CHAPTER 20

Mechanisms of Evolution

Reflecting Questions

- How does an understanding of genetics help explain how changes within a species can occur?
- How can we measure genetic variation in a population?
- What are the mechanisms that result in genetic variation?

Each fall, swarms of monarch butterflies leave southern Canada and begin their southward migration. Along the route of their incredible journey — which, for most, will end in the mountains of southern Mexico — populations of monarchs will be eagerly awaited and counted by keen observers. Monarch butterflies are one of the few migratory insects, and their migratory routes are well-studied. Every year, biologists and volunteer observers monitor monarch butterfly populations. These observers have found that populations shift dramatically from year to year. Numbers rise some years, then fall other years. During their migration and during their time in Canada, the United States, and Mexico, populations of monarchs (like populations of all organisms) are subjected to variable environmental conditions. There can be a drought one year, an early snowfall the next, or the loss of valuable habitat in another year. Populations peak following favourable conditions, while adverse conditions can result in precipitous declines. Populations continue to shift naturally from one generation to the next.

Monarch butterfly populations are estimated to total over 120 million individuals and, for now, their populations are large enough to ensure a sizeable gene pool that can withstand many challenges. But what would happen if a small population became isolated from the larger group? If the smaller population's gene pool changed, how might the smaller population itself change? Would the organisms start to look different? How does population size and the genetic variation within the population affect the evolution of the monarch butterfly population?

As you have learned, evolution is the shift in the frequency of genes in the gene pool of a population from one generation to the next. Genetic variation within a population allows changes to occur within a species. You will examine the relationship between genetics and evolution in greater detail in this chapter. You will also learn about some of the mechanisms that affect genetic variation and learn how to measure this variation.

How does genetic variety, such as the variety that exists in this population of bacteria, make evolution possible?

Chapter Contents

20.1 Population Genetics

OUTCOMES

- **Illustrate how knowledge of Mendelian genetics supported Darwin's theory of evolution.**
- **Analyze evolutionary mechanisms and their effects on biodiversity.**
- **Describe how scientific understanding of evolution has been enhanced by the development of technologies.**

Evolution can be divided into macro-evolution and micro-evolution. **Macro-evolution** is evolution on a grand scale; it is large evolutionary change such as the evolution of new species from a common ancestor or the evolution of one species into two. (You will learn more about the evolution of new species in Chapter 21.) The modern camel, for example, evolved over 65 million years from a small ancestor that was not much larger than a rabbit. This long, visible sequence of changes and the categorization of organisms (extinct and living) in relation to one another are examples of macro-evolution. Figure 20.1 shows the sequence that paleontologists propose for the evolutionary path of the modern camel. (Ancestral camels actually evolved in North America, and then expanded their range to include parts of Asia and Africa.)

Micro-evolution is the change in the gene frequencies within a population over time. It is evolution *within* a species, or evolution on a small scale. For example, adaptation by natural selection is an example of evolutionary change within a species, or micro-evolution. As these changes accumulate, they can lead to the formation of a new species.

This chapter focusses on micro-evolution and the mechanisms that result in genetic variation within a population.

Heredity and Evolution

While Darwin's *The Origin of Species* convinced most biologists that species could change over time, Darwin's mechanism for change — natural selection — took longer to gain acceptance. Part of the difficulty in explaining the mechanism of natural selection was that there needed to be a plausible explanation for how traits could be inherited. If variation within a species was necessary for natural selection, what was the ultimate source of this variation?

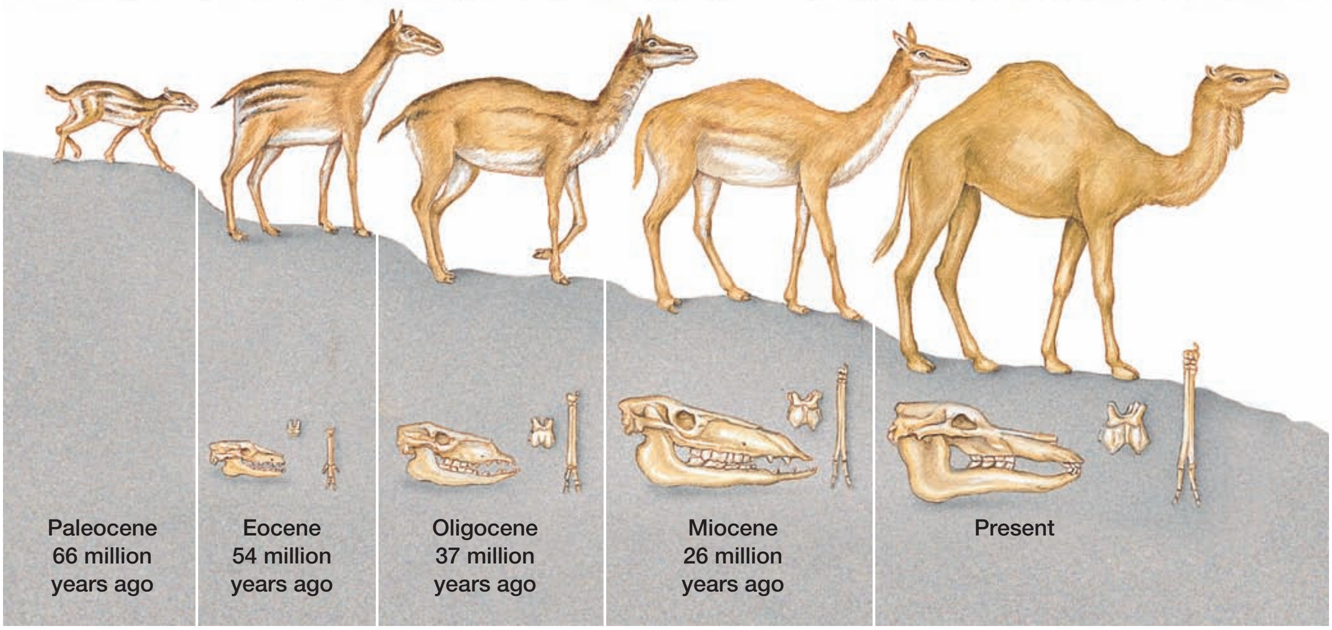

Figure 20.1 Paleontologists have used fossils to trace the evolution of the modern camel.

In Darwin's theory of natural selection, new variants of species arise continually in populations. Some variants thrive and produce more offspring, thus slowly leading to change in a population (this may even lead to new species over time), while other variants die off because they cannot thrive in the environment. This idea did not mesh with the ideas about inheritance at that time, which said that characteristics were blended and an offspring was an "average" of its parents. (For example, according to blended inheritance, the offspring of a plant with a red flower and a plant with a white flower would be pink. This offspring would then pass on the pink colour to its offspring. In reality, this is not always the case.) What was needed to support natural selection was an understanding of how chance variations arise in a population and how these variations are passed from parents to offspring.

Part of this missing information needed to explain inheritance and support the idea of evolution by natural selection was actually discovered during Darwin's lifetime. Gregor Mendel, an Austrian monk who is shown in Figure 20.2, conducted experiments with pea plants in the 1850s, and his work provided the basis for an explanation of inheritance. His experiments showed that, in contrast to the idea of blended inheritance, parents pass on discrete factors of inheritance, which he called genes. Mendel showed that genes do not blend in the offspring; genes retain their characteristics when they are passed to the offspring. Mendel's work and the subsequent work of others on inheritance would eventually help support the idea of natural selection by showing how the variation created through the mechanisms of heredity is the raw material on which natural selection acts.

Figure 20.2 Gregor Mendel (1822–1884) conducted experiments that explained the inheritance of characteristics.

Mendel's work was some of the first that helped to explain mechanisms of inheritance. But his work was not read by Darwin, and it would be several decades before ideas about inheritance were used to help explain natural selection. In the late nineteenth and early twentieth centuries, there was a growing interest in genetics. In the 1930s, a new field of science emerged — population genetics. As scientists began to broaden their understanding of genetics, they demonstrated that there is substantial genetic variation within populations. They showed that variations could arise in populations through changes, or **mutations**, in genes. A mutation is a permanent change in the genetic material of an organism. (Refer back to Chapter 17, section 17.4 to review mutations.) It was recognized that mutations provide the genetic variation within a population. Evolution, therefore, depends on both random genetic mutation (which provides variation) and mechanisms such as natural selection. (You will learn more about mutations in section 20.3.)

Scientists, including geneticist Theodosius Dobzhansky, biogeographer and taxonomist Ernst Mayr, paleontologist George Gaylord Simpson, and botanist G. Ledyard Stebbins, combined ideas from their fields of study with Darwin's ideas about natural selection and the current understanding of inheritance to develop a revised theory of evolution. This modification to evolutionary theory, and the meshing of Mendel's and Darwin's ideas, was called the **modern synthesis**.

Reviewing the Language of Genetics

To understand and discuss genetic variation, it is important to review certain terms. **Alleles** are alternate forms of a gene. In humans, for example, there are three alleles — I^A, I^B, and i — that determine whether an individual has A, B, AB, or O blood type. Since individuals generally have two sets of chromosomes — one received from the male parent and one received from the female parent — there are two alleles for every gene at every locus. (A **locus** [plural loci] is the location of a gene on a chromosome.) So, humans could be I^AI^A, I^AI^B, I^Ai, I^BI^B, I^Bi, or ii at the locus for blood group. If the two alleles at a locus are identical (for example, I^AI^A or ii), the individual is called **homozygous** for that characteristic. An individual with two different alleles at the locus (for example, I^AI^B) is called **heterozygous**. The three blood type alleles, I^A, I^B, or i, exist in the population, but no single person can have all three. In some populations, the allele possibilities are even greater, and far exceed the two possible alleles any human can have.

If the two alleles inherited from parents are different, one of them (the **dominant allele**) will be fully expressed in the organism's appearance and therefore will become the phenotype. (Note that dominant in this sense does not mean that this allele is somehow better. Trait for the dominant allele is simply the one that is always expressed in an individual.) The other allele, the **recessive allele**, has no noticeable effect on the organism's appearance, but it remains as part of the genotype of the organism. Figure 20.3 shows a cross between a pure purple-flowered pea plant and a pure white-flowered pea plant. The alleles for colour are W and w. Since W is the dominant allele, the flowers can only be white when the two alleles are both recessive (that is, ww).

The **genotype**, or genetic make-up, of an *individual* remains constant throughout its life. However, over time, the alleles within a *population* may change. New alleles may arise and may be recombined, thus producing individuals with novel **phenotypes**. Phenotypes are the physical and physiological traits of an organism. (Physical in this sense refers to how the organism with this trait appears.) A phenotype of an individual can be the product of both the environment and heredity. For example, environmental factors such as disease, crowding, injury, or the availability of food can all affect the appearance of an individual. But these acquired characteristics are not heritable; that is, they are not passed on to the next generation. Because of dominant and recessive alleles, an organism's appearance does not always reflect its genetic make-up. For example, Figure 20.4 shows a cross between two pea plants that have the alleles W or w at the locus for colour. The genotypes WW and Ww both result in a purple flower, while the genotype ww results in a white flower. Table 20.1 summarizes how genotype is related to phenotype.

