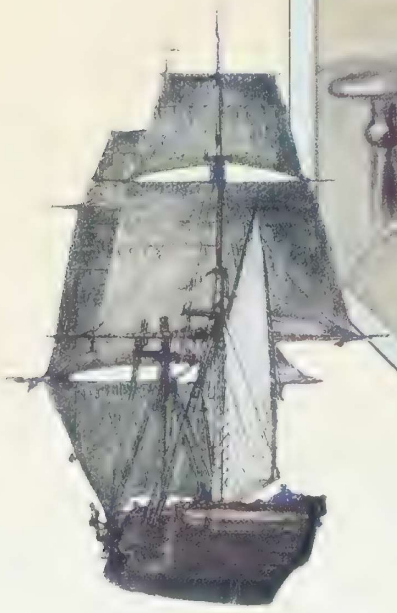
CHAPTER 14

Evolution: How Change Occurs





It was in this ship that Charles Darwin sailed around South America. By today's standards, it was a small ship, and time on board was spent in cramped quarters.

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or one; and that, whilst this planet has gone cycling according to the fixed laws of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

So wrote Charles Darwin in his conclusion to On the Origin of Species, *the book in which he attempted to explain what he among many had observed: that life on Earth has changed over time. But how does change occur? And how can one species evolve into another? It is this explanation in part that you will learn about in the pages that follow.*

CHAPTER OUTLINE

14–1 Developing a Theory of Evolution
- An Early Explanation for Evolutionary Change
- Ideas That Shaped Darwin's Theory of Evolution

14–2 Evolution by Natural Selection
- Peppered Moths: Natural Selection in Action

14–3 Genetics and Evolutionary Theory
- Genes: Units of Variation
- Raw Material for Natural Selection
- Evolution as Genetic Change
- Genes, Fitness, and Adaptation
- A Genetic Definition for Species

14–4 The Development of New Species
- The Niche: How to Make a Living
- The Process of Speciation
- Darwin's Finches: An Example of Speciation
- Speciation and Adaptive Radiation

14–5 Evolutionary Theory Evolves
- Genetic Drift
- Unchanging Gene Pools
- Gradual and Rapid Evolutionary Change
- The Significance of Evolutionary Theory

14–1 Developing a Theory of Evolution

Section Objectives

- Discuss the importance of evolutionary theory.
- Identify the basic assumptions of Lamarck's theory of evolution.
- Explain some of the major ideas that helped shape Darwin's theory of evolution.

Evolutionary theory is the foundation on which the rest of biological science is built. In fact, the biologist Theodor Dobzhansky once wrote that nothing in biology makes sense except in the light of evolution. Much research in genetics, ecology, and medicine is based on evolutionary theory.

The fact that plants and animals have changed over time was obvious to Darwin and has been clear to scientists throughout the last century. Observing that evolution has occurred is relatively simple. Explaining how and why evolution occurs is more difficult.

Certain aspects of Darwin's original theory of evolution have been revised by biologists in the years since the publication of *On the Origin of Species*. But the revisions do not mean that evolutionary change itself is debatable or that evolutionary theory is merely a collection of vague hunches that are not supported by evidence. Evolutionary change is undeniable. **Evolutionary theory is a collection of carefully reasoned and tested hypotheses about how evolutionary change occurs.**

By way of comparison, consider that even today physicists do not completely understand gravity, although there is no doubt in anyone's mind that gravity exists. There are at least two competing modern theories that explain how gravity works. Both theories make important useful predictions of natural events. For example, there is no question that if you jump into the air, you will end up on the ground below. It makes no difference whether you understand—or even believe in—gravity. What goes up must come down. Just as definitely, life on Earth evolves, or changes over time. Explaining the fine points of evolutionary change will continue to be one of the great challenges of biology.



Figure 14–1 *Although the mouse and the pig do not look at all alike, an analysis of their DNA shows that these two animals are more closely related than appearances would indicate.*

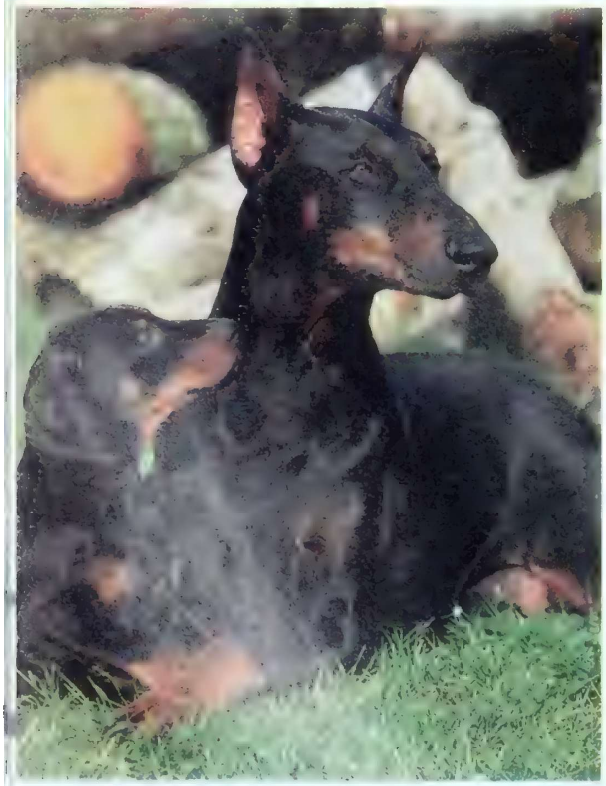
An Early Explanation for Evolutionary Change

Jean Baptiste de Lamarck (1744–1829) was among the first scientists to recognize that living things changed over time. And long before Darwin, Lamarck also realized that organisms were somehow adapted to their environments. In explaining how adaptation occurred, however, Lamarck relied on three assumptions we now know to be incorrect.

A DESIRE TO CHANGE Lamarck thought that organisms change because they have an inborn urge to better themselves and become more fit for their environments. In Lamarck's view, for instance, the ancestors of birds acquired an urge to fly. Over many generations, birds' constant efforts to become airborne led to the development of wings. What a pity for the Wright Brothers that this element of Lamarck's theory proved not to be true!

USE AND DISUSE Lamarck also believed that change occurred because organisms could alter their shape by using their bodies in new ways. Organs could increase in size or change in shape depending on the needs of the organism. For example, by trying to use their front limbs for flying, birds could eventually transform those limbs into wings. In the opposite way, Lamarck believed that if an animal did not use a particular part of its body, that body part would decrease in size and might finally disappear.

Figure 14–2 *The ears of this adult Doberman pinscher have been clipped so that they stand up on her head. But the ears of her puppy still hang down by the side of its head. This is proof that traits acquired during a lifetime are not passed on to the next generation.*



PASSING ON ACQUIRED TRAITS Included in Lamarck's reasoning was the belief, shared by many biologists of that time, that acquired characteristics were inherited. He thought that if an animal acquired a body structure (such as long arms or feathers) during its lifetime, it could pass that change on to its offspring. By the same reasoning, structures that became smaller from disuse would eventually disappear.

Although later discoveries showed that Lamarck's explanation of evolution was incorrect, he is still credited with being one of the first people to devise a theory of evolution and adaptation. He is also credited with bringing the concept of evolution to the attention of scientists. Thus Lamarck paved the way for Darwin's theory of evolution.

Lamarck's ideas may seem strange to you now, yet his theory was consistent with knowledge of that time. It was not until a century after Lamarck proposed his theory that an improved understanding of genetics and the principles of heredity showed that the mechanisms he proposed would not work.

Lamarck, you see, knew nothing about genes. As you know now, only genes and changes in genes—not alterations in body structure—are passed from parents to offspring. There is no evidence that experience during its life can cause specific

changes in an organism's genes. Years of proper exercise and diet, for example, can turn a weakling into a champion weight lifter. But that weight lifter's children cannot benefit genetically from the parent's pumping iron. If the children do not exercise and eat a proper diet, they will not develop large muscles, even if their parents were world champions!

Ideas That Shaped Darwin's Theory of Evolution

Personal experience on the *Beagle*'s voyage awakened Darwin's interest in explaining the diversity and fitness of life on Earth. But both during his trip and after his return, Darwin's thinking was also influenced by the books he read and by discussions with geologists, farmers, and others.

THE INFLUENCE OF GEOLOGY: LYELL'S IDEAS As you will remember from Chapter 13, the geologist Charles Lyell demonstrated that the Earth was very old and that it had changed over time. After reading Lyell's book *Principles of Geology,* Darwin became convinced that the Earth was much older than most people of his time believed. This was an important idea for Darwin. For in order to explain evolution—to even recognize that evolution had occurred—it was essential for Darwin to realize that the Earth was very old. The long periods of time it would have taken for millions of species to have evolved from a common ancestor could be accounted for only if the Earth was very old.



Figure 14–3 *Volcanoes can alter the Earth's face. This volcano, emerging from beneath the ocean, resulted in the formation of a new island. Within a short period of time, living organisms will discover this newly formed island and begin to exploit the opportunities that exist there. A volcanic eruption can produce a completely opposite effect, destroying an area of land and all its inhabitants.*



Figure 14–4 *The cabbage (top), Brussels sprouts (center), and cauliflower (bottom) are all varieties of the same plant species that have been "selected" over time to produce familiar food crops.*

Lyell's writing also caused Darwin to appreciate the geological phenomena he observed on his journey. In Chile, Darwin saw a spectacular volcanic eruption. Shortly thereafter, he observed that an earthquake had lifted a stretch of shoreline three meters higher than it had been before. With Lyell's writings fresh in his mind, Darwin came to realize that geological phenomena such as the ones he had observed could transform the face of the Earth over time. And if the Earth itself could change over time, so too could life on the Earth.

