Poison dart frogs

UNIT 5

Evolution and Life on Earth

1753

Carolus Linnaeus publishes the first of two volumes containing the classification of all known species. In doing so, Linnaeus establishes a consistent system for naming and classifying species. The system is widely used thereafter.

1859

Charles Darwin suggests that natural selection is the mechanism of evolution. Within months, public debates regarding the truth and significance of his theory ensue.

Galápagos tortoises

1907

In his book, *Plant Breeding,* Hugo de Vries, Dutch botanist, joins Mendel's laws of heredity with the newer theory of mutation. De Vries asserts that inheritable mutations are the mechanism by which species change and new species form.

1960

Mary and Jonathan Leakey discover fossil bones of a human ancestor, *Homo habilis,* in Olduvai Gorge, Tanzania.

Mary Leakey, paleoanthropologist

1974

Donald Johansen discovers a fossilized skeleton of one of the first hominids, *Australopithecus afarensis*. This specimen was nicknamed "Lucy."

Skull of A. afarensis

1980

Walter and Luis Alvarez, Frank Asaro, and Helen Michel publish a paper providing evidence that 65 million years ago, an asteroid collided with Earth and caused severe environmental changes. The changes may have led to the extinction of the majority of species that lived during that time.

1994

Reinhardt Kristensen and Peter Funch discover a tiny animal living on the lips of lobsters. They name the new species *Symbion pandora*. This species is so different from other animals that scientists classify it within a new phylum, Cycliophora, within kingdom Animalia.

2006

A team of biologists announces a study of Camiguin Island, the smallest island of the Philippines. They find 54 species of birds and 24 of species of mammals.

As-yet-unnamed parrot species

Beetles—one of the most diverse groups of animals on Earth

BIOLOGY CAREER

Museum Curator

Rob DeSalle

Rob DeSalle is a curator in the Division of Invertebrate Zoology at the American Museum of Natural History in New York City. He is an adjunct professor at Columbia University and City University of New York and is a Distinguished Research Professor at New York University. His current research focuses on molecular evolution in various organisms, including pathogenic bacteria and insects.

DeSalle enjoys being a scientist because he can investigate the diversity of life every day. He also enjoys the opportunity to serve as a mentor to students. Most of all, he enjoys the thrill of discovering something that no one else on the planet has found.

He considers his most significant accomplishment in science to be his work communicating scientific ideas through his writing and museum exhibitions.

Besides his work, DeSalle loves baseball and is a passionate fan of the Chicago Cubs.

Fossil and eggs of dinosaur called *oviraptor*

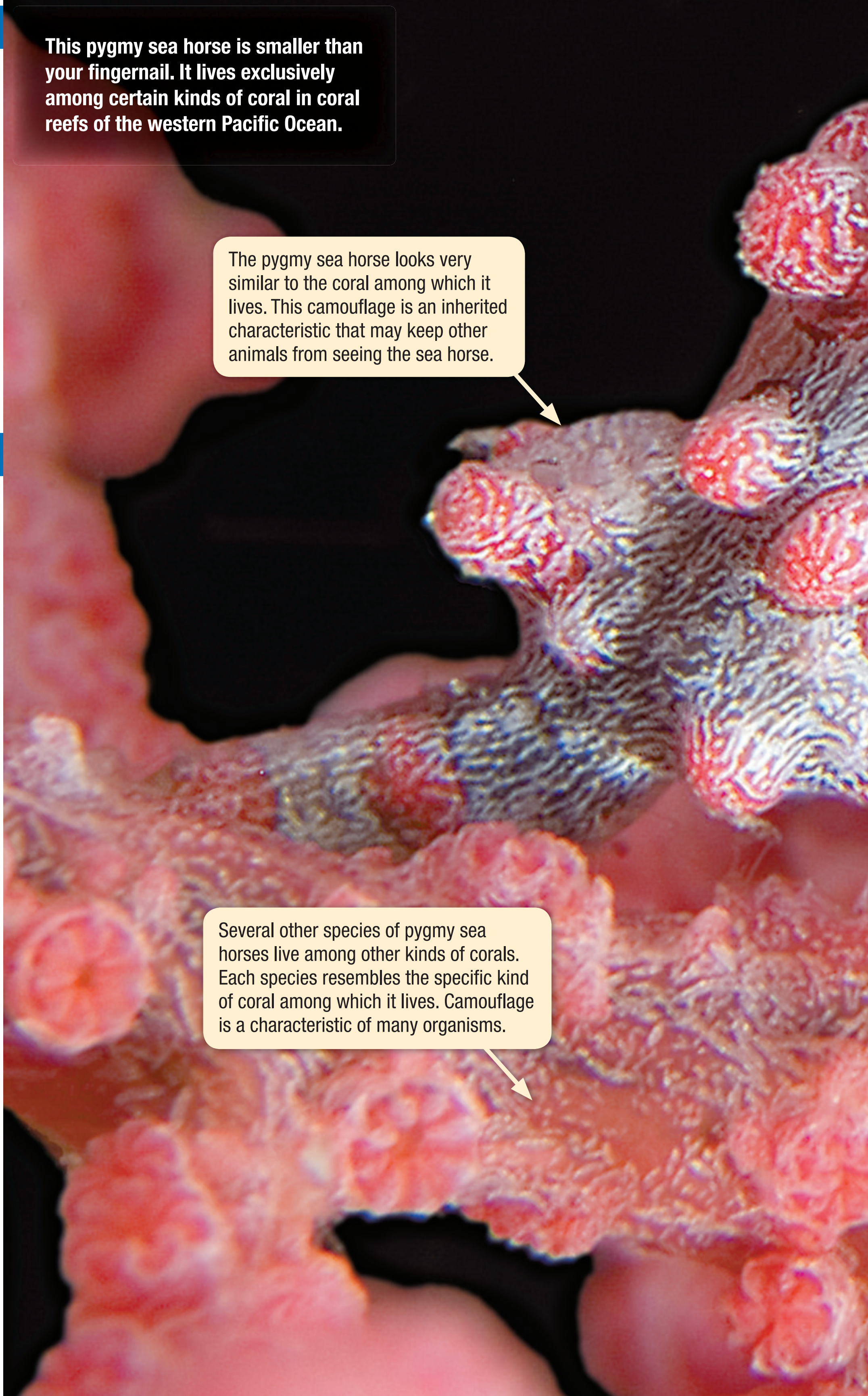
Chapter 16

Evolutionary Theory

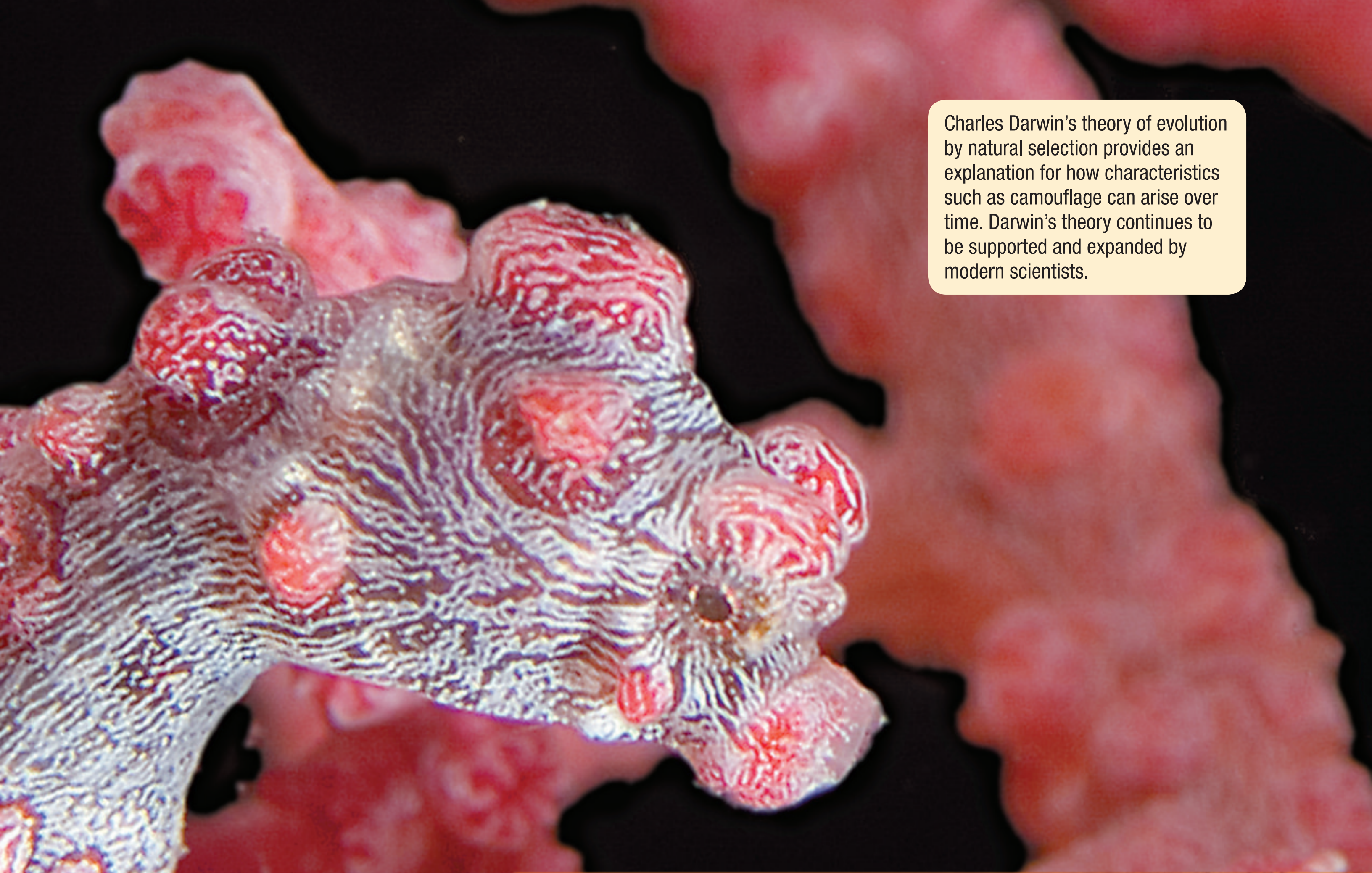
Preview

Why It Matters

Modern evolutionary theory provides strong and detailed explanations for many aspects of biology, such as anatomy and behavior.



This pygmy sea horse is smaller than your fingernail. It lives exclusively among certain kinds of coral in coral reefs of the western Pacific Ocean.



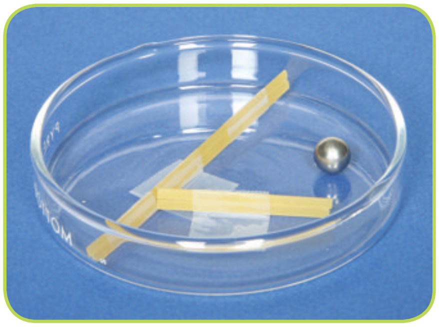
Charles Darwin's theory of evolution by natural selection provides an explanation for how characteristics such as camouflage can arise over time. Darwin's theory continues to be supported and expanded by modern scientists.

Inquiry Lab

15 min

Scientific Inference

Much of science is based on making inferences. Not all inferences can be supported by direct observation. Instead, many are tested by modeling, prediction, and experimentation. Doing so requires attention to detail and, sometimes, creative thinking.



Procedure

1. Break a **piece of flat-noodle pasta** into two smaller segments about 8 cm long and 3 cm long.
2. Erect two "walls" in the bottom of a **Petri dish** by securing the pasta pieces to the dish with **tape.**
3. Place a **ball bearing** in the dish.
4. Secure the lid onto the dish with tape. Keeping the dish upright, place it in a **brown paper bag.**
5. Exchange bags with another student. Without looking inside the bag, try to infer the arrangement of the pasta in the dish.

Analysis

1. **Describe** your inference, and explain how you formed it.
2. **Suggest** how your inference could be supported or confirmed.

READING TOOLBOX

These reading tools can help you learn the material in this chapter. For more information on how to use these and other tools, see **Appendix: Reading and Study Skills.**

Using Words

Key-Term Fold A key-term fold is useful for studying definitions of key terms in a chapter. Each tab can contain a key term on one side and the term's definition on the other.

Your Turn Prepare a key-term fold for the key terms in this chapter. Fill it in as you read. Use it later to quiz yourself on the definitions.

1. Fold a sheet of lined notebook paper in half from left to right.

2. Using scissors, cut along every third line from the right edge of the paper to the center fold to make tabs.

Using Language

Hypothesis or Theory? In everyday language, there is little difference between a *hypothesis* and a *theory*. But in science, the meanings of these words are more distinct. A *hypothesis* is a specific, testable prediction for a limited set of conditions. A *theory* is a general explanation for a broad range of data. A theory can include hypotheses that have been tested and can also be used to generate new hypotheses. The strongest scientific theories explain the broadest range of data and incorporate many well-tested hypotheses.

Your Turn Use what you have learned about a hypothesis and a theory to answer the following questions.

1. List some scientific theories that you have heard of.

2. Make a simple concept map or Venn diagram to show the relationship between hypotheses and theories.

3. The word *theory* may also be used to describe general trends and areas of active investigation in a scientific field. In this context, what does the term *evolutionary theory* mean?

Taking Notes

Summarizing Ideas Summarizing ideas helps you condense important information. When you summarize, use your own words and keep your sentences short. Focus on key ideas.

Your Turn Prepare to take notes for this chapter. Use this table as an example. As you read, be sure to summarize the following concepts:

1. natural selection

2. macroevolution

3. microevolution

Notes about Evolution		
Natural selection	*Macroevolution*	*Microevolution*

Section 1

Developing a Theory

Key Ideas	Key Terms	Why It Matters
❯ Why is evolutionary theory associated with Charles Darwin? ❯ How was Darwin influenced by his personal experiences? ❯ How was Darwin influenced by the ideas of others?	evolution artificial selection	Many aspects of biology are best explained by evolutionary theory.

Recall that in biology, **evolution** is the process by which species change over time. The idea that life evolves is not new. Yet for centuries, scientists lacked clear evidence that evolution happens. They also lacked a strong theory to explain how evolution happens. In 1859, Charles Darwin pulled together these missing pieces. Darwin, shown in **Figure 1,** was an English naturalist who studied the diversity of life and proposed a broad explanation for it.

A Theory to Explain Change over Time

Recall that in science, a *theory* is a broad explanation that has been scientifically tested and supported. ❯ **Modern evolutionary theory began when Darwin presented evidence that evolution happens and offered an explanation of how evolution happens.** Like most scientific theories, evolutionary theory keeps developing and expanding. Many scientists since Darwin have tested and added to his ideas. Most of Darwin's ideas, including his main theory, remain scientifically supported.

❯ **Reading Check** *What does* evolution *mean in biology? (See the Appendix for answers to Reading Checks.)*

evolution the process of change by which new species develop from preexisting species over time

Figure 1 Charles Darwin took many years to publish his theory of evolution by natural selection. Many of his ideas were first inspired by his 1831 global voyage on a ship called the *Beagle*.

Darwin's Ideas from Experience

In Darwin's time, most people did not think that living things had changed over time. In fact, many doubted that Earth itself had ever changed. But Darwin saw evidence of gradual change. **Darwin's experiences provided him with evidence of evolution at work.**

The Voyage of the *Beagle* Darwin's first evidence was gathered during a global voyage on a ship called the *Beagle*. As part of his work as a naturalist, Darwin collected natural objects from each place that he visited. For example, in South America, he collected fossils of giant, extinct armadillos. Darwin noticed that these fossils were similar, but not identical, to the living armadillos in the area.

Darwin also visited the Galápagos Islands in the Pacific Ocean. There, he collected several different species of birds called *finches*. Each of the finches are very similar, but differences can be seen in the size and shape of the bill (or beak), such as those shown in **Figure 2.** Each finch has a bill that seems suited to the finch's usual food.

Darwin noticed that many of the islands' plants and animals were similar, but not identical, to the plants and animals he saw in South America. Later, Darwin proposed that the Galápagos species had descended from species that came from South America. For example, he suggested that all of the finch species descended from one ancestral finch species that migrated from South America. Then, the descendant finches were modified over time as different groups survived by eating different types of food. Darwin called such change *descent with modification*. This idea was a key part of his theory.

