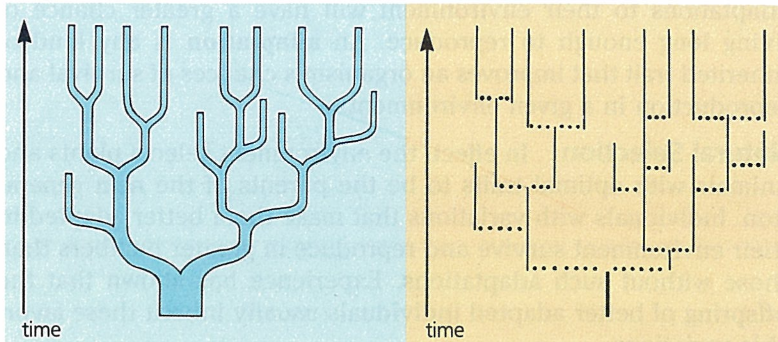


Figure 29–6
Gradualism and Punctuated Equilibrium. The gradualism model (left) sees evolution as proceeding more or less steadily through time. The punctuated equilibrium model (right) views evolution as being concentrated in short periods of time (dotted lines) followed by long periods of little or no change. Note that both models result in the same number of species. ▶

thousands and millions of years. This model is called **gradualism.** The gradualists believe that transitional forms, or links, between species are missing from the fossil record because they were less common. Thus, few of them were preserved.

Steven J. Gould and Niles Eldredge have proposed a different view of evolutionary change, which is known as **punctuated equilibrium.** According to their view, a species remains in equilibrium, or stays the same, for extended periods of time. This view is supported by the fossil record, which shows that each species seems to remain the same for thousands or millions of years. Then, in a relatively short period of time (a few hundred or a few thousand years) according to the fossil record, equilibrium is interrupted by the appearance of a new species. In other words, the long period of equilibrium is interrupted, or punctuated, by a short period of rapid evolution.

The supporters of punctuated equilibrium argue that transitional forms between species are missing because evolution occurs rapidly over a relatively brief period on the geologic time scale. Although the fossil record seems to support this new theory, the mechanisms that could produce new species in such a short interval are unknown. Figure 29–6 compares the Darwinian gradualistic model with the punctuated equilibrium model of evolution.

29-1 Section Review

1. Name the two principles involved in Lamarck's theory of evolution.
2. What is natural selection?
3. List the six main points of Darwin's theory of evolution.
4. Explain how the fossil record supports the theory of punctuated equilibrium.

Critical Thinking

5. Darwin observed similarities and differences between species on the Galapagos Islands and species on the mainland. Why were both similarities and differences necessary for Darwin's conclusion that evolution occurs? (*Reasoning Conditionally*)

29-2 The Synthetic Theory of Evolution

Section Objectives:

- *Define* the term *population genetics* and explain evolution in terms of allele frequencies.
- *Describe* De Vries' contribution to Darwin's theory of evolution.
- *List* the causes of variation in a species according to modern genetic theory.
- *State* the Hardy-Weinberg law and list the conditions under which this law holds true.

Laboratory Investigation: *Test* the Hardy-Weinberg law using traits of students (p. 622).

In Darwin's time, little was known about heredity and genetics. However, modern biologists have combined Darwin's basic theory with the findings of genetics and population biology to form the **synthetic theory** of evolution. According to this theory, evolution happens to populations, not to individuals. Indeed, evolution is now defined as a change in the allele frequency within a population over time. Even with this new definition, however, individuals, not popuiations, are the units of natural selection.

Population Genetics

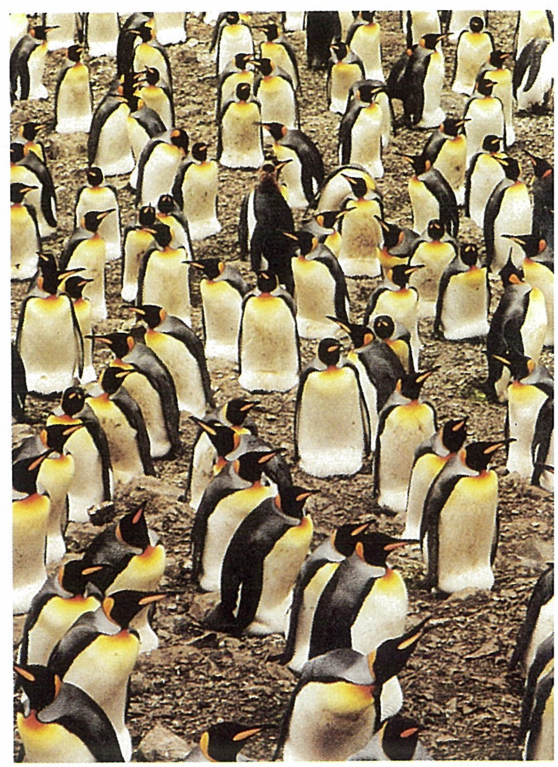
The synthetic theory of evolution stresses the importance of populations. See Figure 29–7. A **population** is a group of organisms of the same species living together in a given region and capable of interbreeding. According to the synthetic theory of evolution, *individuals* do not evolve. Their genetic makeup remains the same throughout their lives. However, *populations* do evolve. A population is made up of many individuals, each with its own unique assortment of alleles. As these individuals reproduce and die, the genetic makeup of the population as a whole may change. As its genetic makeup changes from generation to generation, the population evolves. The study of the changes in the genetic makeup of populations is called **population genetics.**

Each individual of a population has a set of alleles that is not exactly the same as the set of any other individual. Still, these individuals do have many of the same alleles. In a population as a whole, there are a certain number of alleles of each kind. Some alleles may be more common than others. For example, every individual in a population may have the alleles for producing a particular enzyme. The *frequencies* of these alleles in the population is 100 percent. On the other hand, only 1 in 100 individuals may have a mutant allele. Its frequency in the population is then 1/100, or 1 percent.

The total of all the alleles present in a population is called the **gene pool.** At any given time, each allele occurs in the population's gene pool with a certain frequency. This frequency may be any-

Figure 29–7

A Population of Penguins. According to the synthetic theory of evolution, it is a population that evolves over time, not individuals. ▼



▲ **Figure 29–8**
Mutations. De Vries formulated his theory of mutation after observing generations of evening primroses.

where from 100 percent to 1 per 10 000 or 1 per 1 000 000. As time goes on, the allele frequencies found in the gene pool may change as the result of natural selection. According to the synthetic theory, **evolution** is the gradual change of the allele frequencies found in a population.

Genetic Sources of Variation

The Dutch botanist Hugo De Vries introduced the concept of mutation at the beginning of this century. As you read in Chapter 26, De Vries based his theory of mutation on research that he conducted over several years with the evening primrose. See Figure 29–8. In the course of his research, De Vries observed that occasionally a plant appeared with a totally new structure or form. This plant would then breed true in later generations. De Vries considered these sudden changes in the hereditary material to be mutations.

