16–1 Genes and Variation

As Darwin developed his theory of evolution, he worked under a serious handicap. He didn't know how heredity worked! Although Mendel's work on inheritance in peas was published during Darwin's lifetime, its importance wasn't recognized for decades. This lack of knowledge left two big gaps in Darwin's thinking. First, he had no idea how heritable traits pass from one generation to the next. Second, although variation in heritable traits was central to Darwin's theory, he had no idea how that variation appeared.

Evolutionary biologists connected Mendel's work to Darwin's during the 1930s. By then, biologists understood that genes control heritable traits. They soon realized that changes in genes produce heritable variation on which natural selection can operate. Genes became the focus of new hypotheses and experiments aimed at understanding evolutionary change. Another revolution in evolutionary thought began with Watson and Crick's studies on DNA. Their model of the DNA molecule helped evolutionary biologists because it demonstrated the molecular nature of mutation and genetic variation.

Today, molecular techniques are used to test hypotheses about how heritable variation appears and how natural selection operates on that variation. As you will learn in this chapter, fitness, adaptation, species, and evolutionary change are now defined in genetic terms. We understand how evolution works better than Darwin ever could, beginning with heritable variation.

Guide for Reading

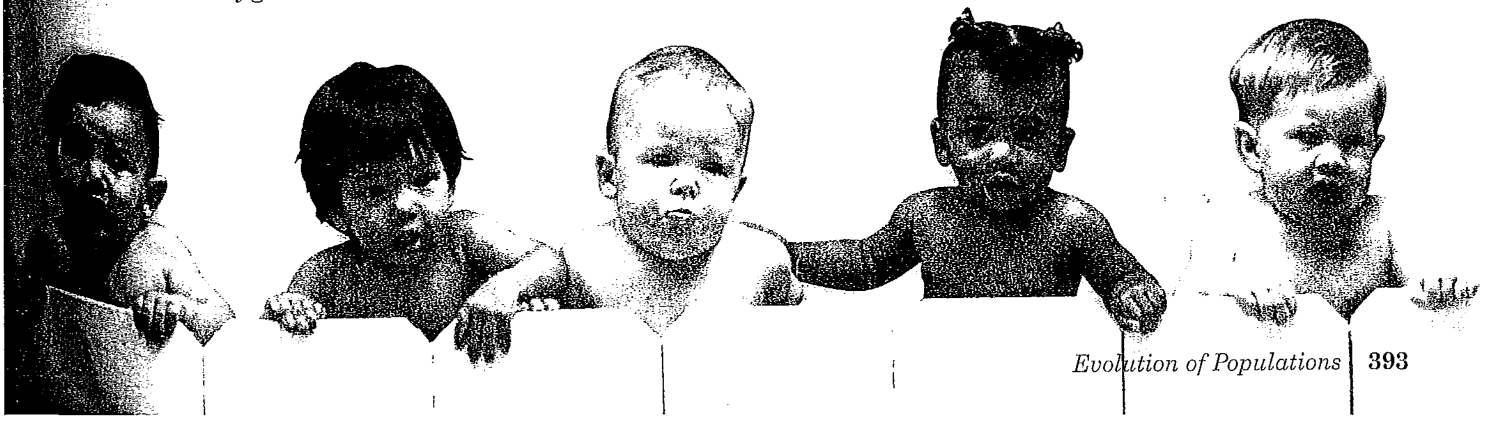
Key Concepts
- What are the main sources of heritable variation in a population?
- How is evolution defined in genetic terms?
- What determines the numbers of phenotypes for a given trait?

Vocabulary
gene pool
relative frequency
single-gene trait
polygenic trait

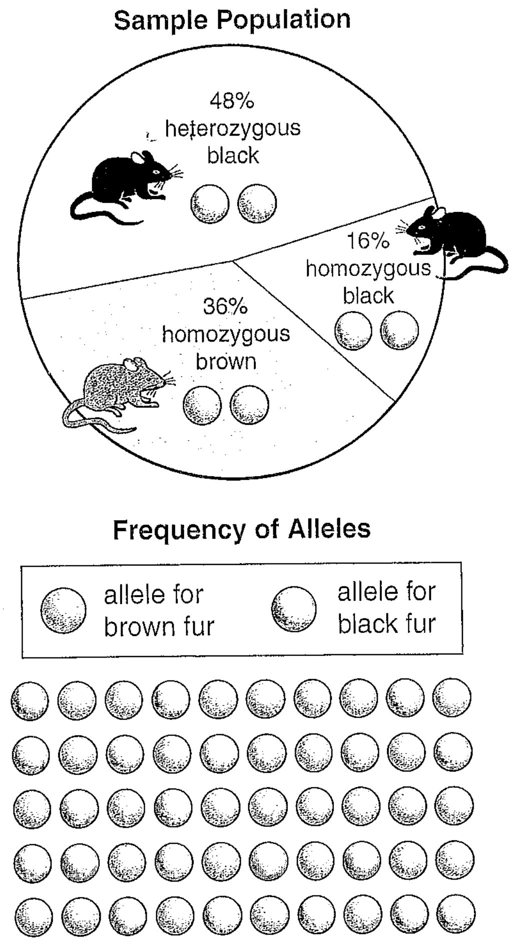
Reading Strategy: Building Vocabulary
Before you read, make a list of the vocabulary terms above. As you read, take notes about the meaning of each term.

How Common Is Genetic Variation?

We now know that many genes have at least two forms, or alleles. Animals such as horses, dogs, and mice often have several alleles for traits such as body size or coat color. Plants, such as peas, often have several alleles for flower color. All organisms have additional genetic variation that is "invisible" because it involves small differences in biochemical processes. In addition, an individual organism is heterozygous for many genes. An insect may be heterozygous for as many as 15 percent of its genes. Individual fishes, reptiles, and mammals are typically heterozygous for between 4 and 8 percent of their genes.



▼ **Figure 16–1** **There are two main sources of genetic variation: mutations and the gene shuffling that results from sexual reproduction.** Each of these babies has inherited a collection of traits. Some, such as hair color, are visible, while others, such as the ability to resist certain diseases, are not.



▲ **Figure 16–2** When scientists determine whether a population is evolving, they may look at the sum of the population's alleles, or its gene pool. This diagram shows the gene pool for fur color in a population of mice. **Calculating** *Here, in a total of 50 alleles, 20 alleles are B (black), and 30 are b (brown). How many of each allele would be present in a total of 100 alleles?*

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Variation and Gene Pools

Genetic variation is studied in populations. A population is a group of individuals of the same species that interbreed. Because members of a population interbreed, they share a common group of genes called a gene pool. A **gene pool** consists of all genes, including all the different alleles, that are present in a population.

The **relative frequency** of an allele is the number of times that the allele occurs in a gene pool, compared with the number of times other alleles for the same gene occur. Relative frequency is often expressed as a percentage. For example, in the mouse population in **Figure 16–2,** the relative frequency of the dominant *B* allele (black fur) is 40 percent, and the relative frequency of the recessive *b* allele (brown fur) is 60 percent. The relative frequency of an allele has nothing to do with whether the allele is dominant or recessive. In this particular mouse population, the recessive allele occurs more frequently than the dominant allele.

Gene pools are important to evolutionary theory, because evolution involves changes in populations over time. **In genetic terms, evolution is any change in the relative frequency of alleles in a population.** For example, if the relative frequency of the *B* allele in the mouse population changed over time to 30 percent, the population is evolving.

CHECKPOINT *What is a gene pool?*

Sources of Genetic Variation

Biologists can now explain how variation is produced. **The two main sources of genetic variation are mutations and the genetic shuffling that results from sexual reproduction.**

Mutations A mutation is any change in a sequence of DNA. Mutations can occur because of mistakes in the replication of DNA or as a result of radiation or chemicals in the environment. Mutations do not always affect an organism's phenotype. For example, a DNA codon altered from GGA to GGU will still code for the same amino acid, glycine. That mutation has no effect on phenotype. Many mutations do produce changes in phenotype, however. Some can affect an organism's fitness, or its ability to survive and reproduce in its environment. Other mutations may have no effect on fitness.