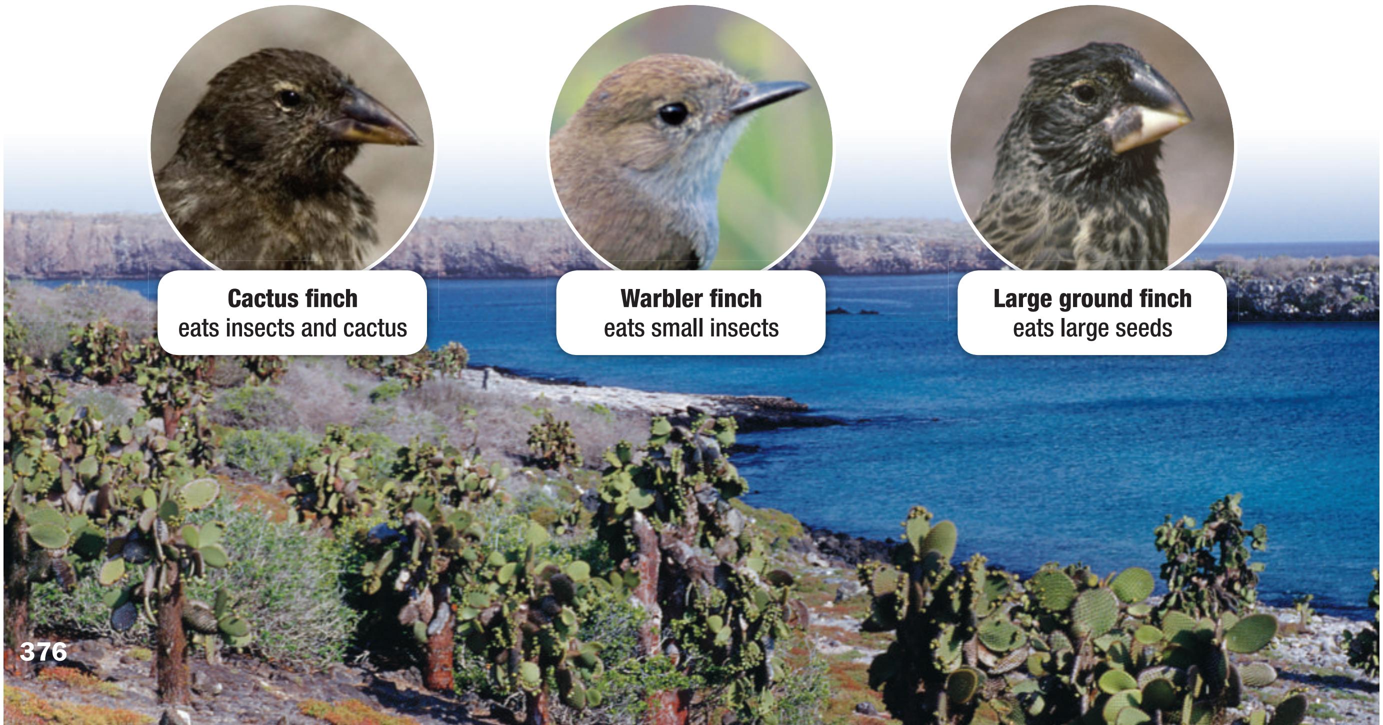
Years of Reflection After returning from his voyage at the age of 27, Darwin spent years studying his data. He also continued studying many sciences. As he studied, his confidence grew stronger that evolution must happen. But Darwin did not report his ideas about evolution until much later. Instead, he took time to gather more data and to form a strong explanation for how evolution happens.

READING TOOLBOX

Key-Term Fold On the back half of your key-term fold, under each flap, write your own definition for the key terms in this section.

artificial selection the human practice of breeding animals or plants that have certain desired traits

Figure 2 Darwin eventually learned that all Galápagos finch species were similar to each other and to one particular South American finch. **What explanation did Darwin propose for this similarity?**



Breeding and Selection Darwin took interest in the practice of breeding, especially the breeding of exotic pigeons. He bred pigeons himself and studied the work of those who bred other kinds of animals and plants, such as dogs, orchids, and food crops. Eventually, Darwin gained a new insight: breeders take advantage of natural variation in traits within a species. If a trait can be inherited, breeders can produce more individuals that have the trait. Breeders simply select individuals that have desirable traits to be the parents of each new generation. Darwin called this process **artificial selection** because the selection is done by humans and not by natural causes.

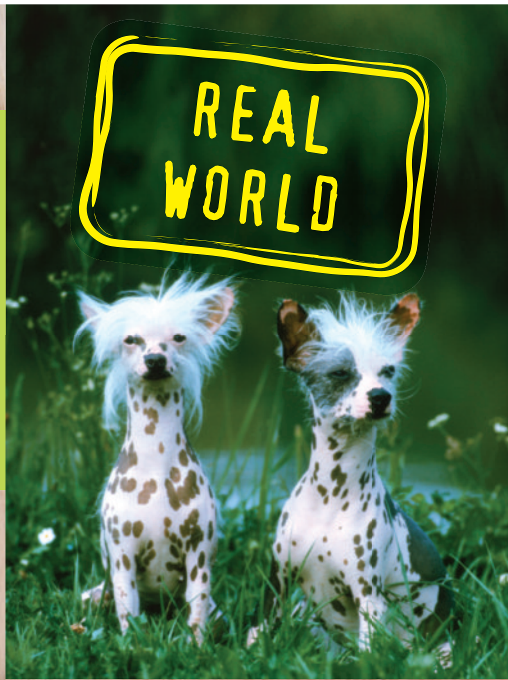
Academic Vocabulary

insight a clear understanding of something

› **Reading Check** *When did Darwin first see evidence of evolution?*

Why It Matters

Breeding



The power of artificial selection can be seen today in the amazing variety of pets, show animals, and agricultural food crops. For example, more than 400 breeds of dogs exist today, from tiny Chihuahuas to Great Danes. All of these breeds, including wolves, are considered part of the same species (*Canis lupus*) because most can interbreed.

Dog Diversity

People have lived with dogs—or the wolf ancestors of dogs—throughout history. Over time, people learned to selectively breed dogs by choosing certain individuals to become parents. People have selected dogs that have various kinds of physical and behavioral traits. So today, each breed of dog is known for its appearance as well as its degree of playfulness, friendliness, watchfulness, or cleverness. Some breeds are also known for certain quirks or problems.

Quick Project Visit a local pet store, and ask which breeds are most popular or most expensive. Ask why.

Hands-On

QuickLab

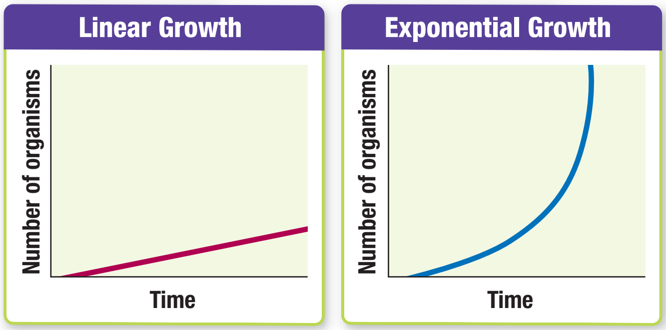
15 min

Two Kinds of Growth

Can you visualize the difference between linear growth and exponential growth?

Procedure

1. Place **grains of rice** in the cups of an **egg carton** in the following sequence: Place one grain in the first cup. Place two grains in the second cup. Place three grains in the third cup. In each of the remaining cups, place *one more* grain of rice than in the cup before.
2. Use a line graph to graph the results of step 1.
3. Repeat step 1, but use the following sequence: Place one grain in the first cup, two in the second cup, and four in the third cup. In each remaining cup, place twice as many grains as placed in the cup before.
4. Use a line graph to graph the results of step 3.



Analysis

1. **Match** your graphs to the graphs shown.
2. CRITICAL THINKING **Analyzing Terminology** Linear growth is also called *arithmetic growth,* and exponential growth is also called *geometric growth*. Propose an explanation for the use of these terms.

Darwin's Ideas from Others

In Darwin's time, most people—including scientists—believed that each species was created once and stayed the same forever. But this view could not explain fossils of organisms that no longer exist, such as dinosaurs. Some scientists tried to explain such observations by saying that species could die out but never change. Others, including Darwin's own grandfather, proposed various mechanisms to explain how species may change over time. **Darwin was influenced by ideas from the fields of natural history, economics, and geology.** The ideas of Lamarck, Malthus, Cuvier, and Lyell were especially important.

Lamarckian Inheritance In 1809, the French scientist Jean Baptiste Lamarck proposed an explanation for how organisms may change over generations. Like Darwin and others, Lamarck noticed that each organism is usually well adapted to its environment. He proposed, as Darwin would later, that organisms change over time as they adapt to changing environments.

However, Lamarck had an incorrect idea about inheritance. He proposed that changes due to use or disuse of a characteristic would be passed on to offspring. For example, he knew that a person's muscles may decrease in size because of disuse or may increase in size because of use, as shown in **Figure 3.** He believed that offspring inherited these kinds of changes. This idea was eventually disproved, but not in Darwin's time. Darwin once accepted this idea because it proposed a role for inheritance in evolution.

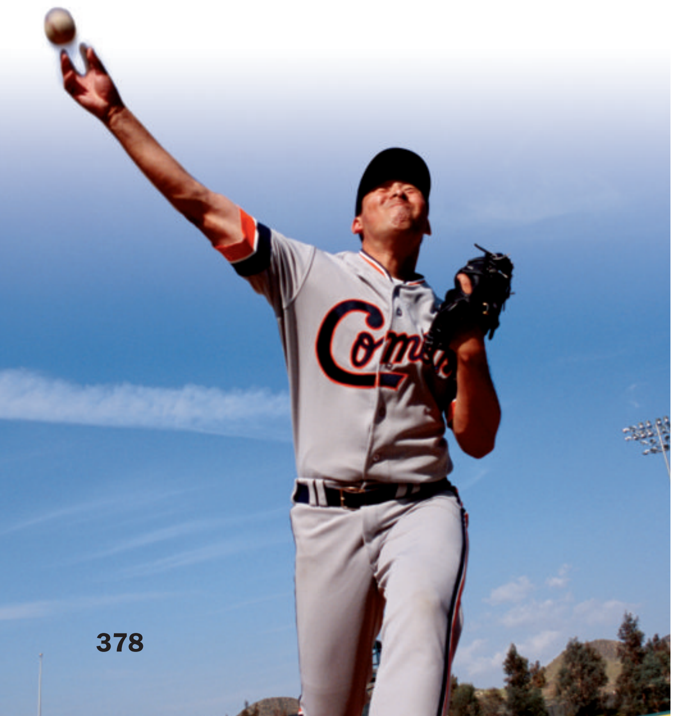


Figure 3 According to Lamarck's idea of inheritance, this baseball player's children would inherit strong arm muscles. **Why was this idea important to Darwin?**

Population Growth Another key influence on Darwin's thinking about evolution was an essay by Thomas Malthus. In 1798, this English economist observed that human populations were increasing faster than the food supply. Malthus pointed out that food supplies were increasing *linearly*. More food was being produced each year, but the amount by which the food increased was the same each year. In contrast, the number of people was increasing *exponentially*. More people were added each year than were added the year before. Malthus noted that the number of humans could not keep increasing in this way, because many people would probably die from disease, war, or famine.

Darwin simply applied Malthus's idea to all populations. Recall that a *population* is all of the individuals of the same species that live in a specific place. Darwin saw that all kinds of organisms tend to produce more offspring than can survive. So, all populations must be limited by their environments.

Figure 4 Layers of rock contain evidence of changes occurring over millions of years in organisms and environments on Earth. Darwin realized that such evidence supported his ideas about evolution.

Geology and an Ancient Earth In Darwin's time, scientists had become interested in the study of rocks and landforms, and thus began the science of *geology*. In particular, scientists such as Georges Cuvier, James Hutton, and Charles Lyell studied fossils and rock layers, such as those shown in **Figure 4.** Cuvier argued that fossils in rock layers showed differences in species over time and that many species from the past differed from those of the present. But Cuvier did not see species as changing gradually over time. He thought that changes in the past must have occurred suddenly.

Hutton and Lyell, on the other hand, thought that geologic processes—such as those that wear away mountains and form new rocks and fossils—work gradually and constantly. Lyell carefully and thoroughly presented his ideas in a book, which Darwin read. Lyell's ideas fit well with Darwin's observations and showed that Earth's history was long enough for species to have evolved gradually.

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www.scilinks.org
Topic: Charles Darwin
Code: HX80262

› Reading Check ***What idea did Darwin and Lamarck once share?***

Section 1 Review

› KEY IDEAS

1. **Describe** Darwin's relationship to modern evolutionary theory.
2. **Identify** personal experiences that contributed to Darwin's thinking about evolution.
3. **Identify** other scientists that influenced Darwin's thinking.

CRITICAL THINKING

4. **Applying Process Concepts** Darwin observed that artificial selection can produce specific traits. Suppose a farmer has a corn crop in which each ear of corn has some yellow kernels and some white kernels. Describe how the farmer could produce a variety of corn that has all white kernels.

METHODS OF SCIENCE

5. **Scientific Testing** According to Lamarck's idea of inheritance, an individual that developed an improved trait within its lifetime, especially through repeated use, could pass that trait on to its offspring. Propose a way to test the accuracy of this idea.

Section 2

Applying Darwin's Ideas

Key Ideas	Key Terms	Why It Matters
❯ What does Darwin's theory predict? ❯ Why are Darwin's ideas now widely accepted? ❯ What were the strengths and weaknesses of Darwin's ideas?	natural selection adaptation fossil homologous	The principles of evolution are used daily in medicine, biology, and other areas of modern life to understand, predict, and develop advancements in each area.

Darwin applied Malthus's idea to all species. Every living thing has the potential to produce many offspring, but not all of those offspring are likely to survive and reproduce.

Evolution by Natural Selection

Darwin formed a key idea: Individuals that have traits that better suit their environment are more likely to survive. For example, the insect in **Figure 5** is less likely to be seen (and eaten) than a brightly colored insect is. Furthermore, individuals that have certain traits tend to produce more offspring than others do. These differences are part of **natural selection.** Darwin proposed that natural selection is a cause of evolution. In this context, *evolution* is a change in the inherited characteristics of a population from one generation to the next.

Steps of Darwin's Theory Darwin's explanation is often called the *theory of evolution by natural selection.* ❯ **Darwin's theory predicts that over time, the number of individuals that carry advantageous traits will increase in a population.** As shown in **Figure 6,** this theory can be summarized in the following four logical steps:

Step 1 Overproduction Every population is capable of producing more offspring than can possibly survive.

Step 2 Variation Variation exists within every population. Much of this variation is in the form of inherited traits.

Step 3 Selection In a given environment, having a particular trait can make individuals more or less likely to survive and have successful offspring. So, some individuals leave more offspring than others do.

Step 4 Adaptation Over time, those traits that improve survival and reproduction will become more common.

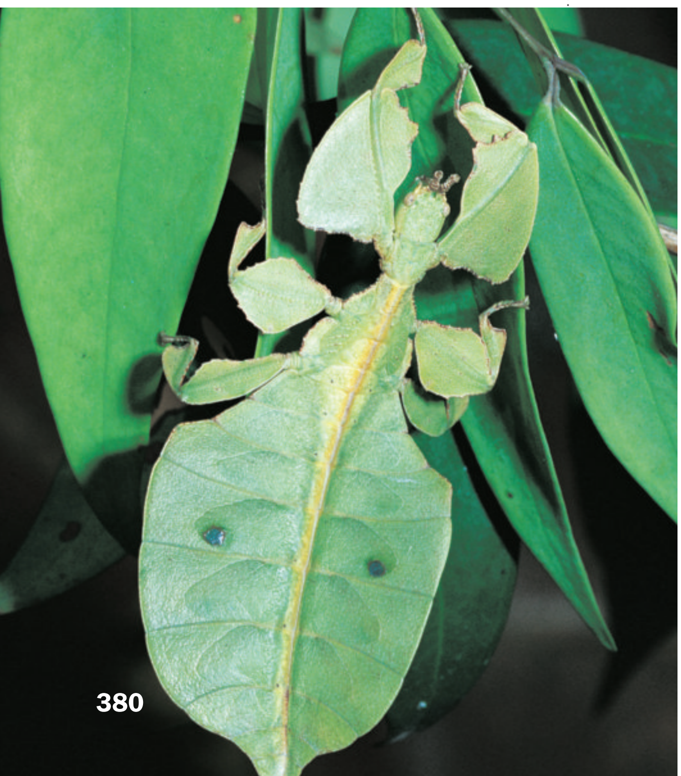

Figure 5 This insect is well adapted to its environment. ❯ **How does Darwin's theory help explain this observation?**

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The Theory of Evolution by Natural Selection