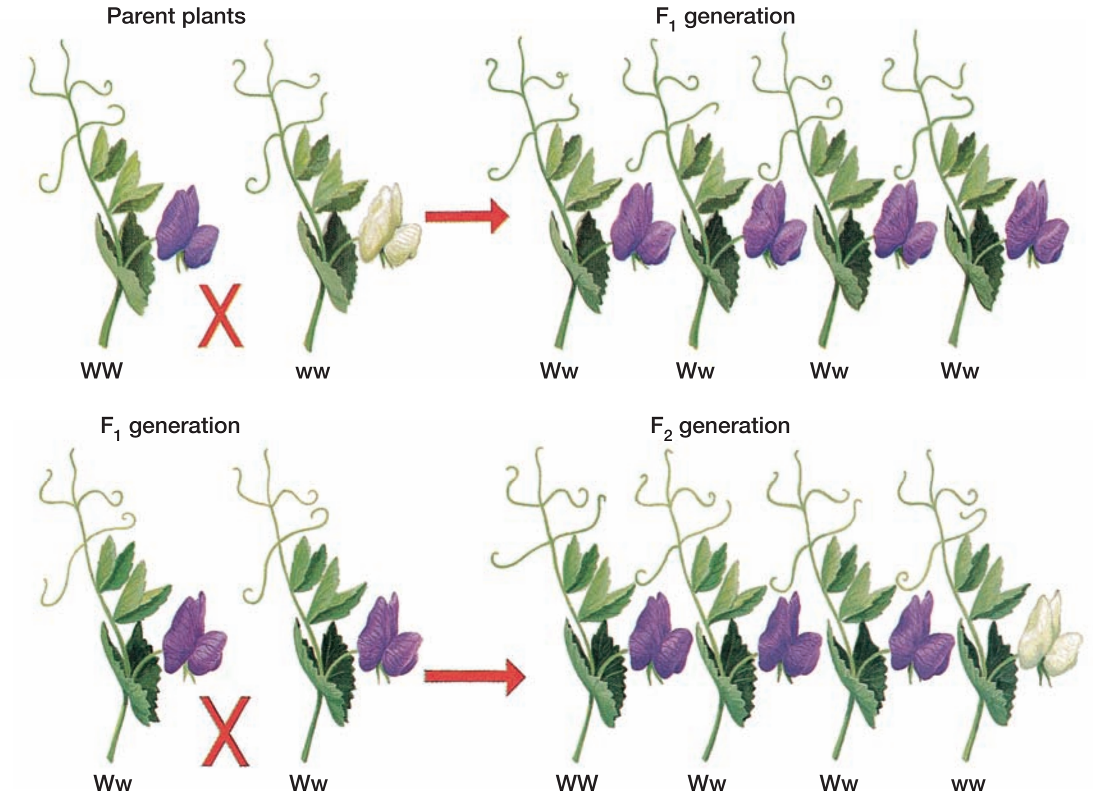

Figure 20.3 Two generations resulting from the cross of a purple-flowered pea plant and a white-flowered pea plant.

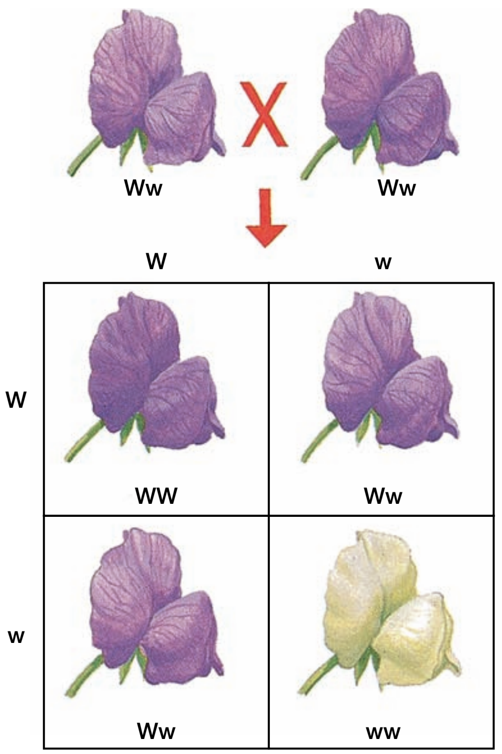

Figure 20.4 The result of a cross of two pea plants is shown in this Punnett square.

Not all traits are purely dominant or purely recessive. Sometimes neither of the alleles controlling a trait are dominant. In this case, blending of the two traits can occur. This is called **incomplete dominance**. Figure 20.5 gives an example of how incomplete dominance can occur. White or red flowers are homozygous, while pink flowers are heterozygous.

Occasionally both alleles for a trait may be dominant. These alleles are said to be **co-dominant** and both alleles are expressed in the heterozygous individual. In some varieties of chickens, for example, two alleles for a trait may be expressed equally. A black rooster crossed with a white hen produces offspring that have some black feathers and some white feathers.

Table 20.1
Genotype and phenotype in peas with alleles W and w

Genotype	Genotype	Phenotype
WW	homozygous dominant	purple flowers
Ww	heterozygous	purple flowers
ww	homozygous recessive	white flowers

Population Genetics

A **population** is a localized group of a single species occupying a particular area. For example, the field of lilies in Figure 20.6A on page 678 is a different population from a field of lilies in an adjacent valley. The two populations are not completely isolated (since pollinating insects may travel between them), but it is more likely that members of the same population will interbreed to produce the next generation. The same is true for the pond of frogs in Figure 20.6B. Although it is not out of the question that these frogs would mate with frogs from a nearby pond, it is more likely they would mate with individuals that live in the same pond.

Monarch butterflies (such as those shown on page 000) are all from the same species, yet there are distinct populations within this species. When the butterflies migrate in winter, they travel in huge flocks and become mixed. In their summer breeding grounds, however, they have strong family groupings. Genetic mixing during migration and in their winter habitat ensures that the species does not begin to diverge into two or more species. However,

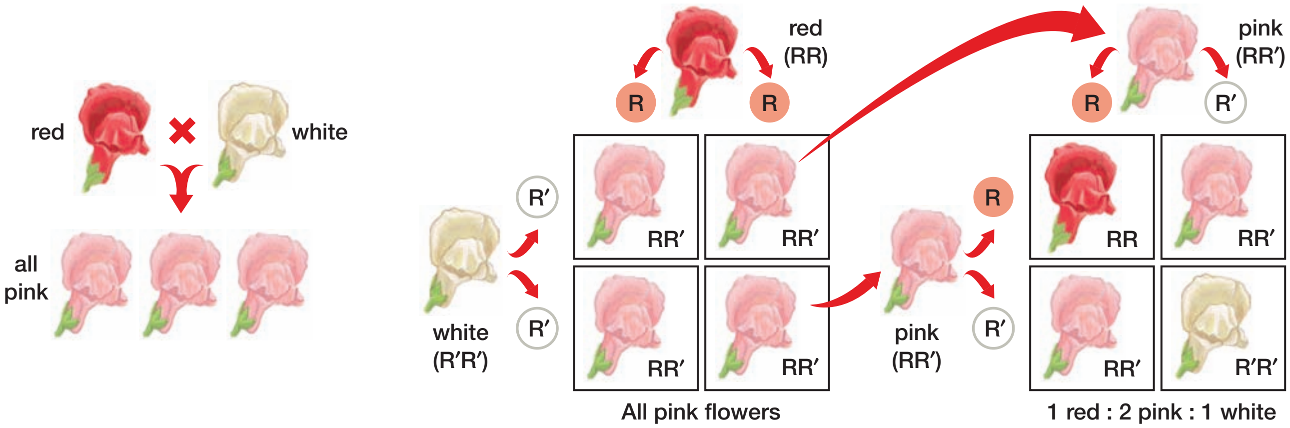

Figure 20.5 Flower colour in the snapdragon is an example of incomplete dominance. Pink flowers are heterozygous (*RR′*), where neither allele is dominant.

Figure 20.6 A field of glacier lilies and a pond of frogs are each considered populations.

the genetic similarity of the smaller summer groupings creates diversity among local populations.

All of the genes in a population or, more specifically, all of the alleles at all gene loci in all individuals of the population, make up the population's gene pool. There can be genetic variation both within individuals (when they are heterozygous for alleles) and within populations. For example, most plants within a population have more than one allele, or are **polymorphic**, at 45 percent of the loci. As well, individual plants are likely to be heterozygous at about 15 percent of their loci. A polymorphic population (with organisms exhibiting different phenotypes and genotypes) and heterozygous individuals contribute to the level of genetic variability within a population. When all members of a population are homozygous for the same allele, that allele is said to be **fixed** in the gene pool. In most circumstances, however, there are two or more alleles for a gene and each exists with a relative frequency within the population. The unique combination of alleles in individuals provides the variation within a population.

Scientists can use the technique of **electrophoresis** to help measure genetic variation within populations. Recall from Chapter 18 (section 18.2) that in the process of electrophoresis, samples of DNA from individuals are placed in a special gel that is then placed in a solution and connected to an electrical circuit. The DNA fragments move through the gel at varying speeds and the resulting pattern of bands — called the DNA fingerprint — is stained and analyzed. Biologists can use this technique to look at the variability of genes (and, consequently, genetic variation) in the population. To do this they compare the samples from different individuals within a population to calculate the percentage of loci that are polymorphic. The more sites that are polymorphic, the greater the genetic variety within the population.

Polymerase chain reactions (PCR) are also used by evolutionary biologists. (Recall that PCR was introduced in section 18.2.) PCR techniques are used to amplify (generate multiple copies of) DNA from small samples. For example, even minute samples of DNA gathered from mummified organisms or fossils can be copied using PCR techniques. Then, the DNA can be analyzed and compared with DNA sequences of other organisms to help determine evolutionary relationships. Electrophoresis and PCR techniques can be used to sequence and analyze DNA taken from long-dead, or even long-extinct, organisms. For example, DNA has been taken from a 76 000-year-old mummified human brain, fossilized bacteria, and a 40 000-year-old frozen woolly mammoth. This information will help determine the evolutionary history of organisms, because the relatedness of species can be reflected in DNA and proteins. Species that are closely related share a greater proportion of their DNA sequences and proteins.

BIO FACT

In the blood hemoglobin molecule of 146 amino acids, humans and gorillas differ by just one amino acid. Humans and frogs, however, differ by 67 amino acids.

