Section 15.1

Reading Preview

Objectives

- **Discuss** the evidence that convinced Darwin that species could change over time.
- **List** the four principles of natural selection.
- **Show** how natural selection could change a population.

Review Vocabulary

selective breeding: process by which a breeder develops a plant or animal to have certain traits

New Vocabulary

artificial selection
natural selection
evolution

Figure 15.1 Charles Darwin (1809-1882)

Darwin's Theory of Evolution by Natural Selection

MAIN Idea **Charles Darwin developed a theory of evolution based on natural selection.**

Real-World Reading Link Today, a jet can travel from London to New York in hours. Imagine how different things were when it took almost five years for Charles Darwin to circle the globe aboard a small, cramped ship.

Developing the Theory of Evolution

When Charles Darwin, shown in **Figure 15.1,** boarded the HMS *Beagle* in 1831, the average person believed that the world was about 6000 years old. Almost everyone, including the young Darwin, thought that animals and plants were unchanging. The concept of gradual change over time was still years away.

Darwin on the HMS *Beagle* The primary mission of the *Beagle* was to survey the coast of South America. In 1831, the *Beagle* set sail from England for Maderia and then proceeded to South America, as shown on the map in **Figure 15.2.** Darwin's role on the ship was as naturalist and companion to the captain. His job was to collect biological and geological specimens during the ship's travels. Darwin had a degree in theology from Christ's College, Cambridge, though he previously had studied medicine and the sciences.

Over the course of the ship's five-year voyage, Darwin made extensive collections of rocks, fossils, plants, and animals. He also read a copy of Charles Lyell's *Principles of Geology*—a book proposing that Earth was millions of years old. This book influenced his thinking as he observed fossils of marine life at high elevation in the Andes, unearthed giant fossil versions of smaller living mammals, and saw how earthquakes could lift rocks great distances very quickly.

The Galápagos Islands In 1835, the *Beagle* arrived in the Galápagos (guh LAH puh gus) Islands off the coast of South America. Darwin was initially disappointed by the stark barrenness of these volcanic islands. But as he began to collect mockingbirds, finches, and other animals on the four islands he visited, he noticed that the different islands seemed to have their own, slightly different varieties of animals. These differences, however, only sparked a mere curiosity. He took little notice of the comment from the colony's vice governor that the island origins of the giant tortoises could be identified solely by the appearance of the tortoises' shells.

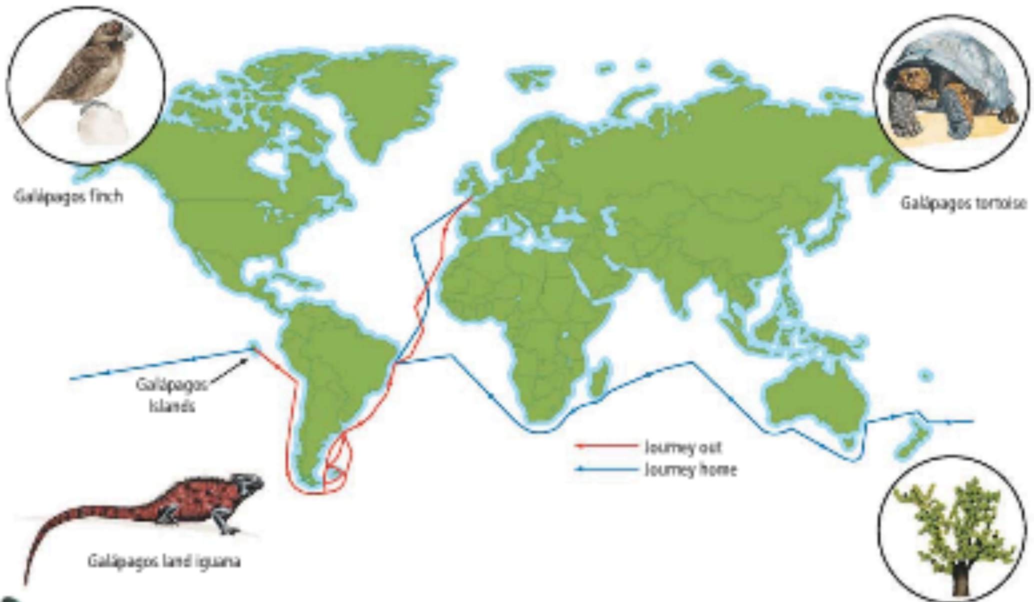


Figure 15.2 The map shows the route of the *Beagle's* voyage. The species shown are all unique to the Galápagos Islands.
Infer ***How did the first organisms reach the Galápagos?***

A few years after Darwin returned to England, he began reconsidering his observations. He took note of the work of John Gould, an ornithologist who was classifying the birds Darwin brought back from the Galápagos. Gould discovered that the Galápagos mockingbirds were separate species and determined that the finches of the Galápagos did not live anywhere else in South America. In fact, almost every specimen that Darwin had collected on the islands was new to European scientists. These new species most closely resembled species from mainland South America, although the Galápagos and the mainland had different environments. Island and mainland species should not have resembled one another so closely unless, as Darwin began to suspect, populations from the mainland changed after reaching the Galápagos.

Darwin continued his studies Darwin hypothesized that new species could appear gradually through small changes in ancestral species, but he could not see how such a process would work. To understand it better, he turned to animal breeders—pigeon breeders in particular.

Different breeds of pigeons have certain distinctive traits that also are present in that breed's offspring. A breeder can promote these traits by selecting and breeding pigeons that have the most exaggerated expressions of those traits. For example, to produce pigeons with fan-shaped tails, the breeder will breed pigeons with the most fan-shaped tails. The process of directed breeding to produce offspring with desired traits, referred to as selective breeding in Chapter 13, was called **artificial selection** by Darwin.

Artificial selection also occurs when developing new breeds of dogs or new strains of crop plants. Darwin inferred that if humans could change species by artificial selection, then perhaps the same process could work in nature. Further, Darwin thought that, given enough time, perhaps this process could produce new species.

Natural selection While thinking about artificial selection, Darwin read an essay by the economist Thomas Malthus. The essay suggested that the human population, if unchecked, eventually would outgrow its food supply, leading to a competitive struggle for existence. Darwin realized that Malthus's ideas could be applied to the natural world. He reasoned that some competitors in the struggle for existence would be better equipped for survival than others. Those less equipped would die. This is the process of **natural selection.** Here, finally, was the framework for a new theory about the origin of species.

Darwin's theory of evolution by natural selection has four basic principles that explain how traits of a population can change over time. First, individuals in a population show differences, or variations. Second, variations can be inherited, meaning that they are passed down from parent to offspring. Third, organisms have more offspring than can survive on available resources. The average cardinal, for example, lays nine eggs each summer. If each baby cardinal survived and reproduced just once, it would take only seven years for the first pair to have produced one million birds. Finally, variations that increase reproductive success will have a greater chance of being passed on than those that do not increase reproductive success. If having a fantail helps a pigeon reproduce successfully, future generations would include more pigeons with fan-shaped tails.