THE INFLUENCE OF FARMERS: ARTIFICIAL SELECTION

While assembling his thoughts back in England, Darwin spoke extensively with plant and animal breeders. He learned that farmers altered and improved their crops and livestock through breeding programs. But how, Darwin wondered, did such programs work?

Farmers told Darwin that domesticated animals and plants vary a great deal. For example, in every corn field, some plants are larger than average; others are smaller than average. Certain cows produce a large amount of milk; other cows produce a small amount of milk. Here and there among a flock of white chickens, a gray or black chicken appears. The farmers convinced Darwin that many of these variations were often passed on to the animals' offspring. In other words, these were inheritable variations.

Darwin realized that farmers could not cause variation to occur. Variation either happened naturally or it did not. But once farmers encountered variation, they could use it to their advantage. They noted the variations they found and decided which organisms to use as breeding stock. Individuals with undesirable variations—scrawny bulls or cows that produced little milk, for example—were not allowed to mate. Superior animals—husky bulls or cows that produced much milk—would be mated as often as possible.

This process, which Darwin called **artificial selection**, allowed only the best organisms to produce offspring. Over the years, breeders have used artificial selection to produce plants and animals far superior to—and often dramatically different in



Figure 14–5 *Variation in a species is quite common in nature. These ladybug beetles show different markings.*

appearance from—their original stock. **In artificial selection, the intervention of humans allows only the best organisms to produce offspring.**

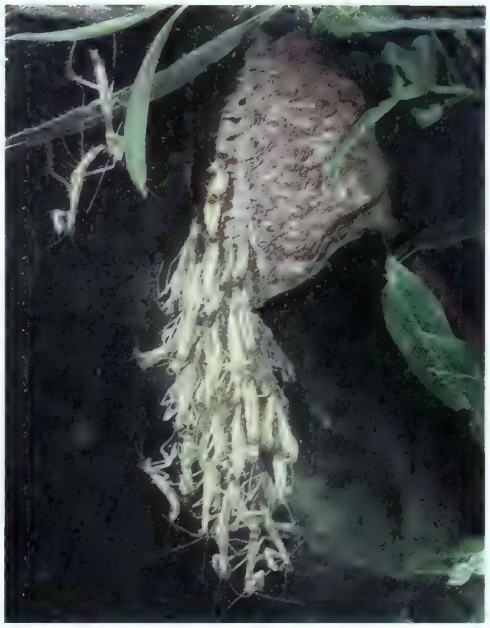
Darwin became convinced that a process similar to artificial selection must be at work in nature. This process would allow only those organisms best suited to their environment to survive and reproduce. But in nature there is no human intervention; so how, Darwin wondered, could such a process operate?

THE INFLUENCE OF MALTHUS: POPULATION CONTROLS

An important influence on Darwin was the work of the economist Thomas Malthus (1766–1834). Malthus observed that babies were being born at a faster rate than people were dying. If the human population continued to increase in that way, Malthus reasoned, sooner or later there wouldn't be enough living space and food. The only conditions that would prevent the endless growth of human populations, Malthus observed, were famine, disease, and war. In time, these unpleasant observations were called the Malthusian Doctrine.

Darwin realized that the Malthusian Doctrine applied even more to animals and plants than to humans, for most other species produce far more offspring than we do. For example, every summer each mature maple tree produces thousands of seeds. Marine animals, such as the common mussel, produce millions of eggs each time they spawn. If all the offspring of just one of these maple trees or mussels survived, they would overcrowd the area where they lived. If each offspring then produced as many offspring as its parents and if all those offspring reproduced, there would soon be so many maple trees or mussels that they would cover the Earth or fill the oceans!

Obviously, the oceans are not filled with mussels and the continents are not covered with maple trees. Most baby mussels die during their first year of life. Most maple seeds never grow into mature trees. Thousands upon thousands of individuals of each species die and only a few survive. Even fewer successfully raise offspring. That much is clear. But what determines which individuals survive and reproduce?



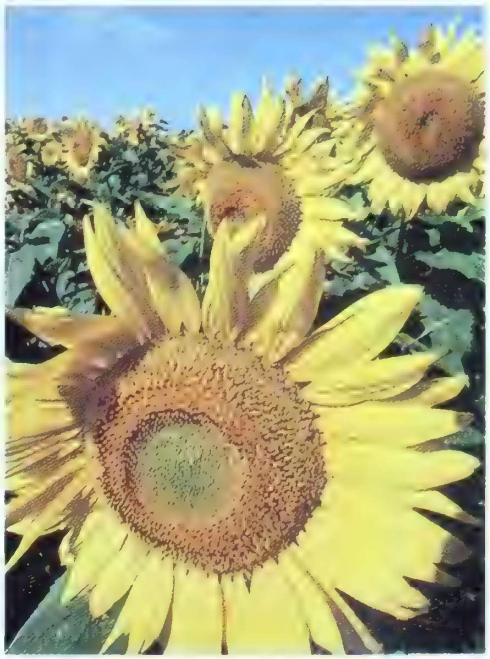


Figure 14–6 *Some animals and plants produce enormous numbers of offspring. Eggs in this praying mantis egg case have begun to hatch (top). If all the young survived to reproduce, you can imagine how the number of mantises in the world would be affected. Each sunflower in this field is capable of producing hundreds of seeds (bottom). If each seed survived and reproduced, there would be uncountable numbers of sunflowers.*

14–1 SECTION REVIEW

1. What is the importance of evolutionary theory?
2. How did Lamarck explain evolution? What are the major problems with his explanation?
3. What is artificial selection? How did this concept influence Darwin's thinking?
4. Would Darwin have developed his theory of evolution if he had not read the works of Lyell and Malthus? Explain.

Section Objectives

- Describe the process of natural selection.
- Provide an example of natural selection in action.

14–2 Evolution by Natural Selection

Ultimately, Darwin recognized in nature a process that operates in a manner similar to the way artificial selection worked on farms and in fields. Darwin called this process **natural selection** and explained its action in terms of several important observations.

Darwin observed that wild animals and plants showed variations just as domesticated animals and plants did. His field notebooks were filled with records of height, weight, color, claw size, tail length, and other characteristics among members of the same species. Darwin did not understand the reasons for these variations, but he realized that many of them were inherited.

Darwin observed that high birthrates and a shortage of life's necessities forced organisms into a constant "struggle for existence," both against the environment and against each other. Plant stems grow tall in search of sunlight; plant roots grow deep into the soil in search of water and nutrients. Animals compete for food and space in which to build nests and raise young. But who among all the contenders wins the struggle for existence?



Figure 14–7 *Life is a constant struggle for all organisms to survive. This smaller lizard has just come to the end of that struggle in the jaws of a gecko.*

Darwin knew that each individual differs from all the other members of its species. Sometimes the differences are easy to observe; sometimes the differences are subtle. **Those individuals with characteristics best suited to their environment survive the struggle for existence. Other individuals lacking the characteristics best suited to their environment die or leave fewer offspring.** This principle Darwin called **survival of the fittest**.

Natural selection thus operates in a similar way to artificial selection, but over much longer periods of time. On farms, human breeders determine which plants and animals will reproduce. In nature, the struggle for existence permits only the fittest individuals to reproduce. The fact that the members of a species that are not the fittest do not survive and reproduce keeps the species from covering the Earth.

Peppered Moths: Natural Selection in Action

England's peppered moth provides an example of natural selection in action. It also offers us a chance to study the sorts of experiments that can be used to test evolutionary theory. The story is as follows. The peppered moth spends much of the daytime resting on the bark of oak trees. In the beginning of the nineteenth century, the trunks of most oak trees in England were light brown speckled with green. Most of the peppered moths of that time were mottled light brown too. There were always a few dark-colored moths around, but light-colored moths were always the most common.

Then the Industrial Revolution began in England. Pollution (mostly soot from burning coal) stained London's tree trunks dark brown. At about the same time, biologists noticed that more and more moths with dark coloration were appearing. Why was the population changing color in this way?

The evolutionary hypothesis suggested by observation was straightforward. Birds are the major predators of peppered moths. It is much harder for birds to see, catch, and eat moths that blend in with the color of the tree bark than it is for them to spot moths whose color makes a strong contrast with the tree trunks. The moths that blend in with their background are said to be camouflaged.

As the tree trunks darkened, the rarer, dark-colored moths were better camouflaged and harder for birds to spot. Being harder to spot, the darker individuals were now better able to survive. The darker forms had greater fitness than the lighter forms. More of the darker moths survived and reproduced, passing on the genes for dark color to their offspring, and the moth population evolved darker coloration.

But a hypothesis that looks good is not enough. Scientific hypotheses must be tested by experiment whenever possible.

