Population Genetics and Speciation

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.

Physical variation in these snails includes variation in shell coloration, number of stripes, shell size, and shell thickness. Each trait affects the survival and reproduction of individual snails.

Banding patterns can give the snails camouflage protection against predators, especially birds. Each pattern may provide better camouflage in some seasons or locations than in others.

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?

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

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?
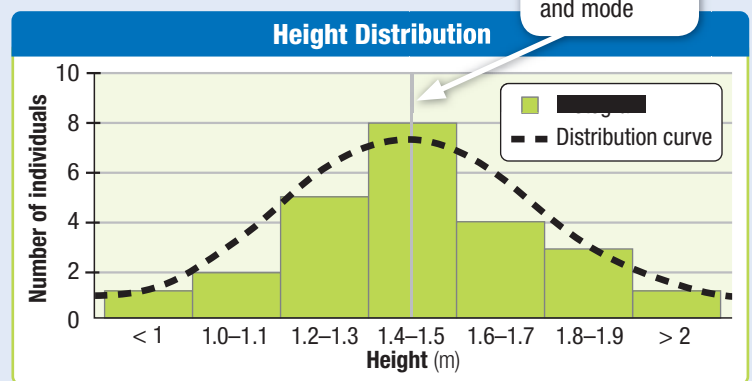

| Size 6 | Size 7 | Size 8 | Size 9 | Size 10 | Size 11 |

Histograms and Distributions

Suppose that you were to measure the height of every student in your school. You would pro-ably 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.

Height Distribution

Mean, median, and mode

- - Distribution curve

Number of individuals

Height (m): < 1, 1.0–1.1, 1.2–1.3, 1.4–1.5, 1.6–1.7, 1.8–1.9, > 2

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?

Genotype Frequencies Vs. Allele Frequencies

ee (homozygous recessive) 37%

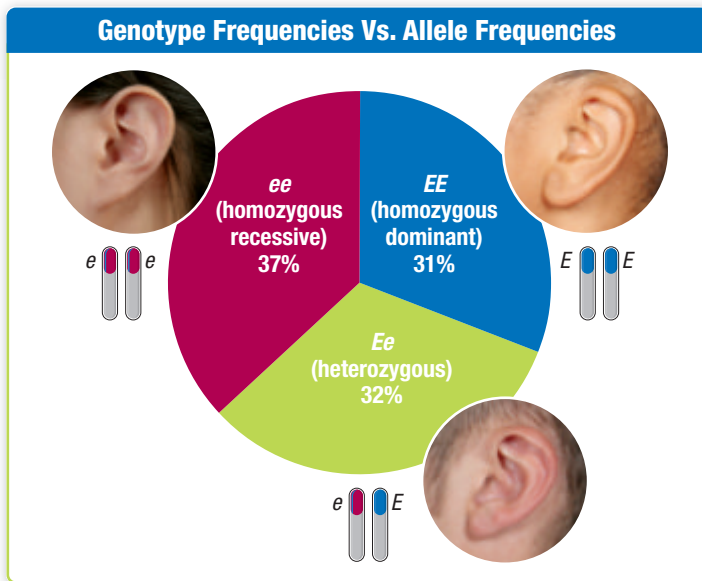EE (homozygous dominant) 31%

Ee (heterozygous) 32%

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?**

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?*

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.

❯ **Reading Check** *Why is mutation so important?*

ACADEMIC VOCABULARY

generate produce; bring into being; cause to be

Section 1 Review

❯ KEY IDEAS

1. **Describe** the scope of population genetics.

2. **Explain** how phenotypic variation can be measured.

3. **Relate** the number of genes that affect a phenotype to the variation in traits that may exist.

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.

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.
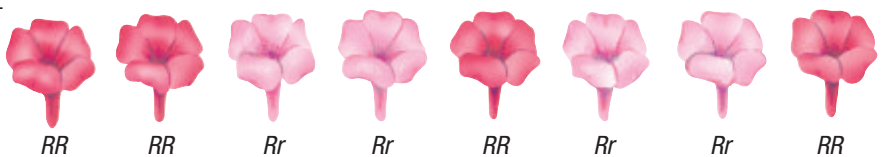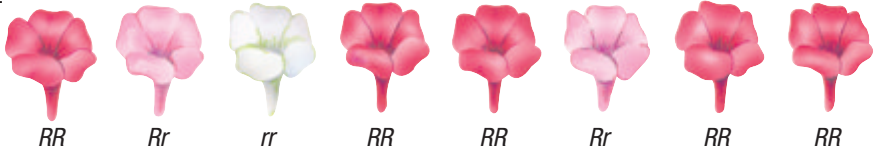
Equilibrium and Change

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*

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:

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

(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 time s 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.