Population geneticists study the frequencies of alleles and genotypes in populations. The study of population genetics is important to the study of micro-evolution because changes in the genetic variability within the population can be used to determine if a population is undergoing micro-evolution. To illustrate how frequencies of alleles and genotypes can be calculated, let's consider a hypothetical population of 400 field mice that are either white or black (see Figure 20.7). The allele for black, A, is dominant to the allele for white, a. (For this example we will assume there are only two alleles for this locus.) In this population of mice, 364 are black and 36 are white. Of the black mice, 196 are homozygous dominant (AA) and 168 are heterozygous (Aa). The 36 white mice are homozygous recessive, aa. Since these mice inherit one set of chromosomes from each parent (that is, they are diploid), there are a total of 800 copies of genes for fur colour in the population of 400 field mice. The dominant allele (A) accounts for 560 of these genes ($196 \times 2 = 392$ for AA mice and $168 \times 1 = 168$ for Aa mice). The recessive allele (a) accounts for 240 of these genes ($36 \times 2 = 72$ for aa mice and $168 \times 1 = 168$ for Aa mice). The overall frequency of the A allele in the gene pool of this population is $560/800 = 0.7 = 70\%$, and the frequency of the a allele is 0.3 or 30%. (**Frequency** is the number of occurrences of a particular allele in a population divided by the total number of alleles in the population.) The genotypic frequencies in this population are: AA = 0.49 (196 out of 400 mice), Aa = 0.42 (168/400), and aa = 0.09 (36/400). The frequencies of alleles and genotypes are called the population's **genetic structure**.

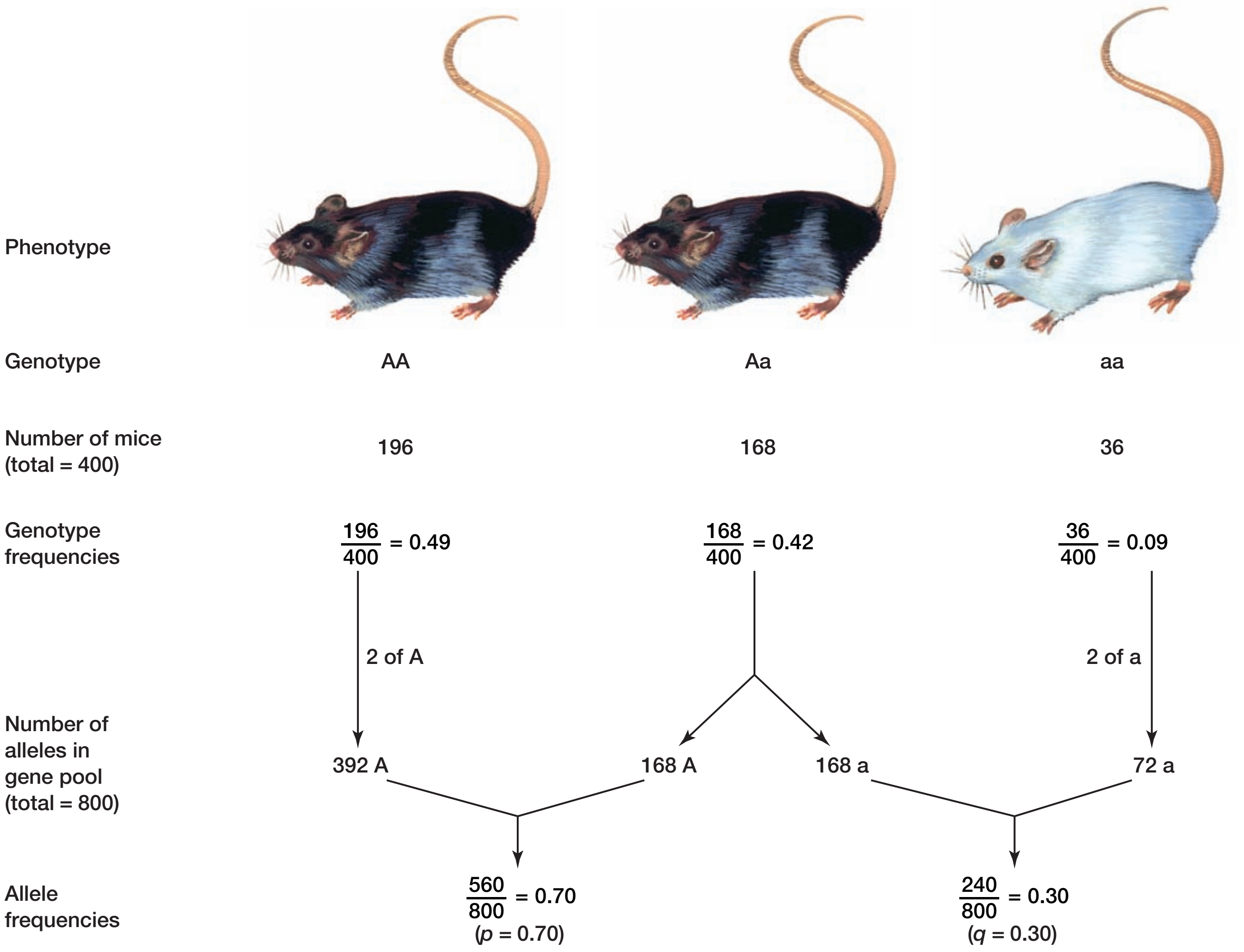

Figure 20.7 Genetic structure of a parent population of field mice

Practice Problems

1. Calculate the allele frequency and genotype frequency in a population of 500 flowers in which 275 are homozygous dominant, 137 are heterozygous, and 88 are homozygous recessive.
2. In a population of 500 plants with purple flowers and white flowers, the genotype frequency is $AA = 0.64$, $Aa = 0.32$, and $aa = 0.04$. Calculate the frequency of each allele in the population. If A is the allele for purple and a is the allele for white, calculate the numbers of each colour of plant. Copy the following chart into your notebook and fill in the data.

<table>
<tr><td>phenotype</td><td colspan="2"></td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td>genotype</td><td colspan="2"></td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td>number</td><td colspan="2"></td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td>genotype frequencies</td><td colspan="2"></td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td>number of alleles in gene pool</td><td colspan="3"></td><td colspan="3"></td></tr>
<tr><td>allele frequencies</td><td colspan="3"></td><td colspan="3"></td></tr>
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SECTION REVIEW

1. Distinguish between macro-evolution and micro-evolution. Give an example of each.
2. Explain how genetic variation and micro-evolution are related.
3. Explain how variations within a species are affected by natural selection.
4. Use the word “population” to explain local differences in a species.
5. Describe the similarities and differences between the following pairs:
   - **(a)** allele and gene
   - **(b)** phenotype and genotype
   - **(c)** dominant and recessive
   - **(d)** homozygous and heterozygous
6. Assume that a white animal is crossed with three other animals of the same species, A, B, and C. (For this example we will assume there are only two alleles for this locus.) Animal A is brown and produces offspring A′, which is also brown. Animal B is white and produces offspring B′, which is brown. Animal C is brown and produces offspring C′, which is white. Give the genotypes and phenotypes of all seven animals. Show how you came to this conclusion.
7. Explain how polymorphic populations and heterozygous individuals contribute to the level of genetic variety in a population.
8. Describe the genetic structure (genotype and allele frequency) using a chart or table for a population of 300 frogs. The frogs are either spotted or spot-less. The allele for spots, A, is dominant to the allele for no spots, a. In this population, 240 frogs have spots and 60 are spot-less. Of the 240 frogs with spots, 200 are homozygous and 40 are heterozygous.
9. If a group of scientists is trying to determine how a particular fossil of a woolly mammoth is related to an animal on Earth today, what techniques could they use? How could they determine relatedness?

20.2 The Hardy-Weinberg Principle

OUTCOMES

- **State the Hardy-Weinberg principle and explain its significance in the development of evolutionary theories.**
- **Use the Hardy-Weinberg equation to solve problems related to evolution.**

For a population to undergo change there must be genetic variation. If all members of a population were genetically identical, all of their offspring would be identical and the population would not change over time. One way to determine how a real population *does* change over time is to develop a model of a population that *does not* change genetically from one generation to the next. Then, actual populations can be compared with this hypothetical model. Such a model was developed independently and published almost simultaneously in 1908 by English mathematician G.H. Hardy and German physician G. Weinberg. These men noted that in a large population in which there is random mating, and in the absence of forces that change the proportions of the alleles at a given locus, the original genotype proportions will remain constant from generation to generation. Their theory is referred to as the **Hardy-Weinberg principle**. In the example shown in Figure 20.7 on page 679, this principle says that the genotypes of 0.49 AA, 0.42 Aa, and 0.09 aa would persist in the mouse population from generation to generation. Because their proportions do not change, the genotypes are said to be in **Hardy-Weinberg equilibrium**.

The Hardy-Weinberg principle is written as an equation. For a gene with two alternative alleles, say A and a, the frequency of allele A (the dominant and, usually, more common allele) is expressed as p, and the alternative allele a (the recessive and, usually, more rare allele) is expressed as q. Because there are only two alleles, $p + q$ must always equal one. The Hardy-Weinberg equation is:

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

where:

p = frequency of dominant allele
q = frequency of recessive allele
p^2 = frequency of individuals homozygous for allele A
$2pq$ = frequency of individuals heterozygous for alleles A and a
q^2 = frequency of individuals homozygous for allele a

Let's apply the Hardy-Weinberg principle to the population of field mice introduced in Figure 20.7. In this population, 70 percent (0.7) of the fur-colour loci in the gene pool have the A allele and 30 percent (0.3) have the a allele. The equation can be applied to see how genetic recombination during sexual reproduction will affect the frequencies of the two alleles in the next generation of field mice. The Hardy-Weinberg principle assumes that mating is completely random and that all embryos will survive. The gametes — sperm and ova — each have one allele for fur colour, and the allele frequencies of the gametes will be the same as the allele frequencies in the parent. Every time a gamete is drawn from the pool at random, the chance that the gamete will bear an A allele is 0.7, and the chance that the gamete will have an a allele is 0.3 (see Figure 11.8). Using the Hardy-Weinberg equation, $p = 0.7$ and $q = 0.3$ ($p + q$ must equal 1).

Figure 20.8 shows the possible scenarios that can result when gametes combine their alleles to form zygotes. The Hardy-Weinberg equation states that the probability of generating an AA genotype is p^2. So, in our population of field mice, the probability of an A sperm fertilizing an A ovum to produce an AA zygote is 0.49 (which is 0.7×0.7).

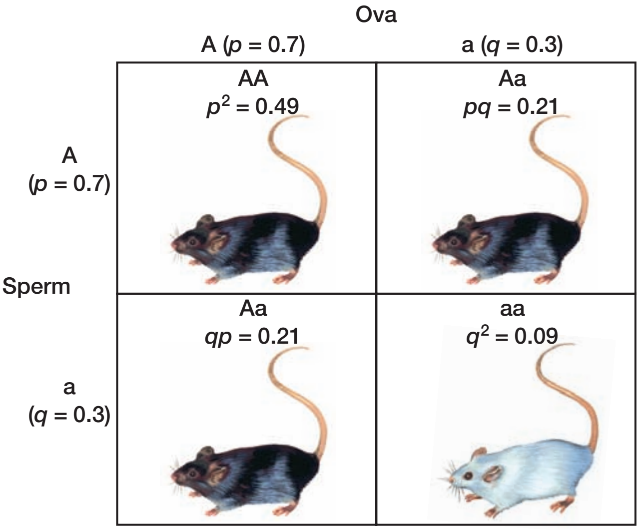


Figure 20.8 The genetic structure of the second generation of field mice

The frequency of individuals homozygous for the other allele (aa) is q^2, or $0.3 \times 0.3 = 0.09$. The genotype Aa can arise in two ways, depending on which parent contributes the dominant allele. Therefore, the frequency of heterozygous individuals in the population is $2pq$ ($2 \times 0.7 \times 0.3 = 0.42$ in our example). All of these possible genotypes add up to 1 ($0.49 + 0.09 + 0.42 = 1$).