Given enough time, natural selection could modify a population enough to produce a new species. Natural selection is now considered the mechanism by which evolution takes place. **Figure 15.3** shows how natural selection might modify a population of sunflowers.

Concepts In Motion

Interactive Table To explore more about the principles of natural selection, visit biologygmh.com.

Table 15.1 Basic Principles of Natural Selection

Principle	Example
Individuals in a population show variations among others of the same species.	The students in a classroom all look different.
Variations are inherited.	You look similar to your parents.
Animals have more young than can survive on the available resources.	The average cardinal lays nine eggs per summer. If each cardinal lived only one year, in seven years there would be a million cardinals if all offspring survived.
Variations that increase reproductive success will be more common in the next generation.	If having a fan-shaped tail increases reproductive success of pigeons, then more pigeons in the next generation will have fan-shaped tails.

The Origin of Species

Darwin had likely formulated his theory of evolution by natural selection by about 1840. Soon after, he began writing a multi-volume book compiling evidence for evolution and explaining how natural selection might provide a mechanism for the origin of species. **Table 15.1** summarizes the principles of natural selection described in Darwin's work. He continued to compile evidence in support of his theory for many years. For example, he spent eight years studying relationships among barnacles.

In 1858, Alfred Russel Wallace, another English naturalist, proposed a theory that was almost identical to Darwin's theory. Both men's ideas were presented to the Linnean Society of London. One year later, Darwin published *On the Origin of Species by Means of Natural Selection*—a condensed version of the book he had started many years before.

In his book, Darwin used the term *evolution* only on the last page. Today, biologists use the term **evolution** to define cumulative changes in groups of organisms through time. Natural selection is not synonymous with evolution; it is a mechanism by which evolution occurs.

VOCABULARY
WORD ORIGIN
Evolve
comes from the Latin word *evolvere*, meaning *unroll* or *unfold*.

Section 15.1 Assessment

Section Summary

- Darwin drew from his observations on the HMS *Beagle* and later studies to develop his theory of evolution by natural selection.
- Natural selection is based on ideas of excess reproduction, variation, inheritance, and advantages of certain traits in certain environments.
- Darwin reasoned that the process of natural selection eventually could result in the appearance of new species.

Understand Main Ideas

1. MAIN Idea **Describe** the evidence Charles Darwin gathered that led to his theory of evolution.
2. **Explain** how the idea of artificial selection contributed to Darwin's ideas on natural selection.
3. **Identify** the four principles of natural selection and provide examples not used in the section.
4. **Discuss** Wallace's contribution to the theory of evolution by natural selection.

Think Critically

5. **Infer** the consequences for evolution if species did not vary.

WRITING in Biology

6. Write a short story about what it might have been like to visit the Galápagos Islands with Darwin.

Section 15.2

Reading Preview

Objectives

- **Describe** how fossils provide evidence of evolution.
- **Discuss** morphological evidence of evolution.
- **Explain** how biochemistry provides evidence of evolution.

Review Vocabulary

fossil: remains of an organism or its activities

New Vocabulary

derived trait
ancestral trait
homologous structure
vestigial structure
analogous structure
embryo
biogeography
fitness
camouflage
mimicry

Evidence of Evolution

MAIN Idea Multiple lines of evidence support the theory of evolution.

Real-World Reading Link The evidence for evolution is like a set of building blocks. Just as you cannot build something with only one building block, one piece of evidence does not make a theory. The evidence for evolution is more convincing when supported by many pieces of evidence, just as a structure is more sturdy when built with many blocks.

Support for Evolution

Darwin's book *On the Origin of Species* demonstrated how evolution might happen. The book also provided evidence that evolution has occurred on our planet. The concepts of natural selection and evolution are different, though related. Darwin's theory of evolution by natural selection is part of the larger theory of evolution. Recall from Chapter 1 that a theory provides an explanation for a natural phenomenon based on observations. Theories explain available data and suggest further areas for experimentation. The theory of evolution states that all organisms on Earth have descended from a common ancestor.

The fossil record Fossils provide a record of species that lived long ago—supplying some of the most significant evidence of evolutionary change. This record can show ancient species that are similar to current ones, as illustrated in **Figure 15.4.** Fossils also show some species, such as the horseshoe crab, have remained unchanged for millions of years. The fossil record is an important source of information for determining the ancestry of organisms and patterns of evolution.

Figure 15.4 The giant armadillo-like glyptodont, *Glyptodon*, is an extinct animal that Darwin thought must be related to the living armadillos.
Observe *What features of the 2000-kg glyptodont are similar to those of the 4-kg armadillo?*

■ **Figure 15.5** This artist's rendering of *Archaeopteryx* shows that it shares many features with modern birds while retaining ancestral dinosaur features.

Connection to Earth Science Though Darwin recognized the limitations of the fossil record, he predicted the existence of fossils intermediate in form between species. Today, scientists studying evolutionary relationships have found hundreds of thousands of transitional fossils that contain features shared by different species. For example, certain dinosaur fossils show feathers of modern birds and the teeth and bony tails of reptiles. **Figure 15.5** shows an artist's rendering of *Archaeopteryx*, one of the first birds. *Archaeopteryx* fossils provide evidence of characteristics that classify it as a bird, and also show that the bird retained several distinct dinosaur features.

Researchers consider two major classes of traits when studying transitional fossils: derived traits and ancestral traits. **Derived traits** are newly evolved features, such as feathers, that do not appear in the fossils of common ancestors. **Ancestral traits,** on the other hand, are more primitive features, such as teeth and tails, that do appear in ancestral forms. Transitional fossils provide detailed patterns of evolutionary change for the ancestors of many modern animals, including mollusks, horses, whales, and humans.

VOCABULARY

WORD ORIGIN

Homologous
from the Greek words *homos,* meaning *same,* and *logos,* meaning *relation* or *reasoning.*

Comparative anatomy Why do the vertebrate forelimbs shown in **Figure 15.6** have different functions but appear to be constructed of similar bones in similar ways? Evolutionary theory suggests that the answer lies in shared ancestry.

Homologous structures Anatomically similar structures inherited from a common ancestor are called **homologous structures.** Evolution predicts that an organism's body parts are more likely to be modifications of ancestral body parts than they are to be entirely new features. The limbs illustrated in **Figure 15.6** move animals in different ways, yet they share similar construction. Bird wings and reptile limbs are another example. Though birds use their wings to fly and reptiles use their limbs to walk, bird wings and reptile forelimbs are similar in shape and construction, which indicates that they were inherited from a common ancestor. While homologous structures alone are not evidence of evolution, they are an example for which evolution is the best available explanation for the biological data.

■ **Figure 15.6** The forelimbs of vertebrates illustrate homologous structures. Each limb is adapted for different uses, but they all have similar bones.