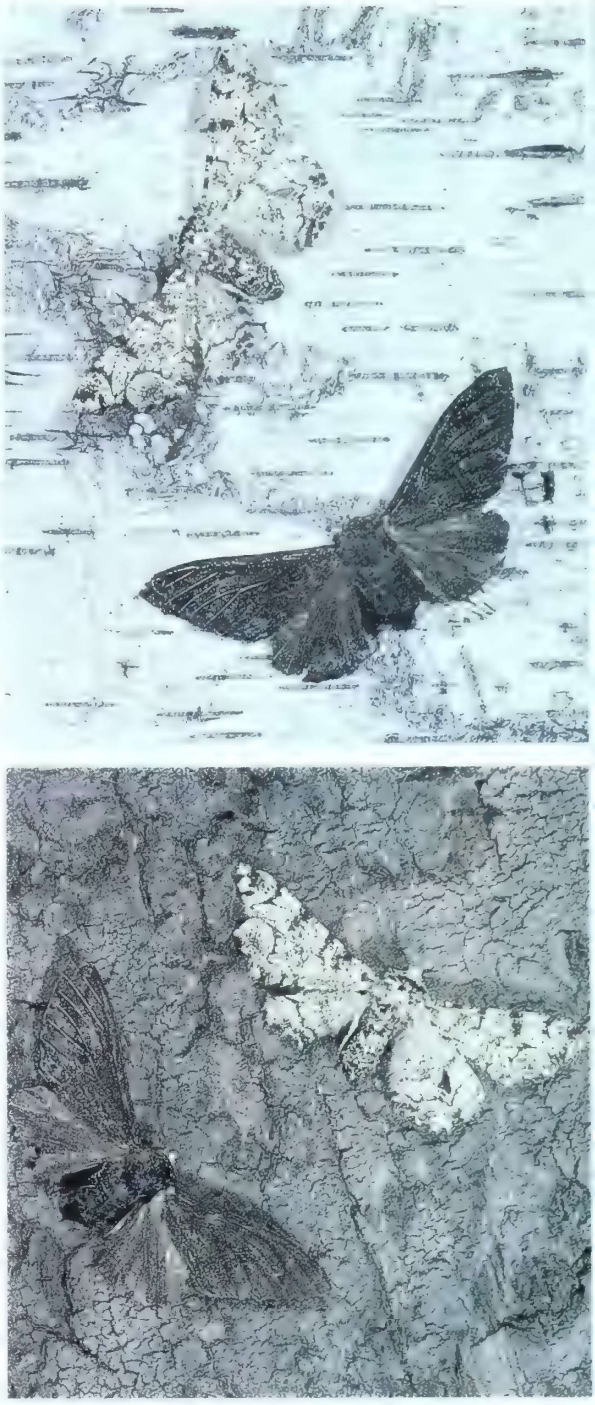


Figure 14–8 *Before the Industrial Revolution, soot was rare in the English countryside. A light-colored moth was difficult to see against the clean tree bark (top). After several years, during which the bark was darkened by the soot of burning coal, a light-colored moth stood out against the darkened tree bark (bottom). In each photograph, which moth would most likely be noticed by a hungry bird?*



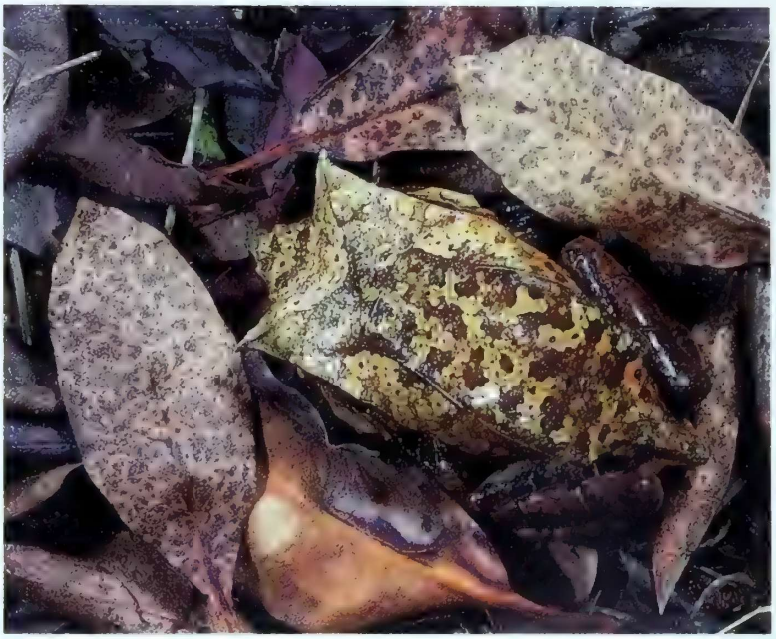




Figure 14–9 *Looking like something it's not can be helpful to an organism. It is difficult to spot the insect disguised as a thorn (top, left), the toad that resembles a fallen leaf (top, right), and the moth that looks like a plant leaf complete with diseased areas (bottom).*

British ecologist H.B.D. Kettlewell devised just such a test for this hypothesis. Kettlewell learned how to capture both light- and dark-colored forms of the peppered moth and then managed to raise them in captivity. He also learned to mark living moths in such a way that birds could not see the marks.

Kettlewell then released equal numbers of light- and dark-colored moths in two types of areas. In one area, trees were normally colored. In the other area, they were blackened by soot. Later on, he recaptured, sorted, and counted all the marked moths he could. What type of results do you think Kettlewell needed to either prove or disprove the hypothesis?

Kettlewell found that in unpolluted areas, more of his light-colored moths had survived. In soot-blackened areas, more of his dark-colored moths had survived. Thus Kettlewell showed that in each environment the moths that were better camouflaged had the higher survival rate. It was logical to conclude that when soot darkened the tree trunks in an area, natural selection caused the dark-colored moths to become more common. Today Kettlewell's work is considered to be a classic demonstration of natural selection in action.

14–2 SECTION REVIEW

1. What is natural selection? What observations led Darwin to develop this concept?
2. Define survival of the fittest. How are the concepts of natural selection and survival of the fittest related?
3. Explain how natural selection might produce a modern giraffe from short-necked ancestors.

14–3 Genetics and Evolutionary Theory

Section Objectives

- Explain how genes affect natural selection.
- Define evolution in genetic terms.
- Relate genes to fitness and adaptation.

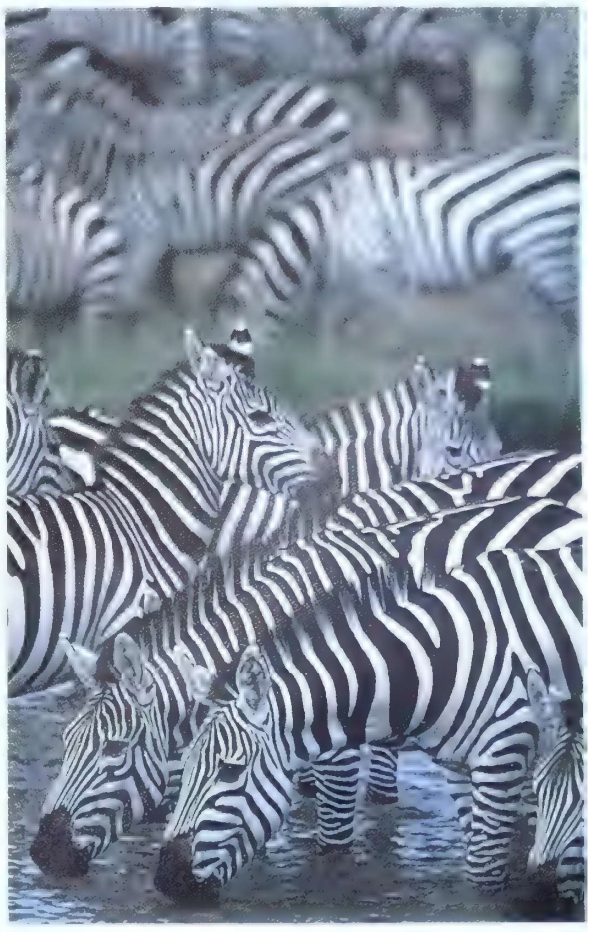
In developing his theory of evolution, Darwin worked under a serious handicap. He had no idea how the inheritable traits so important to his theory were passed from one generation to the next. For although Mendel had formulated his genetic principles during Darwin's lifetime, his work remained unknown to most scientists until the early part of this century. The rediscovery of Mendel's work and the growth of our knowledge of genetics enable us to explain the mechanism of evolution more completely than Darwin could. Genetics and evolutionary theory are inseparable. Today we define fitness, adaptation, species, and the process of evolutionary change in genetic terms.

Genes: Units of Variation

Genes, the carriers of inheritable characteristics, are also the source of the random variation upon which natural selection operates. Mutations cause some variation. Much additional variation arises during meiosis as the parents' chromosomes are copied, shuffled like a deck of playing cards, and dealt out to the gametes.

It is important to remember that genetic variation does not occur because an animal needs or wants to evolve—an idea central to Lamarck's theory. Sometimes genetic variation occurs; sometimes it doesn't. There is no way for an organism to cause a particular change in its DNA. There is also no way for an organism to prevent variations that do occur.

Figure 14–10 *It is a zebra's genes that determine the exact pattern of the animal's stripes. Notice that there are slight variations in the stripes of each animal.*



Raw Material for Natural Selection

In the evolutionary struggle for existence, entire organisms, not individual genes, either survive and reproduce or do not. How then does natural selection operate? Natural selection can operate only on the phenotypic variation among individuals. As you learned in Chapter 9, an organism's phenotype includes all the physical and behavioral characteristics produced by the interaction of genotype and environment.