De Vries added the idea of mutation to Darwin's theory of evolution. This overcame the question of how new traits could arise, one of the major weaknesses of Darwin's theory. De Vries claimed that the important changes leading to new species occurred as sudden, large changes in heredity that resulted from mutation. According to De Vries, a giraffe with a longer-than-normal neck would have been produced by a mutation. Because the long-necked giraffe and its offspring had an advantage over giraffes with necks of normal length, they survived and multiplied in greater numbers. Eventually, only the long-necked variety was left.

Mutations are not the only source of genetic variation. Recombination, as a result of sexual reproduction and the migration of individuals between populations, also contributes to variation.

Mutations

While gene mutations are a major source of variation in the synthetic theory of evolution, the mutation of any particular gene is a rare event. Out of 10 000 gametes, only one may have a mutated gene. The mutation rate for that gene is said to be 1 per 10 000. On the other hand, each gamete has thousands of genes. Among those thousands of genes, it is very likely that at least one of them has mutated. Thus, a few mutations are likely to be present in every zygote.

Most mutations are recessive. As a result, the mutant trait is usually hidden by the normal, dominant trait. Because of the low frequency of gene mutations, it is rare for mutant alleles to be brought together in the homozygous state. When this does happen, the effect may be harmful or helpful to the individual. However, if environmental conditions change, a harmful mutant allele may suddenly become useful to the species. Natural selection will then tend to gradually increase the frequency of this allele in the population.

Chromosomal mutations, which were described in Chapter 26, are another source of variation in a population. Although these mutations do not produce new genes, they do result in new combinations of genes in an organism. Since most physical traits are controlled by several genes, new gene combinations can give rise to new traits in a later generation.

Genetic Recombination The formation of new combinations of alleles during sexual reproduction is called **genetic recombination.** Recombination can occur when two gametes undergo fusion to form a zygote. It is crossing-over and independent assortment that bring about recombination during meiosis. Crossing-over involves the exchange of segments between homologous chromosomes. When crossing-over occurs, it results in new allele combinations. Independent assortment provides that alleles on nonhomologous chromosomes are randomly grouped, which also results in allele recombination.

Migration Another source of variation may result from migration into or out of a population. As individuals move into a population, they may bring in genes not already present. When individuals leave a population, they may remove some genes from the population. Migration tends to have its greatest effect on variations in small populations.

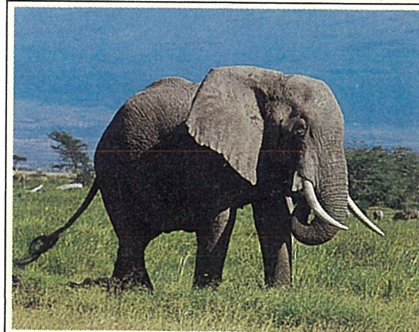
Genetic Drift Another factor that affects small populations is known as genetic drift. **Genetic drift** is a change in the gene pool of a small population that is brought about by chance. In small populations, there is a *chance* that a few individuals have certain alleles that the rest of the population does not have. If these individuals do not mate successfully, the alleles will be lost to the gene pool. For example, imagine that the population of an endangered plant species consists of 80 plants. Suppose that only three plants in this population have a certain allele. If these three plants are killed in a storm before they reproduce, the gene pool is reduced.

Genetic drift usually is harmful to the population because it decreases the variations in the gene pool. In a large population, genetic drift is less likely to occur because there are so many individuals. Therefore, it is unlikely that only a few individuals have an allele that no other individuals possess.

The Hardy-Weinberg Law

In Chapter 25, you read about Mendel's experiments with hybrid pea plants. In these experiments, there were two alleles for each trait that he studied. For example, the allele T produced tall plants, and the allele t produced short plants. The frequencies of T and t in the hybrid plants were equal: 50 percent T and 50 percent t. When the hybrids reproduced, the offspring had a genotype ratio of 1:2:1 and a phenotype ratio of 3:1, but the allele frequencies in the offspring remained the same—50:50. You can check this statement for yourself by counting the T and t alleles in the Punnett square shown in Figure 25-10.

Science, Technology and Society



Issue: Endangered Species

The snow leopard, northern spotted owl, and African elephant are only a few of many species facing a common threat: extinction. Today, the chief causes of extinction are human activities such as poaching (hunting illegally), and destroying natural habitats for industrial or agricultural use. The present extinction rate is over 1000 times higher than in prehistoric times, and it is increasing rapidly.

Environmentalists argue that governments must pass laws to control human activities that result in extinction. All organisms have a right to exist, and many species have potential value as sources of medicine and knowledge.

Other people argue that human needs are more important. Many people depend on the farmland for their food. Others make a living by logging or through other uses of the land. Moreover, competition for survival among species, including humans, is a natural process. Because it is, governments should not interfere.

■ ***Should steps be taken to protect endangered species? Why or why not?***

The condition in which allele frequencies do not change from one generation to the next is called **genetic equilibrium.** To maintain genetic equilibrium, it is not necessary for two alleles in a population to have the same frequency. One may be much more common than the other. Suppose, for example, that there are two alleles for eye color in a certain species. One allele produces white eyes; the other, red eyes. We do not need to worry about dominance or about the eye color of a hybrid. Let us just assume that the allele for white eyes is more common than the allele for red eyes. We will say that 90 percent of the alleles are for white eyes, and 10 percent are for red. As these organisms mate and reproduce, what will happen to the allele frequencies for eye color as generation follows generation? While it might seem logical that the white-eye allele will eventually replace the red-eye allele, in fact, the allele frequency does not change.

In 1908, G. H. Hardy, an English mathematician, and W. H. Weinberg, a German physician, considered this question and came to the same conclusion independently. They showed that segregation and recombination of genes in sexual reproduction could not change allele frequencies by itself. If the frequency of allele p was 90 percent, and the frequency of its allele, q, was 10 percent, random mating would always produce a new generation with the same ratio of 90 percent p and 10 percent q. Their conclusion that sexual reproduction alone does not affect genetic equilibrium is called the **Hardy-Weinberg law.** See Figure 29-9.