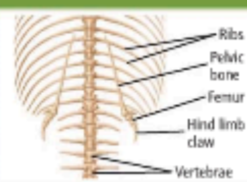
Infer ***Which of the forelimbs shown would most likely resemble a whale's fluke?***

Vestigial structures In some cases, a functioning structure in one species is smaller or less functional in a closely related species. For example, most birds have wings developed for flight. Kiwis, however, have very small wings that cannot be used for flying. The kiwi wing is a kind of homologous structure called a vestigial structure. **Vestigial structures** are structures that are the reduced forms of functional structures in other organisms. **Table 15.2** illustrates some vestigial structures in different species. Evolutionary theory predicts that features of ancestors that no longer have a function for that species will become smaller over time until they are lost.

Concepts In Motion

Interactive Table To explore more about vestigial structures, visit biologygmh.com.

Table 15.2 Vestigial Structures

Trait	Example	Description
Snake pelvis		The pelvis is the attachment point for legs and is therefore nonfunctional in an animal without legs.
Kiwi wings		The wings of kiwis are too small to be of any use in flight.
Human Appendix		This is a 5–15 cm long structure important for digestion in many mammals, but of limited use in humans and some apes.

■ **Figure 15.7** Eagles and beetles use their wings to fly, but their wing structures are different.
Explain ***how scientists know that the wings of eagles and beetles are analogous structures.***

Bald Eagle

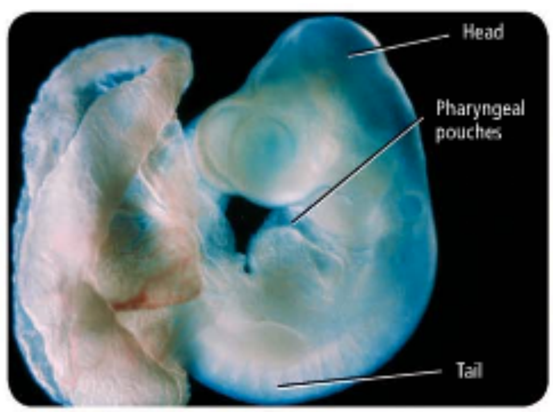
May Beetle

Not all anatomically similar features are evidence of common ancestry. **Analogous structures** can be used for the same purpose and can be superficially similar in construction but are not inherited from a common ancestor. As shown in **Figure 15.7,** the wings of an eagle and the wings of a beetle have the same function—they both enable the organism to fly. But the wings are constructed in different ways from different materials. While analogous structures do not indicate close evolutionary relationships, they do show that functionally similar features can evolve independently in similar environments.

Reading Check **Explain** why vestigial structures are considered examples of homologous structures.

Comparative embryology Vertebrate embryos provide more glimpses into evolutionary relationships. An **embryo** is an early, pre-birth stage of an organism's development. Scientists have found that vertebrate embryos exhibit homologous structures during certain phases of development but become totally different structures in the adult forms. The embryos shown in **Figure 15.8,** like all vertebrate embryos, have a tail and paired structures called pharyngeal pouches. In fish the pouches develop into gills. In reptiles, birds, and mammals, these structures become parts of the ears, jaws, and throats. Though the adult forms differ, the shared features in the embryos suggest that vertebrates evolved from a shared ancestor.

■ **Figure 15.8** Embryos reveal evolutionary history. Bird and mammal embryos share several developmental features.



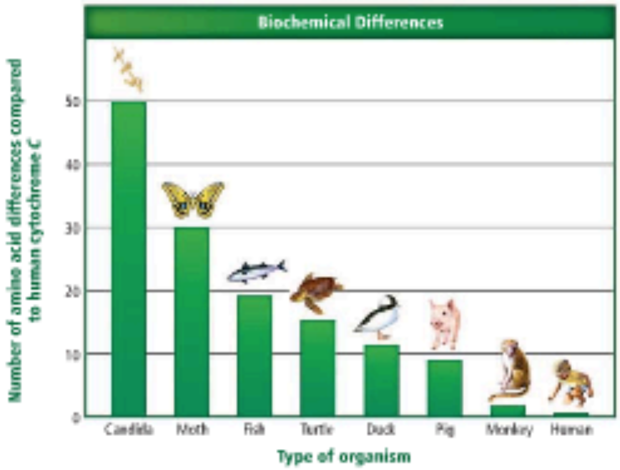


Figure 15.9 This illustration compares amino acid sequences of cytochrome *c* in humans and other organisms.

Infer ***Would the cytochrome c of a reptile or a duck be expected to have more amino acid differences when compared with that of a human? Explain.***

Comparative biochemistry Scientific data also shows that common ancestry can be seen in the complex metabolic molecules that many different organisms share. Cytochrome *c* is an enzyme that is essential for respiration and is highly conserved in animals. This means that despite slight variations in its amino acid sequence, the molecule has changed very little over time.

Evolutionary theory predicts that molecules in species with a recent common ancestor should share certain ancient amino acid sequences. The more closely related the species are, the greater number of sequences will be shared. This predicted pattern is what scientists find to be true in cytochrome *c*. For example, as illustrated in **Figure 15.9**, the cytochrome *c* in the pig and in the monkey share more amino acid sequences with humans than the cytochrome *c* in birds shares with humans.

Connection to Chemistry Scientists have found similar biochemical patterns in other proteins, as well as in DNA and RNA. DNA and RNA form the molecular basis of heredity in all living organisms. The fact that many organisms have the same complex molecules suggests that these molecules evolved early in the history of life and were passed on through the life-forms that have lived on Earth. Comparisons of the similarities in these molecules across species reflect evolutionary patterns seen in comparative anatomy and in the fossil record. Organisms with closely related morphological features have more closely related molecular features.

Geographic distribution The distribution of plants and animals that Darwin saw during his South American travels first suggested evolution to Darwin. He observed that animals on the South American mainland were more similar to other South American animals than they were to animals living in similar environments in Europe. The South American mara, for example, inhabited a niche that was occupied by the rabbit in Europe. You can compare a mara and a rabbit in **Figure 15.10**. Darwin realized that the mara was more similar to other South American species than it was to the rabbit because it shared a closer ancestor with the South American animals.

Figure 15.10 The mara *(Dolichotis patagonum)* exists in a niche similar to that of the English rabbit *(Oryctolagus cuniculus)*.

Mara

English Rabbit

Patterns of migration were critical to Darwin when he was developing his theory. Migration patterns explained why, for example, islands often have more plant diversity than animal diversity: the plants are more able to migrate from the closest mainland as seeds, either by wind or on the backs of birds. Since Darwin's time, scientists have confirmed and expanded Darwin's study of the distribution of plants and animals around the world in a field of study now called **biogeography.** Evolution is intimately linked with climate and geological forces, especially plate tectonics, which helps explain many ancestral relationships and geographic distributions seen in fossils and living organisms today.