The Hardy-Weinberg principle predicts the expected allele and genotype frequencies in idealized populations that are not subjected to selective pressure. Deviations from the frequencies that are expected by the principle indicate that natural selection is occurring. The five conditions required to maintain the Hardy-Weinberg equilibrium are:

- Random mating — Mating must be random with respect to genotype. For example, females cannot select males with a particular genotype or phenotype when they mate.

Biology Magazine TECHNOLOGY • SOCIETY • ENVIRONMENT

Biotechnology and Evolution

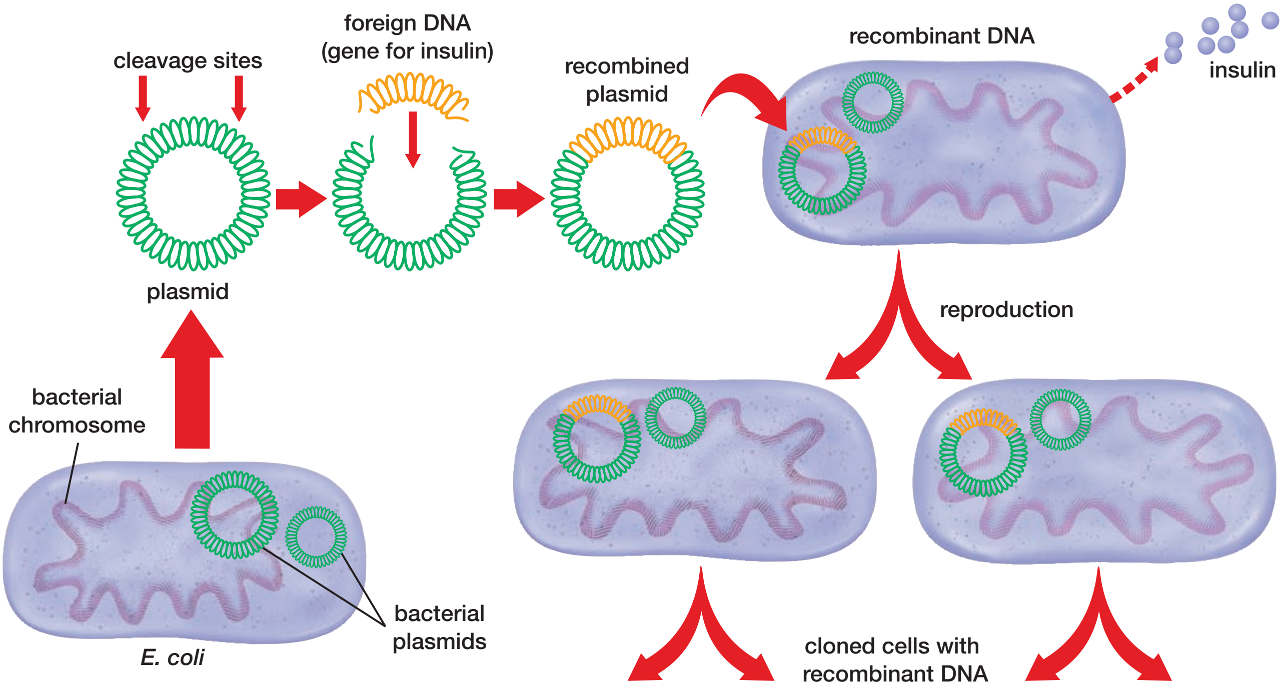
Can technology create new species? This question might bring to mind a scientist putting together bits and pieces from various organisms, like a child making new designs from the parts of a construction toy. Modern biotechnology includes techniques that do make novel combinations of species possible. In many ways, humans have been producing new animals, plants, and micro-organisms for thousands of years.

Charles Darwin himself explained the process of evolution by first describing how livestock, crops, ornamental plants, and pets are developed by artificial selection — breeding only those organisms that have certain desirable inherited characteristics. This early form of reproductive technology gave us cows, chickens, apples, roses, dogs, and many other types of animals and plants previously unknown in nature.

In the twentieth century, other technologies led to the unexpected evolution of new organisms with less desirable characteristics. As farmers added more pesticides to their fields, new forms of resistant weeds and insect pests appeared on farms. As physicians prescribed more antibiotics for their patients, new varieties of antibiotic-resistant bacteria sprang up in hospitals. By adding toxins to the environment, humans unintentionally selected organisms able to survive exposure to the chemicals meant to kill them.

Playing with Genes

The tools of genetic engineering now make it possible to bypass the selection of individual organisms and directly select particular genes with useful characteristics. For example, biotech companies add genes to organisms to give them new traits, such as the ability to produce beneficial enzymes or resist certain herbicides. Unlike



Recombinant DNA can be cloned to produce many copies of a specific segment of DNA.

- No mutations — Alleles must not mutate. In other words, allele choices in the gene pool (as defined in section 10.1) must remain unaltered.
- Isolation — There must be no exchange of genes among populations, since this would alter the gene pool.
- Large population size — The population must be very large.
- No natural selection — No genotype can have a reproductive advantage over another.

These conditions will be explored further in the next section.

In most natural populations, the allele and genotype frequencies *do* change from generation to generation — they are not in Hardy-Weinberg equilibrium since natural populations cannot meet all of the criteria listed above. Therefore, most natural populations are changing. You will explore what causes gene frequencies to deviate from Hardy-Weinberg equilibrium in the next section.

earlier forms of artificial selection, genes from one species can be introduced into other species. For example, one of the earliest applications of genetic engineering created populations of bacteria containing human genes that code for the production of the human insulin molecule. These transgenic bacteria are now the main source of insulin for diabetics.

Many people are concerned that the transfer of genes from one species to another is unnatural. However, gene swapping between species is not entirely a human invention. Different bacteria routinely exchange genetic material by the processes of transformation and conjugation, producing recombinant cells. Viruses also carry genetic material from species to species, even among widely different groups of organisms such as insects and mammals. Because of this ability, viruses are commonly used by molecular biologists.

Another misconception is that transgenic organisms are a type of hybrid, like the result of crossing a lion with a tiger (which has been done in zoos). The offspring of a lion and a tiger have equal genetic contributions from both parents. In contrast, the genetic contribution added to a transgenic organism by genetic engineering is only a tiny fraction of the organism's genome — far less than 1 percent. It is no more of a change in the genome than might be produced by normal random mutation. Even though the change is very small, a directed change can have large impacts on the phenotypes of organisms (for example, the changes made to the genes of people who have certain genetic disorders).

Directed Evolution

The characteristics of each species are determined by their genes. The genes that are of most interest to genetic engineers are those that code for the production of useful molecules such as enzymes and other proteins. These biological molecules have evolved within living organisms over billions of years to perform specific functions. But some of the properties we want enzymes to have for industrial or medical use are not found in any organisms we know of — perhaps because they would clash with the needs of the organism, or because they were never required. For decades, scientists have been applying the principles of evolution to explore a vast universe of novel protein designs that never evolved in nature.

Directed evolution can produce proteins that have capabilities not found in naturally occurring organisms. By speeding up rates of mutation and selection, researchers have created completely new enzymes from purely random pools of DNA sequences in only a few days. For example, one lab increased the catalytic efficiency of an enzyme more than 100-fold by applying random mutagenesis, gene recombination, and screening over a sequence of generations.

As we learn more about the relationships that genes, proteins, and organisms have with their environments, it may be possible to artificially evolve entire organisms. A study of the history of life on Earth shows us that millions of strange and remarkable species have evolved and disappeared. The future will bring new species and new diversity, some of it deliberately introduced by humans but most of it produced by the never-ending process of natural selection.

Follow-up

1. Biotechnology analyzes and manipulates genomes. This makes it seem like each type of organism is simply the product of various molecules working together in a co-ordinated way. Are organisms more than their genes? If so, what else helps define and separate one species from another?
2. The numbers of some rare and endangered animals have been increased by techniques such as cloning and implanting embryos in surrogate mothers of a different species. It is also possible that recently extinct species could be revived by using genetic material from well-preserved specimens. Do you think these techniques might affect the course of evolution?

Investigation 20 • A

SKILL FOCUS

- Predicting
- Performing and recording
- Communicating results

Population Genetics and the Hardy-Weinberg Principle

There are several characteristics that you can easily measure to determine some of the genetic variability that exists within your classroom. Eye and hair colour, the presence or absence of freckles, hair on your fingers, and even how you cross your hands are all genetic traits.

Studies like this investigation often involve interviewing or examining people. All those involved must respect the confidentiality of the subjects of the study. This confidentiality should be maintained in all studies unless permission has been obtained from the subjects.

Pre-lab Question

- Does your class meet all the requirements to maintain the Hardy-Weinberg equilibrium? (Consider your class as a population.)

Problem

How can genetic variety among the students in your classroom be measured?

Prediction

If there are three possible genotypes (and two possible phenotypes) for a particular characteristic, predict the frequency of each allele in your class.

Part A

Trait	Dominant	Recessive
hairline	pointed on forehead	straight across forehead
freckles	present	absent
thumb joint	last joint bends out	last joint is straight
finger hair	present	absent
folded hands	left thumb over right	right thumb over left
tongue rolling	can be rolled in U-shape	cannot be rolled

Procedure

1. Choose one of the traits from the table shown here. (Your entire class should test the same trait.) Copy the table below into your notebook, and fill in the genotype and phenotype for the three possible combinations of alleles. (Use A for the dominant allele, and a for the recessive allele.)

Trait	Possible genotypes	Possible phenotypes

2. Survey the class to determine the total number of students with each phenotype of the selected trait. Copy the following table into your notebook and record these results as percentages. Change each percentage into decimal form.

	Class Phenotypes				Allele Frequency	
	Dominant phenotype $p^2 + 2pq$		Recessive phenotype q^2			
	Number of students	Percentage of students	Number of students	Percentage of students	p	q
class population						
larger population						

3. Use the Hardy-Weinberg equation to calculate the frequency of each allele in your class. Record your calculated frequencies in the last two columns of your table.
4. (Optional) Repeat steps 2 and 3 for a larger population of two or more classes.

Post-lab Questions

1. What is the frequency of homozygous dominant students, p^2, in your classroom? What is the frequency of heterozygous students, $2pq$?
2. What is the frequency of homozygous recessive students, q^2, in your classroom?
3. What are the percentages of the three genotypes in your classroom?
4. (Optional) How did genotype and allele frequencies change when you sampled a larger population size?