You can sample phenotypic variation by measuring the height of all the students in your class. Using mathematics, you can calculate an average height for this group. Many students will be just a little taller or shorter than average. However, a few very tall or very short individuals may be in your class. If you graph the number of individuals of each height, you will get a curve similar to the one shown in Figure 14–11 on page 300. This phenotypic variation is produced by a combination of genetic instructions and environmental influences, such as nutrition and exercise. If your classmates are not malnourished, most (though not all) of the variations in height you observe

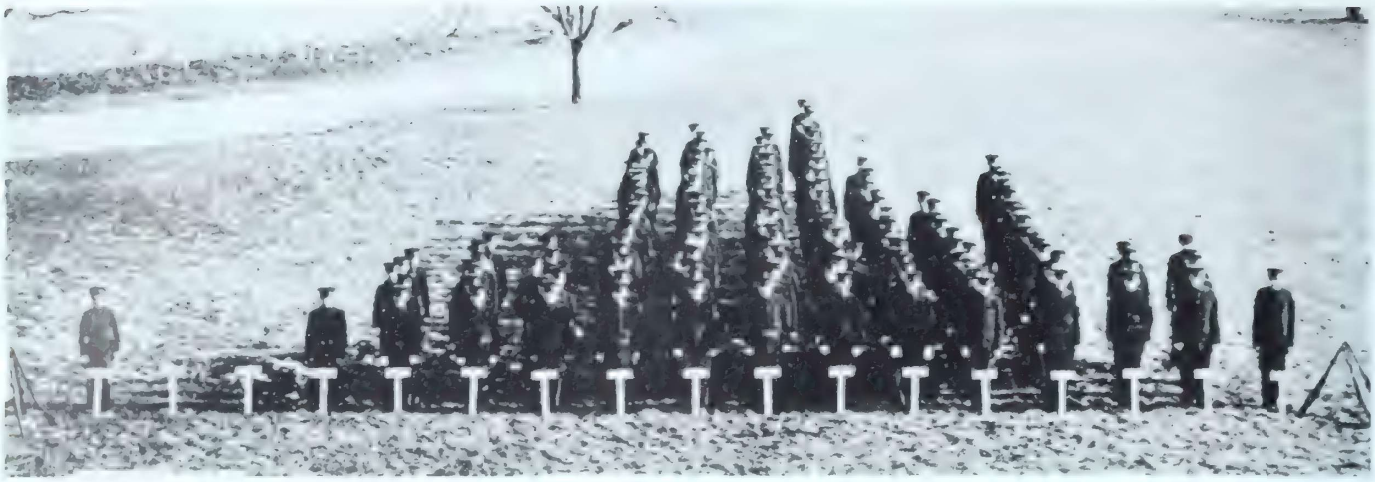


Figure 14–11 *This photograph shows height distribution in a population of U.S. Army recruits. As you can see, most of the recruits fall in the range of average heights in the center of the curve. There are relatively few very tall or very short recruits.*

can be said to result from differences in genotype. Of course, you can also observe many other kinds of phenotypic variation among your classmates. For example, variations in skin, hair, and eye color, and variations in the shapes of noses, the curves of lips, and the amount of body hair can be observed.

In nature, organisms show as many variations as humans, although most humans are not aware of this. For example, to the casual observer, one zebra looks much like any other zebra. But when researchers study the characteristics of many individuals of a species, they find the same sort of distribution for each characteristic that you saw in human height. It is this sort of variation in organisms that provides the raw material for natural selection.

Evolution as Genetic Change

In order to describe the evolution of plants and animals, modern evolutionary biologists study groups of organisms called **populations**. A population is a collection of individuals of the same species in a given area whose members can breed with one another. For example, all the fishes of a certain species in a single pond could be considered one population. Individuals in another, separate pond would belong to a different population, even if that pond was close by.

Because all members of a population can interbreed, they and their offspring share a common group of genes, called a **gene pool**. Each gene pool contains a number of alleles—or forms of a certain gene at a given point on a chromosome—for each inheritable trait, including alleles for recessive traits. The number of times an allele occurs in a gene pool compared with the number of times other alleles for the same gene occur is called the **relative frequency** of the allele.

Sexual reproduction alone does not change the relative frequency of alleles in a population. To understand why, you can compare the combinations of alleles produced by sexual reproduction to the different hands you get when you shuffle and deal a deck of playing cards. Shuffling and reshuffling produce

an enormous variety of different hands. But shuffling alone will not change the relative numbers of aces, kings, fours, or jokers in the deck.

With this in mind, we can define evolution in another way. **Evolution is any change in the relative frequencies of alleles in the gene pool of a population**. And, as you can see in Figure 14–13, when the relative frequencies of alleles in a population change, the curves that describe the distribution of traits controlled by those alleles also change. In the case of the peppered moths, as the alleles for dark color increased, more dark-colored moths appeared in the population. This is the visible result of evolutionary change.

Genes, Fitness, and Adaptation

Each time an organism reproduces, it passes copies of its genes to its offspring. Thus we can define evolutionary fitness as the success an organism has in passing on its genes to the next generation. And we can define an adaptation as any genetically controlled characteristic of an organism that increases its fitness.

Let's return to our discussion of human weight lifters for a moment. Muscles acquired as a result of exercise are not passed on to offspring. Thus they cannot be considered an evolutionary adaptation and cannot contribute to evolutionary fitness. A gene that somehow allowed an individual to develop stronger muscles by doing less work or by eating less food, on the other hand, might be a useful adaptation under certain circumstances. This gene could be passed on to offspring.

A Genetic Definition for Species

In the past, biologists defined a species as a group of organisms that looked alike. Species were defined according to precise physical descriptions, and differences among individuals were seen as imperfections or mistakes. This definition, however, did not recognize that variation in a population is the rule rather than the exception.

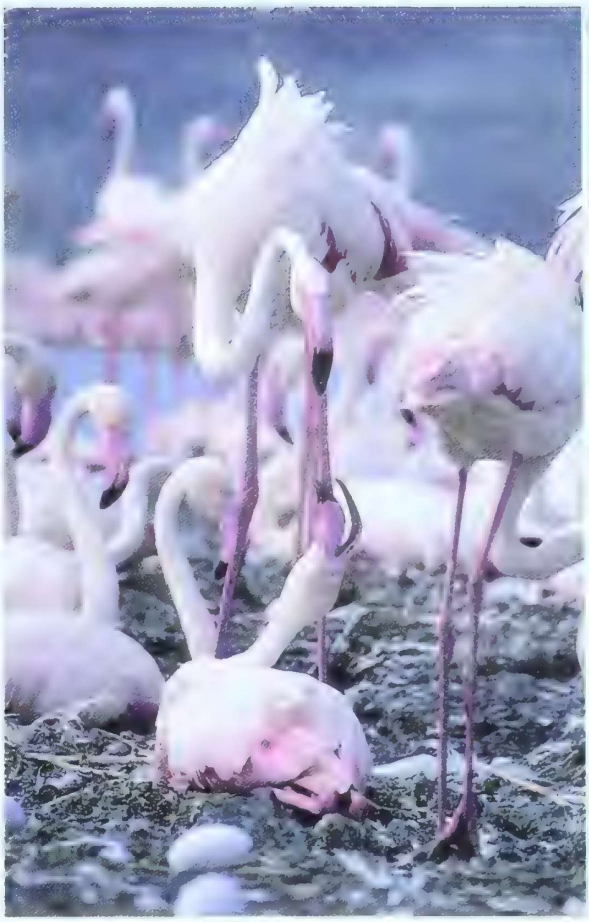


Figure 14–12 *All of the flamingoes in a given area make up a gene pool. Within that pool, it is possible for any one flamingo to breed with any other flamingo. It is individual choice that limits the number of potential mates a single flamingo may have.*

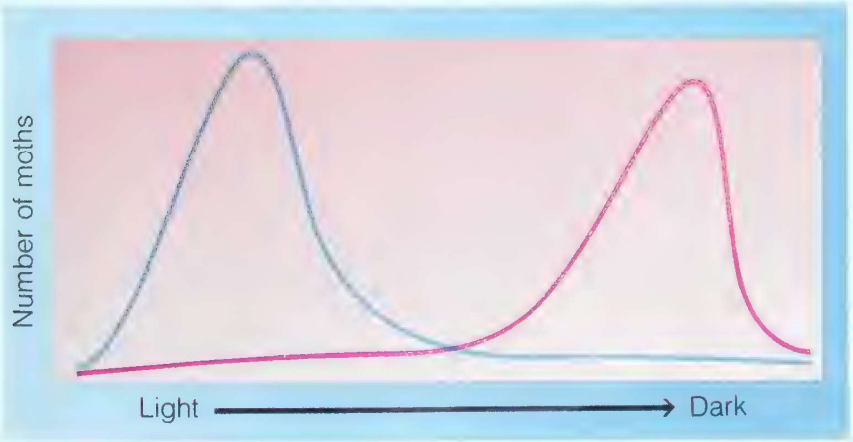


Figure 14–13 *Sometimes the frequency of an allele changes in a population. The light-colored moths occurred with greater frequency before the Industrial Revolution. After the Industrial Revolution, the frequency of dark-colored moths became greater. How do you explain these changes?*



Figure 14–14 *A species is a population of organisms that breed with one another and share a common gene pool. If this baby hippopotamus survives, it can pass on its genes to another generation.*

We now define a species as a group of similar-looking (though not identical) organisms that breed with one another and produce fertile offspring in the natural environment. This definition is important because it allows us to determine what it means to belong to the same or different species.

Because members of a species can breed with one another, they share a common gene pool. Because of that shared gene pool, a genetic change that occurs in one individual can spread through the population as that individual and its offspring mate with other individuals. If the genetic change increases fitness, that gene will eventually be found in many individuals in the population. Members of a species can thus evolve together and interact with their environment in similar ways.

14–3 SECTION REVIEW

1. What causes phenotypic variation? How is phenotypic variation related to natural selection?
2. Define evolution in genetic terms.
3. What are the genetic definitions of fitness and adaptation?
4. Scientists notice that the individuals in a certain plant species are growing taller with each successive generation. Explain what is happening to the gene pool of this population.