Adaptation

The five categories discussed in the previous section—the fossil record, comparative anatomy, comparative embryology, comparative biochemistry, and geographic distribution—offer evidence for evolution. Darwin drew on all of these except biochemistry—which was not well developed in his time—to develop his own theory of evolution by natural selection. At the heart of his theory lies the concept of adaptation.

Types of adaptation An adaptation is a trait shaped by natural selection that increases an organism's reproductive success. One way to determine how effectively a trait contributes to reproductive success is to measure fitness. **Fitness** is a measure of the relative contribution an individual trait makes to the next generation. It often is measured as the number of reproductively viable offspring that an organism produces in the next generation.

The better an organism is adapted to its environment, the greater its chances of survival and reproductive success. This concept explains the variations Darwin observed in the animals on the Galápagos Islands. Because the finches were each adapted to their individual islands, they had variations in their beaks.

Vocabulary
Science usage v. Common usage
Adaptation
Science usage: a trait shaped by natural selection to increase the survival or reproductive success of an organism.
The prehensile tail of monkeys is an adaptation for life in the trees.

Common usage: adjustment or change.
The movie script is an adaptation of the original play.

Camouflage Some species have evolved morphological adaptations that allow them to blend in with their environments. This is called **camouflage** (KA muh flahj). Camouflage allows organisms to become almost invisible to predators, as shown in **Figure 15.11.** As a result, more of the camouflaged individuals survive and reproduce.

Figure 15.11 It would be easy for a predator to overlook a leafy sea dragon, *Phycodurus eques*, in a sea grass habitat because of the animal's effective camouflage.

California Kingsnake **Western Coral Snake**

■ **Figure 15.12** Predators avoid the harmless California kingsnake because it has color patterns similar to those of the poisonous western coral snake.

Mimicry Another type of morphological adaptation is mimicry. In **mimicry,** one species evolves to resemble another species. You might expect that mimicry would make it difficult for individuals in one species to find and breed with other members of their species, thus decreasing reproductive success. However, mimicry often increases an organism's fitness. Mimicry can occur in a harmless species that has evolved to resemble a harmful species, such as the example shown in **Figure 15.12.** Sometimes mimicry benefits two harmful species. In both cases, the mimics are protected because predators can't always tell the mimic from the animal it is mimicking, so they learn to avoid them both.

Reading Check **Compare** mimicry and camouflage.

Antimicrobial resistance Species of bacteria that originally were killed by penicillin and other antibiotics have developed drug resistance. For almost every antibiotic, at least one species of resistant bacteria exists. One unintended consequence of the continued development of antibiotics is that some diseases, which were once thought to be contained, such as tuberculosis, have reemerged in more harmful forms.

■ **Figure 15.13** Spaces between arches set in a square to support a dome are called spandrels and are often decorative. Some features might be like spandrels—a consequence of another adaptation.

Consequences of adaptations Not all features of an organism are necessarily adaptive. Some features might be consequences of other evolved characteristics. Biologists Stephen Jay Gould and Richard Lewontin made this point in 1979 in a paper claiming that biologists tended to overemphasize the importance of adaptations in evolution.

Spandrel example To illustrate this concept, they used an example from architecture. Building a set of four arches in a square to support a dome means that spaces called spandrels will appear between the arches, as illustrated in **Figure 15.13.** Because spandrels are often decorative, one might think that spandrels exist for decoration. In reality, they are an unavoidable consequence of arch construction. Gould and Lewontin argued that some features in organisms are like spandrels because even though they are prominent, they do not increase reproductive success. Instead, they likely arose as an unavoidable consequence of prior evolutionary change.

Human example A biological example of a spandrel is the helplessness of human babies. Humans give birth at a much earlier developmental stage than other primates. This causes them to need increased care early in their life. Many scientists think that the helplessness of human babies is a consequence of the evolution of big brains and upright posture. To walk upright, humans need narrow pelvises, which means that babies' heads must be small enough to fit through the pelvic opening at birth. In contrast, scientists previously thought that the helplessness of human infants provided an adaptive advantage, such as increased attention from parents and more learning.

Section 15.2 Assessment

Section Summary

- Fossils provide strong direct evidence to support evolution.
- Homologous and vestigial structures indicate shared ancestry.
- Examples of embryological and biochemical traits provide insight into the evolution of species.
- Biogeography can explain why certain species live in certain locations.
- Natural selection gives rise to features that increase reproductive success.

Understand Main Ideas

1. MAIN Idea **Describe** how fossils provide evidence of evolution.
2. **Explain** what natural selection predicts about mimicry, camouflage, homologous structures, and vestigial structures.
3. **Indicate** how biochemistry provides evidence of evolution.
4. **Compare** the morphological evidence and the biochemical evidence supporting evolution.

Think Critically

5. **Hypothesize** Evidence suggests that the bones in bird wings share a number of features with the bones of dinosaur arms. Based on this evidence, what hypothesis could you make about the evolutionary relationship between birds and dinosaurs?
6. **Apply** Research has shown that if a prescribed dose of antibiotic is not taken completely, some bacteria might not be killed and the disease might return. How does natural selection explain this phenomenon?

Reading Preview

Objectives

- **Discuss** patterns observed in evolution.
- **Describe** factors that influence speciation.
- **Compare** gradualism with punctuated equilibrium.

Review Vocabulary

allele: alternate forms of a character trait that can be inherited

New Vocabulary

Hardy-Weinberg Principle
genetic drift
founder effect
bottleneck
stabilizing selection
directional selection
disruptive selection
sexual selection
prezygotic isolating mechanism
postzygotic isolating mechanism
allopatric speciation
sympatric speciation
adaptive radiation
gradualism
punctuated equilibrium

Shaping Evolutionary Theory

MAIN Idea The theory of evolution continues to be refined as scientists learn new information.

Real-World Reading Link The longer you operate a complicated piece of electronics, the better you understand how it works. The device does not change, but you become more familiar with its functions. Scientists have been studying evolution for almost 150 years, yet they are still learning new ways in which evolution leads to changes in species.

Mechanisms of Evolution

Darwin's theory of natural selection remains a central theme in evolution. It explains how organisms adapt to their environments and how variations can give rise to adaptations within species. Scientists now know, however, that natural selection is not the only mechanism of evolution. Studies from population genetics and molecular biology have led to the development of evolutionary theory. At the center of this is the understanding that evolution occurs at the population level, with genes as the raw material.

Population genetics At the turn of the twentieth century, genes had not been discovered. However, the allele was understood to be one form of an inherited character trait, such as eye color, that gets passed down from parent to offspring. Scientists didn't understand why dominant alleles wouldn't simply swamp recessive alleles in a population.

In 1908, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg independently came up with the same solution to this problem. They showed mathematically that evolution will not occur in a population unless allelic frequencies are acted upon by forces that cause change. In the absence of these forces, the allelic frequency remains the same and evolution doesn't occur. According to this idea, which is now known as the **Hardy-Weinberg principle,** when allelic frequencies remain constant, a population is in genetic equilibrium. This concept is illustrated in **Figure 15.14.**

Figure 15.14 According to the Hardy-Weinberg principle, even though the number of owls doubled, the ratio of gray to red owls remained the same.