Gene Shuffling Mutations are not the only source of heritable variation. You do not look exactly like your biological parents, even though they provided you with all your genes. You probably look even less like any brothers or sisters you may have. Yet, no matter how you feel about your relatives, mutant genes are not primarily what makes them so different from you.

Most heritable differences are due to gene shuffling that occurs during the production of gametes. Recall that each chromosome of a homologous pair moves independently during meiosis. As a result, the 23 pairs of chromosomes found in humans can produce 8.4 million different combinations of genes!

Another process, crossing-over, also occurs during meiosis. Crossing-over further increases the number of different genotypes that can appear in offspring. Recall that a genotype is an organism's genetic makeup. When alleles are recombined during sexual reproduction, they can produce dramatically different phenotypes. Thus, sexual reproduction is a major source of variation within many populations.

Sexual reproduction can produce many different phenotypes, but it does not change the relative frequency of alleles in a population. To understand why, compare a population's gene pool to a deck of playing cards. Each card represents an allele found in the population. The exchange of genes during gene shuffling is similar to shuffling a deck of cards. Shuffling leads to different types of hands, but it can never change the relative numbers of aces, kings, or queens in the deck. The probability of drawing an ace off the top of the deck will always be 4 in 52, or one thirteenth (4/52 = 1/13). No matter how many times you shuffle the deck, this probability will remain the same. Similarly, sexual reproduction produces many different combinations of genes, but in itself it does not alter the relative frequencies of each type of allele in a population.

CHECKPOINT *What are the sources of heritable variation?*

Single-Gene and Polygenic Traits

Heritable variation can be expressed in a variety of ways. **The number of phenotypes produced for a given trait depends on how many genes control the trait.** Among humans, a widow's peak—a downward dip in the center of the hairline—is a **single-gene trait.** It is controlled by a single gene that has two alleles. The allele for a widow's peak is dominant over the allele for a hairline with no peak. As a result, variation in this gene leads to only two distinct phenotypes, as shown in **Figure 16–3.**

As you can see, the frequency of phenotypes caused by this single gene is represented on the bar graph. This graph shows that the presence of a widow's peak may be less common in a population than the absence of a widow's peak, even though the allele for a widow's peak is the dominant form. In real populations, phenotypic ratios are determined by the frequency of alleles in the population as well as by whether the alleles are in the dominant or recessive form. Allele frequencies may not match Mendelian ratios.

Word Origins

Gene comes from the Greek word *gignesthai,* meaning "to be born," and refers to factors that produce an organism. The prefix *poly-* comes from the Greek word *polys,* meaning "many," so *polygenic* means "having many genes." The prefix *mono-* means "one." **What do you think the term *monogenic* means?**

Figure 16–3 In humans, a single gene with two alleles controls whether a person has a widow's peak (left) or does not have a widow's peak (right). As a result, only two phenotypes are possible. **The number of phenotypes a given trait has is determined by how many genes control the trait.**

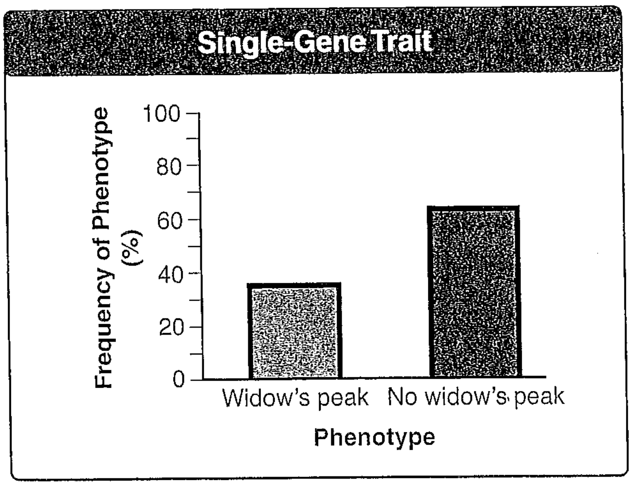
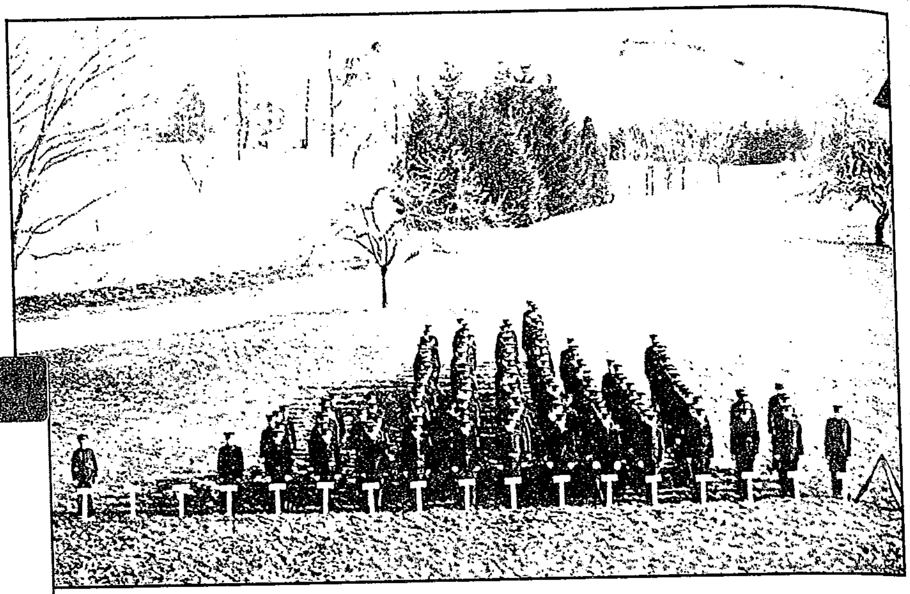
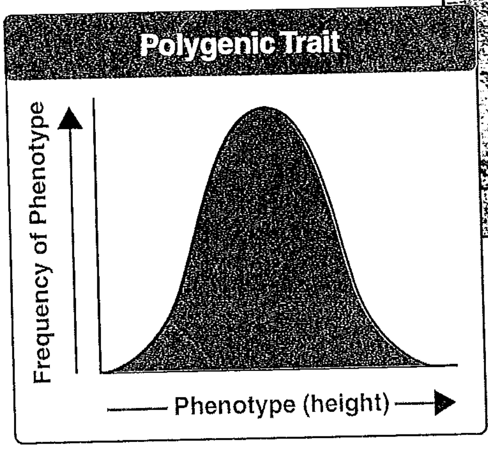


Figure 16–4 The graph below shows the distribution of phenotypes that would be expected for a trait if many genes contributed to the trait. The photograph shows the actual distribution of heights of a group of young men. **Using Tables and Graphs** *What does the shape of the graph indicate about height in humans?*





Many traits are controlled by two or more genes and are, therefore, called **polygenic traits.** Each gene of a polygenic trait often has two or more alleles. As a result, one polygenic trait can have many possible genotypes and phenotypes.

Height in humans is one example of a polygenic trait. You can sample phenotypic variation in this trait by measuring the height of all the students in your class. You can then calculate the average height of this group. Many students will be just a little taller or shorter than average. Some of your classmates, however, will be very tall or very short. If you graph the number of individuals of each height, you may get a graph similar to the one in **Figure 16–4.** The symmetrical bell-like shape of this curve is typical of polygenic traits. A bell-shaped curve is also called a normal distribution.

16–1 Section Assessment

1. **Key Concept** In genetic terms, what indicates that evolution is occurring in a population?
2. **Key Concept** What two processes can lead to inherited variation in populations?
3. **Key Concept** How does the range of phenotypes differ between single-gene traits and polygenic traits?
4. What is a gene pool? How are allele frequencies related to gene pools?
5. **Critical Thinking Evaluating** Evaluate the significance of mutations to the process of biological evolution. (*Hint:* How does mutation affect genetic variation?)