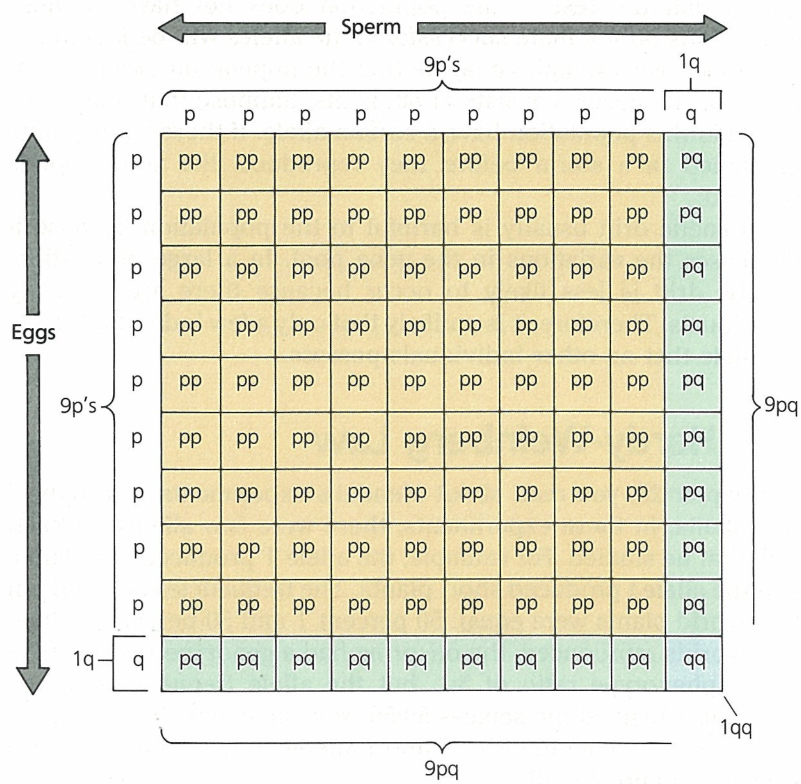


Figure 29–9

Illustrating the Hardy-Weinberg Law. Assume that the frequency of an allele p in a population is 90 percent and that of allele q is 10 percent. Then, out of every 10 sperm cells produced by the population, 9 will carry the p allele and 1 will carry q. The Punnett square shows the results of random fertilizations between these sperm and eggs. Of every 100 gametes formed, 81 are pp, 18 are pq, and 1 is qq. The total number of p's and q's in these 100 gametes is:

81 pp = 162 p's
18 pq = 18 p's and 18 q's
1 qq = 2 q's
Totals: 180 p's and 20 q's

We see that the ratio of p to q in the offspring generation is 180 to 20, or 9 to 1. This is the same as the ratio in the parent generation. ▶

For the Hardy-Weinberg law to hold true, four conditions must be met.

- The population must be large. In a small population, alleles of low frequency may be lost, or the frequency may change due to genetic drift.
- Individuals must not migrate into or out of the population. Any individuals that do so may change the allele frequencies of the population.
- Mutations must not occur because mutations obviously change the frequencies of the population.
- Reproduction must be completely random. This means that every individual, whatever its genetic makeup, should have an equal chance of producing offspring.

While the first two of these conditions can exist in nature, the last two conditions almost never exist. Populations can be large enough, and migration can be practically zero under certain circumstances. Mutations, however, are always occurring at fixed rates, thus changing allele frequencies. Furthermore, reproduction is not random. Individuals with helpful adaptations are more likely to reproduce because of natural selection. This also results in a change in the allele frequencies.

You may wonder about the usefulness of a law that does not apply to any situation in the real world. The Hardy-Weinberg law is important because it allows us to discover whether or not evolution is occurring in a population. The law tells us that under certain conditions, allele frequencies will remain constant and there will be no evolution. The fact that allele frequencies in a population change tells us that there are external factors causing them to change. In other words, the failure of the Hardy-Weinberg law is a sign that evolution is occurring. The extent of the variation from the Hardy-Weinberg prediction is a measure of how rapid the evolutionary change is.

29-2 Section Review

1. Name the sources of variation within a species according to the synthetic theory of evolution.
2. What is a population?
3. Define the term *gene pool.*
4. List the conditions that must exist for the Hardy-Weinberg law to hold true.

Critical Thinking

5. If mutations occur, then the allele frequencies in a population will change. In a population you are studying, the allele frequencies have changed. Does this prove that mutations have occurred? Why or why not? (*Reasoning Conditionally*)

▲ **Figure 29–10**
Adaptations. The dormouse, like many mammals, hibernates in winter. During hibernation, the animal's metabolic rate and body temperature decrease. This adaptation allows the animal to survive long cold periods when food is scarce.

29-3 Adaptations and Natural Selection

Section Objectives:

- *Explain* the term *adaptation* and name some different kinds of adaptations.
- *Define* the terms *camouflage, warning coloration,* and *mimicry.*
- *Distinguish* among *directional selection, stabilizing selection,* and *disruptive selection.*

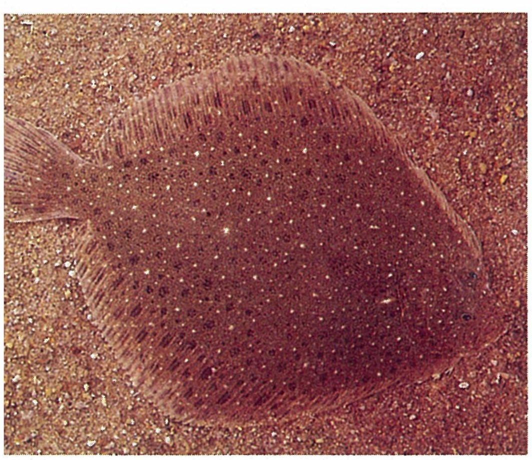
Under what conditions will a species evolve? By focusing on allele frequencies, the Hardy-Weinberg law allows scientists to understand the mechanisms of natural selection. In this section, we will look at how natural selection determines which adaptations are favorable for survival.

Types of Adaptations

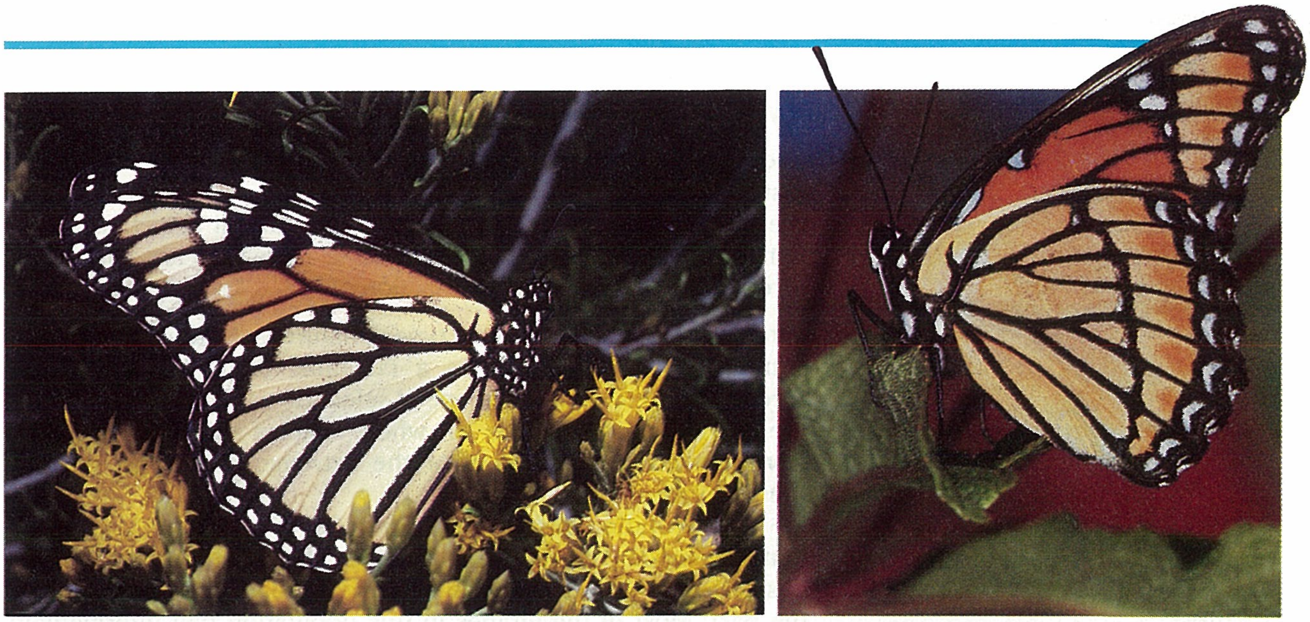
As you read earlier, an adaptation is any kind of inherited trait that improves the chances of survival and reproduction for an organism. The environment is the selecting force that chooses the best and most useful inherited variations. For example, in a population of plants, there may be a genetic variation in the amount of waxy cutin covering the leaves of the plants. Some plants may be heavily covered with this protective layer, while other plants are only thinly covered. Because cutin protects the plant from drying out, plants with a thick cutin layer will be better able to survive and to produce seeds if the climate becomes very dry. In this case, the cutin is an adaptation that has been "selected" by the environment. After many generations, alleles for this adaptation will accumulate in the gene pool. Eventually, only plants with a heavy cutin layer will remain in the population.