Connection to Math To illustrate the Hardy-Weinberg principle, consider a population of 100 humans. Forty people are homozygous dominant for earlobe attachment *(EE)*. Another 40 people are heterozygous *(Ee)*. Twenty people are homozygous recessive *(ee)*. In the 40 homozygous dominant people, there are 80 *E* alleles (2 *E* alleles × 40), and in the 20 homozygous recessive people there are 40 *e* alleles (2 *e* alleles × 20). The heterozygous people have 40 *E* alleles and 40 *e* alleles. Summing the alleles, we have 120 *E* alleles and 80 *e* alleles for a total of 200 alleles. The *E* allele frequency is 120/200, or 0.6. The *e* allele frequency is 80/200, or 0.4.

The Hardy-Weinberg principle states that the allele frequencies in populations should be constant. This often is expressed as $p + q = 1$. For our example, p can represent the *E* allele frequency and q can represent the *e* allele frequency.

Squaring both sides of the equation yields the new equation $p^2 + 2pq + q^2 = 1$. This equation allows us to determine the equilibrium frequency of each genotype in the population: homozygous dominant (p^2), heterozygous (2pq), and homozygous recessive (q^2). From the above example, $p = 0.6$, and $q = 0.4$, so $(0.6)(0.6) + 2(0.6)(0.4) + (0.4)(0.4) = 1$. In the example population, the equilibrium frequency for homozygous dominant will be 0.36, the equilibrium frequency of heterozygous will be 0.48, and the equilibrium frequency of homozygous recessive will be 0.16. Note that the sum of these frequencies equals one.

Reading Check **Determine** when a population is in equilibrium.

Conditions According to the Hardy-Weinberg principle, a population in genetic equilibrium must meet five conditions—there must be no genetic drift, no gene flow, no mutation, mating must be random, and there must be no natural selection. Populations in nature might meet some of these requirements, but hardly any population meets all five conditions for long periods of time. If a population is not in genetic equilibrium, at least one of the five conditions has been violated. These five conditions listed in **Table 15.3** are known mechanisms of evolutionary change.

Table 15.3 The Hardy-Weinberg Principle

Concepts in Motion
Interactive Table To explore more about the Hardy-Weinberg principle, visit biologygmh.com.

Condition	Violation	Consequence
The population is very large.	Many populations are small.	Chance events can lead to changes in population traits.
There is no immigration or emigration.	Organisms move in and out of the population.	The population can lose or gain traits with movement of organisms.
Mating is random.	Mating is not random.	New traits do not pass as quickly to the rest of the population.
Mutations do not occur.	Mutations occur.	New variations appear in the population with each new generation.
Natural selection does not occur.	Natural selection occurs.	Traits in a population change from one generation to the next.

Genetic drift Any change in the allelic frequencies in a population that is due to chance is called **genetic drift.** Recall from Chapter 10 that for simple traits only one of a parent's two alleles passes to the offspring, and that this allele is selected randomly through independent assortment. In large populations, enough alleles "drift" to ensure that the allelic frequency of the entire population remains relatively constant from one generation to the next. In smaller populations, however, the effects of genetic drift become more pronounced, and the chance of losing an allele becomes greater.

Founder effect The founder effect is an extreme example of genetic drift. The **founder effect** can occur when a small sample of a population settles in a location separated from the rest of the population. Because this sample is a random subset of the original population, the sample population carries a random subset of the population's genes. Alleles that were uncommon in the original population might be common in the new population, and the offspring in the new population will carry those alleles. Such an event can result in large genetic variations in the separated populations.

The founder effect is evident in the Amish and Mennonite communities in the United States in which the people rarely marry outside their own communities. The Old Order Amish have a high frequency of six-finger dwarfism. All affected individuals can trace their ancestry back to one of the founders of the Order.

Bottleneck Another extreme example of genetic drift is a **bottleneck,** which occurs when a population declines to a very low number and then rebounds. The gene pool of the rebound population often is genetically similar to that of the population at its lowest level, that is, it has reduced diversity. Researchers think that cheetahs in Africa experienced a bottleneck 10,000 years ago, and then another one about 100 years ago. Throughout their current range, shown in **Figure 15.15,** cheetahs are so genetically similar that they appear inbred. Inbreeding decreases fertility, and might be a factor in the potential extinction of this endangered species.

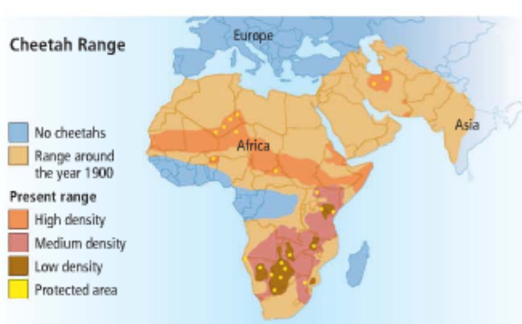


Figure 15.15 The map shows the present range of cheetahs in Africa. It is believed that cheetahs had a much larger population until a bottleneck occurred.
Apply Concepts ***What effect has the bottleneck had on the reproductive rate of cheetahs?***

Gene flow A population in genetic equilibrium experiences no gene flow. It is a closed system, with no new genes entering the population and no genes leaving the population. In reality, few populations are isolated. The random movement of individuals between populations, or migration, increases genetic variation within a population and reduces differences between populations.

Nonrandom mating Rarely is mating completely random in a population. Usually, organisms mate with individuals in close proximity. This promotes inbreeding and could lead to a change in allelic proportions favoring individuals that are homozygous for particular traits.