Focus on the BIG Idea

Information and Heredity
How does the process known as independent assortment relate to the genetic variation that results from sexual reproduction? *Hint:* Refer to Chapter 11.

16–2 Evolution as Genetic Change

Guide for Reading

Key Concepts
- How does natural selection affect single-gene and polygenic traits?
- What is genetic drift?
- What is the Hardy-Weinberg principle?

Vocabulary
directional selection
stabilizing selection
disruptive selection
genetic drift
founder effect
Hardy-Weinberg principle
genetic equilibrium

Reading Strategy: Outlining Before you read, use the headings to make an outline. As you read, add a sentence after each heading to provide key information.

A genetic view of evolution offers a new way to look at key evolutionary concepts. Each time an organism reproduces, it passes copies of its genes to its offspring. We can therefore view evolutionary fitness as an organism's success in passing genes to the next generation. In the same way, we can view an evolutionary adaptation as any genetically controlled physiological, anatomical, or behavioral trait that increases an individual's ability to pass along its genes.

Natural selection never acts directly on genes. Why? Because it is an entire organism—not a single gene—that either survives and reproduces or dies without reproducing. Natural selection, therefore, can only affect which individuals survive and reproduce and which do not. If an individual dies without reproducing, the individual does not contribute its alleles to the population's gene pool. If an individual produces many offspring, its alleles stay in the gene pool and may increase in frequency.

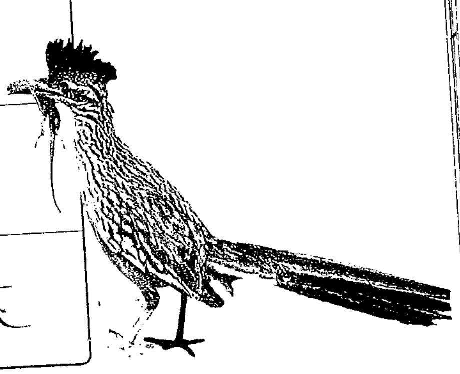
Now recall that evolution is any change over time in the relative frequencies of alleles in a population. This reminds us that it is populations, not individual organisms, that can evolve over time. Let us see how this can happen in different situations.

Natural Selection on Single-Gene Traits

Natural selection on single-gene traits can lead to changes in allele frequencies and thus to evolution. Imagine that a hypothetical population of lizards, shown in **Figure 16-5**, is normally brown, but experiences mutations that produce red and black forms. What happens to those new alleles? If red lizards are more visible to predators, they might be less likely to survive and reproduce, and the allele for red coloring might not become common.

Effect of Color Mutations on Lizard Survival

Initial Population	Generation 10	Generation 20	Generation 30
80%	80%	70%	40%
10%	0%	0%	0%
10%	20%	30%	60%



▼ **Figure 16–5** **Natural selection on single-gene traits can lead to changes in allele frequencies and thus to evolution.** Organisms of one color, for example, may produce fewer offspring than organisms of other colors.

Black lizards, on the other hand, might absorb more sunlight and warm up faster on cold days. If high body temperature allows them to move faster to feed and to avoid predators, they might produce more offspring than brown forms. The allele for black color might then increase in relative frequency. If a color change has no effect on fitness, the allele that produces it would not be under pressure from natural selection.

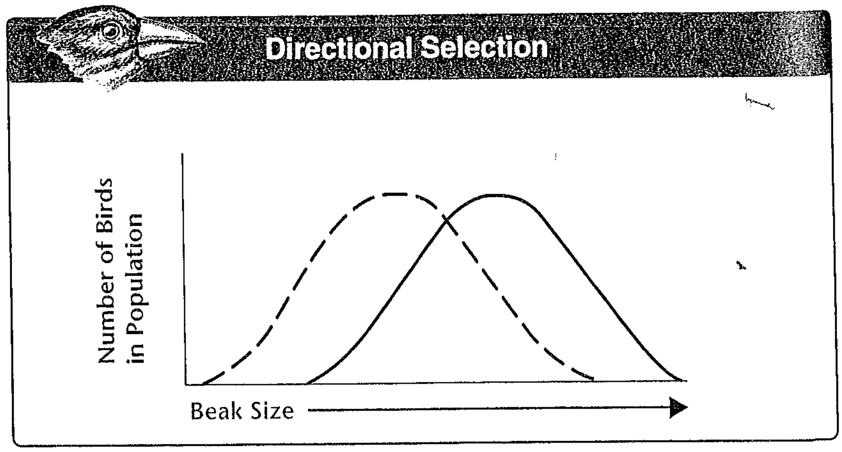
Natural Selection on Polygenic Traits

When traits are controlled by more than one gene, the effects of natural selection are more complex. As you learned earlier, the action of multiple alleles on traits such as height produces a range of phenotypes that often fit a bell curve. The fitness of individuals close to one another on the curve will not be very different. But fitness can vary a great deal from one end of such a curve to the other. And where fitness varies, natural selection can act. **Natural selection can affect the distributions of phenotypes in any of three ways: directional selection, stabilizing selection, or disruptive selection.**

Directional Selection When individuals at one end of the curve have higher fitness than individuals in the middle or at the other end, **directional selection** takes place. The range of phenotypes shifts as some individuals fail to survive and reproduce while others succeed. To understand this, consider how limited resources, such as food, can affect the long-term survival of individuals and the evolution of populations.

Among seed-eating birds such as Darwin's finches, for example, birds with bigger, thicker beaks can feed more easily on larger, harder, thicker-shelled seeds. Suppose a food shortage causes the supply of small and medium-sized seeds to run low, leaving only larger seeds. Birds whose beaks enable them to open those larger seeds will have better access to food. Birds with the big-beak adaptation would therefore have higher fitness than small-beaked birds. The average beak size of the population would probably increase, as shown in **Figure 16–6.**

Figure 16–6 **Directional selection occurs when individuals at one end of the curve have higher fitness than individuals in the middle or at the other end.** In this example, a population of seed-eating birds experiences directional selection when a food shortage causes the supply of small seeds to run low. The dotted line shows the original distribution of beak sizes. The solid line shows how the distribution of beak sizes would change as a result of selection.



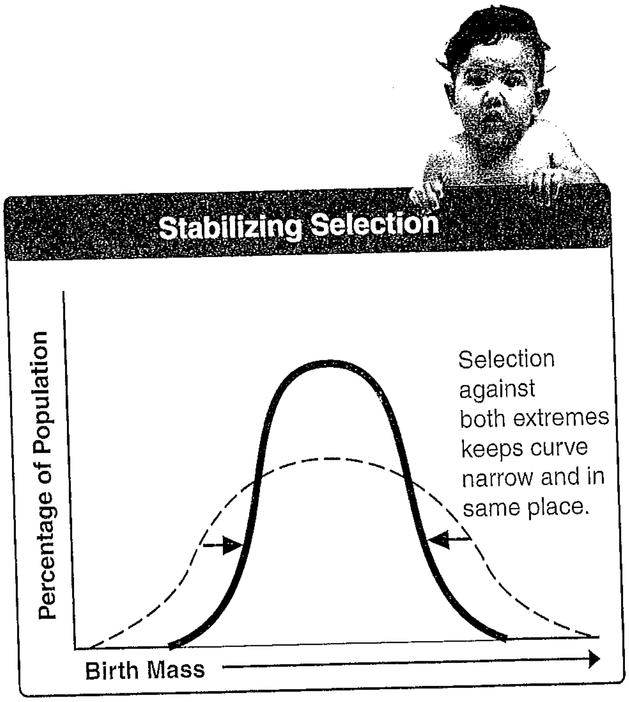
Stabilizing Selection When individuals near the center of the curve have higher fitness than individuals at either end of the curve, **stabilizing selection** takes place. This situation keeps the center of the curve at its current position, but it narrows the overall graph.