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?*

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

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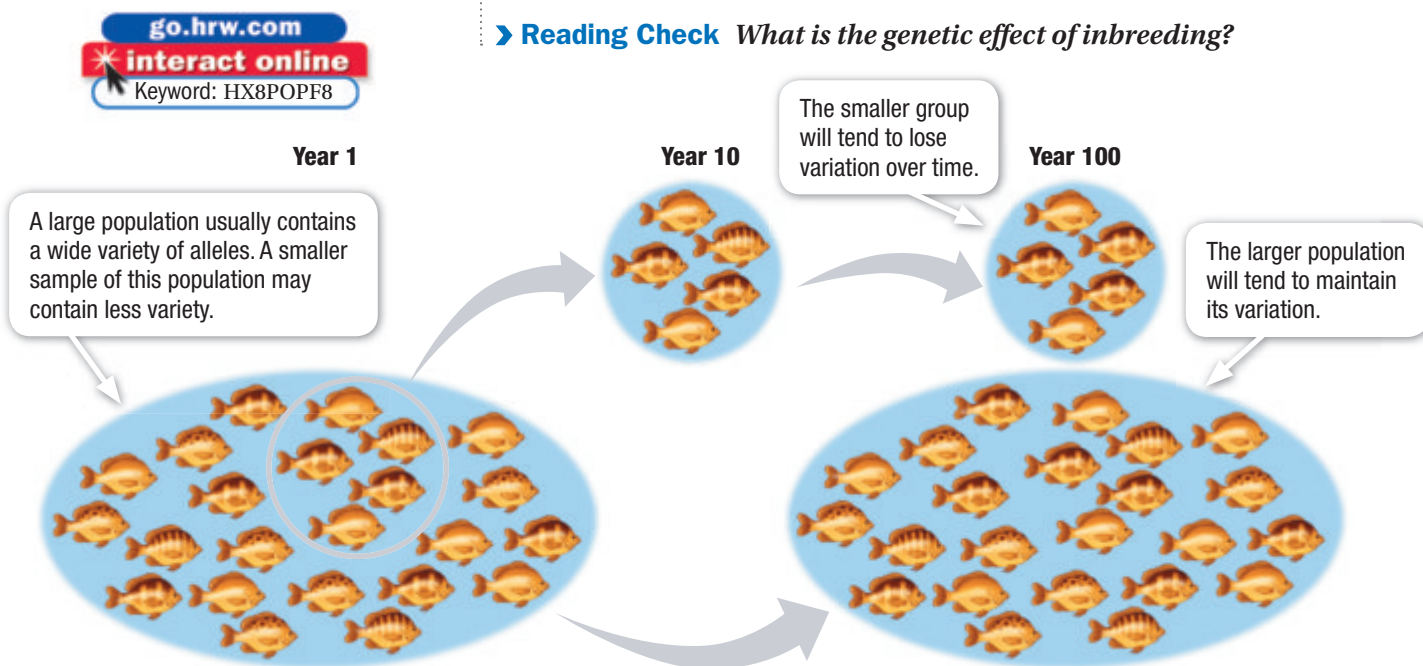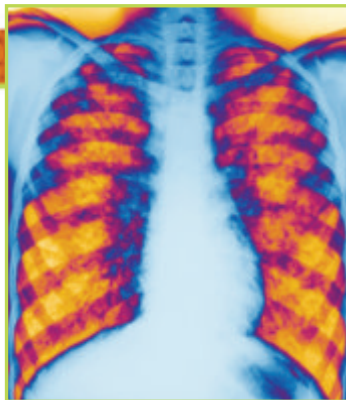
Sexual Reproduction and Evolution

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 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.

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.

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Year 1

A large population usually contains a wide variety of alleles. A smaller sample of this population may contain less variety.

Year 10

The smaller group will tend to lose variation over time.

Year 100

The larger population will tend to maintain its variation.

QuickLab

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 <u>deviations</u> 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?*

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Topic: Natural
     Selection
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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?**

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

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."

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.