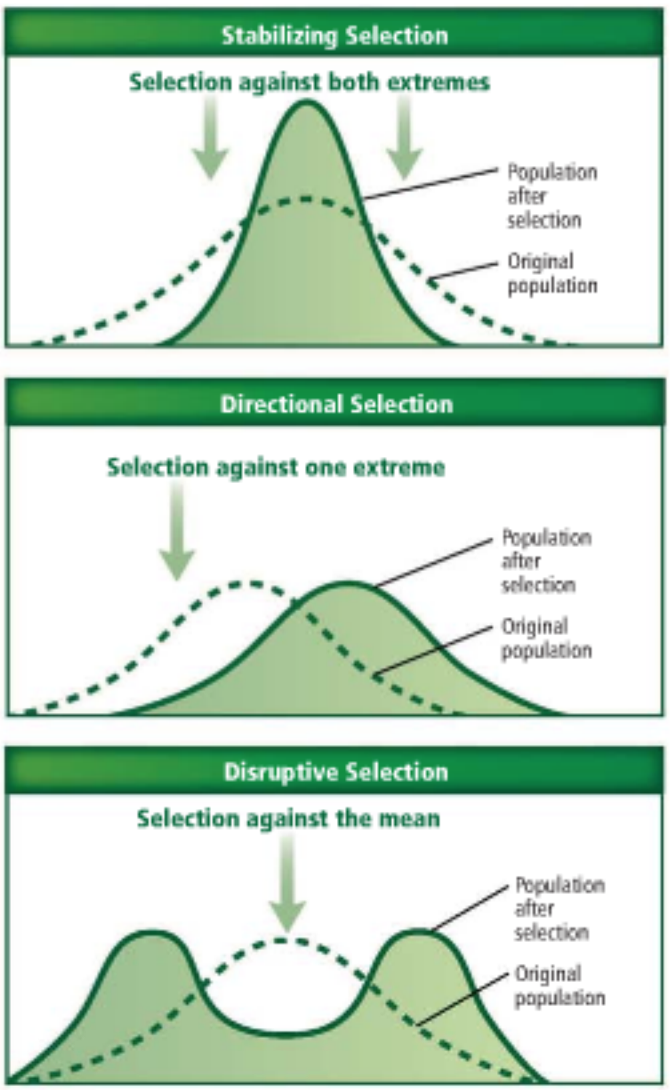
Mutation Recall from Chapter 12 that a mutation is a random change in genetic material. The cumulative effect of mutations in a population might cause a change in allelic frequencies, and thus violate genetic equilibrium. Though many mutations cause harm or are lethal, occasionally a mutation provides an advantage to an organism. This mutation will then be selected for and become more common in subsequent generations. In this way, mutations provide the raw material upon which natural selection works.

Reading Check **Summarize** how mutation violates the Hardy-Weinberg principle.

Natural selection The Hardy-Weinberg principle requires that all individuals in a population be equally adapted to their environment and thus contribute equally to the next generation. As you have learned, this rarely happens. Natural selection acts to select the individuals that are best adapted for survival and reproduction. Natural selection acts on an organism's phenotype and changes allelic frequencies. **Figure 15.16** shows three main ways natural selection alters phenotypes: through stabilizing selection, directional selection, and disruptive selection. A fourth type of selection, sexual selection, also is considered a type of natural selection.

Stabilizing selection The most common form of natural selection is **stabilizing selection.** It operates to eliminate extreme expressions of a trait when the average expression leads to higher fitness. For example, human babies born with below-normal and above-normal birth weights have lower chances of survival than babies born with average weights. Therefore, birth weight varies little in human populations.

Figure 15.16 Natural selection can alter allele frequencies of a population in three ways. The bell-shaped curve shown as a dotted line in each graph indicates the trait's original variation in a population. The solid line indicates the outcome of each type of selection pressure.



Directional selection If an extreme version of a trait makes an organism more fit, **directional selection** might occur. This form of selection increases the expression of the extreme versions of a trait in a population. One example is the evolution of moths in industrial England. The peppered moth has two color forms, or morphs, as shown in **Figure 15.17.** Until the mid 1850s, nearly all peppered moths in England had light-colored bodies and wings. Beginning around 1850, however, dark moths began appearing. By the early 1900s, nearly all peppered moths were dark. Why? Industrial pollution favored the dark-colored moths at the expense of the light-colored moths. The darker the moth, the more it matched the sooty background of its tree habitat, and the harder it was for predators to see. Thus, more dark moths survived, adding more genes for dark color to the population. This conclusion was reinforced in the mid-1900s when the passage of air pollution laws led to the resurgence of light-colored moths. This phenomenon is called industrial melanism.

Directional selection also can be seen in Galápagos finches. For three decades in the latter part of the twentieth century, Peter and Rosemary Grant studied populations of these finches. The Grants found that during drought years, food supplies dwindled and the birds had to eat the hard seeds they normally ignored. Birds with the largest beaks were more successful in cracking the tough seed coating than were birds with smaller beaks. As a result, over the duration of the drought, birds with larger beaks came to dominate the population. In rainy years, however, the directional trend was reversed, and the population's average beak size decreased.

Figure 15.17 The peppered moth exists in two forms— light colored and dark colored.
Infer ***How might natural selection have caused a change in the frequencies of the two forms?***

▪ **Figure 15.18** Northern water snakes have two different color patterns depending on their habitat. Intermediate color patterns would make them more visible to predators.

Disruptive selection Another type of natural selection, **disruptive selection,** is a process that splits a population into two groups. It tends to remove individuals with average traits but retain individuals expressing extreme traits at both ends of a continuum. Northern water snakes, illustrated in **Figure 15.18,** are an example. Snakes living on the mainland shores inhabit grasslands and have mottled brown skin. Snakes inhabiting rocky island shores have gray skin. Each is adapted to its particular environment. A snake with intermediate coloring would be disadvantaged because it would be more visible to predators.

LAUNCH Lab

Review Based on what you have learned about adaptation, how would you now answer the analysis questions?

Sexual selection Another type of natural selection, in which change in frequency of a trait is based on the ability to attract a mate is called **sexual selection.** This type of selection often operates in populations where males and females differ significantly in appearance. Usually in these populations, males are the largest and most colorful of the group. The bigger the tail of a male peacock, as shown in **Figure 15.19,** the more attractive the bird is to females. Males also evolve threatening characteristics that intimidate other males; this is common in species, such as elk or deer, where the male keeps a harem of females.

Darwin wondered why some qualities of sexual attractiveness appeared to be the opposite of qualities that might enhance survival. For example, the peacock's tail, while attracting females, is large and cumbersome, and it might make the peacock a more likely target for predators. Though some modern scientists think that sexual selection is not a form of natural selection, others think that sexual selection follows the same general principle: brighter colors and bigger bodies enhance reproductive success, whatever the chances are for long-term survival.

▪ **Figure 15.19** Peacocks that have the largest tails tend to attract more peahens. The frequency of this trait increases because of sexual selection.

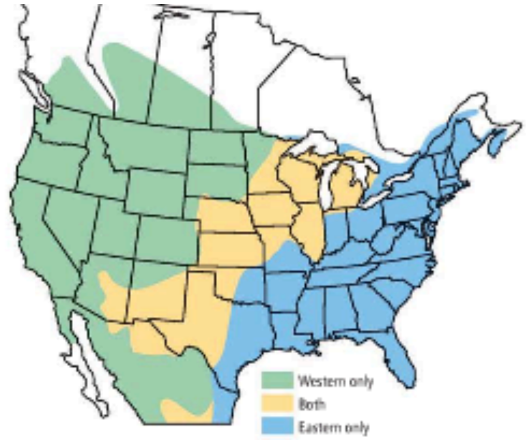


Figure 15.20 The map shows the overlapping ranges of the Eastern meadowlark and Western meadowlark. While the two are similar in appearance, their songs separate them behaviorally.
Infer ***how different songs prevent the meadowlarks from breeding.***

Reproductive Isolation

Mechanisms of evolution—genetic drift, gene flow, nonrandom mating, mutation, and natural selection—violate the Hardy-Weinberg principle. To what extent each mechanism contributes to the origin of new species is a major topic of debate in evolutionary science today. Most scientists define speciation as the process whereby some members of a sexually reproducing population change so much that they can no longer produce fertile offspring with members of the original population. Two types of reproductive isolating mechanisms prevent gene flow among populations. **Prezygotic isolating mechanisms** operate before fertilization occurs. **Postzygotic isolating mechanisms** operate after fertilization has occurred to ensure that the resulting hybrid remains infertile.