As shown in **Figure 16–7**, the mass of human infants at birth is under the influence of stabilizing selection. Human babies born much smaller than average are likely to be less healthy and thus less likely to survive. Babies that are much larger than average are likely to have difficulty being born. The fitness of these larger or smaller individuals is, therefore, lower than that of more average-sized individuals.

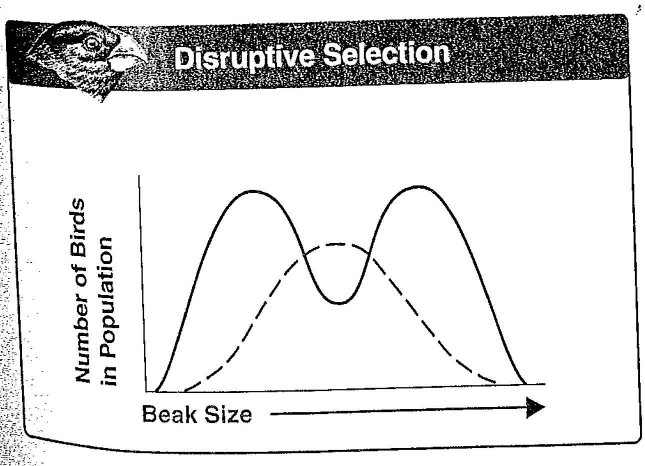
Disruptive Selection When individuals at the upper and lower ends of the curve have higher fitness than individuals near the middle, **disruptive selection** takes place. In such situations, selection acts most strongly against individuals of an intermediate type. If the pressure of natural selection is strong enough and lasts long enough, this situation can cause the single curve to split into two. In other words, selection creates two distinct phenotypes.

For example, suppose a population of birds lives in an area where medium-sized seeds become less common and large and small seeds become more common. Birds with unusually small or large beaks would have higher fitness. As shown in **Figure 16–8**, the population might split into two subgroups: one that eats small seeds and one that eats large seeds.

✓CHECKPOINT *How do stabilizing selection and disruptive selection differ?*



▲ **Figure 16–7** **Stabilizing selection takes place when individuals near the center of a curve have higher fitness than individuals at either end.** This example shows that human babies born at an average mass are more likely to survive than babies born either much smaller or much larger than average.



◀ **Figure 16–8** **When individuals at the upper and lower ends of the curve have higher fitness than individuals near the middle, disruptive selection takes place.** In this example, average-sized seeds become less common, and larger and smaller seeds become more common. As a result, the bird population splits into two subgroups specializing in eating different-sized seeds.

Genetic Drift

Natural selection is not the only source of evolutionary change. In small populations, an allele can become more or less common simply by chance. Recall that genetics is controlled by the laws of probability. These laws can be used to predict the overall results of genetic crosses in large populations. However, the smaller a population is, the farther the results may be from what the laws of probability predict. This kind of random change in allele frequency is called **genetic drift.** How does genetic drift take place? **In small populations, individuals that carry a particular allele may leave more descendants than other individuals, just by chance. Over time, a series of chance occurrences of this type can cause an allele to become common in a population.**

Genetic drift may occur when a small group of individuals colonizes a new habitat. These individuals may carry alleles in different relative frequencies than did the larger population from which they came. If so, the population that they found will be genetically different from the parent population. Here, however, the cause is not natural selection but simply chance—specifically, the chance that particular alleles were in one or more of the founding individuals, as shown in **Figure 16–9.** A situation in which allele frequencies change as a result of the migration of a small subgroup of a population is known as the **founder effect.** One example of the founder effect is the evolution of several hundred species of fruit flies found on different Hawaiian Islands. All of those species descended from the same original mainland population. Those species in different habitats on different islands now have allele frequencies that are different from those of the original species.

CHECKPOINT What is genetic drift?

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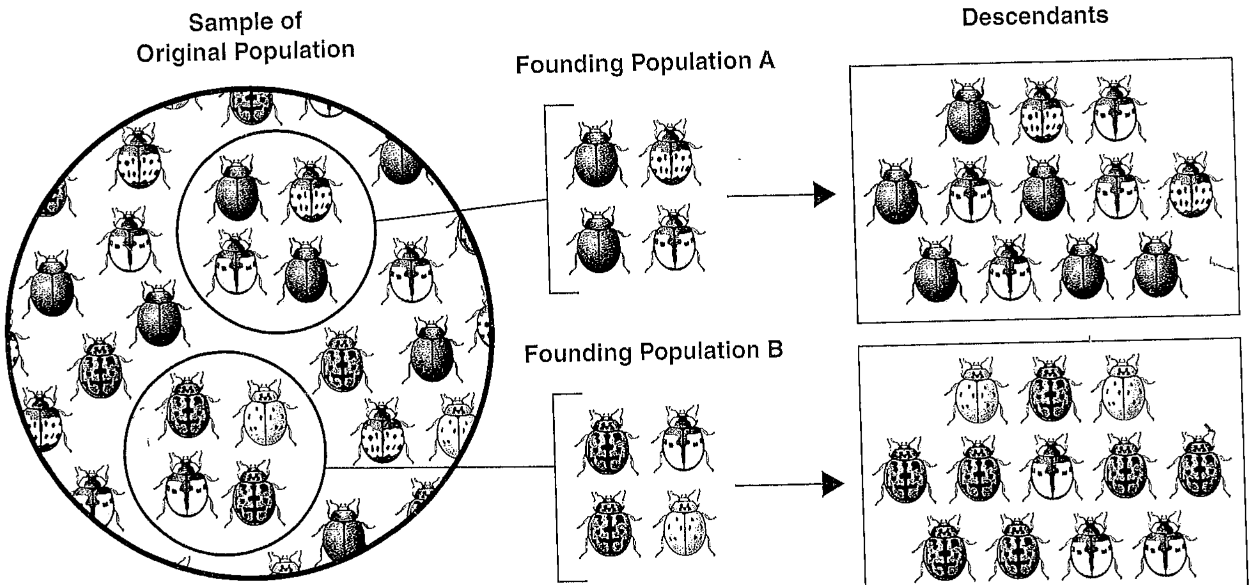
Figure 16–9 In small populations, individuals that carry a particular allele may have more descendants than other individuals. Over time, a series of chance occurrences of this type can cause an allele to become more common in a population. This model demonstrates how two small groups from a large, diverse population could produce new populations that differ from the original group.



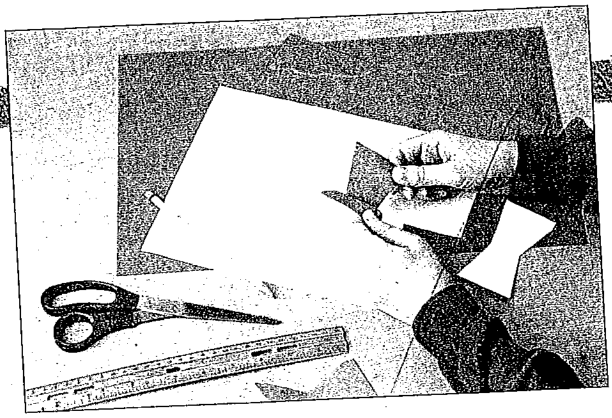
Quick Lab

Can the environment affect survival?

Materials scissors, construction paper (several colors), transparent tape, 15-cm ruler, watch with a second hand

Procedure

1. **Predicting** Predict what would happen to a population of butterflies that includes some individuals that are easy for predators to see and some that blend in with the environment.
2. Choose three different-colored sheets of construction paper. Cut out a butterfly shape from each sheet, 5 × 10 cm in size, as shown. **CAUTION:** *Be careful with scissors.*
3. Tape your butterflies to different-colored surfaces. Then, return to your seat.



4. Record how many shapes of each color you can count from your desk in 5 seconds.
5. Exchange your observations with your classmates to determine the class total for each color.