Evolution in Action

Evolution did not just happen millions of years ago. Evolutionary change occurs around us constantly. Scientists today have observed many examples of evolutionary change that have occurred in living organisms.

Many species of insects and microorganisms damage crops, spoil food, or make us ill. Farmers spray their crops with poisons that kill harmful insects. Doctors and veterinarians use antibiotics and other medicines to kill disease-causing bacteria and other microorganisms.



However, scientists have observed that many of the insect species are not killed by insecticides that killed others of that species several years ago. And some microorganisms are no longer eliminated by antibiotics. The resistance of certain pest species to chemicals that once controlled them are examples of evolutionary change.

How can this resistance be explained? The work of Darwin provides an answer. Remember, Darwin suggested that there is great variation among organisms. Suppose there were a few insects that were not killed by an insecticide that killed other members of their species. Suppose there existed a bacterium that was unaffected by an antibiotic proven to control other members of its species. The surviving organisms would be more fit. They could pass on their genes to their offspring.

Normally these resistant organisms are uncommon in a population. However, the use of insecticides and antibiotics changes the environment. These chemicals kill organisms that are not resistant. But at the same time, these chemicals increase the fitness to survive of resistant organisms. With less competition, these fit individuals survive and reproduce. And because they reproduce quickly, the genes that made them more fit are rapidly spread in a population. Soon many more resistant individuals are found in the population. And the chemicals that once controlled a pest population are no longer effective.

This example of evolution in action poses problems for human society. New chemical controls must constantly be developed. However, some physicians feel that we will run out of new and effective antibiotics before microorganisms run out of variations. To control crop pests, farmers now use chemicals that are potentially more dangerous—chemicals that may also threaten humans and the environment. So there is much work for future biologists.

Section Objectives

- Define niche.
- Relate the availability of niches to speciation.
- Describe the process of speciation.

14–4 The Development of New Species

We are now nearly ready to explain how new species evolve from old ones, a process biologists call **speciation**. But before we can explain how speciation occurs and how it can lead to diversity, we must first understand some basic concepts about the way species interact in their environment.

The Niche: How to Make a Living

Organisms, like members of a human community, need to survive and acquire the necessities of life. But like people crowded into a city, organisms would have difficulty surviving if they all tried to do the same kinds of work, eat the same kinds of food, and live in the same place. Isn't it hard to imagine, for example, an entire city of butchers or tailors? And certainly you wouldn't want the population of an entire city living in your house!

In human cities, thousands of people survive near one another. They have different jobs, they shop in different stores, and they live in different places. Animals and plants do much the same thing. The combination of an organism's "profession" and the place in which it lives is called its **niche** (NIHCH). If two species occupy the same niche in the same location at the same time, they will compete with each other for food and space. One of the species will not survive. **No two species can occupy the same niche in the same location for a long period of time**. Chances are, one of the species will be more efficient than the other. The more efficient species will survive, reproduce, and drive the less efficient species to extinction.





Figure 14–15 *Reproductive isolation can lead to the development of a new species. The fish on the left is a member of the same species as the fish on the right, although it is quite different in appearance. In time, if it is reproductively isolated, it may evolve into another species.*

If two species occupy different niches, however, they will not compete with each other as much. With less competition, there is less chance that one species will cause the other to become extinct. So in the evolutionary struggle for existence, any species (or a population within a species) that occupies an unoccupied niche will be better able to survive. We will soon see how this phenomenon can lead to the formation of entirely new species.

The Process of Speciation

Remember that biologists define a species as a group of organisms that can breed with one another and produce fertile offspring in a natural environment. This definition means that individuals in the same species share a common gene pool. Individuals in different species have different gene pools.

Scientists have learned that new species usually form only when populations are isolated, or separated. This separation of populations so that they do not interbreed to produce fertile offspring is called **reproductive isolation**. If two populations are not reproductively isolated, their gene pools will blend with each other. No new species will be formed. Reproductive isolation is the agent for the formation of new species.

Reproductive isolation may occur in a variety of ways. Geographic barriers such as rivers, mountains, and even roads may separate populations and prevent them from interbreeding. Differences in courtship behavior or fertile periods may result in organisms that breed only with individuals that are most similar to themselves.

Once reproductive isolation occurs, natural selection usually increases the differences between the separated populations. As the populations become better adapted to different

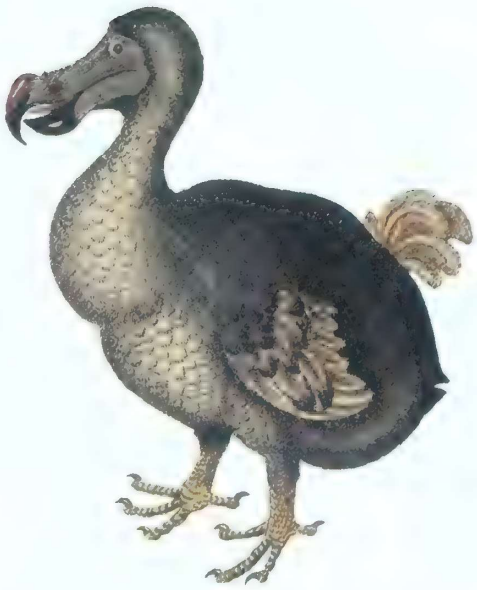


Figure 14–16 *Hundreds of years ago, the dodo was quite common on the island of Mauritius. This large bird, unable to fly, made its nest on the ground. In time, settlers arrived with dogs and other domestic animals. The helpless dodos were killed and their nests destroyed. The expression "dead as a dodo" is used today to refer to any organism that is now extinct.*



Figure 14–17 *The bower bird makes a nest, or bower, on the ground for his mate. In order to entice a suitable female, the male decorates his bower with bits of glass, colored stones, and shiny paper. This complicated behavior contributes to the bower bird's reproductive success.*

environments, their separate gene pools gradually become more dissimilar. Now the populations are separated not only by the physical or behavioral barriers that once separated them, but by vastly different genes. If the populations remain separated for a long time, their gene pools eventually become so different that their reproductive isolation becomes permanent. When this occurs, the groups of organisms are no longer separate populations. They have become separate species.

Darwin's Finches: An Example of Speciation

We can now use our understanding of evolution to explain the fascinating case of Darwin's finches, a group of 14 bird species on the Galapagos Islands. All these finch species evolved from a single ancestral species. Yet each of the 14 species exhibits body structures and behaviors that enable it to live in a different niche. For example, each species shows adaptations that allow it to feed differently. Some of the finch species eat small seeds, whereas others crack open much larger seeds or seeds with thicker shells. Some species pick ticks—small insectlike animals—off the islands' tortoises and iguanas. One finch species uses twigs or cactus spines to remove insects from inside dead wood. And some finches, often called vampire finches, drink the blood of large sea birds after pecking them at the base of their tail! How did so many strange and unusual finch species evolve on these islands? The evolution of the various species of finches on the Galapagos Islands shows how geographic and behavioral barriers and reproductive isolation eventually lead to the formation of new species.



Name	Vegetarian tree finch	Large insectivorous tree finch	Woodpecker finch	Cactus ground finch	Sharp-beaked ground finch	Large ground finch
Shape of Bill	Parrotlike bill	Grasping bill	Uses cactus spines	Large crushing bill	Pointed crushing bill	Large crushing bill
Main Food	Fruit	Insects	Insects	Cactus	Seeds	Seeds
Habitat	Trees	Trees	Trees	Ground	Ground	Ground

Figure 14–18 *The many kinds of finches that Darwin observed on the Galapagos Islands evolved from a single species that emigrated from the South American mainland some kilometers away. How have the shapes of these birds' beaks contributed to their survival?*



Figure 14–19 This map shows the location of the Galapagos Islands off the coast of Ecuador (left). Variation exists even among the giant tortoises that live on the Galapagos Islands. The shell of one type of tortoise is raised in the front (right), enabling it to lift its head farther off the ground than the tortoise with a shell rounded in the front (center). How does the shell shape contribute to the survival of each tortoise?

STEP 1: FOUNDING FATHERS AND MOTHERS Darwin's finches are descendants of a few ancestral finches that found their way to the Galapagos Islands from the South American mainland. Finches are small birds that do not usually fly far over open water. They may have gotten lost, or they may have been blown off course by a storm. In any case, once they arrived at one of the Galapagos Islands, which we can call Island A, they managed to survive and reproduce.

STEP 2: SEPARATION OF POPULATIONS Then, some birds from Island A crossed to another island in the Galapagos group. We will call this Island B. Remember, these birds do not like to fly over open water. So the populations on Islands A and B were essentially isolated from each other. Even though they were still members of the same species, the ocean between them prevented the blending of their gene pools.

STEP 3: CHANGES IN THE GENE POOL Over time, the populations on each island became adapted to the needs of their environments. For example, suppose the plants growing on Island A produced mainly small thin-shelled seeds, whereas the plants on Island B had larger thick-shelled seeds. Individual finches in the Island B population with larger, heavier beaks would be able to crack open and eat the seeds more easily. So birds with large beaks would be better able to survive on Island B. Over time, natural selection could have caused that population to evolve larger beaks.

STEP 4: REPRODUCTIVE ISOLATION Now imagine that a few birds from Island A cross to Island B. Will the birds from Island A be able to breed with the birds on Island B? Probably not. It happens that the finches prefer to mate with birds that have the same size beak they do. Thus differences in beak size, combined with mating behavior, act as a mechanism for reproductive isolation. The gene pools of the two bird groups do not mix. The two populations have become separate species.