Conclude and Apply

5. Explain the relationship between population size and genotype and allele frequency.

6. What does the answer to question 5 imply about the need for an appropriate sample size in order to obtain an accurate picture of what is occurring within a population?
7. Explain how the Hardy-Weinberg equation can be used to study genetic diversity in populations.

Part B

Materials

4 playing cards for each participant (2 from red suits and 2 from black suits)

Procedure

1. Each playing card represents an allele. Cards from red suits are recessive alleles, and cards from black suits are dominant alleles.
2. Find a partner. Place your four cards face down randomly on your desk, but do not mix your cards with your partner's.
3. Each person in this partnership, or random mating, should turn over one card. This is the offspring of the first generation. Copy this table into your notebook and record the genotype of the first offspring.

Generations		Class total for each phenotype		
		AA	Aa	aa
first generation mating	first offspring			
	second offspring			
second generation mating	first offspring			
	second offspring			
third generation mating	first offspring			
	second offspring			
fourth generation mating	first offspring			
	second offspring			
fifth generation mating	first offspring			
	second offspring			
	Class Totals			

4. Retrieve your card and shuffle your four original cards again. Repeat step 3. This is the second offspring of the first generation. Record the genotype of the second offspring in your table.
5. You and your partner must now each assume the genotype of one of your offspring. For example, if the first offspring was AA, one partner now begins with four black cards. The other partner should assume the genotype of the second offspring. If this offspring was Aa, for example, this person now begins with two red cards and two black cards.
6. Randomly select a different partner in your class. Repeat steps 3 and 4 and record the first and second offspring from the second generation.
7. Repeat step 5, selecting new cards if necessary to reflect the alleles of the offspring from the second generation.
8. Continue choosing a different partner at random to create third, fourth, and fifth generation mating, with two offspring from each generation.
9. Collect and record class totals for each genotype from each mating in each generation.

Post-lab Questions

1. What is the initial allele frequency in your class population? Express this as a percentage converted to a decimal.
2. Consider the data you collected over the five generations as a single large population, so your class totals in the last row of your table are the genotypes of an entire population. Calculate the frequency of each genotype as a percentage converted to decimal form. Calculate the allele frequency in the population.
3. Use the Hardy-Weinberg equation to determine the genotype frequencies of the beginning population where $p = 0.5$ and $q = 0.5$.
4. Calculate the genotype and allele frequencies of the class population for the fifth generation only.

Conclude and Apply

5. How do the allele frequencies change from generation to generation? Explain whether this population is in Hardy-Weinberg equilibrium.
6. Predict what would happen if you completed this activity with only half of your class.

Exploring Further

7. Repeat this activity with only half of your class. Compare the results between the two populations of different sizes.
8. What limitations does this simulation have in imitating what is actually occurring in the population?
9. Describe how this activity could be changed to replicate an actual, natural population that is evolving rather than a hypothetical, non-evolving population.

Practice Problems

1. An investigator has determined that 16 percent of a certain human population *cannot* roll their tongue. The ability to roll the tongue is controlled by a dominant allele. Calculate the genotype and allele frequencies for the population.
2. In a certain population, 30 percent are homozygous dominant, 49 percent are heterozygous, and 21 percent are homozygous recessive. What percentage of the next generation is predicted to be homozygous recessive, assuming a Hardy-Weinberg equilibrium?
3. In a population of pea plants, 1 percent are short, which means they are homozygous recessive. What are the frequencies of the recessive allele t and the dominant allele T? What are the genotypic frequencies in this population?

WEB LINK

www.mcgrawhill.ca/links/atlbiology

One application of the Hardy-Weinberg equation is to predict how many people in one generation of a human population are carriers of a particular recessive allele. If the number of babies born annually with a particular disease (such as phenylketonuria [PKU] or cystic fibrosis) are known, the number of adults that carry the allele can be predicted. This information can be used to track trends in the conditions, help medical researchers garner support for their work, and help public-health workers allocate their time and resources effectively. To learn more about these diseases and the frequency of these recessive alleles in our population, go to the web site above, and click on **Web Links**. Determine the frequency of the recessive traits for PKU and cystic fibrosis using the Hardy-Weinberg equation.

SECTION REVIEW

1. The Hardy-Weinberg principle is a model that uses a hypothetical situation that would rarely, if ever, be replicated in nature. Explain why it is useful to use the Hardy-Weinberg principle to help understand population genetics.
2. A biologist has found that 10 percent of a population of bats are hairless, which is a recessive trait. Assuming that the population is in Hardy-Weinberg equilibrium, determine the genetic structure (genotype and allele frequencies) of the population.
3. List the conditions necessary to maintain the Hardy-Weinberg equilibrium.
4. Select one condition that is necessary for the Hardy-Weinberg equation to work, and explain why this condition must be met for no change to occur.
5. A population of flowers are in Hardy-Weinberg equilibrium with 32 white flowers and 168 yellow flowers. The white flowers are bb and the yellow flowers are Bb or BB, where b is recessive and B is dominant. Draw a table showing the phenotypes, genotypes, frequency of the genotypes in the population, and frequency of alleles B and b. Create a Punnett square that shows the potential crosses for this population of flowers.
6. If a plant breeder started selecting either the white or the yellow flowers from Question 5 above, would the population be in Hardy-Weinberg equilibrium?
7. Is the human population of North America to be in Hardy-Weinberg equilibrium? Explain your answer.
8. Why would you expect the whooping crane population of North America to not be in Hardy-Weinberg equilibrium?

20.3 Mechanisms for Genetic Variation

OUTCOMES

- **Explain the role of mutations in micro-evolution.**
- **Analyze evolutionary mechanisms and their effects on biodiversity and extinction.**
- **Explain how sexual selection can affect genetic variation.**

Even though rattlesnakes (such as the one in Figure 20.9) are found throughout much of North America, few humans have close encounters with them. Most rattlesnakes take cover in the underbrush if danger is present or, at least, give warning with their distinctive rattle. Nonetheless, thousands of people are bitten by rattlesnakes each year, although only 0.2 percent of victims will die. In recent decades, however, there have been several reports of unusual reactions to certain rattlesnake venoms. As well, doctors are reporting that they often have to use many more vials of antivenom to treat bites. In some cases, a species whose venom was previously not considered a threat to humans delivered bites that were deadly. In other cases, patients showed symptoms that were not usual for the venom of the snake that bit them. (Rattlesnake venom usually contains either neurotoxins that affect the nerve impulses to muscles and can restrict breathing, or hemotoxins that affect the tissue near the bite.) Victims showed signs of neurotoxin poisoning when they had been bitten by snakes that previously were thought to deliver only hemotoxins. Why do the toxins seem to be changing? Are venoms evolving?

Figure 20.9 What factors might have caused rattlesnake venom to become more potent in recent decades?

Scientists studying this phenomenon have presented several explanations. Some scientists suspect that closely related snakes with differing types and potencies of venom are interbreeding in places where their populations overlap. Others suggest that in some populations, snakes with more potent venoms are being naturally selected because their prey are developing increasingly powerful substances in their blood to block venoms. For example, studies have shown that populations of California ground squirrel that overlap the range of the northern Pacific rattlesnake have a factor in their blood that makes them better able to combat the snake's venom.

A third suggested explanation for the changes in rattlesnake venom relates to the change in age-structure of snake populations. Juvenile rattlesnakes have stronger venom than larger adult snakes. Because humans usually hunt, capture, or even run over larger snakes, the overall age of some snake populations may be shifting to favour young snakes with more potent venom.

All of these possible explanations for the increased toxicity in rattlesnake venom provide scenarios of micro-evolution in action. The gene pools of these populations are changing because of natural selection or because individual snakes are entering or leaving the population. These situations deviate from the Hardy-Weinberg equilibrium. In this section, you will investigate the five conditions that have the potential to result in micro-evolution: mutation, genetic drift, gene flow, non-random mating, and natural selection.

BIO FACT

Of the five causes of micro-evolution, only natural selection always adapts a population to its environment. The other agents of change — gene flow, genetic drift, non-random mating, and mutation — can affect populations in positive, negative, or neutral ways.

WEB LINK

www.mcgrawhill.ca/links/atlbiology

To learn more about the possible evolution of rattlesnake venom, go to the web site above, and click on **Web Links**. Read through the article and identify specific situations in which the gene pool in the population might be changing. Using resources from the Internet and library, find an example of how the gene pool of a Canadian species is changing.

Mutations

Mutations may provide new alleles in a population and, as a result, may provide the variation required for evolution to occur. (Recall that you learned about mutations in Chapter 17, section 17.4.) When DNA mutates, a cell may die, malfunction, or multiply rapidly into a tumour. Whatever the result, the mutation disappears when the organism dies. If, however, the mutation alters the DNA in a gamete, the mutation may be passed on to subsequent generations. Mutations can have effects that are favourable, unfavourable, or neutral, and the fate of the mutation depends on how it acts in the population.

Mutations alone are not likely to cause evolution. But if a mutation provides a selective advantage (such as the ability of the California ground squirrel to break down rattlesnake poison), it may result in certain individuals producing a disproportionate number of offspring as a result of natural selection. Eventually the favourable mutation will appear with increased frequency in a population.

The fate of particular mutations may also change. Neutral, or perhaps even harmful, mutations can be a source of variation that ultimately helps a population survive given the right circumstances, such as when environments change. For example, the water flea *Daphnia* (shown in Figure 20.10) normally lives in water that is around 20°C and cannot survive in water 27°C or warmer. However, there is a mutation that enables *Daphnia* to survive in temperatures between 25°C and 30°C. This mutation is only advantageous — and thus only perpetuated in the population — when water temperatures are so warm that the other *Daphnia* die off.

In situations in which the environment is changing extremely rapidly, mutant alleles that were previously insignificant in the population may, by chance, fit the new environmental conditions better. As a result, the organisms containing the mutant allele survive and the mutant allele is perpetuated because it provides a selective advantage. The once neutral, or even negative, mutation can in some cases mean the survival of a population. For instance, there are many examples of insects, bacteria, and viruses quickly becoming adapted to new environments because of mutations that prove to be beneficial. Populations of mosquitoes have rapidly developed resistance to certain ingredients in insecticides because of a mutation that resulted in alleles that could break down and withstand the chemical poisons. When the mosquitoes were first sprayed by the insecticide, most died. However, those with the mutant allele that withstood the chemicals were naturally selected for and thus were more likely to survive and reproduce. This scenario is repeated generation after generation until there is a mosquito population resistant to the insecticide. Another scenario is being played out today as strains of bacteria become increasingly resistant to once-effective antibiotics.

Figure 20.10 Populations of *Daphnia* can have a mutation that allows them to survive at higher-than-normal water temperatures.