Analyze and Conclude

1. **Analyzing Data** According to your class data, which colors of butterfly are easiest to see? Which color of butterfly would be most easily caught by a predator?
2. **Inferring** What will happen to the butterfly population after many generations if predators consume most of the easy-to-see butterflies?

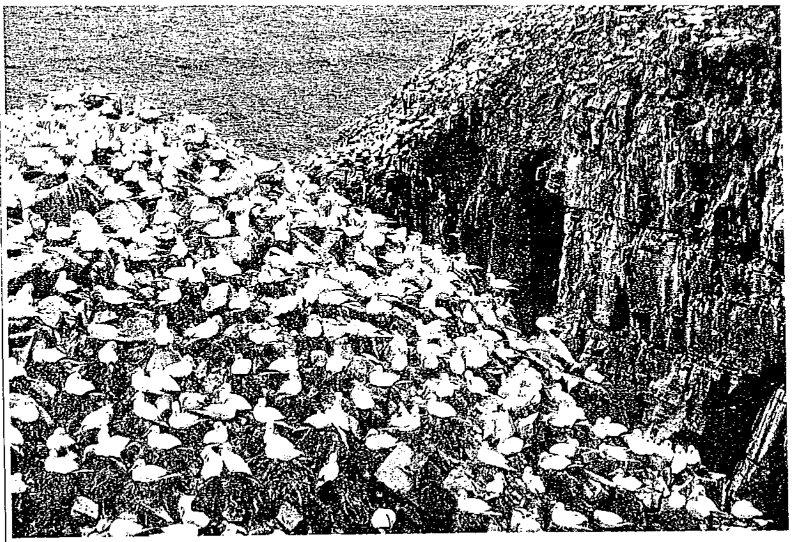
Evolution Versus Genetic Equilibrium

To clarify how evolutionary change operates, scientists often find it helpful to determine what happens when *no* change takes place. So biologists ask: Are there any conditions under which evolution will not occur? Is there any way to recognize when that is the case? The answers to those questions are provided by the Hardy-Weinberg principle, named after two researchers who independently proposed it in 1908.

The **Hardy-Weinberg principle** states that allele frequencies in a population will remain constant unless one or more factors cause those frequencies to change. The situation in which allele frequencies remain constant is called **genetic equilibrium.** If the allele frequencies do not change, the population will not evolve.

Under what conditions does the Hardy-Weinberg principle hold? **Five conditions are required to maintain genetic equilibrium from generation to generation: (1) There must be random mating; (2) the population must be very large; and (3) there can be no movement into or out of the population, (4) no mutations, and (5) no natural selection.**

In some populations, these conditions may be met or nearly met for long periods of time. If, however, the conditions are not met, the genetic equilibrium will be disrupted, and the population will evolve.



▲ **Figure 16–10** **One of the five conditions that are needed to maintain genetic equilibrium from one generation to the next is large population size.** The allele frequencies of large populations, such as this group of birds, are less likely to be changed through the process of genetic drift.

Random Mating All members of the population must have an equal opportunity to produce offspring. Random mating ensures that each individual has an equal chance of passing on its alleles to offspring.

In natural populations, however, mating is rarely completely random. Many species, including lions and wolves, select mates based on particular heritable traits, such as size or strength. Such nonrandom mating means that the genes for those traits are *not* in equilibrium but are under strong selection pressure.

Large Population A large population size is also important in maintaining genetic equilibrium. That is because genetic drift has less effect on large populations, such as the population of birds shown in **Figure 16–10**, than on small ones.

No Movement Into or Out of the Population Because individuals may bring new alleles into a population, there must be no movement of individuals into or out of a population. In genetic terms, the population's gene pool must be kept together and kept separate from the gene pools of other populations.

No Mutations If genes mutate from one form into another, new alleles may be introduced into the population, and allele frequencies will change.

No Natural Selection All genotypes in the population must have equal probabilities of survival and reproduction. No phenotype can have a selective advantage over another. In other words, there can be no natural selection operating on the population.

16–2 Section Assessment

1. **Key Concept** Describe how natural selection can affect traits controlled by single genes.
2. **Key Concept** Describe three patterns of natural selection on polygenic traits. Which one leads to two distinct phenotypes?
3. **Key Concept** How does genetic drift lead to a change in a population's gene pool?
4. **Key Concept** What is the Hardy-Weinberg principle?
5. **Critical Thinking Comparing and Contrasting** How are directional selection and disruptive selection similar? How are they different?

Sharpen Your Skills

Using Models
Demonstrate natural selection on polygenic traits by cutting a sheet of paper into squares of five different sizes to represent sizes in a population. Use the squares to model directional, stabilizing, and disruptive selection. Then, think of an alternative way to model one type of selection. Decide which model works best, and give your reasons.

16–3 The Process of Speciation

Guide for Reading

Key Concepts
- What factors are involved in the formation of new species?
- Describe the process of speciation in the Galápagos finches.

Vocabulary
speciation
reproductive isolation
behavioral isolation
geographic isolation
temporal isolation

Reading Strategy: Using Visuals Before you read, preview **Figure 16–16.** As you read about speciation of Darwin's finches, notice what happens at each step in the diagram.

Factors such as natural selection and chance events can change the relative frequencies of alleles in a population. But how do these changes lead to the formation of new species, or **speciation**?

Recall that biologists define a species as a group of organisms that breed with one another and produce fertile offspring. This means that individuals in the same species share a common gene pool. Because a population of individuals has a shared gene pool, a genetic change that occurs in one individual can spread through the population as that individual and its offspring reproduce. If a genetic change increases fitness, that allele will eventually be found in many individuals of that population.

Isolating Mechanisms

Given this genetic definition of species, what must happen for a species to evolve into two new species? The gene pools of two populations must become separated for them to become new species. **As new species evolve, populations become reproductively isolated from each other.** When the members of two populations cannot interbreed and produce fertile offspring, **reproductive isolation** has occurred. At that point, the populations have separate gene pools. They respond to natural selection or genetic drift as separate units. Reproductive isolation can develop in a variety of ways, including behavioral isolation, geographic isolation, and temporal isolation.

Behavioral Isolation One type of isolating mechanism, **behavioral isolation,** occurs when two populations are capable of interbreeding but have differences in courtship rituals or other reproductive strategies that involve behavior. For example, the eastern and western meadowlarks shown in **Figure 16–11** are very similar birds whose habitats overlap in the center of the United States. Members of the two species will not mate with each other, however, partly because they use different songs to attract mates. Eastern meadowlarks will not respond to western meadowlark songs, and vice versa.