STEP 5: SHARING THE SAME ISLAND The fate of the two species on Island B depends on the relationship between the birds and their environment. There are three possibilities: coexistence, extinction, or further evolution. If the two species occupy different niches, they can coexist, or live together without changing. But if the niches of the species are too similar, the species will compete with each other. If one species is much better at making a living than the other, it may cause its competitor to become extinct.

If, however, one species exhibits enough genetic variation, the competition it encounters may cause it to evolve further. A new species may result. For example, if the species' beak changes size again, it will be able to eat another kind of food for which it does not have to compete. Scientists believe that the 14 species of finches on the Galapagos Islands evolved from a single ancestor when speciation happened in this way again and again on different islands over time.

Speciation and Adaptive Radiation

The process we have just described on the Galapagos Islands, in which one species gives rise to many species, is called **adaptive radiation**. The process of adaptive radiation is also known as **divergent evolution**. In adaptive radiation, a number of different species diverge, or move away, from a common ancestral form, much as the spokes of a bicycle wheel radiate from the hub. During a period of adaptive radiation, organisms evolve a variety of characteristics that enable them to survive in different niches. Throughout the history of life on Earth, adaptive radiations have occurred many times and in many places. Adaptive radiation occurred on the Hawaiian Islands among a group of birds called Hawaiian honeycreepers. The dinosaurs experienced an adaptive radiation in their day, only to eventually become extinct. The mammals alive today were produced by another wave of adaptive radiation.

Evidence of past adaptive radiations can be observed in many organisms. The homologous structures discussed in the last chapter are evidence of past adaptive radiations in which the similar body parts of related organisms evolved to perform different tasks.

As you can see from Figure 14–20, adaptive radiations among different organisms often produce species that are similar in appearance and behavior. This phenomenon is known as **convergent evolution**. Convergent evolution has produced many of the **analogous structures** in organisms today. Analogous structures are similar in appearance and function, but they have different origins. Because they have different origins, analogous structures usually have very different internal structures. For example, the wings of butterflies, birds, and bats are analogous structures that allow the organisms to fly. However, a closer examination of these wings shows that a butterfly's

wing is made of a thin nonliving membrane with an intricate network of supports. A bird's wing is made of skin, muscles, and arm bones. And a bat's wing is made of skin stretched between elongated finger bones.

Figure 14–20 *Adaptive radiation is the process by which many different species develop from a common ancestor. As you can see from this illustration, some of the descendants of the* Cotylosaur *do not resemble it in the least.*

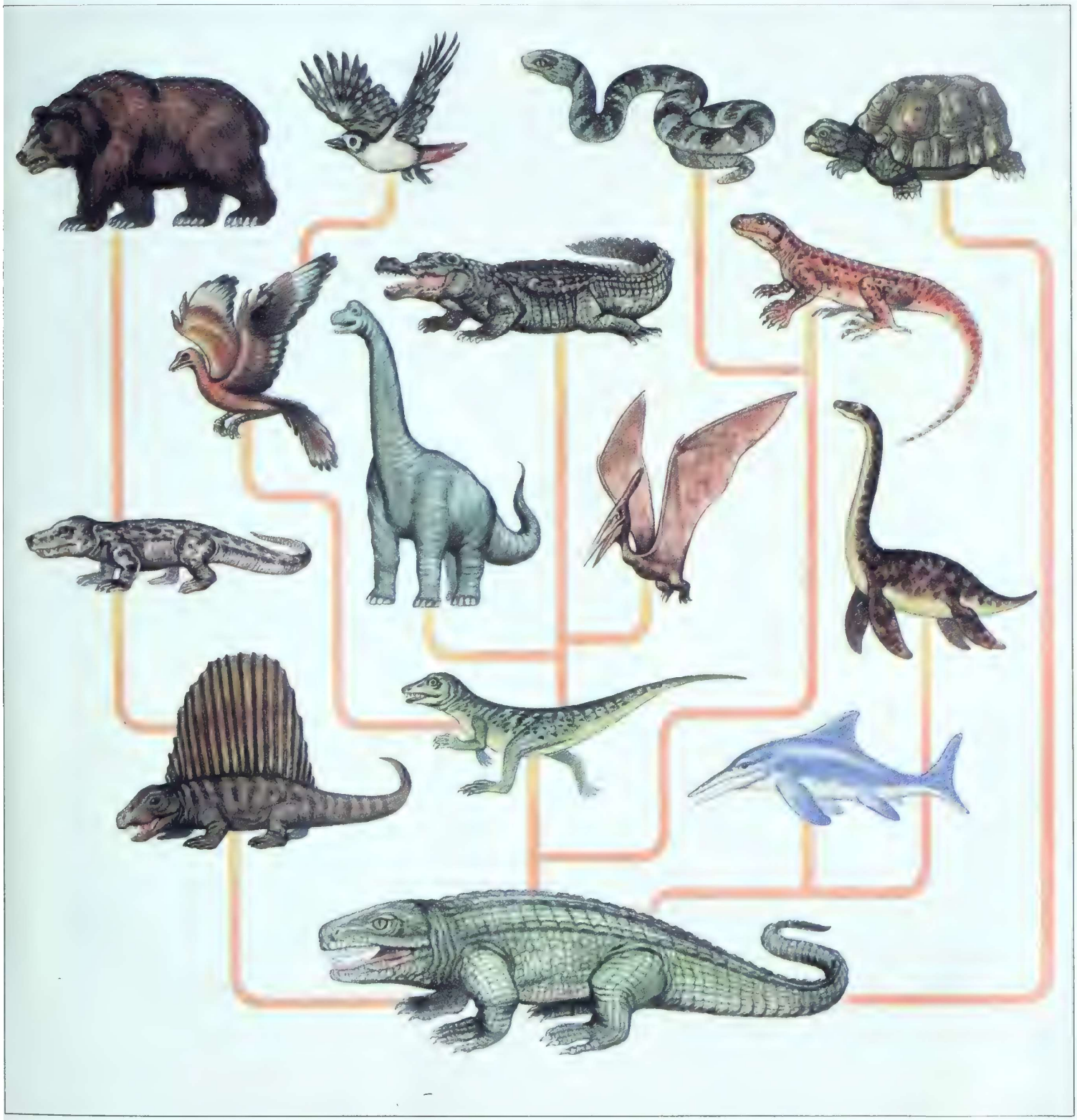




Figure 14–21 *The wings of a butterfly and the wings of a bat are analogous structures—similar in appearance and function. Although the wings of both the butterfly and the bat show adaptations for flight, they are made up of different tissues.*

14–4 SECTION REVIEW

1. What is a niche? How do niches contribute to speciation?
2. How are speciation and reproductive isolation related?
3. What is adaptive radiation? Explain how Darwin's finches illustrate this process.
4. The first species to reach a newly formed volcanic island often undergoes an adaptive radiation. Explain this observation.

Section Objectives

- Discuss how gene pools can change in the absence of natural selection.
- Explain why some gene pools may change very little over time.
- Describe the theory of punctuated equilibria.

14–5 Evolutionary Theory Evolves

It should now be apparent to you that evolutionary theory has been modified over the years. With the contributions of scientists such as Lamarck and Darwin and a better understanding of heredity, scientists can now explain how variation occurs and define evolutionary concepts in terms of genetics. But even today, evolutionary theory continues to evolve as scientists formulate theories about the details of evolutionary change.

Genetic Drift

Natural selection is not always necessary for genetic change to occur. **With the aid of theories and genetic experiments, biologists have realized that gene pools can change—in other words, evolution can occur—in the absence of natural selection.** This does not mean that natural selection is not important. However, biologists now realize that chance plays an even larger part in evolutionary change than Darwin thought.

Geneticists have shown that an allele can become common in a population by chance. This kind of random change in the frequency of a gene is called **genetic drift**.

How does genetic drift work? One possibility is that an individual with a particular allele may produce more offspring than other members of its species—not because it is better adapted but just by chance. It is also possible for environmental events to wipe out many individuals who do not carry a particular allele. For example, the distribution of some alleles in the population of mountain goats in Washington State may have changed when Mount St. Helens erupted in 1980, killing many mountain goats in the area of the volcano. Thus, in very special circumstances, a new or previously rare allele may become common in a population after only a few generations. Genetic drift occurs most efficiently in small populations because chance events, such as a volcanic eruption, are less likely to affect all members of a very large population. Genetic drift could also have played a role in the evolution of Darwin's finches, since each new population was founded by relatively few birds.

Genetic drift implies that all characteristics of an organism do not have to contribute to its fitness. For example, consider the differences between the Indian rhinoceros (which has one horn) and the African rhinoceros (which has two). Both rhinoceros species use their horns to fight predators and to joust among themselves, so having a horn or two is useful. But it is not clear whether having two horns is better for survival than having one horn. If the two types of rhinoceros lived in the same area, the rhinoceros with one horn would probably have the same fitness as the rhinoceros with two horns. Thus the extra horn does not necessarily contribute to fitness. Most likely, the ancestral populations that gave rise to the two modern rhinoceros species developed slightly different horn systems just by chance. Natural selection provided a distinct advantage to individuals with horns; but the two populations developed different numbers of horns because of random genetic drift. Genetic drift probably led also to the evolution of one hump on African camels and two humps on Asian camels.