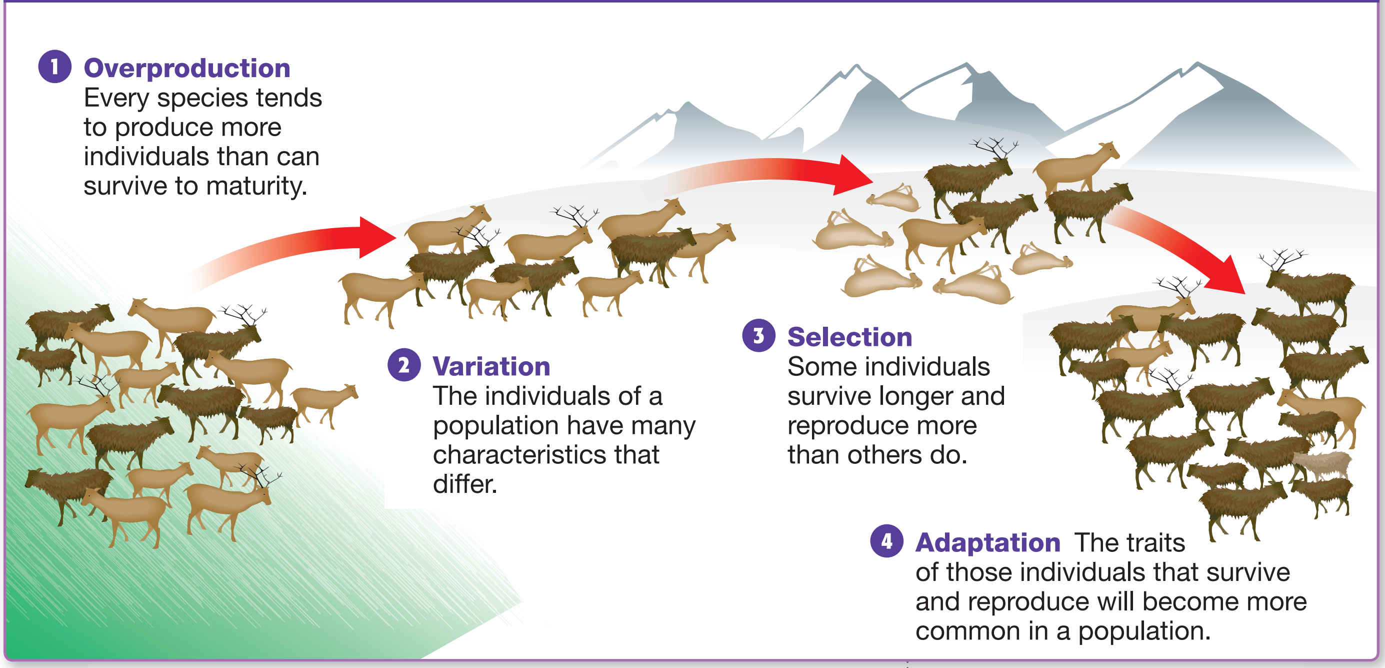


Figure 6 Darwin proposed a logical process by which evolution may occur. **Can this process act on individuals?**

Selection and Adaptation Darwin's theory explains why living things vary in form yet seem to fit their environment. Each habitat presents unique challenges and opportunities to survive and reproduce. So, each species evolves because of the "selection" of those individuals that survive the challenges or make best use of the opportunities. Put another way, each species becomes *adapted* to its environment as a result of living in it over time. An **adaptation** is an inherited trait that is present in a population because the trait helps individuals survive and reproduce in a given environment.

In sum, Darwin's theory explains evolution as a gradual process of adaptation. Note that Darwin's theory refers to *populations* and *species*—not *individuals*—as the units that evolve. Also, keep in mind that a species is a group of populations that can interbreed.

Publication of the Theory In 1844, Darwin finally wrote an outline of his ideas about evolution and natural selection. But he showed it only to a few scientists that he knew well. He was afraid that his ideas would be controversial. Then in 1858, he received a letter from another young English naturalist named Alfred Russel Wallace. Wallace asked for Darwin's opinion on a new theory—a theory much like Darwin's! Because of this similarity, Darwin and Wallace jointly presented their ideas to a group of scientists. Darwin was finally motivated to publish a full book of his ideas within the next year.

Darwin's book *On the Origin of Species by Means of Natural Selection* presented evidence that evolution happens and offered a logical explanation of how it happens. Biologists began to accept that evolution occurs and that natural selection helps explain it.

Reading Check ***Is natural selection the same thing as evolution?***

READING TOOLBOX

Hypothesis or Theory? Why isn't Darwin's explanation simply called *the theory of evolution*? Why isn't it called a *hypothesis*?

natural selection the process by which individuals that are better adapted to their environment survive and reproduce more successfully than less well adapted individuals do

adaptation a trait that improves an organism's ability to survive and reproduce; the process of becoming adapted

What Darwin Explained

Darwin's book was more than an explanation of his theory. It also included a thorough presentation of the evidence that living species evolved from organisms that lived in the past. Darwin had studied much of the data that was available in his time. **Darwin presented a unifying explanation for data from multiple fields of science.** Today, these sciences include geology, geography, ecology, developmental biology, anatomy, genetics, and biochemistry. Scientists continue to draw upon the power of Darwin's explanations.

fossil the trace or remains of an organism that lived long ago, most commonly preserved in sedimentary rock

The Fossil Record Have you ever looked at a series of historical maps of a city? You can infer that buildings and streets have been added, changed, or destroyed over time. Similarly, you can infer past events by looking at **fossils,** traces of organisms that lived in the past. All fossils known to science make up the *fossil record*.

ACADEMIC VOCABULARY

infer to derive by reasoning

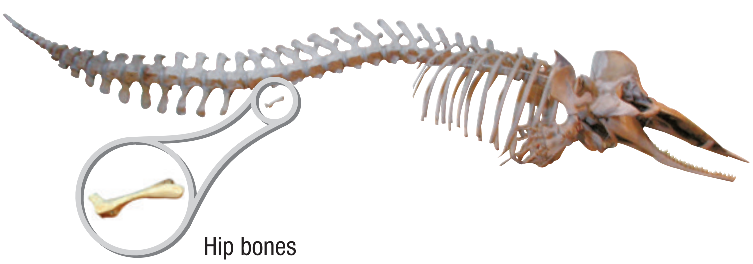
Sometimes, comparing fossils and living beings reveals a pattern of gradual change from the past to the present. Darwin noticed these patterns, but he was aware of many gaps in the patterns. For example, Darwin suggested that whales might have evolved from a mammal that lived on land. But at the time, no known fossils were "in between" a land mammal and a whale.

Figure 7 Darwin once hypothesized that modern whales evolved from ancient, four-legged, land-dwelling, meat-eating mammals. Over the years since, scientists have collected a series of fossil skeletons that support this hypothesis.

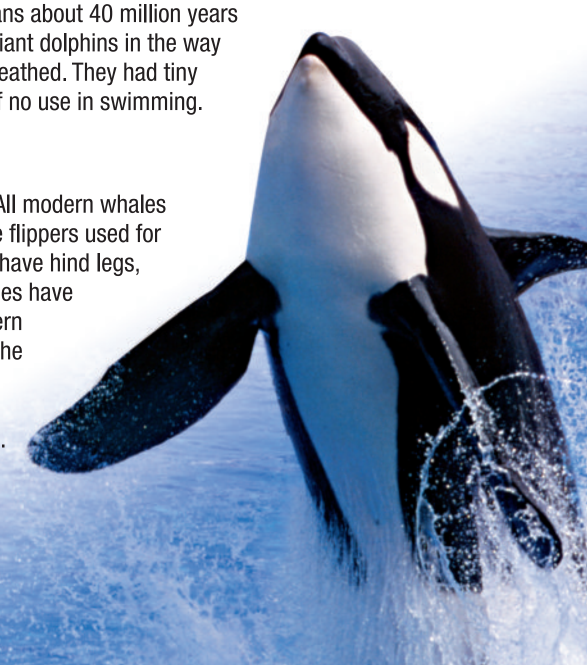
1 ***Pakicetus*** **(PAK uh SEE tuhs)** Scientists think that whales evolved from land-dwelling mammals such as those in the genus *Pakicetus*. The fossil skeleton of a pakicetid is shown here. These mammals lived about 50 million years ago, walked or ran on four legs, and ate meat.

2 ***Ambulocetus*** **(AM byoo loh SEE tuhs)** Mammals of this genus lived in coastal waters about 49 million years ago. These mammals could swim by kicking their legs and using their tail for balance. They could also use their short legs to waddle on land. They breathed air through their mouth.

3 ***Dorudon*** **(DOHR oo DAHN)** Mammals of this genus lived in the oceans about 40 million years ago. They resembled giant dolphins in the way that they swam and breathed. They had tiny hind limbs that were of no use in swimming.



4 **Modern Whales** All modern whales have forelimbs that are flippers used for swimming. No whales have hind legs, but some toothed whales have tiny hipbones. All modern whales must come to the surface of the water to breathe through a hole at the top of their head.



Rhea (South America)

Ostrich (Africa)

Emu (Australia)

Figure 8 Three unique bird species are shown here. Each of these is similar in size, shape, eating habits, and habitat. However, each species lives on a separate continent. **What does this pattern suggest about evolution?**

Darwin predicted that *intermediate forms* between groups of species might be found. And indeed, many new fossils have been found, such as those shown in **Figure 7.** But the conditions that create fossils are rare, so we will never find fossils of every species that ever lived. The fossil record will grow but will never be complete.

Biogeography *Biogeography* is the study of the locations of organisms around the world. When traveling, Darwin and Wallace saw evolution at work when they compared organisms and environments. For example, Darwin saw the similarity of the three species of large birds in **Figure 8.** He found each bird in a similar grassland habitat but on a separate continent. This finding was evidence that similar environments shape the evolution of organisms in similar ways.

Sometimes, geography separates populations. For example, a group of organisms may become separated into two groups living on two different islands. Over time, the two groups may evolve in different patterns. Generally, geologists and biologists have found that the movement of landforms in Earth's past helps to explain patterns in the types and locations of both living and fossil organisms.

Developmental Biology The ancestry of organisms is also evident in the ways that multicellular organisms develop from embryos. The study of such development is called *embryology*. This study is interesting because embryos undergo many physical and genetic changes as they develop into mature forms.

Scientists may compare the embryonic development of species to look for similar patterns and structures. Such similarities most likely derive from an ancestor that the species have in common. For example, at some time during development, all vertebrate embryos have a tail. *Vertebrates* are animals that have backbones.

Reading Check ***Why is the fossil record incomplete?***

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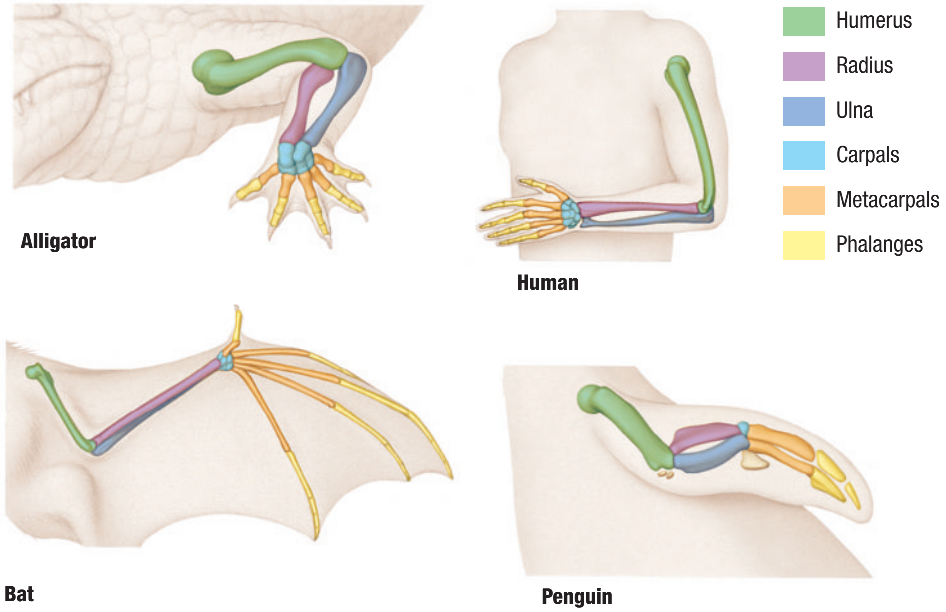
Topic: Fossil Record
Code: HX80615

Figure 9 Although they look very different from one another on the outside, the forelimbs of most tetrapods (vertebrates that have four limbs) include a similar group of bones. **What hypothesis does this observation support?**



Anatomy Another place to observe the results of evolution is inside the bodies of living things. The bodily structure, or *anatomy,* of different species can be compared. Many internal similarities are best explained by evolution and are evidence of how things are related.

For example, the hypothesis that all vertebrates descended from a common ancestor is widely accepted. Observations of the anatomy of both fossil and living vertebrates support this hypothesis. When modern vertebrates are compared, the difference in the size, number, and shape of their bones is clear. Yet the basic pattern of bones is similar. In particular, the forelimbs of many vertebrates are composed of the same basic groups of bones, as **Figure 9** shows. This pattern of bones is thought to have originated in a common ancestor. So, the bones are examples of **homologous** structures, characteristics that are similar in two or more species and that have been inherited from a common ancestor of those species.

Biochemistry To explain the patterns of change seen in anatomy, scientists make testable predictions. For example, if species have changed over time, the genes that determine their characteristics should also have changed. Recall that genes can change by mutation and that such change can make new varieties appear. Then, natural selection may "select against" some varieties and so "favor" others.

Scientists have observed that genetic changes occur over time in all natural populations. A comparison of DNA or amino-acid sequences shows that some species are more genetically similar than others. These comparisons, like those in anatomy, are evidence of hereditary relationships among the species. For example, comparing one kind of protein among several species reveals the pattern shown in **Figure 10.** The relative amount of difference is consistent with hypotheses based on fossils and anatomy.

Reading Check ***What explains similarities in bone structure?***

Hemoglobin Comparison

Animal with hemoglobin	Amino acids that differ from human hemoglobin
Gorilla	1
Rhesus monkey	8
Mouse	27
Chicken	45
Frog	67
Lamprey	125

Figure 10 Scientists have compared the amino acids that make up hemoglobin proteins in several species. Organisms that have fewer differences are more likely to be closely related. **How does this pattern relate to genetic change?**

Evaluating Darwin's Ideas

Why was Darwin such an important scientist? **Darwin's work had three major strengths: evidence of evolution, a mechanism for evolution, and the recognition that variation is important.** Today, Darwin is given credit for starting a revolution in biology.

Strengths Darwin was *not* the first to come up with the idea that evolution happens, but he was the first to gather so much evidence about it. He described his most famous book as "one long argument" that evolution is possible. Before publishing, Darwin collected and organized many notes, observations, and examples, such as the illustration shown in **Figure 11.** So, one strength of Darwin's work is that it is supported by, and helps explain, so much data.

Darwin also presented a logical and testable mechanism that could account for the process of evolution. His theory of natural selection was well thought out and convincing to scientists of his time as well as today. It has since become a foundation of biology.

Finally, Darwin changed the way scientists thought about the diversity of life. Before Darwin, most scientists saw species as stable, unchanging things. They classified species based on average appearances and ignored variation. But Darwin showed that variation was everywhere and could serve as the starting point for evolution.

Weaknesses Darwin's explanations were incomplete in one major way: He knew very little about genetics. **Inherited variation was crucial to Darwin's theory of natural selection, yet his theory lacked a clear mechanism for inheritance.** At different times, Darwin proposed or accepted several ideas for such a mechanism, but none of them were correct. He thought about this problem for much of his life.

Darwin never knew it, but Gregor Mendel had begun to solve this problem. However, Mendel's findings about heredity were not widely published until 1900. Those findings opened the door to a new age in the study of evolution. Today, an understanding of genetics is essential to understanding evolution.

Reading Check *What did Darwin do before publishing his ideas?*

Figure 11 This drawing of a rhea was printed in one of Darwin's books. Darwin collected and organized a large amount of data to help explain his ideas. **How else did Darwin support his main theory?**

homologous (hoh MAHL uh guhs) describes a character that is shared by a group of species because it is inherited from a common ancestor

Section 2 Review

KEY IDEAS

1. **Outline** Darwin's theory of evolution by natural selection. Be sure to include four logical steps.
2. **List** the kinds of data that Darwin helped explain.
3. **Compare** the strengths and weaknesses of Darwin's ideas.

CRITICAL THINKING

4. **Applying Information** Use the theory of natural selection to explain how the average running speed of a population of zebras might increase over time.
5. **Elaborating on Explanations** Describe how a single pair of seed-eating bird species could have arrived on an island and evolved into an insect-eating species. (Hint: Consider the food available.)

USING SCIENCE GRAPHICS

6. **Process Cartoon** Create your own version of **Figure 6** in the form of a four-panel cartoon. Choose a unique type of organism to represent the population undergoing natural selection. Also, depict a unique set of traits and limiting conditions for the population.

Section 3

Beyond Darwinian Theory

Key Ideas	Key Terms	Why It Matters
❯ How has Darwin's theory been updated? ❯ At what scales can evolution be studied?	speciation	The study of evolution was new in Darwin's day, but it is essential to biology today.

Does modern evolutionary theory differ from Darwin's theory? Yes and no. Darwin observed and explained much about the large-scale patterns of biology, but some patterns have yet to be explained. He proposed a logical process (natural selection) for evolution, even though he could not explain evolution at the genetic level. Biology has made great progress since Darwin's time. Modern evolutionary theory relates patterns and processes at many levels.