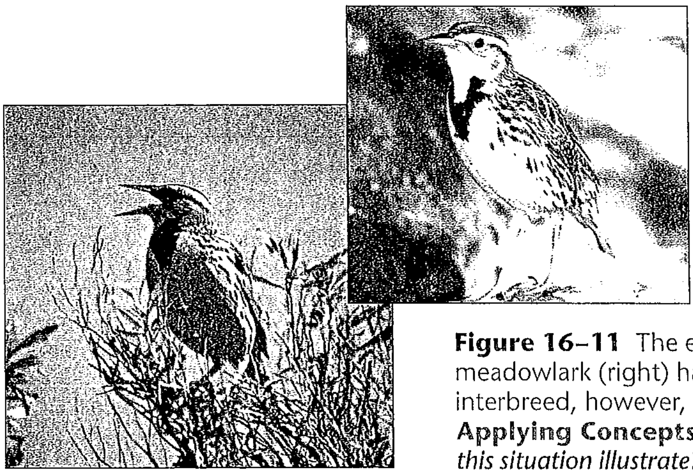
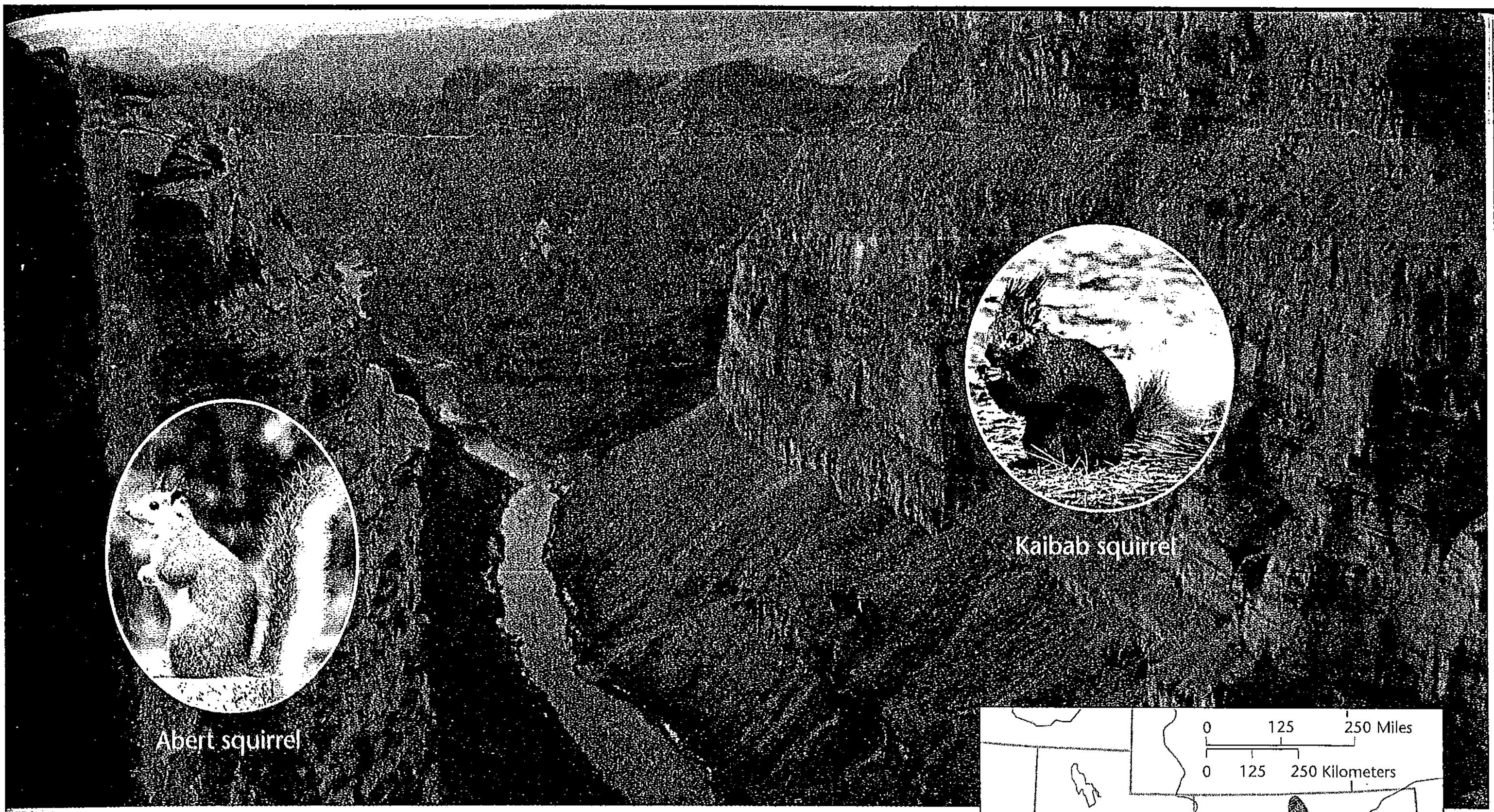


Figure 16–11 The eastern meadowlark (left) and western meadowlark (right) have overlapping ranges. They do not interbreed, however, because they have different mating songs. **Applying Concepts** *What type of reproductive isolation does this situation illustrate?*



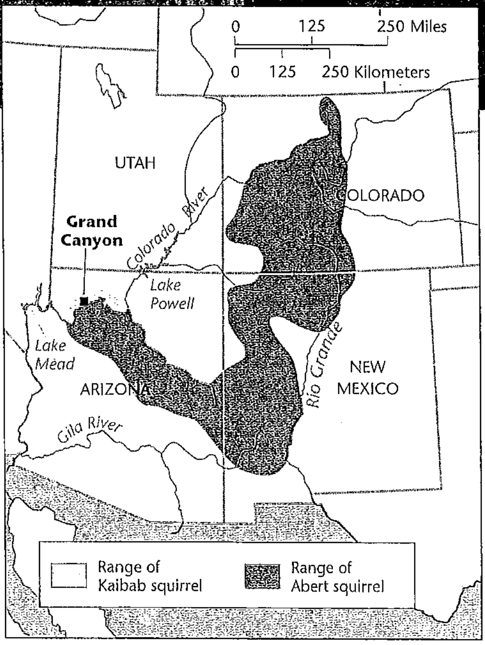


Figure 16–12 **When two populations of a species become reproductively isolated, new species can develop.** The Kaibab squirrel evolved from the Abert squirrel. The Kaibab squirrels were isolated from the main population by the Colorado River.

Geographic Isolation With **geographic isolation,** two populations are separated by geographic barriers such as rivers, mountains, or bodies of water. The Abert squirrel in **Figure 16–12,** for example, lives in the Southwest. About 10,000 years ago, the Colorado River split the species into two separate populations. Two separate gene pools formed. Genetic changes that appeared in one group were not passed to the other. Natural selection worked separately on each group and led to the formation of a distinct subspecies, the Kaibab squirrel. The Abert and Kaibab squirrels have very similar anatomical and physiological characteristics, indicating that they are closely related. However, the Kaibab squirrel differs from the Abert squirrel in significant ways, such as fur coloring.

Geographic barriers do not guarantee the formation of new species, however. Separate lakes may be linked for a time during a flood, or a land bridge may temporarily form between islands, enabling separated populations to mix. If two formerly separated populations can still interbreed, they remain a single species. Also, any potential geographic barrier may separate certain types of organisms but not others. A large river will keep squirrels and other small rodents apart, but it does not necessarily isolate bird populations.

Temporal Isolation A third isolating mechanism is **temporal isolation,** in which two or more species reproduce at different times. For example, three similar species of orchid all live in the same rain forest. Each species releases pollen only on a single day. Because the three species release pollen on different days, they cannot pollinate one another.

✓CHECKPOINT *How can temporal isolation lead to speciation?*

Galápagos Islands Finches						
Shape of Head and Beak						
Common Name of Finch Species	Vegetarian tree finch	Large insectivorous tree finch	Woodpecker finch	Cactus ground finch	Sharp-beaked ground finch	Large ground finch
Main Food	Fruits	Insects	Insects	Cacti	Seeds	Seeds
Feeding Adaptation	Parrotlike beak	Grasping beak	Uses cactus spines	Large crushing beak	Pointed crushing beak	Large crushing beak
Habitat	Trees	Trees	Trees	Ground	Ground	Ground

▲ **Figure 16–13** Detailed genetic studies have shown that these finches evolved from a species with a more-or-less general-purpose beak. **Formulating Hypotheses** *Suggest how one of these beaks could have resulted from natural selection.*

Testing Natural Selection in Nature

Now that you know the basic mechanisms of evolutionary change, you might wonder if these processes can be observed in nature. The answer is yes. In fact, some of the most important studies showing natural selection in action involve descendants of the finches that Darwin observed in the Galápagos Islands.

Those finch species looked so different from one another that when Darwin first saw them, he did not realize they were all finches. He thought they were blackbirds, warblers, and other kinds of birds. The species he examined differed greatly in the sizes and shapes of their beaks and in their feeding habits, as shown in **Figure 16–13.** Some species fed on small seeds, while others ate large seeds with thick shells. One species used cactus spines to pry insects from dead wood. One species, not shown here, even pecked at the tails of large sea birds and drank their blood!

Once Darwin discovered that these birds were all finches, he hypothesized that they had descended from a common ancestor. Over time, he proposed, natural selection shaped the beaks of different bird populations as they adapted to eat different foods.