Bacteria and other micro-organisms reproduce quickly, and mutations that affect the population's genetic variation can have a significant impact in a short period of time. Bacteria can reproduce asexually by dividing as frequently as every 20 minutes. This could result in a single cell having close to a billion descendants in about 10 hours. Because of these astounding reproductive rates, any new mutation that proves beneficial can increase its frequency in the population quickly. This phenomenally rapid asexual cloning of individuals resistant to the new environment (the "poison" of an antibiotic, for example) makes the development of new antibiotics increasingly challenging for biochemists.

Genetic Drift

In small populations, the frequencies of particular alleles can be changed drastically by chance alone. This is called **genetic drift**. As an example, imagine flipping a coin 1000 times. Every time you flip a coin you have a 50–50 chance of having an outcome of heads or of tails. In a large sample size (for example, 1000 flips), you would logically expect the number of outcomes of heads and tails to be fairly close. If, however, you flipped heads 700 times and tails 300 times, you might start to wonder about your coin. On the other hand, in a small sample size (for example, 10 flips), it would not be too unusual to flip heads seven times and tails three. The smaller the sample size, the greater the chance of sampling error. In population genetics, the sample size can greatly affect the gene pool of a population; the smaller the population, the less likely that the parent gene pool will be reflected in the next generation. In a large population, there is a better chance that the parent gene pool will be reflected in subsequent generations.

Figure 20.11 on the following page illustrates how genetic drift can happen in a small population and how these changes can be rapid and significant. In any population, not all of the individuals in each generation will necessarily reproduce. This further amplifies the effect of genetic drift. For example, in the first generation of flowers in Figure 20.11, only four plants produce seeds that give rise to fertile offspring. In such a small population size, the allele frequencies shift in the second generation. Allele frequencies again change in the third generation when only two of the plants in the second generation leave fertile offspring. In this example, genetic drift reduced variability because one allele was lost (it "drifted" out of the population) and the other allele became fixed in the population. By the third generation, only mutation or migration of new individuals into the population could re-introduce the lost allele.

THINKING LAB

An Evolving Disease: Tuberculosis

Background

Tuberculosis is an infectious lung disease caused by the bacterium *Mycobacterium tuberculosis*. Tuberculosis is a contagious disease that can be spread by the inhalation of the bacteria. Although anyone can get tuberculosis, people who are already in poor health and who live in crowded conditions are particularly susceptible. Tuberculosis was once fairly easy to treat — an antibiotic discovered about 60 years ago treated the disease effectively. At one time it was thought that tuberculosis could one day be eradicated. Today, however, new drug-resistant strains of tuberculosis are causing great concern to medical researchers.

In one recent study, researchers have been working with officials from the Russian prison system to help stave off the rapid evolution of drug-resistant forms of tuberculosis. Prisons in Russia are very crowded and it is thought that up to 100 000 prisoners carry strains of tuberculosis resistant to at least one antibiotic. Tuberculosis is readily spread in the prisons and bacteria move quickly from host to host. *Myobacterium* can be destroyed with a long course of antibiotics. However, since few prisoners get the full course of antibiotics (either because it cannot be provided or because patients are discharged before the treatment is completed), resistant bacteria spread easily through their bodies. When prisoners are released and left untreated, they can spread a new drug-resistant version of the bacteria to the general public. The tuberculosis rate increased five-fold in Russia between 1990 and 1996, and it is now one of the leading causes of death of young Russian men. Health officials who monitor tuberculosis are beginning to see drug-resistant strains of *Myobacterium* in places such as North America, where tuberculosis is relatively uncommon. As well, *Myobacterium* is just one of the many bacteria that are becoming resistant to antibiotics.

You Try It

1. Create a model showing how a population of *Myobacterium* could become resistant to antibiotics.
2. Is poorly supervised or incomplete treatment of antibiotics better than no treatment? Discuss this statement with a partner.
3. Using the Internet or library resources, investigate how researchers are treating drug-resistant tuberculosis or another disease that can be treated by antibiotics. Also, find out how they are trying to limit the spread of the disease.

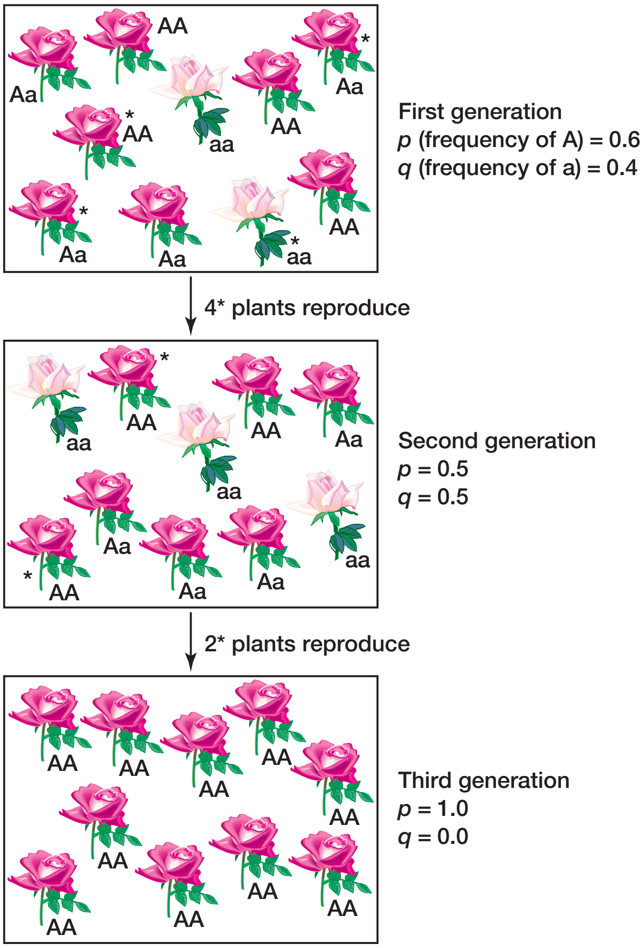


Figure 20.11 The frequency of alleles changes in this population over three generations because of genetic drift.

Most natural populations are large enough that the effects of genetic drift are negligible. However, two situations — population bottlenecks and the founding of new colonies by a few individuals (the founder effect) — lead to genetic drift.

The Bottleneck Effect

Populations can be subject to near extinction as a result of natural disasters such as earthquakes, floods, or fires, or of human interferences such as overhunting or habitat destruction. The surviving population is unlikely to represent the gene pool of the original population. The **bottleneck effect** is a situation in which, as a result of chance, certain alleles are overrepresented and others are underrepresented (or even absent) in the reduced population. Genetic drift then follows and the genetic variation in the surviving population is reduced.

The population of northern elephant seals (see Figure 20.12) passed through a bottleneck in the 1890s when overhunting reduced the population to, possibly, as few as 20 individuals. Since the species became protected, the population has increased to over 30 000 individuals. Biologists have studied 24 gene loci of several of the 30 000 individuals and have found no genetic variation; electrophoresis showed that at each of the 24 loci there is only one kind of allele. This is markedly different from what is found in populations of southern elephant seals that were not subject to the bottleneck effect, in which there is a high degree of genetic variation.

Whooping cranes, which breed in Wood Buffalo National Park in the Northwest Territories, also went through a genetic bottleneck. In 2001, the population at Wood Buffalo National Park was 177 whooping cranes. According to the data, scientists hypothesized that these birds were descendants of at most 12 (and more likely six or eight) founding birds. In addition to these 177 birds, another 86 whooping cranes are found in flocks that scientists are trying to establish in the Rocky Mountains (two individuals) and in Florida (84 individuals.) Biologists are working on strategies to limit loss of diversity due to genetic drift.

Figure 20.12 The reduced genetic variation in populations of northern elephant seals is the result of the bottleneck effect and genetic drift.

WEB LINK

www.mcgrawhill.ca/links/atlbiology

To learn what biologists in Canada and the United States are doing to help preserve genetic diversity in whooping cranes, go to the web site above, and click on **Web Links**. Read the essays on the web sites and summarize some of the problems associated with the small population size of whooping cranes. What strategies are being used to help preserve the species?

The Founder Effect

When a small number of individuals colonize a new area, chances are high that they do not contain all the genes represented in the parent population. The change in allele frequencies that result in this new population is called the **founder effect**. The particular alleles carried by these founders are dictated by chance only. As well, since the new population is in a new environment, its members will experience different selective pressures than the members of the parent population do. In practice, it is difficult to tell how much of the genetic difference between two populations is because of the founder effect and how much is a result of natural selection and the different selective pressures working on the populations. The ancestral population of Hawaiian honeycreepers shown in Figure 20.13 was thought to have migrated from North America about five million years ago. Individuals from the population became isolated on different islands and evolved into different species. Each population started with a small assortment of genes (founder effect), which were subjected to different selective pressures depending on the local environmental conditions.

While the founder effect is important on islands and other isolated habitats, other populations that have limited input of new genetic material also show the effects of a limited gene pool. Isolated human populations occasionally have high frequencies of inherited genetic disorders. An example of the founder effect is found in a small village in Venezuela, where the incidence of Huntington's disease is remarkably high. Huntington's disease is a debilitating, degenerative disease of the nervous system. It is caused by a lethal dominant allele that is not manifested in any particular phenotype. Because of this, individuals show no symptoms of the condition until they are about 30 years old (or older), when the deterioration of their nervous system begins. The presence of this condition in this particular village can be traced back to one woman who carried the dominant allele. Since the symptoms of the disease do not appear until later in life, carriers can reproduce (thereby potentially passing on the allele for this disease) before it is clear whether they carry the dominant allele or not.