Prezygotic isolation Prezygotic isolating mechanisms prevent reproduction by making fertilization unlikely. These mechanisms prevent genotypes from entering a population's gene pool through geographic, ecological, behavioral, or other differences. For example, the eastern meadowlark and the western meadowlark, pictured in **Figure 15.20,** have overlapping ranges and are similar in appearance. These two species, however, use different mating songs and do not interbreed. Time is another factor in maintaining a reproductive barrier. Closely related species of fireflies mate at different times of night, just as different species of trout live in the same stream but breed at different times of the year.

Postzygotic isolation When fertilization has occurred but a hybrid offspring cannot develop or reproduce, postzygotic isolation has occurred. Postzygotic isolating mechanisms prevent offspring survival or reproduction. A lion and a tiger are considered separate species because even though they can mate, the offspring—a liger, shown in **Figure 15.21**—is sterile.

Figure 15.21 The offspring of a male lion and a female tiger is a liger. Ligers are sterile.

Speciation

For speciation to occur, a population must diverge and then be reproductively isolated. Biologists usually recognize two types of speciation: allopatric and sympatric.

Allopatric speciation In **allopatric speciation,** a physical barrier divides one population into two or more populations. The separate populations eventually will contain organisms that, if enough time has passed, will no longer be able to breed successfully with one another. Most scientists think that allopatric speciation is the most common form of speciation. Small subpopulations isolated from the main population have a better chance of diverging than those living within it. This was the conclusion of the biologist Ernst Mayr, who argued as early as the 1940s that geographic isolation was not only important but required for speciation.

Vocabulary

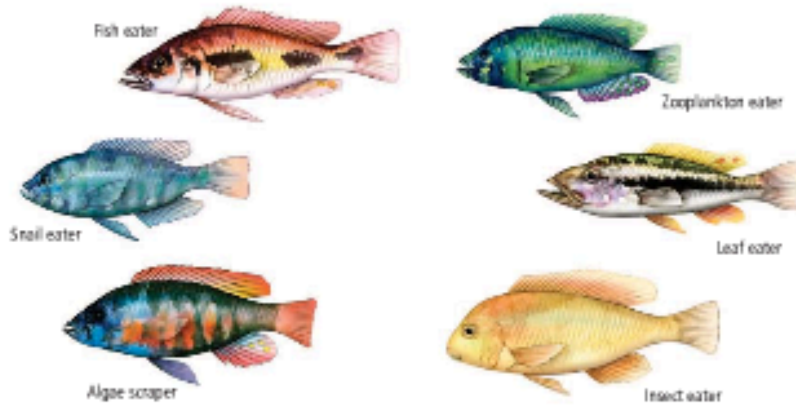
Academic Vocabulary

Isolation:
the condition of being separated from others.
After infection, a patient is kept in isolation from other patients to prevent the infection from spreading.

Geographic barriers can include mountain ranges, channels between islands, wide rivers, and lava flows. The Grand Canyon, pictured in **Figure 15.22,** is an example of a geographic barrier. The Kaibab squirrel is found on the canyon's north rim, while the Abert squirrel lives on the south rim. Scientists think that the two types of squirrels diverged from an ancestral species and today are reproductively isolated by the width of the canyon. While these animals officially belong to the same species, they demonstrate distinct differences and, in time, they might diverge enough to be classified as separate species.

Sympatric speciation In **sympatric speciation,** a species evolves into a new species without a physical barrier. The ancestor species and the new species live side by side during the speciation process. Evidence of sympatric evolution can be seen in several insect species, including apple maggot flies, which appear to be diverging based on the type of fruit they eat. Scientists think that sympatric speciation happens fairly frequently in plants, especially through polyploidy. Recall from Chapter 10 that polyploidy is a mutation that increases a plant's chromosome number. As a result, the plant is no longer able to interbreed with the main population.

Figure 15.22 The Grand Canyon is a geographic barrier separating the Abert and Kaibab squirrels.



■ **Figure 15.23** More than 300 species of cichlid fishes once lived in Lake Victoria. Their adaptive radiation is remarkable because it is thought to have occurred in less than 14,000 years.

Patterns of evolution

Many details of the speciation process remain unresolved. Relative to the human life span, speciation is a long process, and first-hand accounts of speciation are expected to be rare. However, evidence of speciation is visible in patterns of evolution.

Adaptive radiation More than 300 species of cichlid fish, six of which are illustrated in **Figure 15.23,** once lived in Africa's Lake Victoria. Data shows that these species diverged from a single ancestor within the last 14,000 years. This is a dramatic example of a type of speciation called **adaptive radiation.** Adaptive radiation, also called divergent evolution, can occur in a relatively short time when one species gives rise to many species in response to the creation of new habitat or another ecological opportunity. Likely, a combination of factors caused the explosive radiation of the cichlids, including the appearance of a unique double jaw, which allowed these fish to exploit various food sources. Adaptive radiation often follows large-scale extinctions. Adaptive radiation of mammals at the beginning of the Cenozoic following the extinction of dinosaurs likely produced the diversity of mammals visible today.

Coevolution Many species evolve in close relationship with other species. The relationship might be so close that the evolution of one species affects the evolution of other species. This is called coevolution. Mutualism is one form of coevolution. Recall from Chapter 2 that mutualism occurs when two species benefit each other. For example, comet orchids and the moths that pollinate them have coevolved an intimate dependency: the foot-long flowers of this plant perfectly match the foot-long tongue of the moth, shown in **Figure 15.24.**

In another form of coevolution, one species can evolve a parasitic dependency on another species. This type of relationship is often called a coevolutionary arms race. The classic example is a plant and an insect pathogen that is dependent on the plant for food. The plant population evolves a chemical defense against the insect population. The insects, in turn, evolve the biochemistry to resist the defense. The plant then steps up the race by evolving new defenses, the insect escalates its response, and the race goes on. Complex coevolutionary relationships like these might reflect thousands of years of evolutionary interaction.

■ **Figure 15.24** By coevolving, this moth and the comet orchid it pollinates exist in a mutualistic relationship.

Table 15.4 **Convergent Evolution**

Interactive Table To explore more about convergent evolution, visit biologygmh.com.