Structural adaptations are adaptations that involve the body of the organism. The wings of birds and insects, for example, are structural adaptations for flight. The fins of fish and the webbed feet of ducks are structural adaptations for swimming. *Physiological adaptations* involve the metabolism of organisms. The protein web made by spiders and the poison venom made by snakes are examples of physiological adaptations. Still other adaptations involve particular behavior patterns. Of course, many adaptations are combinations of various types of adaptations. For example, the mating behavior and migration of birds, the spawning of fishes, and the hibernation of animals involve several types of adaptations. See Figure 29–10.

Figure 29–11
Camouflage. The sundial flounder is camouflaged against the sandy ocean floor. ▼

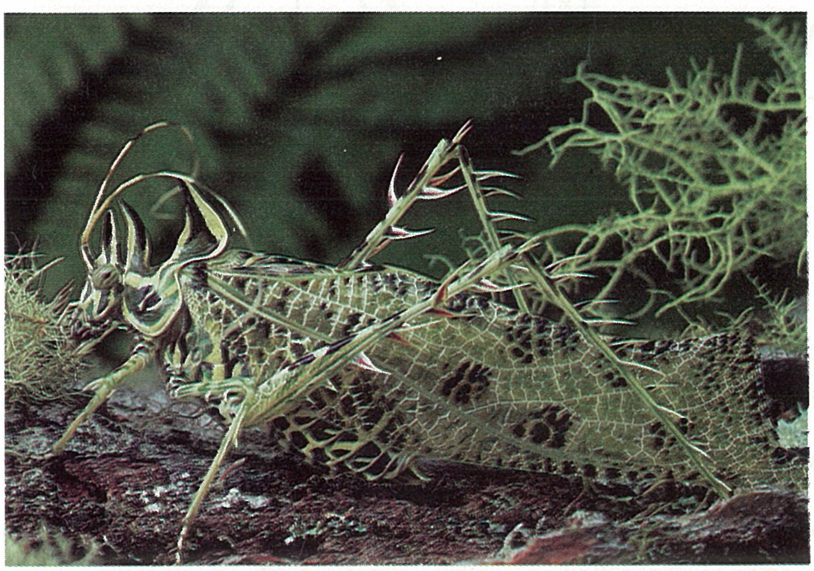


Many adaptations provide protection. In **camouflage,** the organism blends into the environment, as shown in Figure 29–11. Flounders can become practically invisible against a variety of backgrounds. Fawns are hard to see among the shadows in their usual environment. In **warning coloration,** the colors of the animal



▲ **Figure 29–12**
Mimicry and Warning Coloration. The inedible monarch butterfly (left) warns away potential predators with its bright colors. The edible viceroy butterfly (right) is avoided by predators because it so closely resembles the monarch in color and markings.

actually make it easier to see. This is an advantage for certain insects that birds and other enemies find unpleasant to eat. If a young bird happens to eat one of these insects, it quickly learns to avoid that species in the future. The brightly colored monarch butterfly, which is shown in Figure 29-12, is an example of this kind of warning coloration. In **mimicry,** one organism is protected from its enemies by its resemblance to another species. Birds can eat the viceroy butterfly without suffering unpleasant effects, but they tend to avoid it because it looks like the monarch butterfly. In contrast to mimicry, camouflage helps an organism avoid its enemies by making it difficult to see. As Figure 29-13 shows, shape and structure, as well as coloration, can contribute to an organism's camouflage.



◄ **Figure 29–13**
Camouflage. The lichen katydid is hidden from predators because it resembles the lichen on which it feeds.

Types of Natural Selection

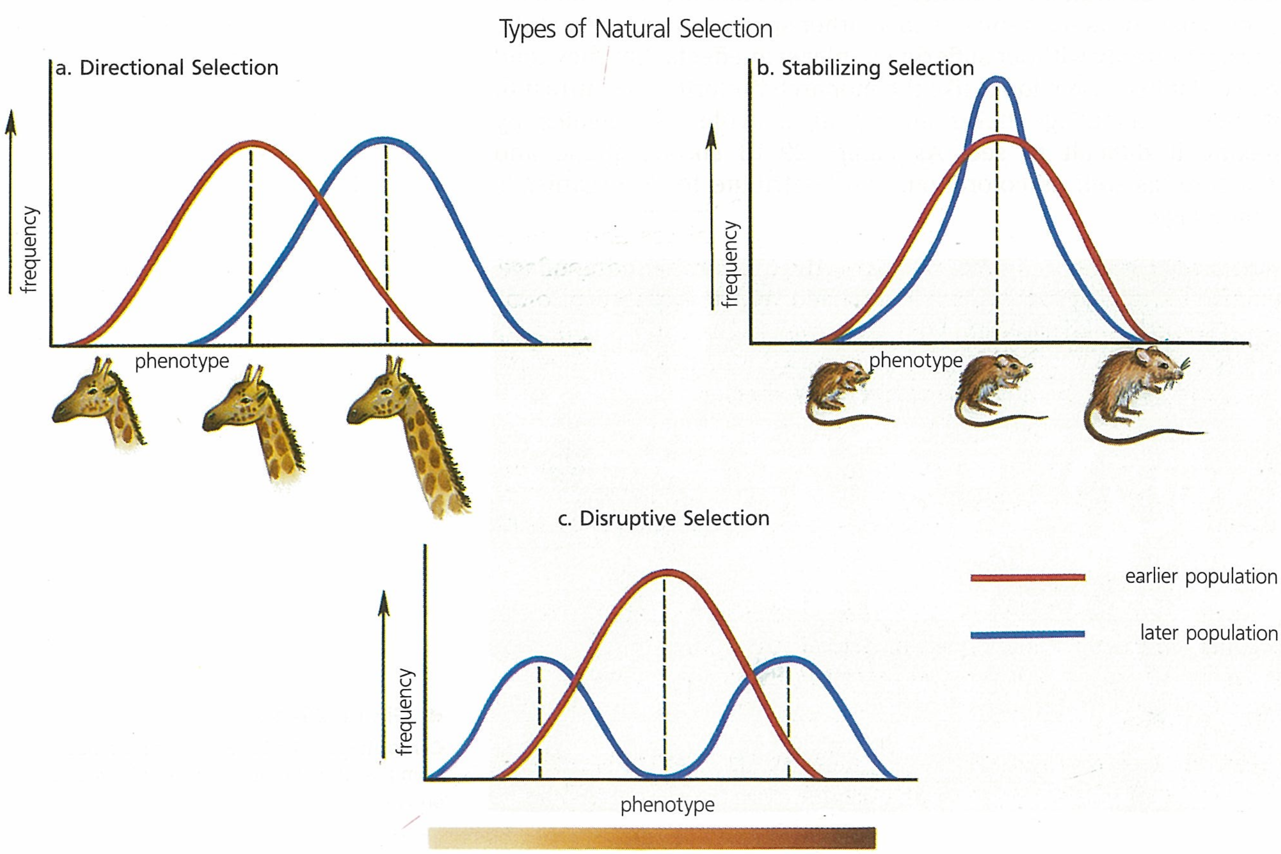
According to the synthetic theory of evolution, natural selection disturbs genetic equilibrium. As a result, the allele frequencies in the population will change. In this way, natural selection determines which adaptations are favorable for a species. There are three main types of natural selection.