That was a reasonable hypothesis. But was there any way to test it? No one thought so, until the work of Peter and Rosemary Grant from Princeton University proved otherwise. For more than twenty years, the Grants, shown in **Figure 16–14,** have been collaborating to band and measure finches on the Galápagos Islands. They realized that Darwin's hypothesis relied on two testable assumptions. First, in order for beak size and shape to evolve, there must be enough heritable variation in those traits to provide raw material for natural selection. Second, differences in beak size and shape must produce differences in fitness that cause natural selection to occur.

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The Grants tested these hypotheses on the medium ground finch on Daphne Major, one of the Galápagos Islands. This island is large enough to support good-sized finch populations, yet small enough to enable the Grants to catch and identify nearly every bird belonging to the species under study.

Variation The Grants first identified and measured as many individual birds as possible on the island. They recorded which birds were still living and which had died, which had succeeded in breeding and which had not. For each individual, they also recorded anatomical characteristics such as wing length, leg length, beak length, beak depth, beak color, feather colors, and total mass. Many of these characteristics appeared in bell-shaped distributions typical of polygenic traits. These data indicate that there is great variation of heritable traits among the Galápagos finches.

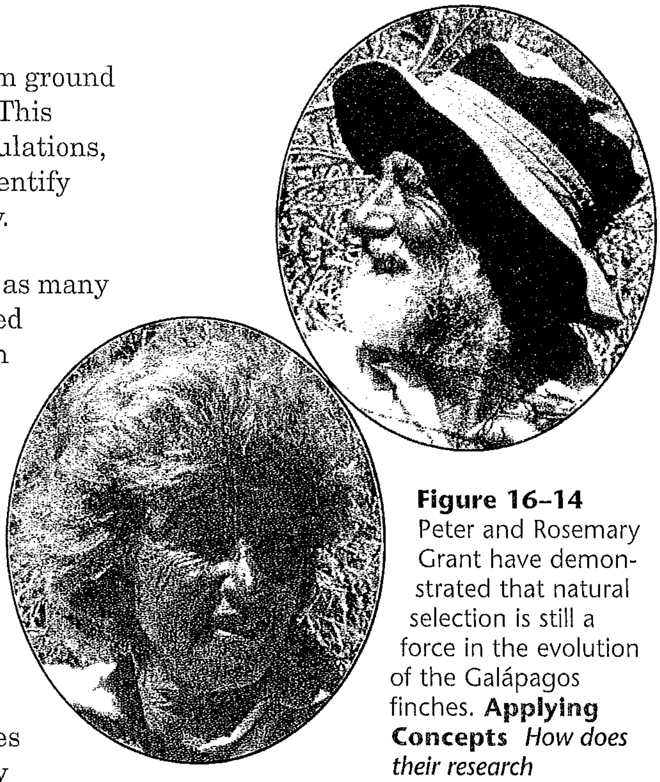


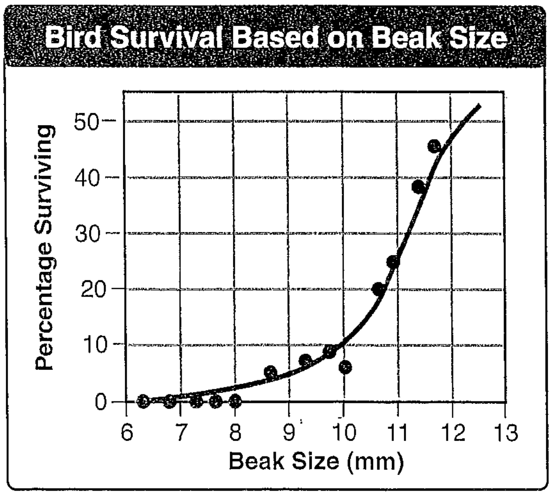
Figure 16–14 Peter and Rosemary Grant have demonstrated that natural selection is still a force in the evolution of the Galápagos finches. **Applying Concepts** *How does their research demonstrate natural selection?*

Natural Selection Other researchers who had visited the Galápagos did not see the different finches competing or eating different foods. During the rainy season, when these researchers visited, there is plenty of food. Under these conditions, finches often eat the most available type of food. During dry-season drought, however, some foods become scarce, and others disappear altogether. At that time, differences in beak size can mean the difference between life and death. To survive, birds become feeding specialists. Each species selects the type of food its beak handles best. Birds with big, heavy beaks, for example, select big, thick seeds that no other species can crack open.

The Grants' most interesting discovery was that individual birds with different-sized beaks had different chances of survival during a drought. When food for the finches was scarce, individuals with the largest beaks were more likely to survive, as shown in **Figure 16–15.** Beak size also plays a role in mating behavior, because big-beaked birds tend to mate with other big-beaked birds. The Grants observed that average beak size in that finch population increased dramatically over time. This change in beak size is an example of directional selection operating on an anatomical trait.

By documenting natural selection in the wild, the Grants provided evidence of the process of evolution: The next generation of finches had larger beaks than did the generation before selection had occurred. An important result of this work was their finding that natural selection takes place frequently—and sometimes very rapidly. Changes in the food supply on the Galápagos caused measurable fluctuations in the finch populations over a period of only decades. This is markedly different from the slow, gradual evolution that Darwin envisioned.

▼ **Figure 16–15** This graph shows the survival rate of one species of ground-feeding finches, the medium ground finch, *Geospiza fortis.* **Using Tables and Graphs** *What trend does this graph show?*



✔ CHECKPOINT *What type of natural selection did the Grants observe in the Galápagos?*

Discovery Education To find out more about ongoing research on the Galápagos, view track 5 "The Galápagos Islands: A Glimpse Into the Past" on the *BioDetectives* DVD.

Speciation in Darwin's Finches

The Grants' work demonstrates that finch beak size can be changed by natural selection. If we combine this information with other evolutionary concepts you have learned in this chapter, we can show how natural selection can lead to speciation. We can devise a hypothetical scenario for the evolution of all Galápagos finches from a single group of founding birds. **Speciation in the Galápagos finches occurred by founding of a new population, geographic isolation, changes in the new population's gene pool, reproductive isolation, and ecological competition.**

Founders Arrive Many years ago, a few finches from the South American mainland—species A—flew or were blown to one of the Galápagos Islands, as shown in **Figure 16–16.** Finches are small birds that do not usually fly far over open water. These birds may have gotten lost, or they may have been blown off course by a storm. Once they arrived on one of the islands, they managed to survive and reproduce.

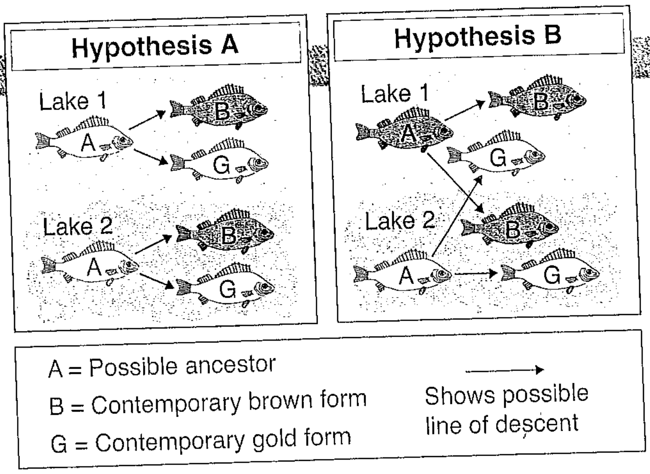
Geographic Isolation Later on, some birds from species A crossed to another island in the Galápagos group. Because these birds do not usually fly over open water, they rarely move from island to island. Thus, finch populations on the two islands were essentially isolated from each other and no longer shared a common gene pool.

✓CHECKPOINT How did finches arrive in the Galápagos Islands?