Darwin's Theory Updated

Since Darwin's work was published, his theory has been thoroughly investigated. ❯ **Discoveries since Darwin's time, especially in genetics, have been added to his theory to explain the evolution of species.** Some parts of Darwin's theory have been modified, and new parts have been added. But mostly, Darwin's theory has been supported.

The first major advance beyond Darwin's ideas was the rediscovery, in 1900, of Mendel's *laws of heredity*. These ideas opened the door for a genetic explanation of evolution. By the 1940s, scientists began to weave Darwin's theory together with newer studies of fossils, anatomy, genetics, and more. This unification is called the *modern synthesis* of evolutionary theory.

In particular, biologists have learned that evolution can result from processes other than natural selection. For example, survival and reproduction can be limited by chance or by the way that genes work. In the modern view, any or all of these forces may combine with natural selection (as described by Darwin). This synthesis helps explain some of the patterns of evolution that were unexplained by natural selection alone.

Remaining Questions Some of the most important questions about evolution have been asked only recently. So, many questions are still being investigated, as shown in **Figure 12.** Modern biologists have tentative answers to the following questions:

- **Can an individual evolve?** Darwin correctly inferred that individuals do not evolve. They may respond to outside forces, but individuals do not pass on their responses as heritable traits. Rather, populations evolve when natural selection acts (indirectly) on genes.

Figure 12 Modern genetic science and Darwin's theory have been united. ❯ **How could this genetic scientist study evolution?**

Hands-On

QuickLab

Selection Model

15 min

In this lab, you will model the process of natural selection. Can you predict the outcome?

Procedure

1. Work with a partner. Spread out a **handful of small, colored candies** onto a **piece of cloth or paper that has a colorful design.** One person should act as "predator" of the candies while the other uses a **stop-watch** to monitor time and then records the results.
2. The "predator" should use **tweezers** to try to "capture" as many candies as possible within 10 s.
3. Record the results, and switch roles. Repeat 10 times.

Analysis

1. **Graph** the total number of each color of candy that was "captured." Use a bar graph.
2. CRITICAL THINKING **Evaluating Results** Explain why some colors were "captured" more often than others.
3. CRITICAL THINKING **Forming Hypotheses** Predict the outcome if the background is changed to solid red.

- **Is evolution the survival of the fittest?** Natural selection can act only on the heritable variation that exists in a population. Chance variations do not always provide the best adaptation for a given time and place. So, evolution does not always produce the "fittest" forms, just those that "fit" well enough to leave offspring.
- **Is evolution predictable?** Evolution sometimes results in larger or more-complex forms of life, but this result cannot be predicted. Many forms of life are simple yet successful. For example, bacteria have been abundant for billions of years. In contrast, some complex organisms, such as dinosaurs, have appeared, been successful for a time, and then almost completely disappeared. Mostly, scientists cannot predict the exact path that evolution will take.

Studying Evolution at All Scales

Because it affects every aspect of biology, scientists can study evolution at many scales. Generally, these scales range from microevolution to macroevolution, with speciation in between. Informally, *microevolution* refers to evolution as a change in the genes of populations, whereas *macroevolution* refers to the appearance of new species over time.

Speciation The link between microevolution and macroevolution is speciation. **Speciation,** the formation of new species, can be seen as a process of genetic change or as a pattern of change in the form of organisms. Recall that a *species* is a group of organisms that are closely related and that can mate to produce fertile offspring. So, speciation can begin with the separation of populations of the same species. For example, the two kinds of squirrels shown in **Figure 13** seem to be evolving from one species into two because of separation.

Reading Check *At what scales can evolution be studied?*

speciation (SPEE shee AY shuhn) the formation of new species as a result of evolution

Figure 13 These squirrels are closely related but are almost different enough to be unique species. Their populations are separated by the Grand Canyon.

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Processes of Microevolution To study microevolution, we look at the processes by which inherited traits change over time in a population. Five major processes can affect the kinds of genes that will exist in a population from generation to generation. These processes are summarized below. Notice that natural selection is only one of the five. You will learn more about these processes soon.

- **Natural Selection** As you have learned, natural selection can cause an increase or decrease in certain alleles in a population.
- **Migration** *Migration* is the movement of individuals into, out of, or between populations. Migration can change the numbers and types of alleles in a population.
- **Mate Choice** If parents are paired up randomly in a population, a random assortment of traits will be passed on to the next generation. However, if parents are limited or selective in their choice of mates, a limited set of traits will be passed on.
- **Mutation** Mutation can change the numbers and types of alleles from one generation to the next. However, such changes are rare.
- **Genetic Drift** The random effects of everyday life can cause differences in the survival and reproduction of individuals. Because of these differences, some alleles may become more or less common in a population, especially in a small population.

Academic Vocabulary

random without aim or plan; purposeless

Patterns of Macroevolution To study macroevolution, we look at the patterns in which new species evolve. We may study the direction, diversity, or speed of change. Patterns of change are seen when relationships between living and fossil species are modeled.

- **Convergent Evolution** If evolution is strongly directed by the environment, then species living in similar environments should evolve similar adaptations. Many examples of this pattern were observed by Darwin and can be seen today.
- **Coevolution** Organisms are part of one other's environment, so they can affect one another's evolution. Species that live in close contact often have clear adaptations to one another's existence, as shown in **Figure 14.**

Figure 14 This moth species and this orchid species have coevolved in a close relationship. The moth feeds exclusively on the orchid, and the orchid's pollen is spread by the moth.

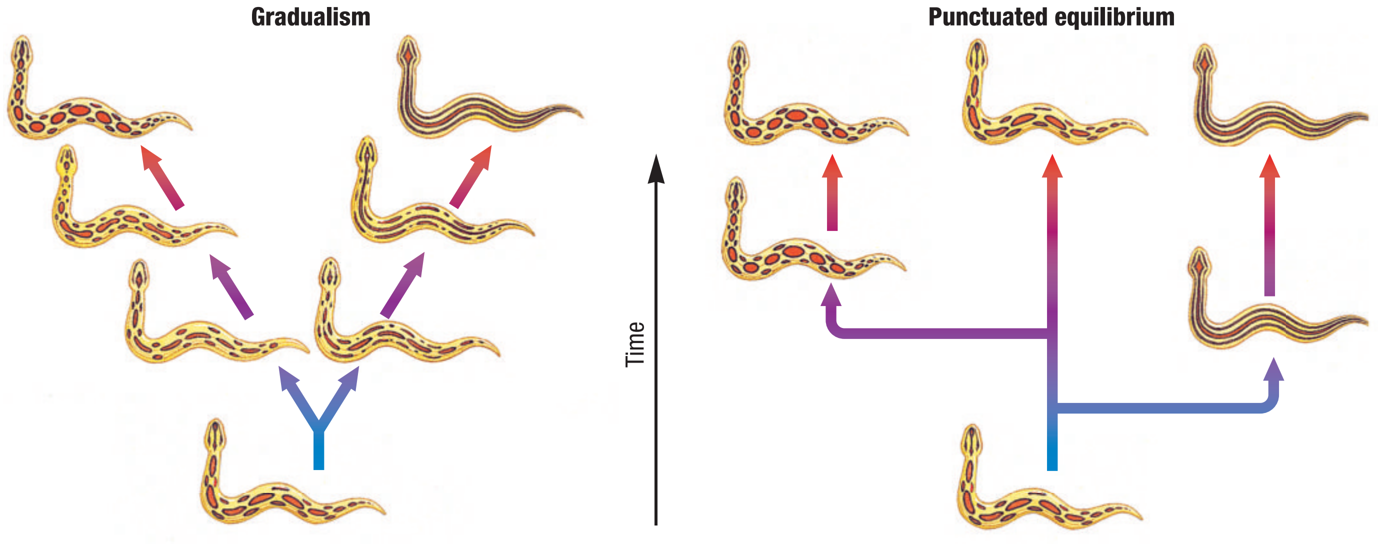


Figure 15 Two differing models of the pace of evolution have been proposed. **Do these models show microevolution or macroevolution?**

- **Adaptive Radiation** Over time, species may split into two or more lines of descendants, or *lineages*. As this splitting repeats, one species can give rise to many new species. The process tends to speed up when a new species enters an environment that contains few other species. In this case, the pattern is called *adaptive radiation*.
- **Extinction** If all members of a lineage die off or simply fail to reproduce, the lineage is said to be *extinct*. The fossil record shows that many lineages have arisen and radiated, but only a few of their descendants survived and evolved into the species present today.
- **Gradualism** In Darwin's day, the idea of slow, gradual change was new to geology as well as biology. Darwin had argued that large-scale changes, such as the formation of new species, must require many small changes to build up gradually over a long period of time. This model is called *gradualism* and is shown in **Figure 15.**
- **Punctuated Equilibrium** Some biologists argue that species do not always evolve gradually. Species may remain stable for long periods until environmental changes create new pressures. Then, many new species may "suddenly" appear. This model is called *punctuated equilibrium* and is shown in **Figure 15.**

READING TOOLBOX

Taking Notes Complete your notes summarizing the major concepts from this chapter. Be sure to include microevolution and macroevolution.

Section 3 Review

KEY IDEAS

1. **Describe** how Darwin's ideas have been updated. Be sure to mention the role of natural selection in modern evolutionary theory.
2. **List** the scales at which evolution can be studied, and list the patterns and processes studied.

CRITICAL THINKING

3. **Arguing Logically** A classmate states that because land animals evolved from fishes and then flying things evolved from walking things, we can predict that future life will evolve to travel in outer space. Write a logical argument against this statement. Be sure to support your argument with examples.

ALTERNATIVE ASSESSMENT

4. **Who's Who** Make a brochure or poster entitled "Who's Who of Evolutionary Theory." Use reference sources to find basic facts about major evolutionary scientists that lived during or after Darwin's lifetime.

Skills Practice

Chapter 16 Lab

Objectives

- Model natural selection.
- Relate favorable mutations to selection and evolution.

Materials

- construction paper
- meterstick or tape measure
- scissors
- cellophane tape
- soda straws
- marker, felt-tip
- penny or other coin
- die, six-sided

Safety

Natural Selection Simulation

In this lab, you will use a paper model of a bird to model the selection of favorable traits in a new generation. This imaginary bird, the Egyptian origami bird (*Avis papyrus*), lives in dry regions of North Africa. Imagine that the birds must fly long distances between water sources in order to live and reproduce successfully.

Procedure

Model Parental Generation

1. Cut a sheet of paper into two strips that are 2 cm × 20 cm each. Make a loop with one strip of paper. Let the paper overlap by 1 cm, and tape the loop closed. Repeat for the other strip.
2. Tape one loop 3 cm from one end of the straw and one loop 3 cm from the other end, as pictured. Use a felt-tip marker to mark the front end of the "bird." This bird represents the parental generation.
3. Test how far your parent bird can fly by releasing it with a gentle overhand pitch. Test the bird twice. Record the bird's average flight distance in a data table like the one shown.

Model First (F_1) Generation

4. Each origami bird lays a clutch of three eggs. Assume that one of the chicks is identical to the parent. Use the parent data to fill in your data table for the first new chick (Chick 1).
5. Make two more chicks (Chick 2 and Chick 3). Assume that these chicks have mutations. Follow Steps A through C for each chick to determine the effects of each mutation.

Data for All Generations

Bird	Coin flip (H or T)	Die throw (1–6)	Anterior wing (cm)			Posterior wing (cm)			Average distance flown (m)
			Width	Circum.	Distance from front	Width	Circum.	Distance from back	
Parent	NA	NA	2	19	3	2	19	3	
Generation 1									
Chick 1									
Chick 2									
Chick 3									
Generation 2									
Chick 1									

Step A Flip a coin to find out which end is affected by the mutation.

Heads = Front wing is affected.

Tails = Back wing is affected.

Step B Throw a die to find out how the mutation affects the wing.

⚀ = Wing position moves 1 cm toward the end of the straw.

⚁ = Wing position moves 1 cm toward the middle.

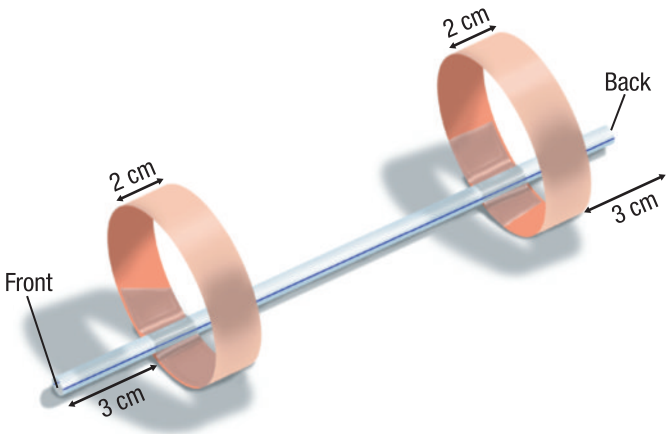
⚂ = Wing circumference increases by 2 cm.

⚃ = Wing circumference decreases by 2 cm.

⚄ = Wing width increases by 1 cm.

⚅ = Wing width decreases by 1 cm.

Step C If a mutation causes a wing to fall off the straw or makes a wing's circumference smaller than the circumference of the straw, the chick cannot "survive." If such a mutation occurs, record it as "lethal," and then produce another chick.



6. For each new chick, record the mutation and the new dimensions of each wing.

7. Test each bird twice by releasing it with a gentle overhand pitch. Release the bird as uniformly as possible. Record the distance that each bird flies. The most successful bird is the one that flies the farthest.

Model Subsequent Generations

8. Assume that the most successful bird in the previous generation is the sole parent of the next generation. Using this bird, repeat steps 4–7.

9. Continue to produce chicks and to test and record data for eight more generations.

Clean Up and Dispose

10. Clean up your work area and all lab equipment. Return lab equipment to its proper place. Dispose of paper scraps in the designated waste container. Wash your hands thoroughly before you leave the lab and after you finish all work.

Analyze and Conclude

1. **Summarizing Results** Describe any patterns in the evolution of the birds in your model.
2. **Evaluating Models** How well does this lab model natural biological processes? What are the limitations of this model?
3. **Analyzing Data** Compare your data with your classmates' data. Identify any similarities and differences. Try to explain any trends that you notice in terms of the theory of natural selection.

Extensions

4. **Design an Experiment** Propose a new hypothesis about natural selection that you could test by observing real organisms. Write a brief proposal describing an experiment that could test this hypothesis. Be sure to give your prediction, explain your methods, identify variables, and plan for control groups.

Chapter 16 Summary

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SUPER SUMMARY
Keyword: HX8EVOS

Key Ideas	Key Terms

1 Developing a Theory

- Modern evolutionary theory began when Darwin presented evidence that evolution happens and offered an explanation of how evolution happens.
- Darwin's experiences provided him with evidence of evolution at work.
- Darwin was influenced by ideas from the fields of natural history, economics, and geology.

Key Terms

evolution (375)
artificial selection (377)

2 Applying Darwin's Ideas

- Darwin's theory of evolution by natural selection predicts that over time, the number of individuals that carry advantageous traits will increase in a population.
- Darwin presented a unifying explanation for data from multiple fields of science.
- The strengths of Darwin's work—evidence of evolution, a mechanism for evolution, and the recognition that variation is important—placed Darwin's ideas among the most important of our time. However, Darwin lacked a mechanism for inheritance.

Key Terms

natural selection (380)
adaptation (381)
fossil (382)
homologous (384)

3 Beyond Darwinian Theory

- Discoveries since Darwin's time, especially in genetics, have been added to his theory to explain the evolution of species.
- Because it affects every aspect of biology, scientists can study evolution at many scales. Generally, these scales range from microevolution to macroevolution, with speciation in between.

Key Terms

speciation (387)

Chapter 16 Review

READING TOOLBOX

1. **Hypothesis or Theory?** Explain why Darwin's theory is not *the* theory of evolution.
2. **Concept Map** Make a concept map that describes the origins of Darwin's theory. Try to include the following words: *Darwin, ideas, evolution, experience, others, travels, reflection, breeding, Lamarck, Malthus,* and *Lyell*.

Using Key Terms

3. Explain the difference between the terms *natural selection* and *artificial selection*.
4. Use the following terms in the same sentence: *macroevolution, microevolution,* and *speciation.*

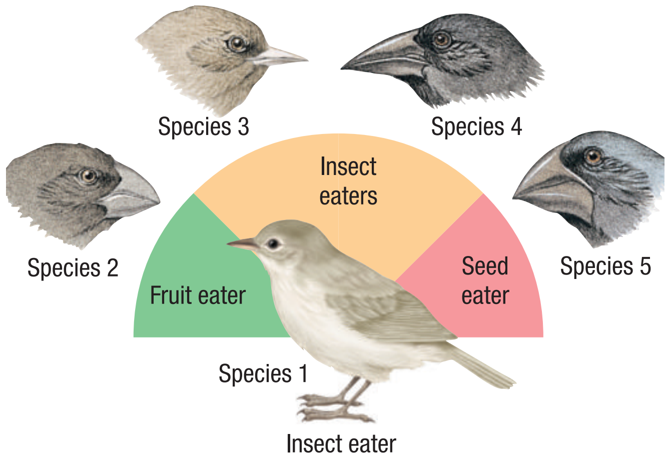
For each of the following terms, write a definition in your own words.