Directional Selection One type of natural selection, in which an extreme phenotype becomes a favorable adaptation, is called **directional selection.** This type of selection usually operates when the environment changes or when species migrate. The new environmental conditions favor the extreme phenotype, causing the population to evolve.

The evolution of long-necked giraffes is an example of directional selection. The red graph in Figure 29–14a shows the continuous variation of neck length in a giraffe population at some time in the past. Most of the giraffes in this population had intermediate neck lengths, although some had short necks and some had long necks. Several alleles for short and long necks probably were present, with low frequencies, in the population. A change in the environment may have given the individuals with the alleles for longer necks a favorable adaptation. In later generations, their offspring made up a larger fraction of the population. Therefore, the

Figure 29–14

Types of Selection. Directional selection favors a relatively rare phenotype. Stabilizing selection favors average phenotypes and acts against extreme phenotypes. Disruptive selection favors two extreme phenotypes and acts against the average phenotype. ▼



alleles they carried for long necks would be present at a greater frequency, and the population would have longer necks, on average. This is shown by the blue curve. Notice that the blue curve looks like the red curve, but it is shifted to the right. Thus, directional selection selects in the direction of an extreme phenotype.

Stabilizing Selection Sometimes, the average phenotype may be a favorable adaptation, and extreme phenotypes are unfavorable. This is called **stabilizing selection.** For example, mice that are too small may not be strong enough to burrow underground in cold weather, while mice that are too large may use too much energy in keeping warm. If the climate becomes colder, fewer large and small mice will survive to reproduce. See Figure 29–14b. Notice that the average size of the population, shown by the dashed line, is the same in the two populations. However, the blue curve representing the population after the climate change is narrower because there is less variation in the population. This is because the frequencies of some alleles carried by the extreme phenotypes have decreased.

Stabilizing selection operates most of the time in most populations. This type of selection limits evolution by keeping allele frequencies relatively constant. In this way, populations of organisms, such as sharks and ferns, have remained stable for millions of years.

Disruptive Selection A third, rare type of natural selection is called disruptive selection. In **disruptive selection,** two opposite phenotypes are favorable adaptations, while the average phenotypes are unfavorable. As you can see in Figure 29–14c, this creates two subpopulations. For example, a species of crab might show a continuous variation in color from light tan to dark brown. If the environment changed to include both sandy beaches and brown mud, both extremes of coloration could be favorable camouflage against predators. In time, alleles carried by the extreme phenotypes would increase in frequency, resulting in the evolution of two subpopulations. If these populations could not mate with each other, they would be considered two new species.

29-3 Section Review

1. Define the term *adaptation*.
2. Name two different types of adaptations and give an example of each.
3. What are the three main types of natural selection?
4. Which type of natural selection tends to prevent evolution?

Critical Thinking

5. How is mimicry of the environment different from camouflage? How is it similar? (*Comparing and Contrasting*)

Can You Explain This?

Several centuries ago, a ship carrying emigrant families was blown off course and wrecked on a deserted tropical island. All of the people were very light skinned. After many years under the tropical sun, however, everyone became dark skinned.

- ***What color skin would babies born to the children of these couples have? What color skin would babies in the fifth generation have? Explain your answers.***

29-4 Speciation

Section Objectives:

- *Define* the terms *range* and *speciation.*
- *Describe* the processes of isolation and adaptive radiation.
- *Distinguish* between convergent evolution and coevolution.

Concept Laboratory: *Explore* the evolutionary adaptations predators and their prey (p. 617).

Under certain circumstances, one species can evolve into two more species. This formation of new species is called **speciati** (spee shee AY shun).

Speciation and Geographic Separation

Each species is found in a particular region of the earth. This regi is called the species' **range.** The characteristics of a species a often different in different parts of its range. Differences in envirc mental conditions have exerted different selective pressures, lea ing to different adaptive characteristics. The leopard frog, *Ra pipiens,* for example, has a wide range that extends over most North America. Across this range, the frogs differ in body si patterns of coloration, and the temperatures at which their embı os will develop. The species actually consists of separate popu tions with different gene pools. However, adjacent populations c mate and produce normal offspring. These separate populatio are therefore called subspecies, or varieties, of the same specie

The frogs at opposite ends of the range show the great differences in characteristics and in gene pools. In fact, frogs frc widely separated regions cannot mate successfully. They are s considered to be the same species because there is continuc interbreeding among adjacent subspecies. If, however, a populati varies so much from its neighbors that it loses the ability interbreed, a new species has developed.

Types of Speciation

Isolation One of the most important factors involved in spec tion is isolation. *Isolation* refers to anything that prevents t groups within a species from interbreeding. Isolating a group organisms separates its gene pool from the gene pool of the rest the species. Through mutation, genetic recombination, and natu selection, a different gene pool will evolve in each group.

It is generally believed that speciation is a two-step proc that first involves geographic isolation, followed by reproduct isolation. **Geographic isolation** occurs when a population is div ed by a natural barrier, such as a mountain, desert, river or otl body of water, or a landslide caused by an earthquake. See Figı 29-15. As a result, the gene pool of each group becomes isolat and the two can no longer intermix. Over a period of time, ea group will become adapted to its particular environment. When t differences between the isolated groups become great enough, they will no longer be able to interbreed, even if they could get together. The loss of the ability to interbreed by two isolated groups is called **reproductive isolation.**

Reproductive isolation can be produced by several mechanisms. Differences may arise in courtship behavior, times of mating, or the structure of the sex organs. Such changes make it unlikely that mating will occur. Other changes affect events after mating and involve the inability of sperm to fertilize eggs, the death of the embryo early in development, or the development of offspring that are sterile. According to most biologists, if two groups of organisms cannot interbreed successfully, they can be considered different species.