Niche	Placental Mammals	Australian Marsupials
Burrower	 **Mole**	 **Marsupial mole**
Anteater	 **Lesser anteater**	 **Numbat (anteater)**
Mouse	 **Mouse**	 **Marsupial mouse**
Glider	 **Flying squirrel**	 **Flying phalanger**
Wolf	 **Wolf**	 **Tasmanian wolf**

Convergent evolution Sometimes unrelated species evolve similar traits even though they live in different parts of the world. This is called convergent evolution. Convergent evolution occurs in environments that are geographically far apart but that have similar ecology and climate. The mara and rabbit discussed in Section 15.2 provide an example of convergent evolution. The mara and the rabbit are unrelated, but because they inhabit similar niches, they have evolved similarities in morphology, physiology, and behavior. **Table 15.4** shows examples of convergent evolution between Australian marsupials and the placental mammals on other continents.

Rate of speciation Evolution is a dynamic process. In some cases, as in a coevolutionary arms race, traits might change rapidly. In other cases, traits might remain unchanged for millions of years. Most scientists think that evolution proceeds in small, gradual steps. This is a theory called **gradualism.** A great deal of evidence favors this theory. However, the fossil record contains instances of abrupt transitions. For example, certain species of fossil snails looked the same for millions of years, then the shell shape changed dramatically in only a few thousand years. The theory of **punctuated equilibrium** attempts to explain such abrupt transitions in the fossil record. According to this theory, rapid spurts of genetic change cause species to diverge quickly; these periods punctuate much longer periods when the species exhibit little change.

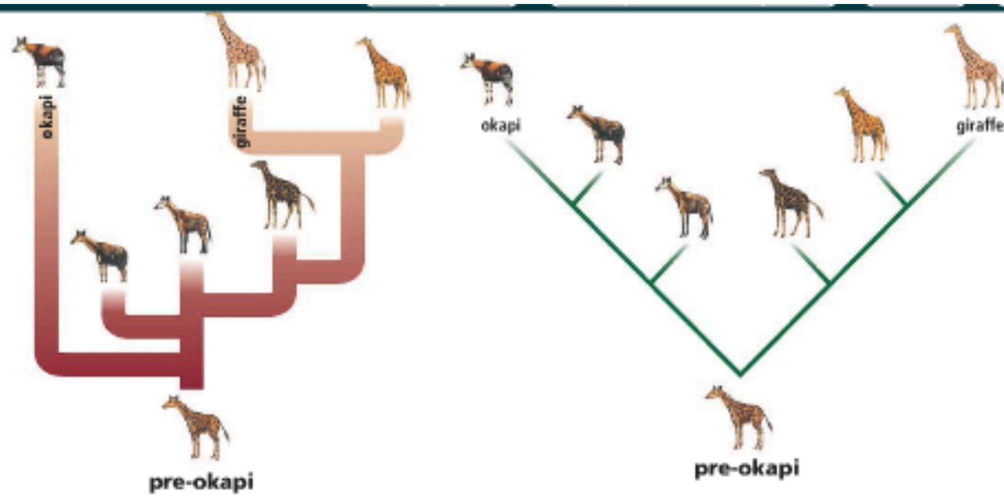


Figure 15.25 Gradualism and punctuated equilibrium are two competing models describing the tempo of evolution.

Concepts in Motion

Interactive Figure To see an animation of gradualism and punctuated equilibrium, visit biologygmh.com.

The two theories for the tempo of evolution are illustrated in **Figure 15.25.** The tempo of evolution is an active area of research in evolutionary theory today. Does most evolution occur gradually or in short bursts? Fossils can show only morphological structures. Changes in internal anatomy and function go unnoticed. How, then, does one examine the past for evidence?

The question of the tempo of evolution is an excellent illustration of how science works. Solving this puzzle requires insights from a variety of disciplines using a variety of methods. Like many areas of scientific endeavor, evolution offers a complex collection of evidence, and it does not yield easily to simple analysis.

Section 15.3 Assessment

Section Summary

- The Hardy-Weinberg principle describes the conditions within which evolution does not occur.
- Speciation often begins in small, isolated populations.
- Selection can operate by favoring average or extreme traits.
- Punctuated equilibrium and gradualism are two models that explain the tempo of evolution.

Understand Main Ideas

1. MAIN Idea **Describe** one new line of evidence supporting evolution that scientists learned after Darwin's book was published.
2. **List** three of the conditions of the Hardy-Weinberg principle.
3. **Discuss** factors that can lead to speciation.
4. **Indicate** which pattern of evolution is shown by the many species of finches on the Galápagos Islands.

Think Critically

5. **Design an Experiment** Biologists discovered two populations of frogs separated by the Amazon River. What experiment could be designed to test whether the two populations are one species or two?

MATH in Biology

6. What type of mathematical results would you expect from the experiment you designed above if the two populations diverged only recently?

CHAPTER 15

Study Guide

Download quizzes, key terms, and flash cards from biologygmh.com.

FOLDABLES Research Consider how natural selection has changed the plants and animals in your community. Select a plant or animal that is native to your community. Research and diagram some of the evolutionary changes the plant or animal went through from ancestors to the present organism.

Vocabulary	Key Concepts
Section 15.1 Darwin's Theory of Evolution by Natural Selection	
• artificial selection (p. 419) • evolution (p. 422) • natural selection (p. 420)	MAIN Idea Charles Darwin developed a theory of evolution based on natural selection. • Darwin drew from his observations on the HMS *Beagle* and later studies to develop his theory of evolution by natural selection. • Natural selection is based on ideas of excess reproduction, variation, inheritance, and advantages of certain traits in certain environments. • Darwin reasoned that the process of natural selection eventually could result in the appearance of new species.
Section 15.2 Evidence of Evolution	
• analogous structure (p. 426) • ancestral trait (p. 424) • biogeography (p. 428) • camouflage (p. 428) • derived trait (p. 424) • embryo (p. 426) • fitness (p. 428) • homologous structure (p. 424) • mimicry (p. 429) • vestigial structure (p. 425)	MAIN Idea Multiple lines of evidence support the theory of evolution. • Fossils provide strong direct evidence to support evolution. • Homologous and vestigial structures indicate shared ancestry. • Examples of embryological and biochemical traits provide insight into the evolution of species. • Biogeography can explain why certain species live in certain locations. • Natural selection gives rise to features that increase reproductive success.
Section 15.3 Shaping Evolutionary Theory	
• adaptive radiation (p. 439) • allopatric speciation (p. 438) • bottleneck (p. 433) • directional selection (p. 435) • disruptive selection (p. 436) • founder effect (p. 433) • genetic drift (p. 433) • gradualism (p. 440) • Hardy-Weinberg principle (p. 431) • postzygotic isolating mechanism (p. 437) • prezygotic isolating mechanism (p. 437) • punctuated equilibrium (p. 440) • sexual selection (p. 436) • stabilizing selection (p. 434) • sympatric speciation (p. 438)	MAIN Idea The theory of evolution continues to be refined as scientists learn new information. • The Hardy-Weinberg principle describes conditions within which evolution does not occur. • Speciation often begins in small, isolated populations. • Selection can operate by favoring average or extreme traits. • Punctuated equilibrium and gradualism are two models that explain the tempo of evolution.