In another example, in 1814 a population of 15 people founded a British colony on the Tristan da Cunha, a small group of islands in the Atlantic

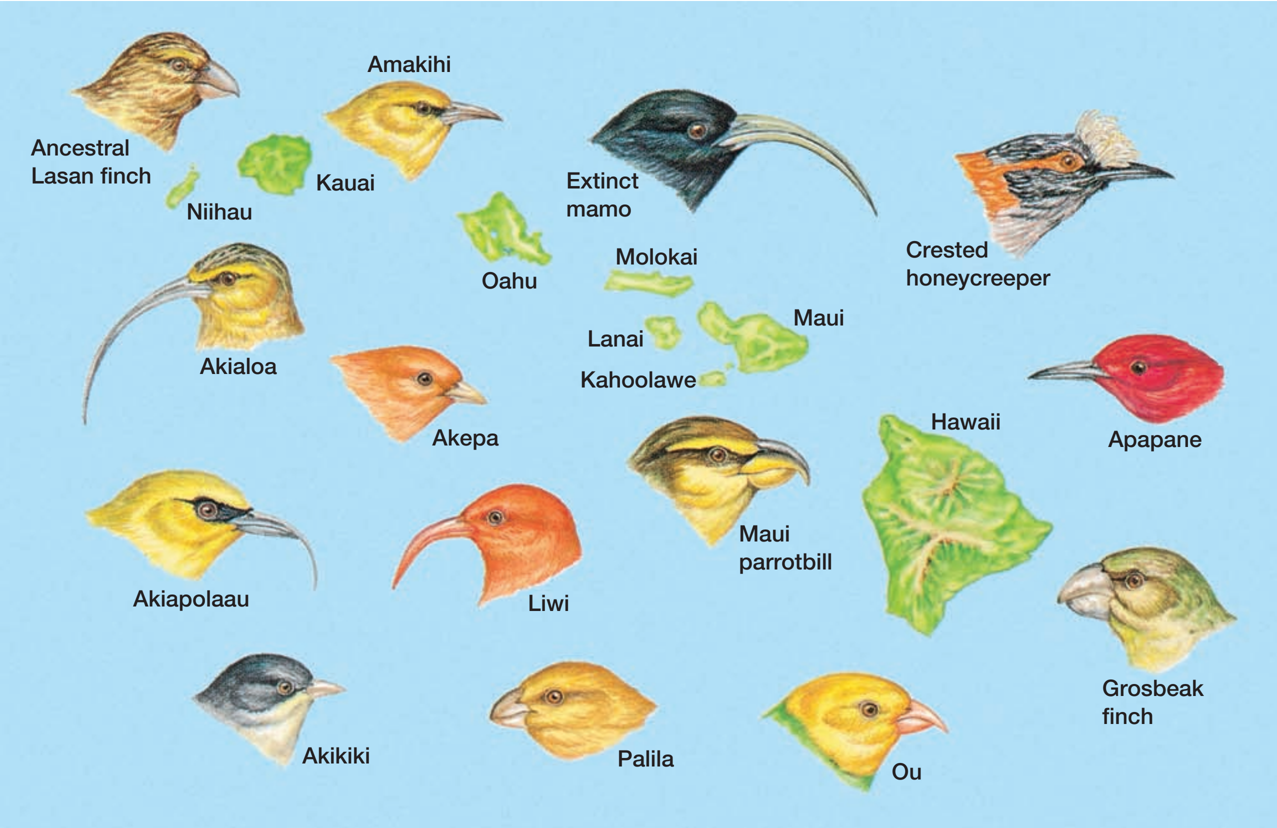


Figure 20.13 Hawaiian honeycreepers evolved into different species from a common ancestral population as a result of the founder effect and selective pressures.

Ocean. Apparently, one of these individuals carried the recessive allele for a type of blindness called retinitis pigmentosa. Studies have shown that the frequency of this allele in the current population on Tristan da Cunha is much higher than in populations from which the original founders came.

Gene Flow

To maintain genetic equilibrium, the gene pool of a population must be completely isolated. In practice, this is rarely the case. A windstorm or tornado can deliver new seeds or pollen to a population. This movement of new alleles into a gene pool, and the movement of genes out of a gene pool, is called **gene flow**.

Gene flow can reduce the genetic differences between populations that may have arisen because of natural selection or genetic drift. Previously isolated populations, including human populations, can accumulate differences over generations because of selective pressure or as a result of having a closed gene pool (no new alleles entering or leaving) in a small population. If the gene flow is extensive enough between two neighbouring populations, they can eventually become amalgamated into a single population with a common genetic structure. How do you think the relative ease of travel has contributed to micro-evolutionary change in human populations? What factors have limited the extent to which micro-evolutionary change can take place even with the accessibility of travel?

Non-random Mating

Genetic equilibrium can be maintained in a population only if that population mates on a random basis. However, not all organisms mate in such a way. Individuals will usually mate more often with neighbours than with more distant members of the population. **Inbreeding** (mating between closely related partners) is a type of **non-random mating** that causes frequencies of certain genotypes to change in the population. Inbreeding does not change allele frequencies; it results in a population with more homozygous individuals. Self-fertilization is particularly common in plants and is the most extreme case of inbreeding. Pea flowers, for example (as shown in Figure 20.14), include both the male and female reproductive structures. This ensures that self-fertilization will take place unless the flower is disturbed by an insect or other means.

Assortative mating is another type of non-random mating, in which individuals choose partners that have a similar phenotype such as size. For example, many animals (such as toads) select mates that are

THINKING LAB

Genetic Diversity and Fish Hatcheries

Background

Fish hatcheries have helped to preserve fish stocks for commercial and sport fishers. Hatcheries have stepped in to help make up for losses in the numbers of fish due to habitat destruction and overfishing. However, several genetic risk factors have the potential to affect the genetic diversity of both hatchery and wild stocks.

Hatcheries take the gametes from wild salmon, fertilize them, raise the salmon to a small size, and then release them back into their native stream. Fish in hatcheries are raised in controlled situations in which the objective is to maximize the output from the hatchery. In most cases, native salmon also spawn in the same areas. Each stream has a genetically unique salmon species. Therefore, hatcheries are careful to release their salmon only in the same streams from which the gametes were taken. The exception to this would be a situation in which the salmon that run in a river are extinct — hatcheries may release fish grown from gametes taken from other streams into a river that no longer has native salmon.

Analyze

Note: You may use the Internet, library, or other resources (such as interviews with fisheries biologists) to help you with this activity.

1. Speculate on how, or if, the following practices or situations might happen in hatcheries:
   - loss of variability within a population
   - loss of variability between populations
   - genetic drift
   - artificial selection
2. What are the advantages and disadvantages of hatchery-raised fish?
3. In many places, there is now a movement to save and/or improve spawning habitat in even the smallest creek that bears a population of salmon. How does this trend support improving the genetic diversity of wild salmon populations?

similar sized. Assortative mating is the basis of artificial selection, in which animals such as dogs are bred for particular characteristics. This inbreeding has led to a decrease in the genetic diversity in breeds of dogs and the perpetuation of certain diseases and conditions (such as hip dysplasia) in some breeds.

Natural Selection

The Hardy-Weinberg equilibrium says that all individuals are equal in their ability to survive and reproduce. In actual situations, however, this condition can rarely, if ever, be met. Populations have a range of phenotypes and genotypes, and some individuals in the population will leave more offspring than others. As you learned in Chapter 19, natural selection is the mechanism that results in this differential reproductive success. Selective forces such as predation and competition work on populations, and consequently some individuals are more likely to survive and reproduce than others. If having a single allele gives even a slight yet consistent selective advantage, the frequency of the allele in the population will increase from one generation to the next at the expense of the less favourable allele. There is a greater chance of the organisms with the slightly favourable allele living and reproducing and then passing this slightly favourable allele to their offspring. Therefore, selection causes changes in a population's gene frequencies that shift the population away from Hardy-Weinberg equilibrium.

There are three ways in which natural selection can affect the frequency of a heritable trait in a population: stabilizing selection, directional selection, and disruptive selection.

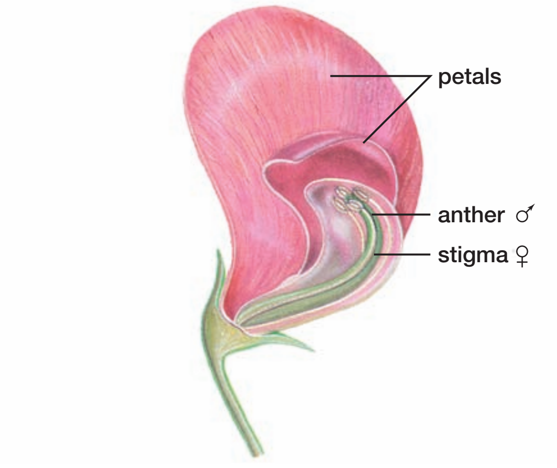


Figure 20.14 Pea flowers are designed so that self-fertilization is ensured if the flower is not disturbed.

Stabilizing selection favours an intermediate phenotype and acts against extreme variants. This type of selection reduces variation and improves the adaptation of the population to aspects of the environment that remain relatively constant. Figure 20.15 shows how stabilizing selection keeps the majority of baby weights between 3 and 4 kg. Infant mortality is greater for babies who are smaller or larger than this size.

Directional selection favours the phenotypes at one extreme over the other, and results in the distribution curve of phenotypes shifting in that direction. This type of selection is common during times of environmental change or when a population migrates to a new habitat that has different environmental conditions. Figure 20.16 on page 694 shows the directional selection shift that took place as horses evolved from an ancestral form that was adapted to a forest habitat to the modern form, which is adapted to a grassland habitat. This shift took place in response to a changing environment. *Hyracotherium* was about the size of a dog and was well-adapted to the forest environment present during the Eocene epoch. During the Miocene and Pliocene epochs, however, grasslands began to replace the forests and the ancestral horses were selected for larger size, more durable teeth suitable for grinding grasses, and longer legs for increased speed in the more open habitats.

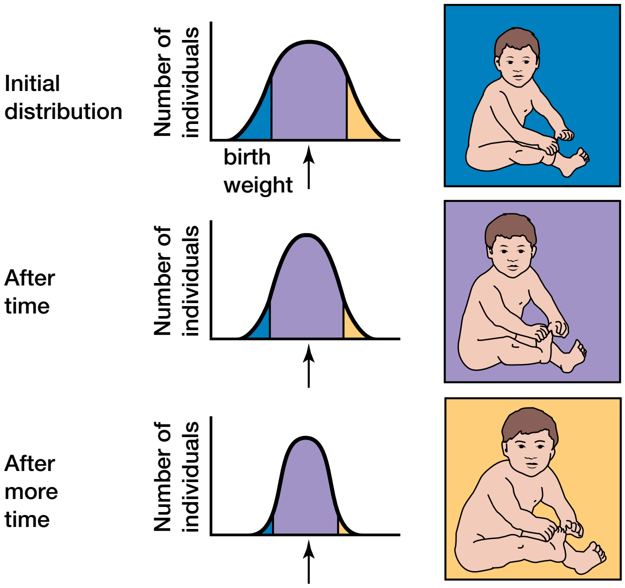


Figure 20.15 Natural selection favours the intermediate phenotype (for example, human baby weight) in stabilizing selection. Now, most babies are of intermediate weight.

Global climate change may also cause directional selection in some populations. Imagine that a hypothetical population of penguins lives near Pacific islands where the water temperatures have been moderate until recently. Global climate change has resulted in a shift in ocean currents such that the water is now consistently much colder. In the changing environment, birds with less body fat are less successful because they need to use more energy (food) to keep themselves warm. Birds with more body fat stay warmer in the water and can afford to use more energy for reproduction. As a result, the fatter penguins have more success raising young, so there is an overall increase in the number of alleles for increased body fat in the penguin population.

The shift in the population of peppered moths you learned about in Chapter 19 is an example of directional selection. The resistance of insects and bacteria to pesticides and antibiotics, respectively, are also examples of directional selection.

Disruptive (diversifying) selection takes place when the extremes of a phenotypic range are favoured relative to intermediate phenotypes (as shown in Figure 20.17). As a result, intermediate phenotypes can be eliminated from the population. In several salmon species (including coho salmon) there are two male phenotypes that are extremely different. When small "jack" males mature, they weigh about 500 g and are approximately 30 cm in length. In comparison, the "normal-sized" males average about 4.5 kg (and can be as large as 8.5 kg) when they are mature.