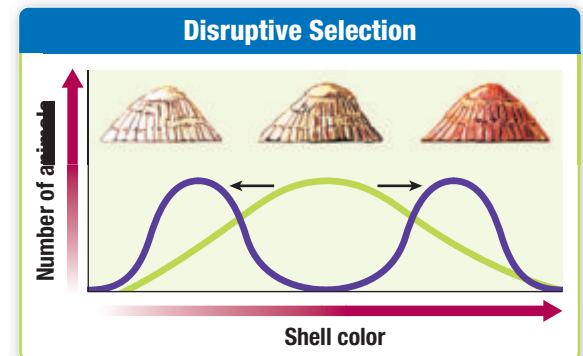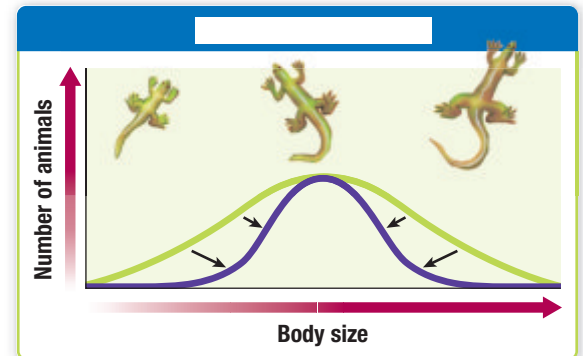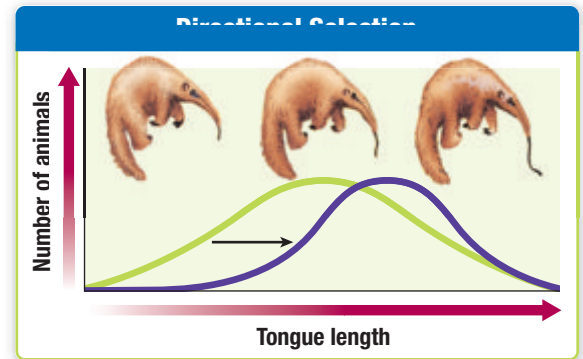❯ **Reading Check** *Which form of selection increases the range of variation in a distribution?*

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.

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?

Rainbow wrasse,
Thalassoma lunasanum

The rainbow wrasse lives in reefs on the western side of the Isthmus of Panama. A close relative, the bluehead wrasse, lives on the eastern side.

The ancestor of both species probably lived in this region before the isthmus rose from the ocean about 3 million years ago.

Bluehead wrasse,
Thalassoma bifasciatum

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.
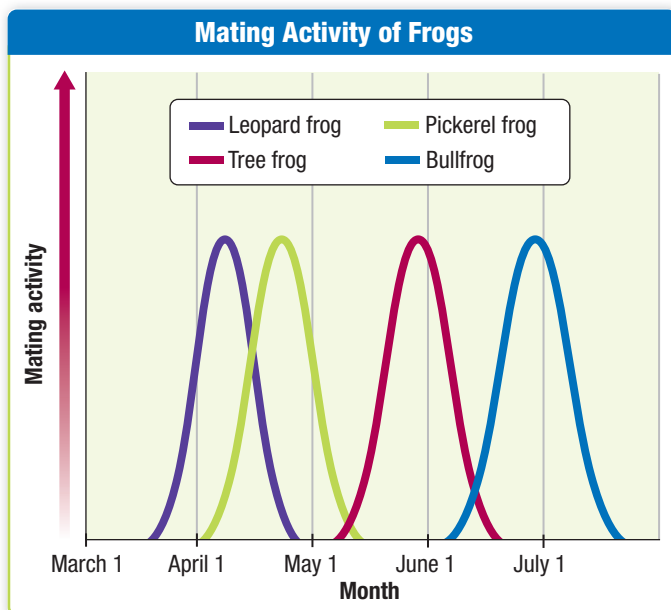
- **Ecological Niche** Recall that the *niche* of a species is the role that the species has in its environment, including all of its interactions with other species. Divergence can occur when populations use different niches. The divergence of multiple lineages into many new species in a specific area 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.

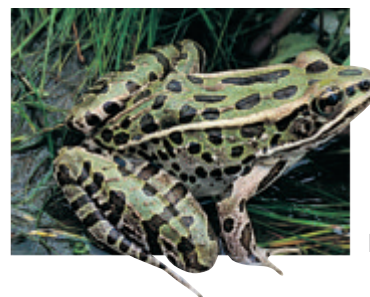❯ **Reading Check** *Is hybridization always successful?*

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*

Mating Activity of Frogs

Legend: Leopard frog, Pickerel frog, Tree frog, Bullfrog

y-axis: Mating activity
x-axis: Month — March 1, April 1, May 1, June 1, July 1

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?

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 meteor 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.

Key Ideas	Key Terms

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.

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 phentoypes 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.

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.

reproductive isolation (412)
subspecies (412)