The Kaibab squirrel and Abert squirrel are thought to be cases of speciation by geographic and reproductive isolation. The Kaibab squirrel inhabits the north side of the Grand Canyon, and the Abert squirrel inhabits the south side. It is believed that these two squirrels evolved from a common ancestor. The Grand Canyon, acting as a geographical barrier, divided the ancestral population, which once occupied the entire area. After a long period of geographical isolation, the Kaibab and Abert squirrels evolved. The two squirrels are similar in appearance but are different species because they cannot interbreed.

Polyploidy Speciation can occur suddenly when abnormal meiosis or mitosis results in polyploidy. As you read in Chapter 25, polyploids are organisms, usually plants, that contain more than the usual number of chromosome sets. When the offspring can interbreed only among themselves, they are considered a new species.

Adaptive Radiation The process by which a species evolves into a number of different species, each occupying a new environment, is called **adaptive radiation.** This spreading, or radiation, of the organisms into different environments is accompanied by adaptations.

For example, a single ancestral species may have migrated—radiated—into several different environments. If the descendants have few predators and little competition for food, they will be successful. Then, through isolation, genetic variation, and natural selection, they will evolve a variety of adaptations to their new environments. After many generations, they will have evolved into several new species, each having certain adaptive traits. However, their common ancestry is indicated by the traits they share in common.

Darwin's finches are an example of adaptive radiation. In this case, an ancestral type of finch probably arrived in the Galapagos Islands and then radiated into a variety of habitats and ways of life. The initial radiation involved living on the ground and living in trees. Further radiation occurred on the basis of food. Some finches live on the ground and feed on seeds of varying size. Some live in forests and feed on insects in trees. Others feed mainly on cactus or

▲ **Figure 29–15**

Speciation through Geographic Isolation. The spring-dwelling salamander (top) and the cave-dwelling salamander (bottom) can no longer interbreed. These two species are believed to share a common ancestor. The population was divided when one group took up residence in a cave. The differing selective pressures of the two environments resulted in the divergence of the species over time.

berries. One species lives in low bushes and feeds on insec Without competition from other birds, the finches slowly radiat into and adapted to the various types of environment that w present.

▲ **Figure 29–16**
Convergent Evolution. The koala bear is a marsupial that looks very much like a bear.

Convergent Evolution

As a result of geographic isolation, organisms that are not clos related may develop similar adaptations and come to resem each other. Natural selection that causes unrelated species resemble one another is called **convergent evolution.** Converg evolution produces analogous structures, which you read about Chapter 28. Bird wings and insect wings are good examples analogous structures that result from convergent evolution.

Another example of convergent evolution is the similar between marsupials and their placental counterparts. The marsu al mouse looks much like a placental mouse. There is also marsupial that resembles a wolf (the Tasmanian wolf) and one t resembles a bear (the koala), which is shown in Figure 29– These resemblances are only "skin deep." They evolved because similar needs in similar environments, leading to the natu selection of analogous structural adaptations.

Coevolution

Two or more species also can evolve in response to each ot through cooperative or competitive adaptations. This is call **coevolution.** One example of coevolution is the relationship b tween flowers and their pollinators. For example, some species flowers have developed adaptations to attract bees. Bees are act during the day, attracted by bright colors and sweet or minty odo and usually land on a petal before feeding. Flowers adapted to be have a sweet or minty odor and are open in the daytime. They ha a petal for the bee to land on and are usually bright blue or yello because bees cannot see red light. In comparison, bats, which a active at night, feed on the nectar of flowers that are open at nig and easily visible in the dark. Coevolution reduces competiti between species and benefits both species.

29-4 Section Review

1. What is speciation? Name the two steps involved in speciation.
2. What is adaptive radiation?
3. Give an example of convergent evolution.
4. Define the term *coevolution.*

Critical Thinking

5. What possible outcomes are likely if a species migrates into area with many predators? Explain your answer. (*Predicting*)

Concept Laboratory

Natural Selection

Goal

To gain an understanding of the process of natural selection.

Scenario

Imagine that you and your classmates are predators, searching for food. Your only source of food is square-shaped organisms. You will eat any square-shaped individual as soon as you see it.

As you perform this experiment, think about how the process of natural selection operates.

Materials

newspaper
solid color construction paper
scissors
empty box

Procedure *

A. Working in groups of four, cut sheets of newspaper into 64 squares of equal size—about 5 cm × 5 cm.

B. Do the same for the colored sheet of paper.

C. Place all the paper squares into a box, shake thoroughly, and dump the squares onto some open, uncut sheets of newspaper. Spread out the squares so they do not overlap.

D. Acting as a predator, each member of your group in turn should quickly look at the spread of squares on the newspaper, grab the square that he or she first sees, then look away. Each person should repeat this procedure five times.

Organizing Your Data

1. Copy the chart below and record how many types of paper square each member of your group captured.

2. Among the members of your group, what differences were there in the number of captured squares of each color? What are some possible explanations?

*For detailed information on safety symbols, see Appendix B.

Student	Newspaper Squares	Colored Squares
1		
2		
3		

3. Calculate the number of squares of each type that were not captured. Graph the data.

4. Compare the results of your group with those of the rest of your class.

Drawing Conclusions

1. What do the two kinds of paper squares represent? What does the open, uncut newspaper represent?

2. Which type of paper square had the lower rate of survival? How would you explain these results?

3. What traits besides coloration might give some individuals of a species an adaptive advantage over others?

4. Based on this investigation, write a brief paragraph explaining how natural selection operates.

Thinking Further

1. Based on your results, what would you expect to happen to the population makeup over the course of many generations?

2. How confident are you that the population would change as you predicted in the previous question? List three factors that might cause the outcome to be different from what you predicted.

3. As you know, predation is only one of many selective forces acting on organisms. Describe a situation in which weather conditions would lead to natural selection in a plant species.

29-5 Observed Natural Selection

Section Objectives:

- *Discuss* industrial melanism and the information gained from the study of the peppered moth in England.
- *Describe* how populations of antibiotic-resistant bacteria and DDT-resistant insects have arisen.

Natural selection may take many thousands of years to produce a change in a population. However, in recent years some excellent examples of natural selection have given scientists an opportunity to study evolution in action. One of these illustrates a kind of adaptation called industrial melanism. **Industrial melanism** is the term used for the development of dark-colored organisms in a population exposed to industrial air pollution.

Industrial Melanism

The peppered moth, *Biston betularia,* is found in wooded areas in England. Before the 1850s, most peppered moths were light in color. Black-colored moths that have a pigment called *melanin* occurred, but they were very rare. During the years from 1850 to 1900, England became heavily industrialized. Where there was a great deal of industry, heavy smoke darkened the tree trunks and killed the light lichens that were growing on them. By the 1890s in these regions, 99 percent of the peppered moths were black in color, while the light-colored variety was rare. In the cleaner, nonindustrial areas of southern England, the light-colored moth continued to predominate. See Figure 29–17.