5. *evolution*
6. *homologous structures*

Understanding Key Ideas

7. After studying plant and animal life in South America and the Galápagos Islands, Darwin proposed that
   - **a.** Galápagos species had descended from South American species.
   - **b.** South American species had descended from Galápagos species.
   - **c.** Galápagos species and South American species were unrelated.
   - **d.** Galápagos species and South American species had descended from European species.
8. Darwin was influenced by Malthus's ideas about
   - **a.** inheritance.
   - **b.** populations.
   - **c.** the fossil record.
   - **d.** natural history.
9. Which of the following is a form of biochemical evidence that can be used to study evolution?
   - **a.** speciation.
   - **b.** intermediate forms.
   - **c.** homologous structures.
   - **d.** amino-acid similarities.
10. Which of the following was a weakness in Darwin's ideas about evolution?
    - **a.** lack of evidence for evolution
    - **b.** lack of a mechanism for evolution
    - **c.** lack of a mechanism for inheritance of traits
    - **d.** lack of recognition of the importance of variation
11. Modern evolutionary theory has incorporated most of Darwin's ideas except
    - **a.** Darwin's laws of heredity.
    - **b.** Darwin's theory of natural selection.
    - **c.** Darwin's idea that species evolve gradually.
    - **d.** Darwin's predictions of intermediate forms.

This image shows several species of finches that are related by evolution. Species 1 is from South America. Species 2–5 live in the Galápagos Islands. Use the image to answer the following question.



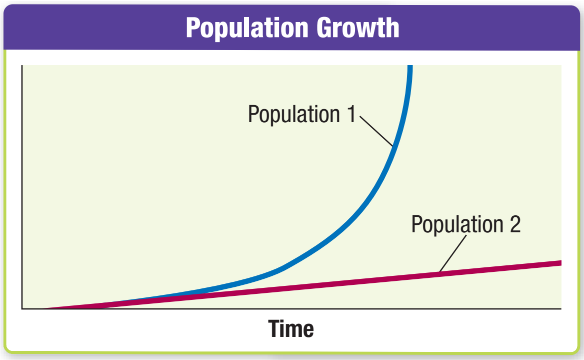
12. The ancestor of all Galápagos finches was probably
    - **a.** a fruit eater.
    - **b.** a seed eater.
    - **c.** a fish eater.
    - **d.** an insect eater.

Explaining Key Ideas

13. **Describe** the relationship between Darwin's ideas and modern evolutionary theory.
14. **List** the four steps of evolution by natural selection.
15. **Explain** how biogeography provides evidence for the influence of environment on evolution.
16. **Identify** two mechanisms other than natural selection that can affect the relative ratios of traits in populations of organisms.

Using Science Graphics

This graph shows the population growth of two different populations over the same period of time. Use the graph to answer the following question(s).



17. From the graph, it is evident that Population 1 underwent
- **a.** no growth.
- **b.** linear growth.
- **c.** exponential growth.
- **d.** equilibrium growth.

18. From the graph, it is evident that Population 2 underwent
- **a.** no growth.
- **b.** linear growth.
- **c.** exponential growth.
- **d.** equilibrium growth.

19. Darwin recognized that all natural populations
- **a.** never increase in the pattern of Population 2.
- **b.** always increase in the pattern of Population 1.
- **c.** are limited to increase in the pattern of Population 2.
- **d.** have the potential to increase in the pattern of Population 1.

Critical Thinking

20. Criticizing an Argument According to Lamarck's ideas about inheritance, people who developed large muscles would pass on those large muscles directly to their offspring. Use another example to show that this conclusion cannot be correct.

21. Explaining Processes Propose a series of steps by which a pair of insect-eating birds could arrive on an island and then evolve into several species, each specializing on a different kind of food.

22. Analyzing Language Explain why the phrase "survival of the fittest" is misleading.

23. Explaining Relationships Why might there be more variation in a population in which individuals mate with random partners each mating season than in a population in which pairs of individuals mate for life?

Why It Matters

24. Applying Concepts Describe how relationships between humans and wolves in ancient history may have led to modern domestic dogs.

25. Quick Project Conduct a survey among any dog owners you know. Ask what breed of dog they have, if the breed is known. Also ask what traits, if any, influenced their selection of this breed.

Alternative Assessment

26. Lyrics Create a song, rap, or poem that explains the difference between everyday uses of the word *theory* and the scientific meaning of the word.

Writing for Science

27. Letter to Scientific Peers Pretend that you are Charles Darwin. Write a letter to one of the people who influenced your ideas about evolution (Lamarck, Malthus, Cuvier, or Lyell). Explain to that person how his ideas helped you understand how organisms evolve.

Math Skills

28. Compound Interest An example of exponential growth is a bank account that earns interest. Often, interest is added once per year, and the new total earns more interest the next year. Thus, the interest is *compounded* each year. The equation for this kind of interest is:

$$P = C(1 + r)^t$$

where P is the future value, C is the initial deposit, r is the interest rate (expressed as a decimal), and t is the number of years invested. Suppose you open an account with an initial deposit of $100.00 and a simple annual interest of 10% (or 0.10). This account would have $110.00 after one year and $121.00 after 2 years. Calculate the account balance over 10 years, and then draw a graph of this growth.

Chapter 16 Standardized Test Prep

TEST TIP Watch out for words that qualify or put conditions on an answer option, such as "only," "always," "some," or "most." These qualifiers are important clues to choosing the correct answer.

Science Concepts

1. Which of the following is the best definition of a scientific theory?
- **A** a group of ideas about a scientific concept
- **B** an explanation that is accepted by most people
- **C** an explanation that has been scientifically tested and supported
- **D** a specific question that can be tested using the scientific method

2. In forming his theory of evolution, Darwin most lacked an adequate understanding of
- **F** geology.
- **G** heredity.
- **H** anatomy.
- **J** geography.

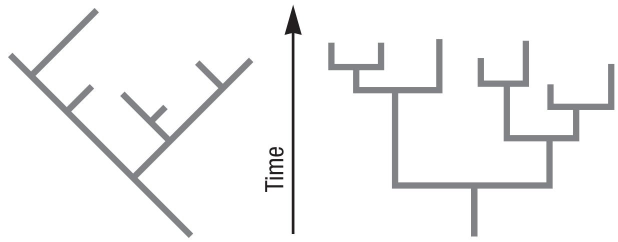
3. An inherited trait that helps an individual survive and reproduce in a particular environment is
- **A** an adaptation.
- **B** a survival trait.
- **C** a genetic trait.
- **D** natural variation.

4. A human arm and a bat wing are each made up of a similar number and arrangement of bones. This similarity is evidence that humans and bats
- **F** evolved at the same time.
- **G** have the same parents.
- **H** have an ancestor in common.
- **J** once shared the same habitat.

5. Which of the following is a true statement about evolution?
- **A** Individuals cannot evolve, but populations can evolve.
- **B** Natural selection is the only mechanism for evolution.
- **C** Evolution always results in more complex forms of life.
- **D** Organisms always evolve to have the best adaptations for their environment.

Using Science Graphics

This diagram shows two contrasting models of the pace of evolution. Use the diagram to answer the following question(s).



6. Model 1 is usually referred to as the model of
- **F** selection.
- **G** gradualism.
- **H** adaptive radiation.
- **J** punctuated equilibrium.

7. Model 2 is usually referred to as the model of
- **A** selection.
- **B** selectionism.
- **C** artificial selection.
- **D** punctuated equilibrium.

8. In Model 1, each point where one line splits into two lines represents
- **F** selection.
- **G** speciation.
- **H** adaptation.
- **J** punctuation.

This table shows the differences between the human hemoglobin protein and that of some animals. Use the table to answer the following question(s).

Animal with hemoglobin	Amino acids that differ from human hemoglobin
Mouse	27
Chicken	45
Frog	67
Lamprey	125

9. These data support the hypothesis that among the animals listed, the animal that is most closely related to humans by ancestry is the
- **A** mouse.
- **B** chicken.
- **C** frog.
- **D** lamprey.

Chapter 17 Population Genetics and Speciation

Preview

1 Genetic Variation
- Population Genetics
- Phenotypic Variation
- Measuring Variation and Change
- Sources of Genetic Variation

2 Genetic Change
- Equilibrium and Change
- Sexual Reproduction and Evolution
- Population Size and Evolution
- Natural Selection and Evolution
- Patterns of Natural Selection

3 Speciation
- Defining Species
- Forming New Species
- Extinction: The End of Species

Why It Matters

The fields of ecology, genetics, and evolutionary theory are brought together to understand how genetic changes in populations result in changes to species over time.

Every population, such as this group of banded wood snails, contains variation. Some of this variation can be seen, but much is hidden in DNA.

InquiryLab

15 min

Normal Variation

Variation is normal and is evident in all populations. Just look down.

Procedure

1. Read step 2, and prepare a table for the class data.
2. Use a **ruler or tape-measure** to measure the length of one of **your shoes** to the nearest centimeter. Record this number, as well as your shoe size and gender. Share these data with the class.
3. Make a table of the shoe lengths of everyone in your class. In the first column, record the name of each student. In the second column, record each shoe length.
4. Make a tally of the numbers of each shoe size in your class.

Analysis

1. **Compare** the table that you made in step 3 to the tally that you made in step 4.
2. **Describe** how the table you made in step 3 could be converted into a tally like that of step 4.
3. **Propose** additional methods by which these kinds of data could be collected and analyzed.
4. **Predict** how the tally that you made in step 4 would change if the data for males were deleted.

Banded wood snails (also called *grovesnails*) eat plant parts and are very common in gardens and moist habitats.

READING TOOLBOX

These reading tools can help you learn the material in this chapter. For more information on how to use these and other tools, see **Appendix: Reading and Study Skills.**

Using Words

Everyday Words in Science Many words that we use every day have special meanings in science. For example, *matter* in everyday use is a topic, issue, or problem. In science, *matter* is the substance of which all things are made.

Your Turn Make a table like the one shown here.

1. Before you read, write in your own words the everyday meaning of the terms in the table.
2. As you read, fill in the scientific meaning for the terms in the table.

Everyday Words in Science

Word	Everyday Meaning	Science Meaning
normal		
distribution		
drift		
fitness		

Using Language

General Statements A general statement often summarizes the features of a group or describes an average or typical feature of members of the group. But if many features are summarized, some individuals in the group probably do not share all of those features. And if an average feature is described, some members of the group will not match the average. So, general statements may be true most of the time, but not always.

Your Turn Use what you know about general statements to complete the following tasks.

1. Write a general statement about apples, bananas, tomatoes, and peanuts.
2. List exceptions to the statement "Humans are bigger than monkeys."

Taking Notes

Outlining Outlining is a note-taking skill that helps you organize information. An outline can give you an overview of the topics in a chapter and help you understand how the topics are related.

Your Turn Create outlines for each section of this chapter. Start with the example shown here.

1. Copy all of the headings for a section, in order, on a piece of paper.
2. Leave plenty of space between each heading.
3. As you read the material under each heading of a section, write the important facts under that heading on your outline.

Population Genetics and Speciation

- *Genetic Variation*
  - *Population Genetics*
  - *Phenotypic Variation*
  - *Measuring Variation and Change*
    - *Studying Alleles*
    - *Allele Frequencies*
  - *Sources of Genetic Variation*
- *Genetic Change*
  - *Equilibrium and Change*

Section 1

Genetic Variation

Key Ideas	Key Terms	Why It Matters
How is microevolution studied? How is phenotypic variation measured? How are genetic variation and change measured? How does genetic variation originate?	population genetics normal distribution	Without variation, evolution cannot occur.

One of Charles Darwin's contributions to biology was his careful study of variation in characteristics, such as the many flower colors shown in **Figure 1.** As you have learned, Darwin knew that heredity influences characteristics, but he did not know about genes. We now know a great deal about genes. We are able to study and predict the relationships between genotypes and phenotypes. We can also study the genetic variation and change that underlie evolution.

Population Genetics

Recall that evolution can be studied at different scales, from that of microevolution to macroevolution. And recall that *microevolution* is evolution at the level of genetic change in populations. **Microevolution can be studied by observing changes in the numbers and types of alleles in populations.** The study of microevolution in this sense is **population genetics**. Thus, the studies of genetics and evolution are advancing together. Furthermore, the link from micro-evolution to macroevolution—*speciation*—can be studied in detail.

Reading Check *What do we now know about heredity that Darwin did not know? (See the Appendix for answers to Reading Checks.)*

population genetics the study of the frequency and interaction of alleles and genes in populations

Figure 1 Genetic variation is found in all living things and forms the basis on which evolution acts. **What kinds of variation can be seen in this photograph?**

Figure 2 Eye color is a polygenic character. Different genes control different pigments, which combine to produce various shades of blue, green, or brown.

Phenotypic Variation

Before anyone understood genetics, the only kind of variation that could be observed and measured was phenotypic variation. Gregor Mendel was the first to suspect that some kind of inherited units determined the various phenotypes that he observed. (In Mendel's day, the term *phenotype* was not used.) We now know that the inherited units are alleles. Mendel used his data on phenotypes to mathematically deduce the ratio of alleles in each individual. Today, we call these ratios *genotypes*.

Mendel's work was made simple by the fact that he studied pea plants with only two phenotypes for each character. As you have learned, genetics is rarely so simple. For example, listing every possible phenotype for height in humans would be difficult. If you compare many humans, you find a range of possible heights, with many slight variations.

The variety of phenotypes that exist for a given character depends on how many genes affect that character. Recall that a character that is influenced by several genes is a *polygenic* character. Human height and human eye color, for example, are polygenic. Polygenic characters may exist as a variety of traits, as shown in **Figure 2,** or a range of trait values, as shown in **Figure 3.**

Biologists study polygenic phenotypes by measuring each individual in the population and then analyzing the distribution of the measurements. A *distribution* is an overview of the relative frequency and range of a set of values. Mathematically, a distribution is a tally or a histogram with a smooth line to show the overall pattern of the values.

Often, some values in a range are more common than others. For example, suppose that you were to collect one shoe from each student in your class. If you ordered and grouped the shoes by size, you would probably form a hill-shaped curve such as the one shown in **Figure 3.** This pattern of distribution is called a **normal distribution** or a *bell curve*. "Normal" in this case simply means a tendency to cluster around an average value (mean, median, or mode).

Reading Check ***Why do polygenic characters vary so much?***

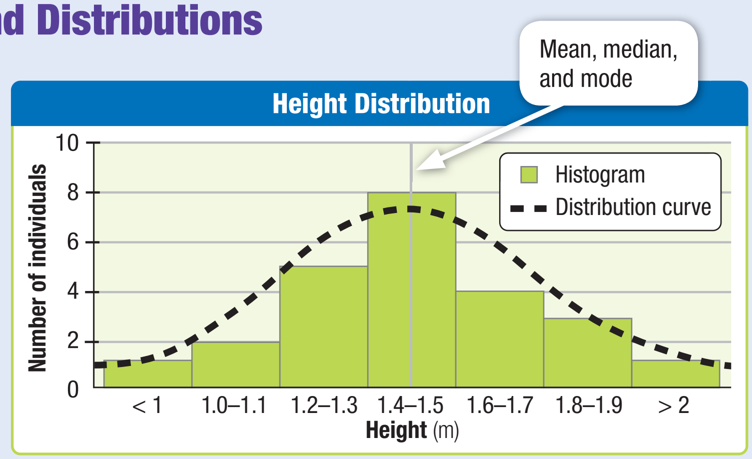
Figure 3 Measurements of characters that have a wide range of variation, such as shoe size, can be arranged into a histogram and are likely to form a bell curve. **How do the number of genes for a character relate to its variation?**

Math Skills Histograms and Distributions

Suppose that you were to measure the height of every student in your school. You would probably gather a wide range of data. The best way to graph this data would be to use a histogram. A *histogram* is a special kind of bar graph for displaying a range of values. The histogram clearly shows the range of values as well as the values that are most common.

To make a histogram, list the values in order from smallest to largest. Then, determine the *range* from the smallest value to the largest. Draw the *x*-axis of the histogram to cover this range. Then, group the values into convenient intervals. For example, values for height in meters could be grouped into intervals of 0.2 m each, as shown here.

Next, count the number of values that fall within each interval. (Hint: Making a tally of the counts is helpful.) Draw the *y*-axis of the histogram to allow for the highest count in any one interval. Finally, draw bars to show the count for each interval. The bars should touch each other because the graph is showing a continuous range of data.



You can use math software to make a histogram and further analyze these kinds of data. For example, you can "fit a curve" to the data, adding a line through the bars to show the general shape, or *distribution*, of the data. You can group the data into smaller or larger intervals, or add or subtract values, and then see changes in the shape of the curve. Finally, you can find the mean, median, and mode(s) of the data. A *normal distribution* will have similar values for the mean, median, and mode.