Analyzing Data

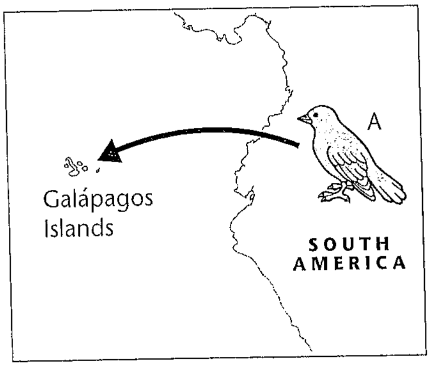
How Are These Fish Related?

A research team studied two lakes in an area that sometimes experiences flooding. Each lake contained two types of similar fish: a dull brown form and an iridescent gold form. The team wondered how all the fish were related, and they considered the two hypotheses diagrammed on the right.

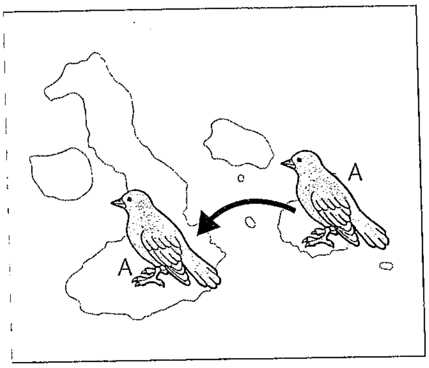


1. **Interpreting Graphics** Study the two diagrams. What does hypothesis A indicate about the ancestry of the fish in Lake 1 and Lake 2? What does hypothesis B indicate?
2. **Comparing and Contrasting** According to the two hypotheses, what is the key difference in the way the brown and gold fish populations might have formed?
3. **Drawing Conclusions** A DNA analysis showed that the brown and gold fish from Lake 1 are the most closely related. Which hypothesis does this evidence support?
4. **Asking Questions** To help determine whether the brown and gold fish are members of separate species, what question might scientists ask?

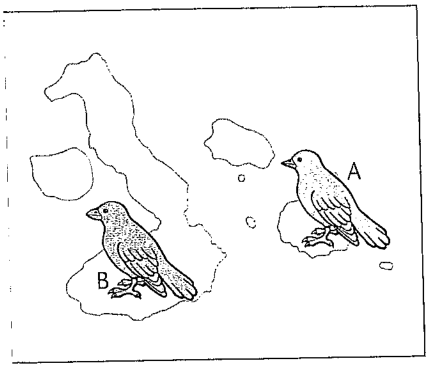
Figure 16–16 **Speciation in the Galápagos finches occurred by founding of new populations, geographic isolation, gene pool changes, reproductive isolation, and ecological competition.** Small groups of finches moved from one island to another, became reproductively isolated, and evolved into new species.



Founders Arrive
A few finches travel from South America to one of the islands. There, they survive and reproduce.



Geographic Isolation
Some birds from species A cross to a second island. The two populations no longer share a gene pool.



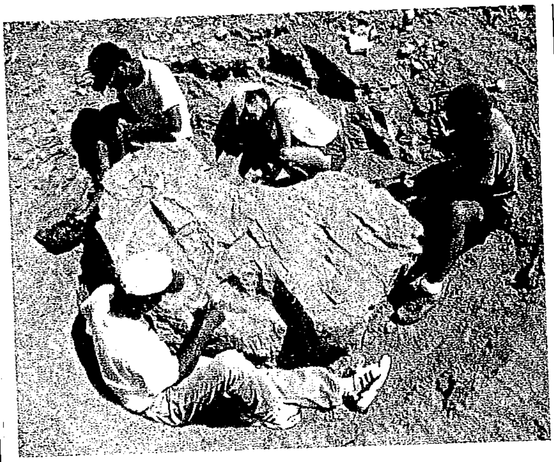
Changes in the Gene Pool
Seed sizes on the second island favor birds with larger beaks. The population on the second island evolves into a population, B, with larger beaks. Eventually, populations A and B evolve into separate species.

Changes in the Gene Pool Over time, populations on each island became adapted to their local environments. The plants growing on the first island may have produced small thin-shelled seeds, whereas the plants on the second island may have produced larger thick-shelled seeds. On the second island, directional selection would favor individuals with larger, heavier beaks. These birds could crack open and eat the large seeds more easily. Thus, birds with large beaks would be better able to survive on the second island. Over time, natural selection would have caused that population to evolve larger beaks, forming a separate population, B.

Reproductive Isolation Now, imagine that a few birds from the second island cross back to the first island. Will the population-A birds breed with the population-B birds? Probably not. These finches choose their mates carefully. As part of their courtship behavior, they inspect a potential partner's beak very closely. Finches prefer to mate with birds that have the same-sized beak as they do. In other words, big-beaked birds prefer to mate with other big-beaked birds, and smaller-beaked birds prefer to mate with other smaller-beaked birds. Because the birds on the two islands have different-sized beaks, it is likely that they would not choose to mate with each other. Thus, differences in beak size, combined with mating behavior, could lead to reproductive isolation. The gene pools of the two bird populations remain isolated from each other—even when individuals live together in the same place. The two populations have now become separate species.

Ecological Competition As these two new species live together in the same environment (the first island), they compete with each other for available seeds. During the dry season, individuals that are most different from each other have the highest fitness. The more specialized birds have less competition for certain kinds of seeds and other foods, and the competition among individual finches is also reduced. Over time, species evolve in a way that increases the differences between them. The species-B birds on the first island may evolve into a new species, C.

Continued Evolution This process of isolation on different islands, genetic change, and reproductive isolation probably repeated itself time and time again across the entire Galápagos island chain. Over many generations, it produced the 13 different finch species found there today. Use the steps in this illustration to explain how other Darwin finches, such as the vegetarian tree finch that feeds on fruit, might have evolved.



▲ **Figure 16–17** Paleontologists study fossils to find clues about previous life-forms.

Studying Evolution Since Darwin

It is useful to review and critique the strengths and weaknesses of evolutionary theory. Darwin made bold assumptions about heritable variation, the age of Earth, and relationships among organisms. New data from genetics, physics, and biochemistry could have proved him wrong on many counts. They didn't. Scientific evidence supports the theory that living species descended with modification from common ancestors that lived in the ancient past.

Limitations of Research The Grants' research clearly shows the effects of directional selection in nature. The Grants' data also show how competition and climate change affect natural selection. The work does have limitations. For example, while the Grants observed changes in the size of the finches' beaks, they did not observe the formation of a new species. Scientists predict that as new fossils are found, they will continue to expand our understanding of how species evolved.

Unanswered Questions The studies of the Grants fit into an enormous body of scientific work supporting the theory of evolution. Millions of fossils show that life has existed on Earth for more than 3 billion years and that organisms have changed dramatically over this time. These fossils form just a part of the evidence supporting the conclusion that life has evolved. Remember that a scientific theory is defined as a well-tested explanation that accounts for a broad range of observations. Evolutionary theory fits this definition. To be sure, many new discoveries have led to new hypotheses that refine and expand Darwin's original ideas. No scientist suggests that all evolutionary processes are fully understood. Many unanswered questions remain.

Why is understanding evolution important? Because evolution continues today, driving changes in the living world such as drug resistance in bacteria and viruses, and pesticide resistance in insects. Evolutionary theory helps us understand and respond to these changes in ways that improve human life.

16–3 Section Assessment

1. **Key Concept** How is reproductive isolation related to the formation of new species?
2. **Key Concept** What type of isolating mechanism was important in the formation of Galápagos finch species?
3. Explain how behavior can play a role in the evolution of species.
4. What recent research findings support Darwin's theory of evolution?
5. **Critical Thinking Inferring** Suppose that a drought on an island eliminates all but plants that produce large, tough seeds. All the finches on the island have very small beaks. How might this environmental change impact the survival of this finch population?

Writing in Science

Summarizing

Write a paragraph that summarizes the Grants' research with Galápagos finches. Your summary should include the main points of the research. *Hint:* The first sentence in your summary might state the Grants' hypothesis.