A hypothesis for the change from light-colored to dark-colored moths can be found in natural selection. The light and dark color of the moth is genetically controlled. The dark color is a mutation that

Figure 29–17
Industrial Melanism. On the light tree (left), the lighter colored peppered moth is better camouflaged. On the dark tree (right), the darker moth is better camouflaged. ▼

occurs at a constant low frequency. During daylight, peppered moths rest on tree trunks. Before England became industrialized, the light-colored moths blended in well with the lichens that covered the tree bark. As a result of this camouflage, birds that feed upon the peppered moth could not easily find the light-colored moths. Dark-colored moths were easily seen and eaten by hungry birds. This situation gave the light-colored moths an obvious reproductive advantage. When the fumes and soot killed the lichens and blackened the trees, however, the light-colored moths were easy to see against the dark background of the tree trunks and became easy prey for birds. Now, the dark-colored moths had a distinct advantage. The blackened trees offered them good camouflage, as shown in Figure 29-17. Through natural selection, more dark moths survived and reproduced than light-colored moths. During the years from 1850 to 1900, a period of 50 generations for peppered moths, the dark-colored moths became the more frequent color in the population.

In the 1950s, H. B. D. Kettlewell and Niko Tinbergen performed controlled experiments that attempted to test the above hypothesis. Light- and dark-colored peppered moths were released in a polluted industrial area and in an unpolluted nonindustrial area. In the polluted area, where the trees were blackened with soot, Kettlewell and Tinbergen recorded more light-colored moths eaten than dark-colored moths. In the unpolluted area, birds ate more dark-colored moths than light-colored moths.

This research on the color change in peppered moths shows that a species can change gradually from one form to another over a period of time. Two details of the evolutionary process are clearly illustrated. One is the presence of variability in the population. Alleles for light color and dark color are in the gene pool. The other is the effect of the changing environment in selecting one color trait over another. The trait that makes the moth best adapted to the environment is preserved.

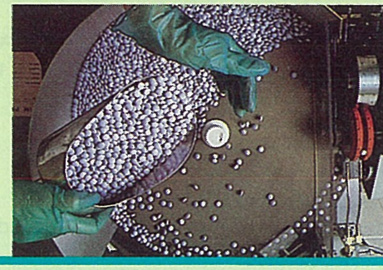
In the United States, the insects around many major cities are darker in color than the ones in the unpolluted countryside. Interestingly, since the 1950s, air pollution control in England has resulted in an increase in the number of light-colored peppered moths.

Bacterial Resistance to Antibiotics

Antibiotics usually kill bacteria. However, once the use of antibiotics became common, resistant strains of bacteria began to appear. Antibiotics were no longer effective in killing those strains.

Scientists wanted to know how this resistance developed. One possibility was that exposure to an antibiotic caused certain bacterial cells to develop resistance to it. This would be similar to the immunity an individual acquires to a disease organism after recovery from the disease. Another possibility was that in a large population of bacteria, there are always a few individuals with

Biology and You



Q: Can resistance to antibiotics spread from one bacterium to another? If so, will antibiotics soon be useless?

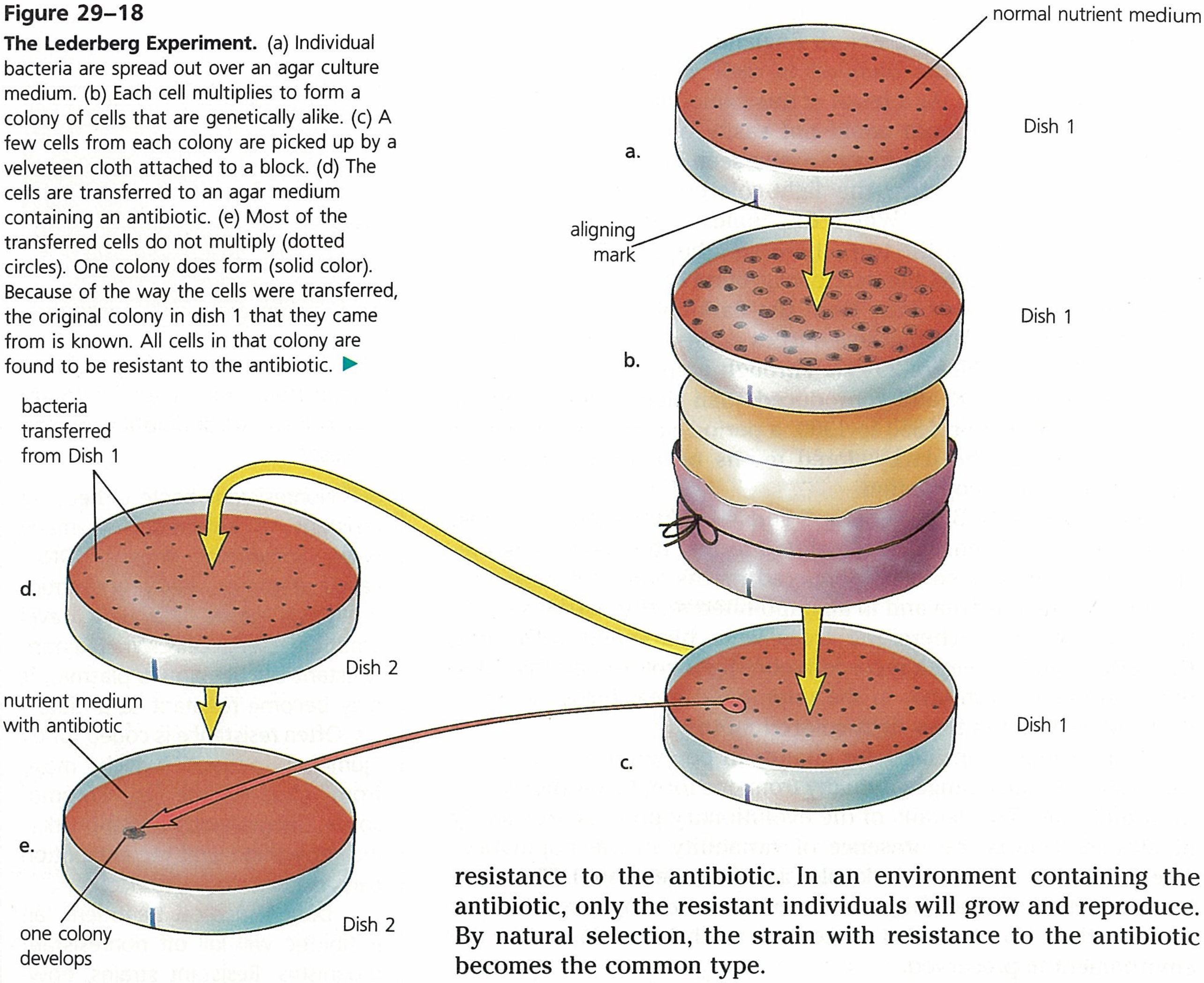
A: Nonresistant bacteria become resistant to antibiotics in many ways. Sometimes rings of DNA, called plasmids, carry antibiotic-resistance genes. Plasmids travel among bacterial cells. When a nonresistant cell acquires a plasmid, it may become resistant to antibiotics. Often resistance is coded for by "jumping genes," which move from chromosome to chromosome. Spontaneous mutation during replication and recombination can also lead to resistance.