Measuring Variation and Change

To study population genetics, we need to study how genes in populations change over time. To measure these changes, we must look at how alleles are passed on from generation to generation as organisms mate and produce offspring. The particular combination of alleles in a population at any one point in time makes up a *gene pool*.

Studying Alleles To study genetic variation, we need to estimate the number of alleles in a population. For characters with simple Mendelian inheritance, we can estimate by using simple math combined with our knowledge of genetics. For example, we may start by counting the number of individuals in the population and recording the phenotype of each. Then, we can deduce each genotype.

As you have learned, to keep track of alleles, we can represent alleles with letters. For example, a particular gene may have two alleles, *R* and *r*. In addition, we represent genotypes as combinations of alleles. So, if two alleles exist for a particular gene, then there are three genotypes: *RR*, *Rr*, and *rr*. To compare the numbers of alleles or genotypes, we measure or calculate the frequency of each. **Genetic variation and change are measured in terms of the frequency of alleles in the gene pool of a population.** A *frequency* is the proportion or ratio of a group that is of one type.

Reading Check *What is the main measure of genetic variation?*

normal distribution a line graph showing the general trends in a set of data of which most values are near the mean

READING TOOLBOX

Everyday Words in Science The word *normal* in science and math is often used to describe measurements that fit within a normal distribution. What does a doctor mean when talking about "normal height" for a person of your age?

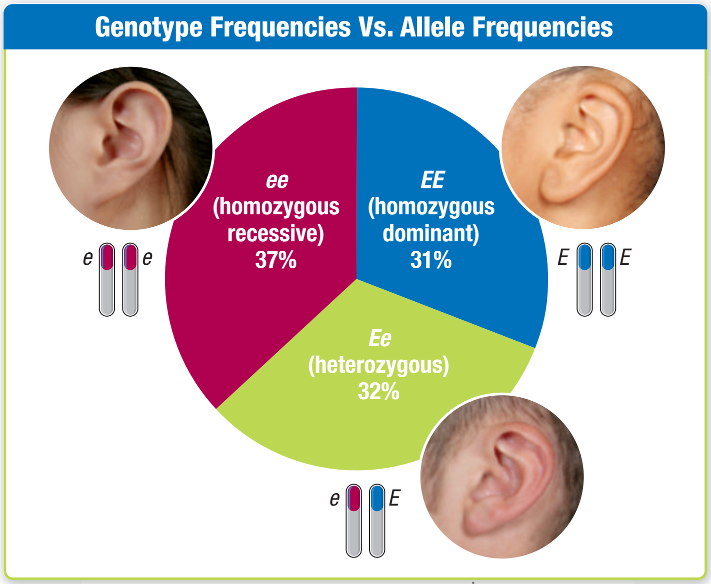


Figure 4 You cannot see alleles, and you cannot always tell genotype based on phenotype. You have to use math and know dominance patterns to calculate allele frequencies. **❯ Is the dominant allele always the most frequent?**

SciLinks
www.scilinks.org
Topic: Genotype/Phenotype
Code: HX80662

Tracking Frequencies To study genetic change, biologists want to keep track of the frequency of each allele in a population over time. They can keep track in several ways. A direct way would be to detect and count every allele in every individual, which is rarely practical. An indirect way is to use mathematics along with a knowledge of how alleles combine. Recall that alleles combine to form genotypes that, in turn, produce recognizable phenotypes.

To understand the basic mathematics of allele frequencies, consider the simple example shown in **Figure 4.** Human ear lobes have two phenotypes: unattached (free hanging) or attached at the base. The ear lobe character is thought to be controlled by a single gene, and the unattached trait is thought to be dominant. So, the unattached allele is represented as *E*, and the attached allele is represented as *e*. People with attached ear lobes are homozygous recessive, or genotype *ee*. People with unattached ear lobes are either homozygous dominant (*EE*) or heterozygous (*Ee*).

Genotype Frequencies Notice how genotype frequencies differ from allele frequencies. Suppose that the population in **Figure 4** consists of 100 people. In this case, 37% of the population, or 37 people, are genotype *ee*; 32 are *Ee*; and 31 are *EE*. Keep in mind that in ratios and percentages, all of the parts add up to one whole, or 100%. So, the sum of genotype frequencies in a population should always be equal to 1 (or 100%). This fact leads to the following equation:

$$(\text{frequency of } EE) + (\text{frequency of } Ee) + (\text{frequency of } ee) = 1$$

Using the numbers in our example, the equation proceeds as follows:

$$0.31 + 0.32 + 0.37 = 1$$

Allele Frequencies Similarly, the sum of allele frequencies for any gene must equal 1, as in the following equation:

$$(\text{frequency of } E) + (\text{frequency of } e) = 1$$

or

$$\frac{(\text{count of } E)}{(\text{total})} + \frac{(\text{count of } e)}{(\text{total})} = 1$$

In our example population, there are 94 *E* alleles and 106 *e* alleles, and the total is 200 alleles. The equation proceeds as follows:

$$\frac{94}{200} + \frac{106}{200} = 0.47 + 0.53 = 1$$

As you can see, the frequency of the *E* allele is 0.47, and the frequency of the *e* allele is 0.53. Notice that the dominant allele is not necessarily the most frequent! Also keep in mind that you often cannot tell genotypes by looking at phenotypes. However, you will soon learn how these equations can be used to track changes in populations.

❯ Reading Check ***What is the sum of all allele frequencies for any one gene?***

Hands-On

QuickLab

15 min

Alleles: The Next Generation

Model the allele frequencies in a population over time.

Procedure

1. Work in a group, which will represent a population. Obtain **two colors of marbles (one pair) for each member in the group.** Each color will represent a unique allele. Choose one color to be "dominant."
2. Mix the marbles. Each member of the "population" should randomly take two "alleles." Record the resulting genotype and phenotype of each member.
3. Each member should hide one marble in each hand and then randomly exchange one of these "alleles" with another member. Record the resulting genotypes and phenotypes of each member.
4. Repeat the steps to model four more "generations."

Analysis

1. **Determine** the genotype and phenotype ratios for each "generation." Do the ratios change over time?
2. **Propose** a way to change the ratios in your population from one generation to the next. Propose a way that this change could happen in a real population.

Sources of Genetic Variation

Evolution cannot proceed if there is no variation. As you have learned, this variation must originate as new alleles. **The major source of new alleles in natural populations is mutation in germ cells.**

Mutation is important, but it generates new alleles at a slow rate. New alleles first arise in populations as changes to DNA in the sperm and ova (called *germ* cells) of individuals. If a germ cell with a mutation goes on to form offspring, then a new allele is added to the gene pool. Mutations can also occur in nongerm cells (called *somatic* cells), but these mutations are not passed on to offspring.

Academic Vocabulary

generate produce; bring into being; cause to be

Reading Check *Why is mutation so important?*

Section 1 Review

KEY IDEAS

1. **Describe** the scope of population genetics.
2. **Explain** how polygenic phenotypes are studied.
3. **Describe** how genetic variation and change can be measured.
4. **Identify** the major source of genetic variation in a population.

CRITICAL THINKING

5. **Analyzing Concepts** Even in cases of simple Mendelian inheritance within a population, the ratio of phenotypes of a specific character is rarely the same as the ratio of alleles for that character. Explain why these ratios differ.
6. **Applying Logic** Can an individual organism evolve in the Darwinian sense? Explain your answer in terms of genetic variation within populations.

MATH SKILLS

7. **Distribution Curves** Suppose that **Figure 3** represents the distribution of shoe sizes in a class of twelfth graders. How might the distribution change if the shoes of a class of first graders were added to those of the twelfth graders? Explain your answer.

Section 2

Genetic Change

Key Ideas	Key Terms	Why It Matters
› What does the Hardy-Weinberg principle predict? › How does sexual reproduction influence evolution? › Why does population size matter? › What are the limits of the force of natural selection? › What patterns can result from natural selection?	genetic equilibrium	The mathematics of genetics can be used to make predictions about future generations.

You might think that a dominant trait would always be the most common trait in a population. When biologists began to study population genetics, they found that this was not always true.

Equilibrium and Change

In 1908, the English mathematician G. H. Hardy and the German physician Wilhelm Weinberg began to model population genetics by using algebra and probabilities. They showed that in theory, the frequency of alleles in a population should not change from one generation to the next. Moreover, the ratio of heterozygous individuals to homozygous individuals (the genotype frequencies) should not change. Such a population, in which no genetic change occurred, would be in a state of **genetic equilibrium.**

Measuring Change Genetic change in a population can be measured as a change in genotype frequency or allele frequency. A change in one does not necessarily mean a change in the other. For example, as shown in **Figure 5,** the genotype frequencies changed between generations, but the allele frequencies did not.

Figure 5 Allele frequencies can remain stable while genotype frequencies change.

Allele Frequencies in Two Generations

Genotype frequency	Allele frequency	Generation
RR (red) = 0.5 *Rr* (pink) = 0.5 *rr* (white) = 0	*R* = 0.75 *r* = 0.25	1  *RR* *RR* *Rr* *Rr* *RR* *Rr* *Rr* *RR*
RR (red) = 0.625 *Rr* (pink) = 0.25 *rr* (white) = 0.125	*R* = 0.75 *r* = 0.25	2  *RR* *Rr* *rr* *RR* *RR* *Rr* *RR* *RR*

Math Skills — Hardy-Weinberg Equation

The Hardy-Weinberg principle can be expressed as an equation that can be used to predict stable genotype frequencies in a population.

The equation is usually written as follows:

$$p^2 + 2pq + q^2 = 1$$

p^2	$2pq$	q^2	1
(frequency of *RR* individuals)	(frequency of *Rr* individuals)	(frequency of *rr* individuals)	(sum of all frequencies)

Recall that the sum of the genotype frequencies in a population must always equal 1.

By convention, the frequency of the more common of the two alleles is referred to as p, and the frequency of the rarer allele is referred to as q.

Individuals that are homozygous for allele *R* occur at a frequency of p times p, or p^2. Individuals that are homozygous for allele *r* occur at the frequency of q times q, or q^2.

Heterozygotes have one copy of *R* and one copy of *r*, but heterozygotes can occur in two ways—*R* from the father and *r* from the mother, or *r* from the father and *R* from the mother. Therefore, the frequency of heterozygotes is $2pq$.

Hardy-Weinberg Principle Hardy and Weinberg made a mathematical model of genetic equilibrium. This model is the basis of the *Hardy-Weinberg principle.* **The Hardy-Weinberg principle predicts that the frequencies of alleles and genotypes in a population will not change unless at least one of five forces acts upon the population.**

genetic equilibrium a state in which the allele frequencies of a population remain in the same ratios from one generation to the next

Forces of Genetic Change In reality, populations are subject to many forces and undergo genetic change constantly. **The forces that can act against genetic equilibrium are gene flow, nonrandom mating, genetic drift, mutation, and natural selection.**

Gene Flow *Gene flow* occurs when genes are added to or removed from a population. Gene flow can be caused by *migration,* the movement of individuals from one population to another, as shown in **Figure 6.** Each individual carries genes into or out of the population, so genetic frequencies may change as a result.

Nonrandom Mating In sexually reproducing populations, any limits or preferences of mate choice will cause nonrandom mating. If a limited set of genotypes mates to produce offspring, the genotype frequencies of the population may change.

Genetic Drift Chance events can cause rare alleles to be lost from one generation to the next, especially when populations are small. Such random effects on allele frequencies are called *genetic drift*. The allele frequencies are changed directly and genotype frequencies change as a result.

Mutation A mutation can add a new allele to a population. Allele frequencies are changed directly, if only slightly.

Natural Selection Natural selection acts to eliminate individuals with certain traits from a population. As individuals are eliminated, the alleles for those traits may become less frequent in the population. Thus, both allele and genotype frequencies may change.

Reading Check *What can cause gene flow?*

Figure 6 These caribou are migrating from one place to another. If they meet other groups of caribou and interbreed, gene flow may occur.

Figure 7 Sexual selection favors the development of extreme phenotypic traits in some species. The vibrant red stripe on the blue muzzle of this male mandrill baboon does not appear in females.

Sexual Reproduction and Evolution

Recall that sexual reproduction creates chances to recombine alleles and thus increase variation in a population. So, sexual reproduction has an important role in evolution. **Sexual reproduction creates the possibility that mating patterns or behaviors can influence the gene pool of a population.** For example, in animals, females sometimes select mates based on the male's size, color, ability to gather food, or other characteristics, as shown in **Figure 7.** This kind of behavior is called *sexual selection* and is an example of nonrandom mating.

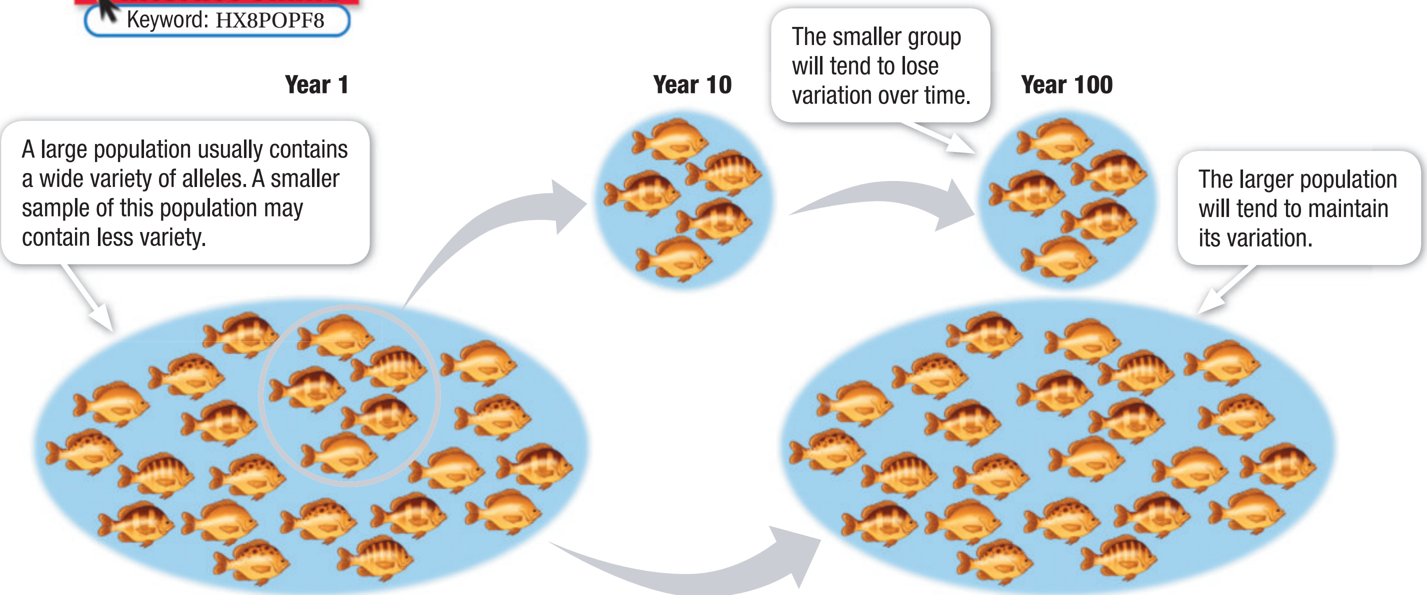
Another example of nonrandom mating is *inbreeding*, in which individuals either self-fertilize or mate with others like themselves. Inbreeding tends to increase the frequency of homozygotes, because a smaller pool of alleles is recombined. For example, populations of self-fertilizing plants consist mostly of homozygotes. However, inbreeding does not change the overall frequency of alleles. Inbreeding is more likely to occur if a population is small.

Population Size and Evolution

Population size strongly affects the probability of genetic change in a population. **Allele frequencies are more likely to remain stable in large populations than in small populations.** In a small population, the frequency of an allele can be quickly reduced by a chance event. For example, a fire or drought can reduce a large population to a few survivors. At that point, each allele is carried in a few individuals. The loss of even one individual from the population can severely reduce an allele's frequency. So, a particular allele may disappear in a few generations, as shown in **Figure 8.** This kind of change is called *genetic drift* because allele frequencies drift around randomly. The force of genetic drift is strongest in small populations. In a larger population, alleles may increase or decrease in frequency, but the alleles are not likely to disappear.

Reading Check ***What is the genetic effect of inbreeding?***

Figure 8 Alleles are more likely to be lost from smaller populations. So, variation tends to decrease over time in smaller populations but not in larger populations.



Data

QuickLab

15 min

Genetic Risk Assessment

How can the Hardy-Weinberg equation be used? It can be used to predict the risk of genetic disorders in a population. For example, medical professionals may know how many people have been diagnosed with a genetic disorder. From this information, they can predict how many people are at risk of passing on the disorder.