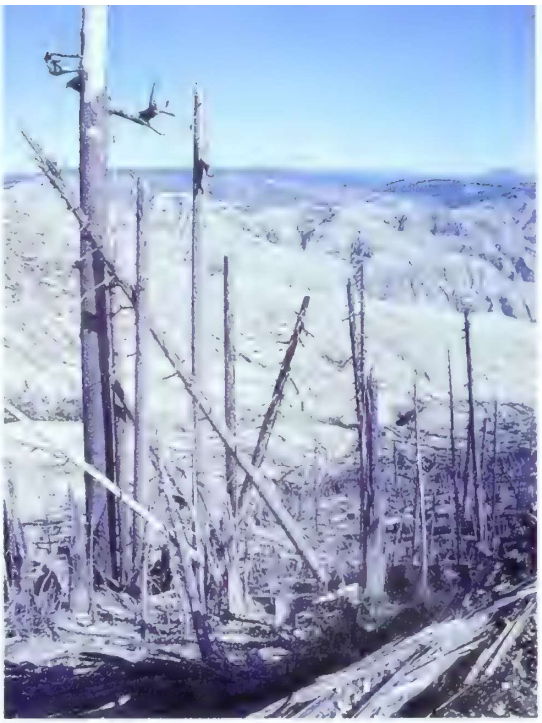
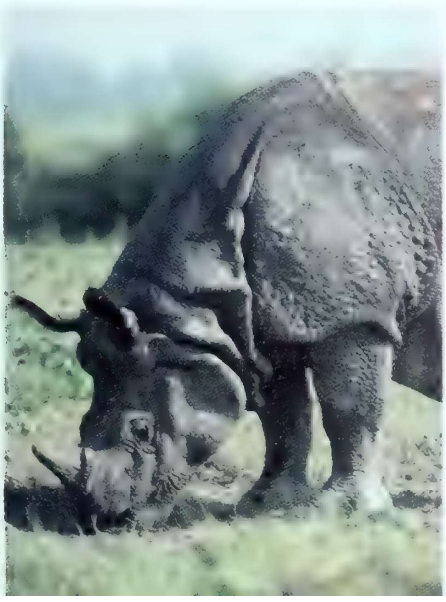


Figure 14–22 *The eruption of Mount St. Helens in 1980 drastically changed the environment. Trees were killed, as were many animals. Presently, plants are growing and some animals have returned to reclaim the altered landscape they called home.*

Figure 14–23 *The Indian rhinoceros (left) has a single horn; the African rhinoceros (right) has two. The number of horns may not contribute to survival, since one horn is as good as two in defending animals as grand as these.*



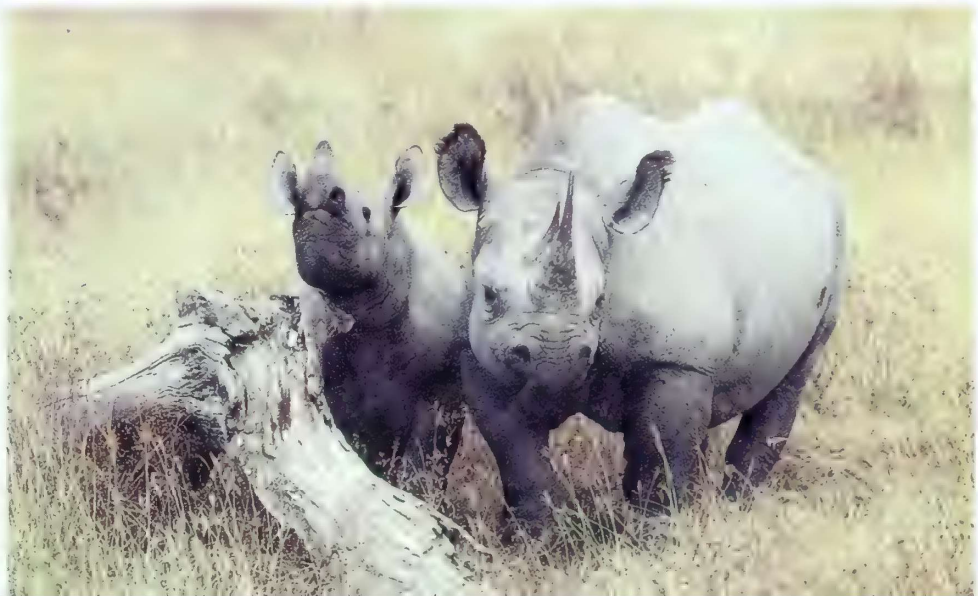




Figure 14–24 *This plant-eating dinosaur, which once munched plants in a quiet pond on ancient Earth, is today extinct. The environment on Earth changed, but, alas, the dinosaur did not.*

Unchanging Gene Pools

Modern evolutionary biologists recognize that although natural selection and genetic drift are both powerful forces of change, they do not cause genetic alterations in all species all the time under all conditions. And because sexual reproduction by itself does not change the frequency of alleles in a population, it is possible for the gene pool of a species to remain the same for a long time.

Every now and then there arises a species, particularly well adapted to an environment, that does not change over time. If no new species enter into competition with that species and if certain other conditions are met, that species may remain nearly unchanged for long periods of time. One example of such a species is the horseshoe crab, *Limulus*, whose living members are nearly identical to ancestors that lived hundreds of millions of years ago. Such organisms are often called living fossils. Though relatively rare among both plants and animals, living fossils are fascinating indications that under some conditions evolution can slow down.

Gradual and Rapid Evolutionary Change

Darwin, convinced by the work of Lyell of the slow and steady nature of geologic change, felt that biological change was also slow and steady. The theory that evolutionary change occurs slowly and gradually is known as **gradualism**. In many cases the fossil record shows that a particular group of organisms has indeed changed gradually over time.

But there is also evidence that many other species did not change very much from the time they appeared in the fossil record to the time they disappeared. In other words, much of the time these groups of animals and plants are in a state of **equilibrium** (ee-kwih-LIHB-ree-uhm), which means they do not change very much.

But every now and then, something happens to upset the equilibrium. At several points in the fossil record, changes in animals and plants occurred over relatively short periods of time. Some biologists argue that these rapid changes—rather than long, slow changes—are what create new species. Remember that when we say "short" and "rapid" we are talking about the geological time scale. Short periods of time for geologists can be hundreds of thousands, even millions, of years!

Rapid evolution after long periods of equilibrium can occur in several ways. It may occur when a small population of a species becomes isolated from the main part of the population. This small population can evolve more rapidly than the larger one because genetic changes can spread more quickly among fewer individuals. Or rapid evolution may occur when a small group of organisms migrates to a new environment, as happened with the Galapagos finches. The organisms then evolve rapidly to fill available niches.

Rapid evolution may also result from dramatic changes on the Earth. Every now and then, many species have vanished in a phenomenon known as a **mass extinction**. Some mass extinctions were caused by changes in global climates that altered many environments. The causes of other mass extinctions remain uncertain. But whatever their causes, the effects of mass extinctions are clear. When many species die, many niches are left unoccupied. The species that remain suddenly find lots of empty niches. Groups of animals with enough genetic variability can undergo adaptive radiations. These adaptive radiations can produce a large number of new species to fill those empty niches.

Scientists use the term **punctuated equilibria** to describe this pattern of long stable periods interrupted by brief periods of change. Punctuated equilibria theory, which has generated much debate, is still controversial among biologists today. It is clear, however, that evolution has often proceeded at different rates for different organisms at different times during the long history of life. But whatever the pace of change might have been, it is certain that organisms have evolved over time.

The Significance of Evolutionary Theory

Evolutionary theory is, in the minds of many biologists, the foundation on which all biological science is built. Only because all living organisms are related through common descent can we talk about universal characteristics of life. Only because the physiological properties of all multicellular organisms are so similar can we study other animals to learn how our own bodies operate. And only through application of evolutionary theory can we truly understand the way that organisms interact with each other and with their environments.

But the influence of evolutionary thought extends far beyond biology. Philosopher J. Collins has written that "there are no living sciences, human attitudes, or institutional powers that remain unaffected by the ideas . . . released by Darwin's work." We cannot even touch on these remote disciplines in this book, although we hope you will be inspired to read about them later in life. We will, however, use the remainder of this book to discuss the products of evolution: Earth's "most beautiful and wonderful" living organisms.

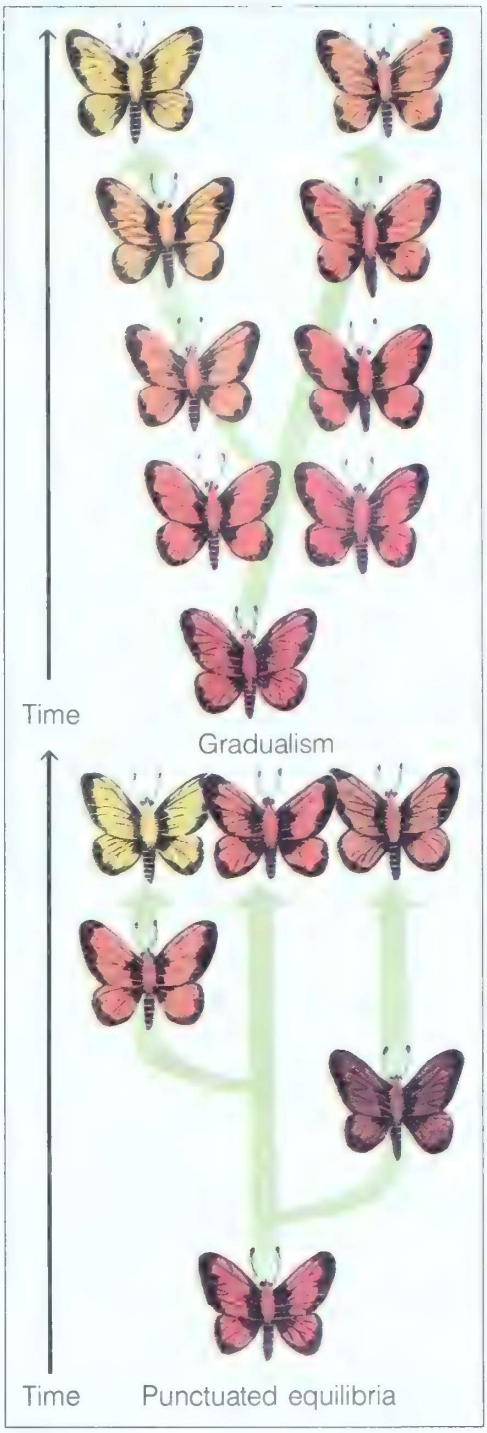


Figure 14–25 *This illustration shows two possible ways in which a population of butterflies changes over time. The insects may change color gradually, with each succeeding generation showing only small color changes. Or the color of the population may remain fairly stable for long periods of time and then make great changes suddenly.*

14–5 SECTION REVIEW

1. What is genetic drift? How does genetic drift affect a gene pool?
2. What three factors can cause an increase in the rate of evolution of a species?
3. Describe the theory of punctuated equilibria.