During medical treatment, an antibiotic will kill off nonresistant organisms. Resistant strains, however, will survive. Because bacteria reproduce quickly, resistant strains can rapidly spread. This rise in resistant organisms causes antibiotics such as penicillin or streptomycin to be ineffective. One way to reduce this problem is to minimize the use of antibiotics. Another way is to give two unrelated antibiotics at the same time, assuming that resistance to both is unlikely.

■ ***Survey five people to find out how many have taken antibiotics in the past three months. Do they know the type taken?***

Figure 29–18

The Lederberg Experiment. (a) Individual bacteria are spread out over an agar culture medium. (b) Each cell multiplies to form a colony of cells that are genetically alike. (c) A few cells from each colony are picked up by a velveteen cloth attached to a block. (d) The cells are transferred to an agar medium containing an antibiotic. (e) Most of the transferred cells do not multiply (dotted circles). One colony does form (solid color). Because of the way the cells were transferred, the original colony in dish 1 that they came from is known. All cells in that colony are found to be resistant to the antibiotic. ▶



resistance to the antibiotic. In an environment containing the antibiotic, only the resistant individuals will grow and reproduce. By natural selection, the strain with resistance to the antibiotic becomes the common type.

In the early 1950s, Esther and Joshua Lederberg carried out a series of experiments that showed that the second explanation, natural selection, was the correct one. The Lederbergs worked with the common intestinal bacterium *Escherichia coli,* which is normally killed by the antibiotic streptomycin. The first step of their experiment was to spread a culture of the bacteria very thinly on an agar nutrient medium in a petri dish. See Figure 29–18. This technique, which is called streaking, had the effect of separating the culture into individual bacteria. Each bacterial cell then multiplied on the agar, forming a distinct colony. In each colony, all the cells were genetically alike since they had developed from a single original cell.

The Lederbergs then looked for cells resistant to streptomycin. Since it would have taken too much time to investigate each colony separately, they used a velveteen cloth to pick up bacteria from all the colonies at once. The cloth was then touched to a second agar plate that contained streptomycin, thus transferring bacteria from all the colonies to the agar. Usually, none of the transferred bacteria formed a colony; they could not survive and multiply in the streptomycin environment. Occasionally, however, a colony did grow on the streptomycin plate. When this happened, the Lederbergs could identify the original colony the transferred cells had come from. They could because the velveteen cloth placed the bacteria in the same relative positions on the new agar as the colonies from which they were picked up. It was then a simple matter to test the original colony for streptomycin resistance.

When this test was carried out, it was found that all cells in the original colony were resistant. Remember that these cells had never been exposed to streptomycin. Their resistance was a genetic trait that they already possessed.

The Lederbergs concluded that a few bacteria with resistance to streptomycin had been in the original population. When no antibiotic was present in their environment, these cells had no advantage or disadvantage. However, when the environment was changed to include the antibiotic, the resistant cells had a survival advantage and multiplied, while the normal type died out. The population became 100 percent streptomycin-resistant.

This experiment showed that the change in the environment had not caused the resistance to develop. It had acted only as a selector for organisms that already had the gene for resistance to streptomycin.

Insect Resistance to DDT

When DDT was first introduced, it was an effective killer of insects, including mosquitos. Apparently, however, a small proportion of insects in various insect populations possessed a natural resistance to DDT. When the DDT-sensitive members of a population were killed by spraying, the DDT-resistant insects survived and passed on their natural DDT-resistance to their offspring. Eventually, many insect populations were completely resistant to DDT.

The DDT did *not* create the resistance of the insects. Rather, the DDT acted as the environmental agent for the selection of the resistant strains.

29-5 Section Review

1. What is industrial melanism?
2. Which moths were eaten more easily by birds in industrial areas?
3. Who discovered how antibiotic-resistant bacteria develop?

Critical Thinking

4. Explain why air pollution control in England since the 1950s has led to a greater number of light-colored moths. (*Identifying Causes*)

Laboratory Investigation

The Hardy-Weinberg Law

The Hardy-Weinberg Law, expressed as $p^2 + 2pq + q^2 = 1$, allows the calculation of allele and genotype frequencies in a population. In this investigation, you will determine allele and genotype frequencies for a single human trait.

Objectives

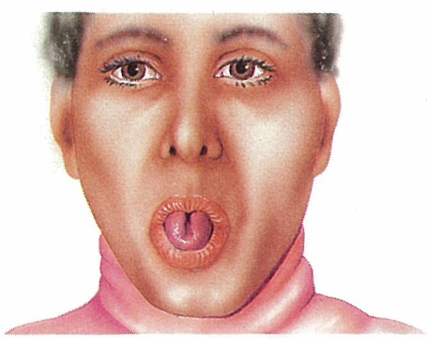
- *Calculate* the frequencies of the dominant and recessive alleles for an inherited trait.
- *Compare* the frequencies of two alleles with the frequencies of their phenotypes.

Materials

calculator

Procedure

A. Tongue rolling is controlled by a single gene. Persons homozygous dominant or heterozygous can roll their tongue. Homozygous recessive individuals cannot. See if you can roll your tongue, as shown below. Following your teacher's instructions, indicate your phenotype on the chalkboard.



B. Make a table like the one shown above. From the class data, calculate q^2, the fraction of individuals who are homozygous recessive for the trait (those who cannot roll their tongue). Express this as a decimal value. For example, if 3 out of 30 people cannot roll their tongues, then (3/30), or 0.1, of the class are homozygous recessive. Record this value under the q^2 column.

C. Calculate q, the frequency of the recessive allele, by finding the square root of q^2. Record your answer.

D. Determine the frequency of the dominant allele, p, by using the formula $p = 1 - q$. Record your answer in the table.

E. Calculate and record in the table the frequencies of the homozygous dominant (p^2) and heterozygous ($2pq$) genotypes.

Phenotypes	Numbers of Rollers	
	Numbers of Nonrollers	
fraction with homozygous recessive genotype (q^2)		
frequency of recessive allele (q; $q = \sqrt{q^2}$)		
frequency of dominant allele (p; $p = 1 - q$)		
fraction with homozygous dominant genotype (p^2)		
fraction with heterozygous genotype ($2pq$)		

Analysis and Conclusions

1. What are the frequencies for the alleles that affect tongue rolling?

2. Is q, the frequency of the recessive allele, larger or smaller than the frequency of people showing the recessive trait? Why?

3. If you tested 10 000 people, do you think the genotype frequencies would be the same as those in your class? Explain.

4. If all Hardy-Weinberg conditions were met, what would be the next generation's allele frequencies?

5. Cystic fibrosis is a recessive, inherited disease whose victims die before they can reproduce. Which Hardy-Weinberg condition would not be met under these circumstances?

6. What do you think would happen to the frequency of the cystic fibrosis allele over several generations?

7. In fact, the allele frequency for cystic fibrosis in the United States seems to be constant over several generations. What could account for this?

8. Evolution is sometimes defined as a change in allele frequencies over time. Comment on this.