Lungs of a person with cystic fibrosis

Procedure

1. Consider these facts: Cystic fibrosis (CF) is a disorder that occurs in 1 out of every 2,500 Caucasians in North America. CF is caused by a recessive allele.
2. Use the Hardy-Weinberg equation to predict the percentage of carriers of the allele that causes CF.

Analysis

1. **Calculate** the frequency of the recessive allele.
2. **Calculate** the frequency of the dominant allele.
3. **Calculate** the frequency of carriers (heterozygotes).
4. **Determine** how many of every 1,000 Caucasian North Americans are likely to carry the cystic fibrosis allele.

Natural Selection and Evolution

Recall that Charles Darwin proposed natural selection as a mechanism that could drive evolution. Scientists have studied many examples of natural selection in action.

How Selection Acts Keep in mind that the process of natural selection is a result of the following facts.

- **All populations have genetic variation.** Any population has an array of individuals that differ slightly from one another in genetic makeup. Although this variation may be obvious in humans, variation also exists in species whose members may appear identical, such as a species of bacteria.
- **Individuals tend to produce more offspring than the environment can support.** Individuals of a population often struggle to survive, whether competing with one another or not.
- **All populations depend upon the reproduction of individuals.** Some biologists have noted that "evolutionary fitness is measured in grandchildren." The statement means that an individual must survive to reproduce, and also produce offspring that can reproduce, to pass its genes on to future generations.

Genetic Results of Selection The result of natural selection is that the frequency of an allele may increase or decrease depending on the allele's effects on survival and reproduction. Natural selection causes deviations from genetic equilibrium by directly changing the frequencies of alleles. Although natural selection is not the only force of evolution, it is a powerful force.

› **Reading Check** *How is "fitness" measured in evolutionary terms?*

SCILINKS®
www.scilinks.org
Topic: Natural Selection
Code: HX81016

ACADEMIC VOCABULARY

deviate to turn aside; to diverge or differ

Figure 9 Crayfish species exist in a variety of colorations. In many cases, the coloration helps the crayfish hide from predators or attract mates. But for crayfish species that live in lightless caves, having color gives no fitness advantage. **❯ What might happen to a colorless crayfish placed in a well-lit pond?**

Why Selection Is Limited The key lesson that scientists have learned about evolution by natural selection is that the environment does the selecting. If the environment changes in the future, the set of characteristics that are most adaptive may change. For example, each of the animals shown in **Figure 9** is adapted to a specific environment and may not be able to survive if placed in another environment.

Natural selection is limited by nature. **❯ Natural selection acts only to change the relative frequency of alleles that exist in a population.** Natural selection cannot direct the creation of new alleles, nor will it necessarily delete every allele that is not adaptive. So, natural selection does not create perfectly adapted organisms.

Indirect Force Natural selection does not act directly on genes. It merely allows individuals who express favorable traits to reproduce and pass those traits on to their offspring. Darwin's idea of natural selection, stated in modern terms, is that **❯ natural selection acts on genotypes by removing unsuccessful phentoypes from a population.** Biologists say that certain phenotypes are "selected against" and that certain genotypes are thus "favored."

READING TOOLBOX

General Statements List possible exceptions to the statement "Natural selection removes unsuccessful phenotypes from a population."

Role of Mutation Think carefully about how natural selection might operate on a new allele that has arisen by mutation. At first, the mutation may make no difference. Even if the mutation results in a nonfunctional protein, the cell may have a functional copy of the original gene as its second allele. However, the new, nonfunctioning version could be passed on as a recessive allele. This kind of mutation is the probable origin of many recessive genetic disorders.

Only characteristics that are expressed can be targets of natural selection. Therefore, selection cannot operate against rare recessive alleles, even if they are unfavorable. A recessive allele must become common before two heterozygous individuals (carriers) are likely to mate and produce homozygous offspring. Only then does natural selection have an opportunity to act. And even then, selection will act only against homozygotes. For this reason, genetic disorders can persist in populations.

❯ Reading Check ***How can unfavorable alleles persist?***

Patterns of Natural Selection

Recall that many traits, such as human height, have a bell-curve distribution in natural populations. When natural selection acts on polygenic traits, it essentially acts to eliminate some part of the bell curve.

Three major patterns are possible in the way that natural selection affects the distribution of polygenic characters over time. These patterns are directional selection, stabilizing selection, and disruptive selection, as **Figure 10** illustrates.

Directional Selection In *directional selection,* the "peak" of a normal distribution moves in one direction along its range. In this case, selection acts to eliminate one extreme from a range of phenotypes. Thus, the alleles for the extreme phenotype become less common in the population. This pattern of selection is often seen in the evolution of single-gene traits, such as pesticide resistance in insects.

Stabilizing Selection In *stabilizing selection,* the bell-curve shape becomes narrower. In this case, selection eliminates individuals that have alleles for any extreme type. So, the ratio of intermediate phenotypes increases. In other words, this pattern of selection tends to "stabilize" the average by favoring a narrow range of phenotypes. Stabilizing selection is very common in nature.

Disruptive Selection In *disruptive selection,* the bell curve is "disrupted" and pushed apart into two peaks. In this case, selection acts to eliminate individuals with average phenotype values. Each peak is pushed in an opposite direction, away from the average. The result is increasingly distinct or variable phenotypes in the population. Mathematically, the new distribution is said to have two mode values, each of which differs from the mean value.

Reading Check ***Which form of selection increases the range of variation in a distribution?***

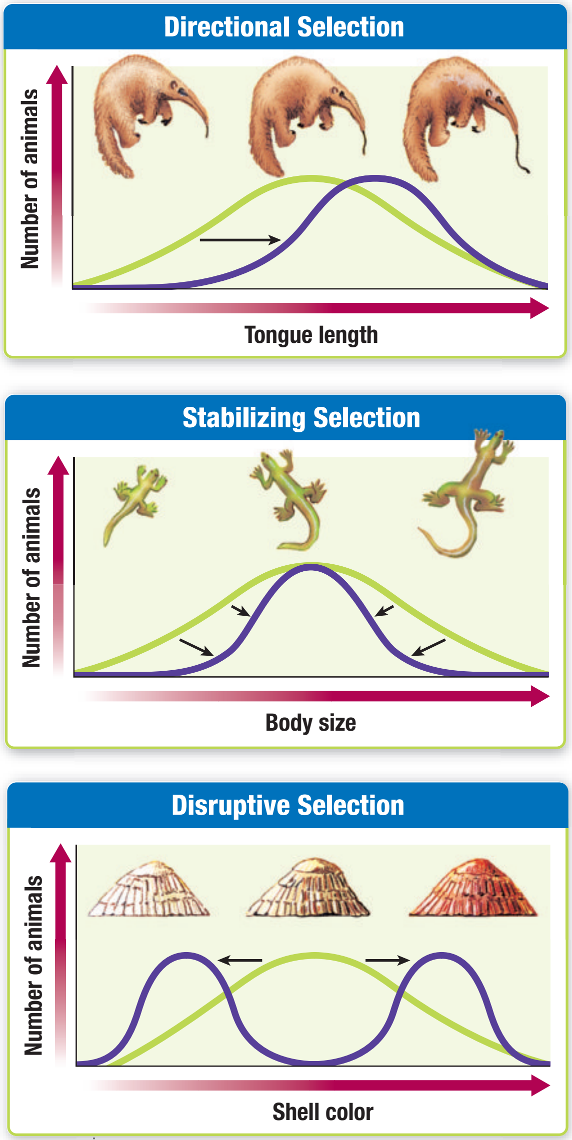


Figure 10 Selection can shift a distribution from an original bell curve (green) toward a new shape (purple).

Section 2 **Review**

KEY IDEAS

1. **Restate** the Hardy-Weinberg principle in your own terms.
2. **Relate** sexual reproduction to evolutionary forces.
3. **Explain** why a small population is subject to genetic drift.
4. **Describe** the limits of the force of natural selection.
5. **List** the patterns that can result from natural selection acting on polygenic traits.

CRITICAL THINKING

6. **Comparing Concepts** In what way is the genetic effect of nonrandom mating similar to the genetic effect of gene flow?
7. **Reasoning Opinions** Are all organisms perfectly adapted for their habitat? Explain.

USING SCIENCE GRAPHICS

8. **Prediction** Redraw each of the graphs in **Figure 10.** Use as examples birds with a range of beak sizes. Describe possible situations that would cause each pattern of selection.

Why It Matters

Wild Laboratories

What do the finches of the Galápagos Islands, the anole lizards of the Caribbean Islands, and the *Drosophila* flies of the Hawaiian Islands have in common? Each of these groups of related species has been extensively studied by evolutionary biologists. And each group has undergone a similar pattern of evolution on each group of islands.

Roles in the Landscape

Darwin found that each Galápagos finch species ate certain types of food and had a beak that was adapted for that food. Similarly, biologists have found that each Caribbean anole species tends to live in a certain part of the landscape and has body parts adapted for running, climbing, or hiding in that area. On each Caribbean island, a unique set of species fulfills each "specialist" role.

Trunk-Ground Specialist *Anolis lineatopus* specializes in running along tree trunks and the ground.

Trunk-Crown Specialist *Anolis allisoni* specializes in crawling along the tops and trunks of tropical plants.

Twig Specialist *Anolis angusticeps* specializes in clinging to twigs.

Grass-Bush Specialist *Anolis bahorucoensis* specializes in clinging to grass and stems.

Quick Project Find out how many species of anoles have been identified in the Carribbean islands as compared with the total number of anole species worldwide. Likewise, find out the number of Hawaiian species of flies in the family Drosophilidae.

Section 3

Speciation

Key Ideas	Key Terms	Why It Matters
❯ How can species be defined? ❯ How do we know when new species have been formed? ❯ Why is studying extinction important to understanding evolution?	reproductive isolation subspecies	How we define species relates to how we study evolution and ecology.

All of the beetles in **Figure 11** belong to the same species, but each looks different. Identifying species or telling species apart is often difficult. Part of the difficulty lies in the very definition of *species*.

Defining Species

Since the days of Darwin, scientists have understood that species are not permanent, stable things. And thanks to Mendel, scientists have learned that genetics underlie the variation and change in species. With this knowledge, they have reconsidered the very definition of *species*. ❯ **Today, scientists may use more than one definition for *species*. The definition used depends on the organisms and field of science being studied.** Increasingly, scientists want to do more than name and describe things—they want to know how things are related.

As you have learned, a *species* is generally defined as a group of natural populations that can interbreed. This definition is based on the *biological species concept*, which adds the requirement that the interbreeding produce healthy, fertile offspring. Applying this concept, any populations that do not share future offspring could be considered separate species.

However, the biological species concept cannot be applied to all organisms. It does not apply to those that reproduce asexually or that are known only from fossils. And any form of reproduction may be difficult to confirm. So, species may instead be defined based on their physical features, their ecological roles, and their genetic relatedness.

❯ **Reading Check** *Why is a species hard to define?*

Figure 11 How many species of beetles are in this photo? Just one! ❯ **What problems arise when defining species based on appearances?**

Figure 12 These two species probably evolved from a single species that was separated into two groups by geographic change. **❯ What other mechanisms can isolate species?**

reproductive isolation a state in which a population can no longer interbreed with other populations to produce future generations

subspecies a taxonomic classification below the level of species; refers to populations that differ from, but can interbreed with, other populations of the same species

Forming New Species

Each population of a single species lives in a different place. In each place, natural selection acts on the population and tends to result in offspring that are better adapted to the environment. If the environments differ, the adaptations may differ. The accumulation of differences between populations is called *divergence* and can lead to the formation of new species.

Recall that *speciation* is the process of forming new species by evolution from preexisting species. Speciation rarely occurs overnight; it usually occurs in stages over generations. **❯ Speciation has occurred when the net effects of evolutionary forces result in a population that has unique features and is reproductively isolated.**

Reproductive Isolation Recall that the biological species concept defines species as interbreeding groups. Thus, if two groups stop interbreeding, they take a step toward speciation. **Reproductive isolation** is a state in which two populations can no longer interbreed to produce future offspring. From this point on, the groups may be subject to different forces, so they will tend to diverge over time.

Through divergence over time, populations of the same species may differ enough to be considered subspecies. **Subspecies** are simply populations that have taken a step toward speciation by diverging in some detectable way. This definition is imprecise because reproductive isolation is only apparent after the passage of time.

Mechanisms of Isolation Divergence and speciation can happen in many ways. Any of the following mechanisms may contribute to the reproductive isolation of populations.

- **Geography** A physical barrier, such as the one shown in **Figure 12,** may arise between populations. Such a barrier could prevent interbreeding. Over time, if the populations diverge enough, they will probably not interbreed even if the barrier is removed.

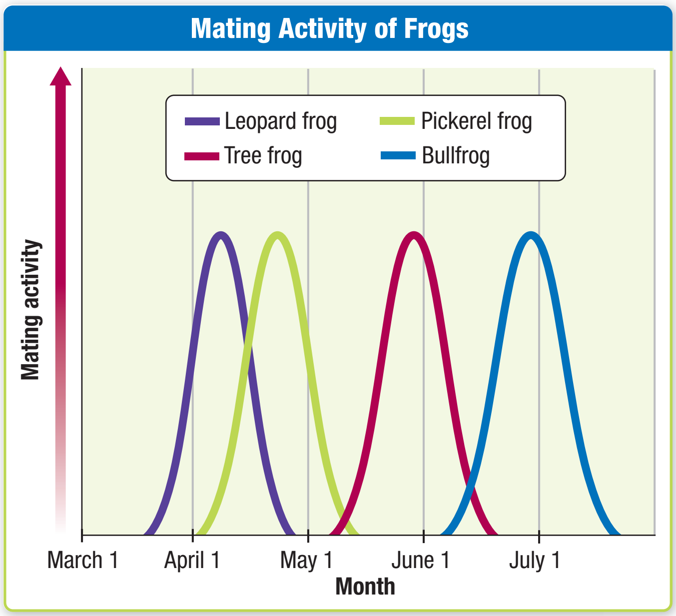
- **Ecological Niche** Recall that the *niche* of a species is the role that the species has in its environment, including all of its interactions with other species. Divergence can occur when populations use different niches. The divergence of multiple lineages into many new species in a specific area and time is called *adaptive radiation.*
- **Mating Behavior and Timing** Many species that sexually reproduce have specific behaviors for attracting mates, such as a pattern of sounds or actions. Some undergo mating at specific times or in response to environmental events. If two populations develop differences in these behaviors, they may no longer attract each other for mating. This mechanism seems to be responsible for the species divergence shown in **Figure 13.**
- **Polyploidy** Recall that a *polyploid* organism has received a duplicate set of chromosomes by accident. A polyploid individual may be reproductively isolated because it cannot pair gametes with others from the original population. However, it may reproduce by vegetative growth, self-fertilize, or find a polyploid mate. In these cases, a new species can arise rapidly. Polyploidy has been observed in many plant species.
- **Hybridization** In some cases, two closely related species may come back into contact with each other and attempt to mate. The offspring of such a mating are called *hybrids.* In cases in which the two parent species are sufficiently diverged from each other, their offspring may be sterile. For example, a mule is a sterile hybrid of a horse and a donkey. Another possibility is that hybrid offspring may not be well adapted to the environment of either parent. Finally, if the parents have many genetic differences, the offspring may not develop successfully. However, there are also many cases in which hybridization leads to new and successful species.

› **Reading Check** ***Is hybridization always successful?***

READING TOOLBOX

Outlining Complete your outline for this chapter. Be sure to include each of the headings on this page, such as "Polyploidy" and "Hybridization." When you finish the chapter, review your outline and add notes to any heading whose meaning is unclear to you.

Figure 13 The pickerel frog and the leopard frog are closely related species. Differences in mating times may have caused their reproductive isolation. › **What other aspects of mating can push populations to diverge?**



Pickerel frog, *Rana palustris*

Leopard frog, *Rana pipiens*

Figure 14 The Tasmanian wolf was driven to extinction by ranchers and dogs in Australia in the early 1900s. ❯ **What is the role of extinction in evolution?**

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Extinction: The End of Species

Extinction occurs when a species fails to produce any more descendants. The animal in **Figure 14** is extinct. Extinction, like speciation, can be detected only after it is complete. And extinction is as much a part of evolution as speciation is. Scientists estimate that more than 99% of all of the species that have ever lived on Earth have become extinct. ❯ **The species that exist at any time are the net result of both speciation and extinction.** If you think of speciation as a branching of a "family tree," then extinction is like the loss of one of the branches.

As you will learn, many cases of extinction are the result of environmental change. Almost all of the dinosaurs died off because of some combination of meteorite impacts, volcanism, and climate change on Earth millions of years ago. Anytime that an environment changes, species that were once well adapted may become poorly adapted. If the environment changes more rapidly than new adaptations arise within a species, the species may be driven to extinction.

❯ **Reading Check** ***When do we know that extinction has happened?***

Section 3 Review

❯ KEY IDEAS

1. **Identify** two definitions of *species* used in evolutionary biology.
2. **Summarize** a general process by which one species can evolve into two species.
3. **Relate** extinction to changes that occur in the numbers and types of species over time.