LABORATORY INVESTIGATION

SIMULATING NATURAL SELECTION

PROBLEM

What happens to harmful genes over time?

MATERIALS *(per group)*

small brown paper bag
400-mL beaker
250 g pinto beans
100 large lima beans
100 red kidney beans
stopwatch or clock with second hand

PROCEDURE

1. After reading the investigation carefully, prepare a data table on a separate sheet of paper.
2. Examine and note the differences and similarities among the three types of beans.
3. Fill the beaker about three-fourths full with the pinto beans. Then pour the beans into the paper bag.
4. Add 50 lima beans and 50 kidney beans to the paper bag. The lima and kidney beans represent organisms. The pinto beans represent the environment in which the organisms are hiding.
5. Have one member of your group time you for 3 minutes. During the 3 minutes, remove one bean at a time from the paper bag. Without looking, try to remove as many lima and kidney beans as you can. Use the shapes of the beans to identify them.
6. Record the number of lima beans and kidney beans that you removed in the appropriate place in the data table.
7. To determine the number of lima beans and kidney beans that remain in the paper bag, subtract the number of lima beans removed from the starting number. Do the same for the kidney beans.
8. Add the numbers of remaining lima and kidney beans together. Record this information in the appropriate place in the data table.
9. To find the frequencies of lima beans and kidney beans that remain in the paper bag, divide the numbers of each of the remaining beans by the total number of remaining lima and kidney beans. Round these numbers off to the nearest hundredths place. Record this information in the appropriate place in the data table.
10. The frequencies of each of the beans that remain in the paper bag represent the distribution of genes in the population. To determine the starting number of lima beans and kidney beans that are present in the next generation, multiply the frequency of each bean by 100. Record the information in the appropriate place in the data table. Add lima beans and kidney beans to the bag to restore the same starting number for the next generation.
11. Repeat steps 5 through 9 until the information in the data table is complete for five generations.

OBSERVATIONS

1. What was the ratio of lima beans to kidney beans?
2. Based on your data, was one type of bean removed from the bag more frequently than the other? If so, which type?
3. What happened to the frequencies of the lima beans in the population over five generations? The frequencies of the kidney beans?
4. What happened to the total number of beans that remained over five generations?

ANALYSIS AND CONCLUSIONS

1. Which beans represent the beneficial genes in a population? The harmful genes? How do you know?
2. Explain why the frequency of remaining genes changes in each generation?
3. What do you think happens to harmful genes over time?

STUDENT STUDY GUIDE

SUMMARIZING THE CONCEPTS

The key concepts in each section of this chapter are listed below to help you review the chapter content. Make sure you understand each concept and its relationship to other concepts and to the theme of this chapter.

14–1 Developing a Theory of Evolution

- Lamarck was one of the first people to propose a theory of evolution and adaptation. He thought that organisms respond to the needs of their environment and pass on acquired characteristics to their offspring.

14–2 Evolution by Natural Selection

- In natural selection, only the organisms with the characteristics best suited for their environment survive and reproduce.

14–3 Genetics and Evolutionary Theory

- Gene mutations and gene recombinations provide the variations upon which natural selection acts.
- Evolution is a change in the relative frequencies of alleles in the gene pool of a population.

14–4 The Development of New Species

- A niche is the combination of an organism's "profession" and the place in which it lives. If two species occupy the same niche in the same location at the same time, they will compete with each other for food and space.
- Reproductive isolation is necessary for speciation.
- In adaptive radiation, one species gives rise to many new species.

14–5 Evolutionary Theory Evolves

- Genetic drift—a random change in the frequency of a gene—occurs most efficiently in small populations.
- The theory of punctuated equilibria states that there are long periods of stability punctuated by brief periods of rapid change.

REVIEWING KEY TERMS

Vocabulary terms are important to your understanding of biology. The key terms listed below are those you should be especially familiar with. Review these terms and their meanings. Then use each term in a complete sentence. If you are not sure of a term's meaning, return to the appropriate section and review its definition.

14–1 Developing a Theory of Evolution

artificial selection
survival of the fittest

14–2 Evolution by Natural Selection

natural selection

14–3 Genetics and Evolutionary Theory

population
gene pool
relative frequency

14–4 The Development of New Species

speciation
niche
reproductive isolation
adaptive radiation
divergent evolution
convergent evolution
analogous structure

14–5 Evolutionary Theory Evolves

genetic drift
gradualism
equilibrium
mass extinction
punctuated equilibria

CHAPTER REVIEW

CONTENT REVIEW

Multiple Choice

Choose the letter of the answer that best completes each statement.

1. Darwin was familiar with the works of all of the following except
   a. Mendel.
   b. Lyell.
   c. Lamarck.
   d. Malthus.
2. Which of the following is needed for new species to form?
   a. a niche
   b. homologous structures
   c. analogous structures
   d. reproductive isolation
3. Farmers change the gene pool of a population by
   a. adaptive radiation.
   b. natural selection.
   c. artificial selection.
   d. convergent evolution.
4. The source of random variation on which natural selection operates are changes in
   a. a niche.
   b. genes.
   c. relative frequency.
   d. the survival of the fittest.
5. An example of analogous structures are a
   a. whale's flipper and a bat's wing.
   b. bird's wing and a butterfly's wing.
   c. hawk's wing and a robin's wing.
   d. dog's leg and a horse's leg.
6. Which of the following ideas proposed by Lamarck was later found to be incorrect?
   a. Acquired characteristics can be inherited.
   b. Analogous structures can be inherited.
   c. Living things change over time.
   d. The Earth is very young.
7. Malthus thought that all of the following would prevent the endless growth of the human population except
   a. famine.
   b. war.
   c. disease.
   d. evolution.
8. Natural selection is also known as
   a. adaptive radiation.
   b. convergent evolution.
   c. survival of the fittest.
   d. divergent evolution.

True or False

Determine whether each statement is true or false. If it is true, write "true." If it is false, change the underlined word or words to make the statement true.

1. The theory of <u>gradualism</u> states that the fossil record shows long periods of stability and short periods of rapid evolution.
2. <u>Lamarck</u> and Wallace both developed a theory of evolution by natural selection.
3. Members of a <u>population</u> share a common group of genes, called a gene pool.
4. <u>Speciation</u> is any change in the relative frequencies of alleles in the gene pool of a population.
5. The combination of an organism's "profession" and the place in which it lives is called its <u>niche</u>.
6. <u>Divergent evolution</u> has produced many of the analogous structures in organisms today.
7. Random change in the frequency of a gene is called <u>relative frequency</u>.
8. More dark-colored peppered moths were found when soot darkened the color of tree trunks. This is an example of <u>artificial selection</u>.

Word Relationships

Give the vocabulary word whose meaning is opposite that of the following words.

1. gradualism
2. convergent evolution
3. natural selection
4. interbreeding

CONCEPT MASTERY

Use your understanding of the concepts developed in the chapter to answer each of the following in a brief paragraph.

1. Explain how the work of Lamarck, Lyell, and Malthus influenced Darwin's thinking.
2. What are two errors in Lamarck's theory of evolution?
3. What is punctuated equilibria?
4. How can farmers change a population of chickens?
5. Why is reproductive isolation needed for a new species to form?
6. How do genes provide the raw material for natural selection?
7. What is survival of the fittest?
8. Two organisms cannot occupy the same niche at the same time. Explain why this is so.

CRITICAL AND CREATIVE THINKING

Discuss each of the following in a brief paragraph.

1. **Applying concepts** How does punctuated equilibria try to explain gaps in the fossil record?
2. **Making predictions** Domesticated turkeys cannot fly. This is an advantage to a farmer who raises thousands of birds. What would happen to these birds if they escaped from the farm into the woods? Explain your answer.
3. **Evaluating theories** Is protecting endangered species defying natural selection? Explain.
4. **Relating cause and effect** The giant panda occupies a very small niche by eating only one kind of food: bamboo. How can being adapted to such a small niche actually endanger this species' survival?
5. **Applying concepts** How might having a small gene pool cause a species to become extinct?
6. **Using the writing process** A friend of yours invents a time machine through which you both embark on a trip far into the future. When you arrive at your destination, you discover that Earth is much warmer and the sunlight more intense. You see many plants and animals that are unlike any you have ever seen before. Write a short story that describes the new life forms that are able to survive under these different conditions. You may wish to accompany your story with one or more drawings depicting these unusual plants and animals.