CRITICAL THINKING

4. **Making Inferences** Would the biological species concept be useful for classifying bacterial species? Explain your answer.
5. **Relating Concepts** Relate the idea of reproductive isolation to the biological species concept.
6. **Describing Relationships** Describe the relationship between speciation and extinction in terms of a "family tree" of descent.

ALTERNATIVE ASSESSMENT

7. **Speciation-in-Action Poster** Sometimes, the easiest way to explain a concept is to illustrate real-world examples of the concept. Create a poster that illustrates examples of reproductive barriers between species. Show how these barriers relate to the biological species concept. Present your poster to the class.

Chapter 17 Lab

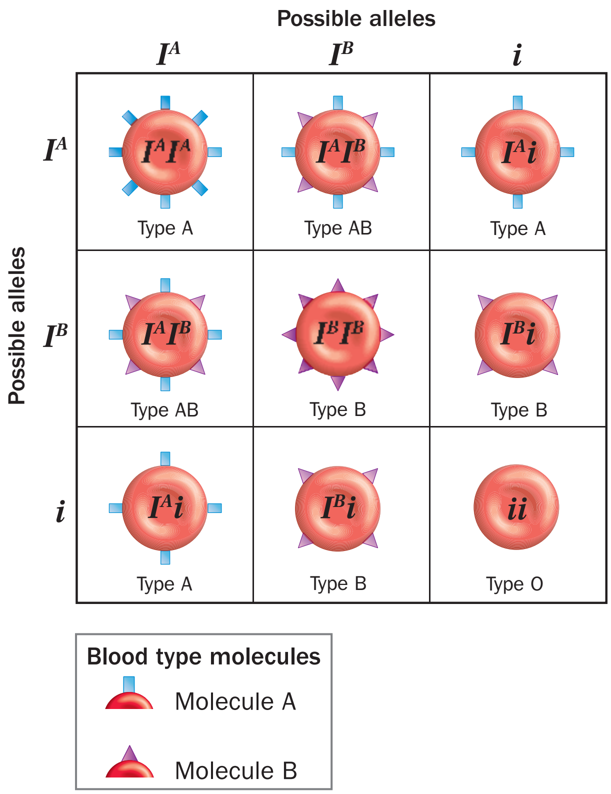
45 min

Objectives

- Investigate the effect of population size on genetic drift.
- Analyze the mathematics of the Hardy-Weinberg principle.

Materials

- buttons, blue (10 to 100)
- buttons, red (10 to 100)
- buttons, white (10 to 100)
- jar or beaker, large, plastic



Genetic Drift

Random chance affects the frequencies of alleles in a population over time. This effect, called *genetic drift,* also depends on population size.

Preparation

1. SCIENTIFIC METHODS **State the Problem** How does population size affect allele frequencies? Read the procedure to see how you will test this.
2. SCIENTIFIC METHODS **Form a Hypothesis** Form a hypothesis that predicts the results of this procedure for three different population sizes.

Procedure

1. Prepare to model the populations. First, assign each color button to one of the alleles (I^A, I^B, or i) of the ABO blood types. Notice how each possible pairing of alleles matches one of the four types (A, B, AB, or O). Then, choose three different population sizes. Also choose one ratio of alleles at which to start all three populations (for example, I^A:I^B:i = 2:2:1). Create tables for your data.
2. Represent the first population's alleles by placing the appropriate number of blue, red, and white buttons in a jar.
3. Randomly select two buttons from the jar to represent one person. Record this person's genotype and phenotype. Place the buttons back into the jar.
4. Repeat step 3 until you have modeled the appropriate number of people in the population. Tally the total number of each allele within this generation.
5. Empty the jar. Refill it with the number and color of buttons that matches the tallies recorded in step 4.
6. Repeat steps 3 through 5 until you have modeled four generations.
7. Repeat steps 2 through 6 to model two more populations.

Analyze and Conclude

1. **Analyzing Data** Describe any changes in genotype and phenotype ratios within each population over time.
2. **Explaining Results** Did any population maintain genetic equilibrium? Explain how you can tell.
3. SCIENTIFIC METHODS **Analyzing Results** Which popultion showed the greatest amount of genetic drift? Explain.

Chapter 17 Summary

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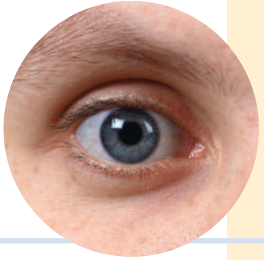
SUPER SUMMARY
Keyword: HX8POPS

Key Ideas

1 Genetic Variation

- Microevolution can be studied by observing changes in the numbers and types of alleles in populations.
- Biologists study polygenic phenotypes by measuring each individual in the population and then analyzing the distribution of the measurements.
- Genetic variation and change are measured in terms of the frequency of alleles in the gene pool of a population.
- The major source of new alleles in natural populations is mutation in germ cells.



Key Terms

population genetics (399)
normal distribution (400)

2 Genetic Change

- The Hardy-Weinberg principle predicts that the frequencies of alleles and genotypes in a population will not change unless at least one of five forces acts upon the population. The forces that can act against genetic equilibrium are gene flow, nonrandom mating, genetic drift, mutation, and natural selection.
- Sexual reproduction creates the possibility that mating patterns or behaviors can influence the gene pool of a population.
- Allele frequencies are more likely to remain stable in large populations than in small populations.
- Natural selection acts only to change the relative frequency of alleles that exist in a population. Natural selection acts on genotypes by removing unsuccessful phenotypes from a population.
- Three major patterns are possible in the way that natural selection affects a distribution of polygenic characters over time. These patterns are directional selection, stabilizing selection, and disruptive selection.

Key Terms

genetic equilibrium (404)

3 Speciation

- Today, scientists may use more than one definition for species. The definition used depends on the organisms and field of science being studied.
- Speciation has occurred when the net effects of evolutionary forces result in a population that has unique features and is reproductively isolated.
- The species that exist at any time are the net result of both speciation and extinction.

Key Terms

reproductive isolation (412)
subspecies (412)

Chapter 17 Review

READING TOOLBOX

1. **Everyday Words in Science** Sometimes, words are used in science in ways that are not far from their everyday meanings, but the words need to be considered in context. For example, *drift* in the context of *genetic drift* means "to float about randomly." What does *pool* mean in the context of *gene pool*?

2. **Concept Map** Construct a concept map that describes the causes of genetic change. Try to include the following words in your map: *Hardy-Weinberg, genetic drift, nonrandom mating, natural selection, mutation,* and *gene flow*.

Using Key Terms

In your own words, write a definition for each of the following terms.

3. *normal distribution*
4. *genetic equilibrium*

Use each of the following terms in a separate sentence.

5. *gene pool*
6. *reproductive isolation*

Understanding Key Ideas

7. The sum of allele frequencies in a population should be
   - **a.** equal to 1.
   - **b.** less than 100.
   - **c.** equal to the phenotype frequencies.
   - **d.** one-half of the genotype frequencies.

8. In the Hardy-Weinberg equation, $p^2 + 2pq + q^2 = 1$, what does the term $2pq$ represent?
   - **a.** frequency of heterozygous individuals
   - **b.** frequency of individuals with two alleles
   - **c.** frequency of homozygous recessive individuals
   - **d.** frequency of homozygous dominant individuals

9. Genetic drift has the greatest impact on
   - **a.** large populations.
   - **b.** small populations.
   - **c.** growing populations.
   - **d.** migrating populations.

10. Which of the following is a reason why natural selection is limited in its influence on evolution?
    - **a.** Natural selection cannot direct the creation of new alleles.
    - **b.** All populations depend on the reproduction of individuals.
    - **c.** Natural selection eliminates certain genotypes from populations.
    - **d.** Individuals tend to produce more offspring than the environment can support.

11. In evolution, *extinction* describes the end of
    - **a.** an allele.
    - **b.** a single species.
    - **c.** an individual organism.
    - **d.** a population of organisms.

Explaining Key Ideas

12. **Describe** the role of population genetics in the study of microevolution.

13. **Identify** the major source of new alleles in natural populations.

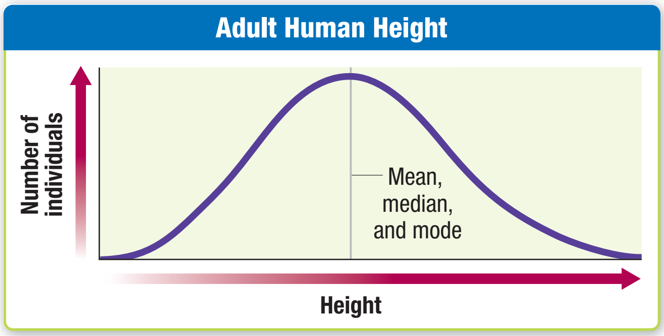
14. **Relate** natural selection to changes in allele frequencies.

15. **Describe** the effect that directional selection has on the phenotypes in a population of organisms.

16. **Describe** the difficulty with defining species.

17. **Explain** how mating behavior can contribute to reproductive isolation.

Use the diagram to answer the following question.

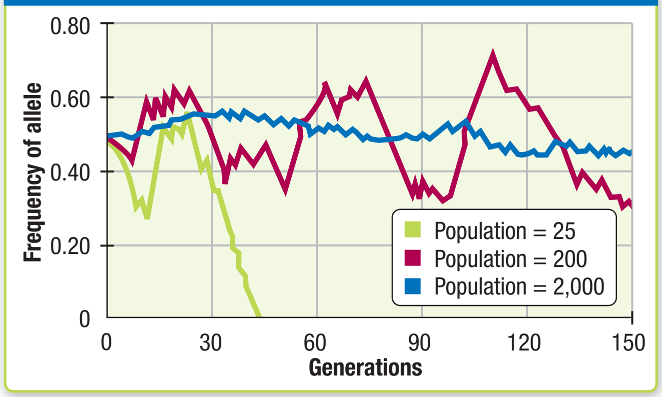


18. **Identify** the kind of characters in a population that will usually form a diagram like this one.

Using Science Graphics

Use the diagram to answer the following question.

Effect of Population Size on Allele Frequency



19. This diagram represents the effect of

a. gene size.
b. genetic drift.
c. speciation.
d. population growth.

This Punnett square shows how each part of the Hardy-Weinberg equation aligns to the possible combinations of two alleles.

	R (*p*)	*r* (*q*)
R (*p*)	*RR* (p^2)	*Rr* (*pq*)
r (*q*)	*rR* (*pq*)	*rr* (q^2)

20. The Hardy-Weinberg equation states that

$$p^2 + 2pq + q^2 = 1$$

Identify from the Punnett square what each part of the equation represents.

Critical Thinking

21. Applying Logic Is a population that is in genetic equilibrium evolving? Explain your answer.

22. Explaining Processes How does inbreeding increase the frequency of homozygotes in a population?

23. Making Inferences Cheetahs have undergone drastic population declines over the last 5,000 years. As a result, the cheetahs alive today are descendants of only a few individuals, and each cheetah is almost genetically uniform with other members of the population. Do you think that genetic drift has affected the cheetah population? Explain your answer.

24. Defining Concepts Propose a definition of *species* that encompasses more than one way that species could be defined.

25. Forming Reasoned Opinions In the laboratory, a scientist studied two identical-looking daisies that belong to the genus *Aster*. The two plants produce fertile hybrids in the laboratory, but they never interbreed in nature because one plant flowers only in the spring and the other flowers only in autumn. Do the plants belong to the same species? Explain.

Writing for Science

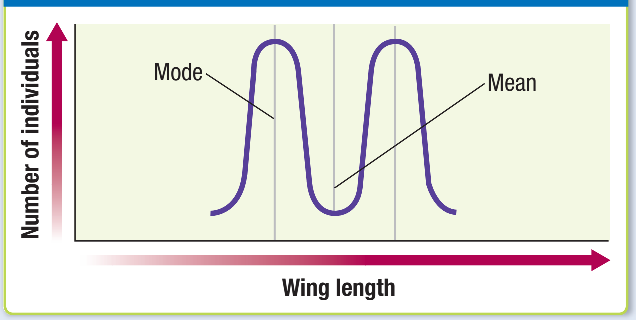
26. Speciation Narration Two species of antelope squirrel live on opposite sides of the Grand Canyon. *Ammospermophilus harrisi,* or Harris's antelope squirrel, lives on the south rim, and *Ammospermophilus leucrurus,* the white-tailed antelope squirrel, lives on the north rim. Imagine that you can speed up time and witness the speciation process ocurring with these squirrels. Write a running commentary—much like that heard at a sports event—on the process of speciation that occurred after the initial population of antelope squirrels became divided on both sides of the canyon. Read or act out your commentary to the class.

Why It Matters

27. Hawaiian Speciation Conduct research to identify another Hawaiian example of adaptive radiation.

Math Skills

Distribution of Wing Length



28. Mean, Median, and Mode Describe this distribution in terms of mean, median, and mode.

29. Math Terminology This kind of distribution is sometimes called a *bimodal* distribution. Why?

Chapter 17 Standardized Test Prep

TEST TIP For a question about a structure or process that has a complex name, write down the name and review its meaning before answering the question.

Science Concepts

1. Population genetics is the study of
   - **A** how individuals evolve.
   - **B** how populations interact.
   - **C** how genes determine traits.
   - **D** how alleles change within populations.

2. Phenotypic variations take the form of
   - **F** genetic differences between organisms.
   - **G** character differences between organisms.
   - **H** molecular differences between organisms.
   - **J** chromosomal differences between organisms.

3. The major source of new alleles in a natural population is
   - **A** mutation.
   - **B** polyploidy.
   - **C** genetic drift.
   - **D** natural selection.

4. Which of the following is an example of non-random mating?
   - **F** Genes are removed from the population when individuals migrate.
   - **G** A change in a populations' allele frequency is due to chance.
   - **H** An individual chooses a mate that has the brightest coloration.
   - **J** An individual is eliminated from the gene pool by natural selection.

5. Random change in allele frequency due to chance alone is called
   - **A** gene flow.
   - **B** genetic drift.
   - **C** natural selection.
   - **D** sexual selection.

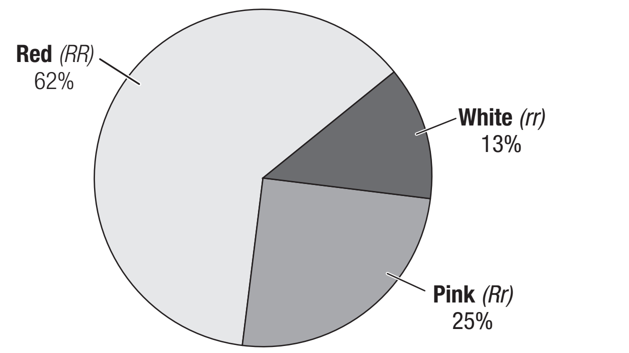
Math Skills

6. The Hardy-Weinberg equation, $p^2 + 2pq + q^2 = 1$, describes a state of equilibrium among all alleles in a population. Expressed in terms of percentages, the sum of allele frequencies in a population would be
   - **F** 1%
   - **G** 2%
   - **H** 50%
   - **J** 100%

Using Science Graphics

Use the diagram to answer the following questions.

Flower Color in a Population of Snapdragons

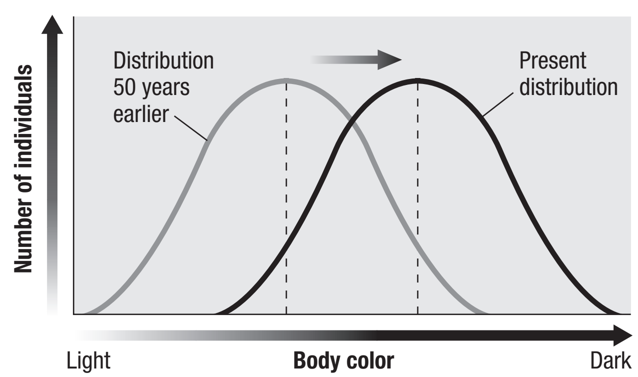


7. In this population, which genotype has the lowest frequency?
   - **A** *RR*
   - **B** *rr*
   - **C** red
   - **D** white

8. In this population, what is the frequency of heterozygotes?
   - **F** 13%
   - **G** 25%
   - **H** 38%
   - **J** 62%

Use the diagram to answer the following question.

Distribution of Body Colors in Bark Beetles



9. The diagram represents which form of selection?
   - **A** sexual selection
   - **B** stabilizing selection
   - **C** disruptive selection
   - **D** directional selection

Chapter 18 Classification

Preview

Why It Matters

More than one million species on Earth have been given scientific names, but many more species exist that have not been identified.

These butterflies look similar, but does that mean they are related? There is more to that answer than meets the eye.

Sometimes, butterflies that look different are actually members of the same species.

Scientists use systems for naming and grouping species. These butterflies have been classified as belonging to the family Pieridae.