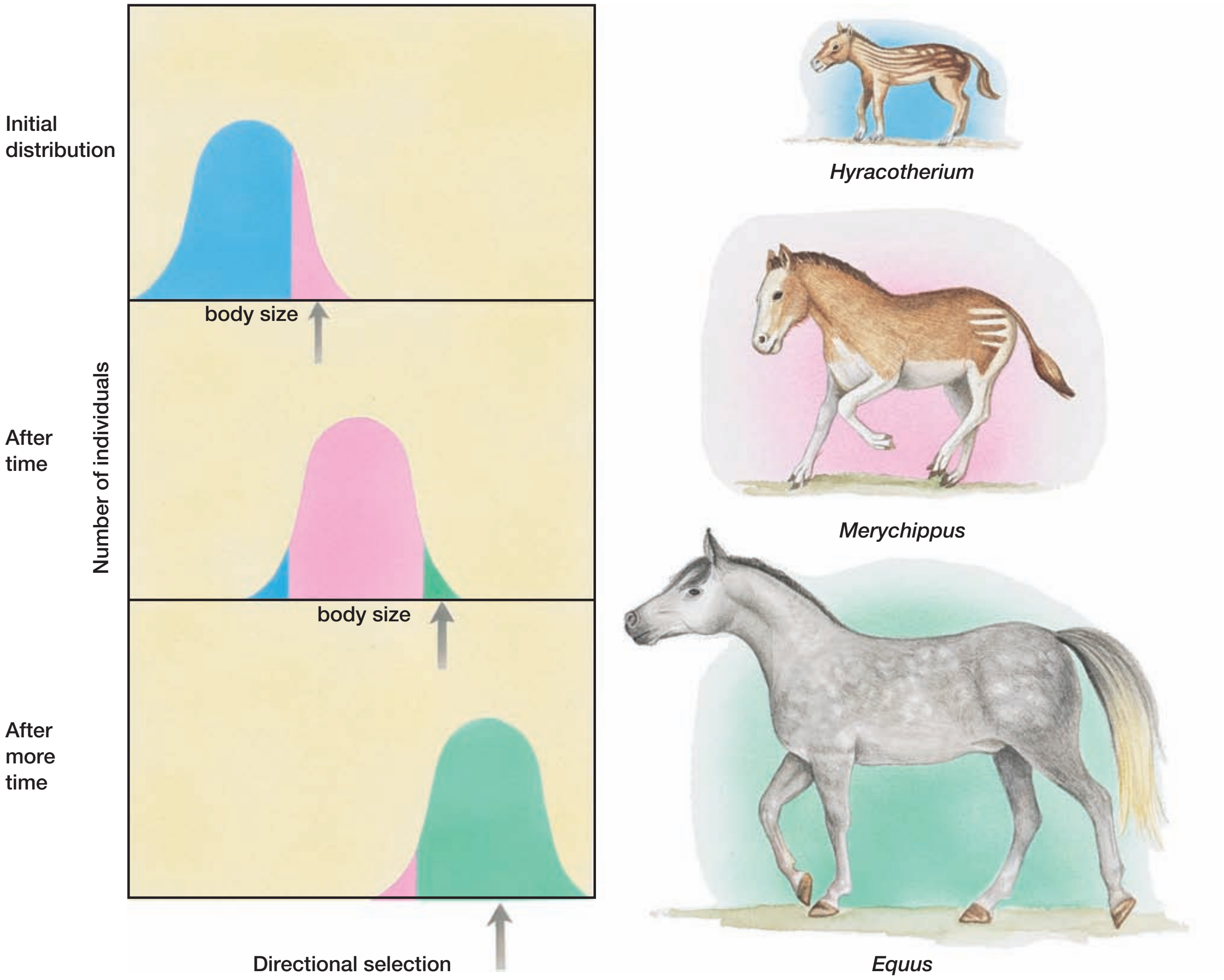


Figure 20.16 The modern horse, which is adapted to a grassland habitat, evolved from an ancestral horse that was adapted to a forest habitat. This shift in phenotype is called directional selection.

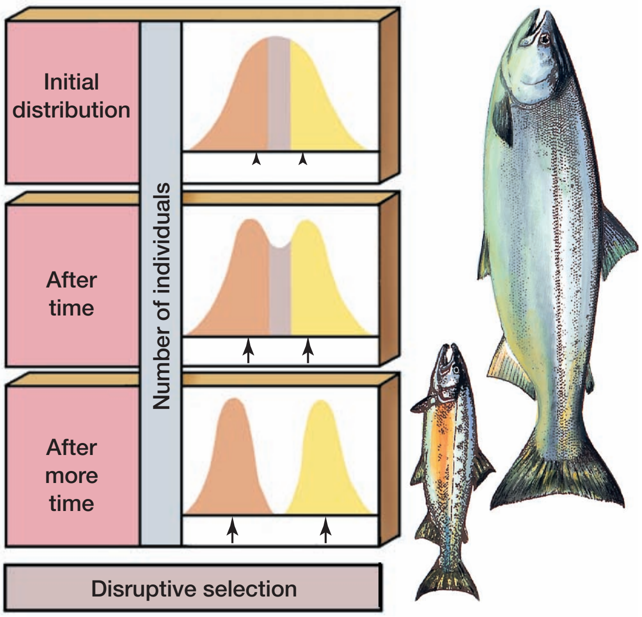


Figure 20.17 In disruptive selection, two extreme phenotypes are favoured over the intermediate form. Shown are two phenotypes of male coho salmon — the smaller "jack" salmon and the noticeably larger, regular-sized male.

Sexual Selection

Sexual reproduction has evolved independently several times throughout the course of evolutionary history. Remarkably, most forms of sexual reproduction share similar characteristics: the ova are large and immobile, while the sperm are small swimmers. Instead of both gametes wandering around searching for each other, it is more practical for one (the ova) to stay in place while the other searches for it. Two things occur to increase the probability of the gametes meeting — the ova releases powerful pheromones and males release millions of sperm.

Evolution has favoured mutations that make a species' sperm smaller and eggs larger. If sperm's only function is to carry genes (and not to carry the energy required for cell division), a species can have more, smaller-sized sperm. To complement this strategy, fewer, larger eggs that have the stored energy needed for cell division are required. This trend towards females with large eggs and males with more than enough sperm to fertilize the entire population of their species has produced a very competitive situation for sexually reproducing species. While one male may be able to fertilize all of his species, virtually every other male is in the same position. This has led to the evolution of a wide array of sexual behaviours and sexual attractants, such as plumage or scents, as males compete for the chance to mate with a female.

Males and females of many animal species often have markedly different physical characteristics, such as colourful plumage in male birds and antlers in male deer. This difference between males and females is called **sexual dimorphism**. Figure 20.18 shows the striking difference between male and female orioles. These obvious characteristics, as well as courtship displays and other mating rituals, result in another type of selection — **sexual selection**. Although the selection of mates has many facets, in general, competition between males (through actual combat or visual displays) and the choices made by females result in sexual selection and enhanced reproductive success.

Characteristics used in sexual selection may not be adaptive in the sense that they help an individual survive in the environment in any way. The larger mane of a lion or the antlers of a moose, for example, do not help these animals better withstand environmental conditions. However, if such characteristics give them the advantage of being chosen by a female, then their alleles can be perpetuated in the population and sexual selection has occurred.

Many organisms, including bacteria and many protozoa, reproduce without sex. Even some plants and animals can reproduce asexually. Sexual reproduction can be costly — it takes vast amounts of energy to grow new plumage, or a large rack of antlers. In many ways, sex seems to make no sense. A very well-adapted individual that could create clones of itself would create offspring that were equally well-adapted, so why has sexual reproduction evolved at all? Recently, scientists proposed a surprising idea: sex is a way of fighting off parasites and disease because sexual reproduction enhances genetic variability within the species.

Figure 20.18 Many birds, such as Baltimore orioles, show a high degree of sexual dimorphism.

Since sexual reproduction mixes the genes from both parents, any ability to fight off parasites or disease can be passed on to offspring. While a population may be perfectly adapted to the current environment, a population of clones will have little genetic variation to work with to survive changing conditions. Biologists tested their hypothesis by studying a type of fish — called topminnows — that live in Mexican ponds and streams. These fish sometimes mate with a closely related species, producing hybrids that are only female and that always reproduce by cloning rather than by mating. Curiously, in order to activate their eggs to grow, these hybrid females get sperm from male fish but they do not incorporate DNA from the sperm into their eggs.

In one pond the scientists studied, they found that the clones, rather than the sexually reproducing fish, were infected by parasitic cysts. Because the clones were exact replicas of one another, this strain of fish was an easy target for the parasites. Once the parasites became established in the population, they began to reproduce quickly.

In a second pond, where there were two different strains of clones, the researchers found that the more common strain of clone was subject to more infections. This also fit their hypothesis, which said that parasites able to attack the most common fish will thrive and spread throughout the population. (Meanwhile, the numbers of the other strain of fish remained low — at least temporarily — since they had less habitat available to them.) Eventually, however, the parasites became so successful that they killed their hosts and the more common strain of clone died out. This gave more habitat for the other strain of fish and their population rose. Of course, this also provided more opportunities for *another* parasite to infect *this* strain, and the cycle began all over again.

In a third pond, scientists saw something that seemed to contradict their hypothesis: they found that the fish that sexually reproduced were more infested than the clones. On closer inspection, however, it was clear that their hypothesis did fit. The pond had dried up years before, and when it refilled it had been recolonized by just a small population of fish. As a result, these fish were highly inbred and therefore deprived of the genetic variety that is the important advantage of sexual reproduction.

So, in many ways, sex is a compromise. A perfectly well-adapted individual will, in most cases, still mix genetic material with another individual to create offspring that are not exact clones. The questions is, who to mix genetic material with? Parasites may also play a role in determining which males are selected as mates by females. The displays demonstrate the fitness (because it takes energy and resources to produce the displays) and genetic potential of the males. Scientists speculate that a strong display — whether a loud song or a particularly bright display of feathers — shows that the male is healthy, strong, and not weakened by parasites or disease.

WEB LINK

www.mcgrawhill.ca/links/atlbiology

Our understanding of evolution grows daily as new ideas are presented and new information is gathered. To learn more about recent ideas and discoveries, go to the web site above, and click on **Web Links**. Investigate one new discovery or scientific study that advances our understanding of evolution. Create a short summary of this new information and post it on a bulletin board in your classroom.

SECTION REVIEW

1. Hunters often seek "trophy" animals — those that have large sets of antlers or horns. You are a wildlife biologist who recommends stopping trophy hunting in a certain area. Justify your reasoning and explain how this hunting behaviour might affect a population.
2. Create a diagram that explains how genetic drift can shift the allele frequency in a population in just a few generations.
3. Explain the difference between how natural selection changes phenotypes observed in populations and how the other four agents of micro-evolutionary change (genetic drift, gene flow, etc.) act on populations.
4. Can the role of a particular mutation present in a population change over time? Explain your answer.
5. Compare and contrast the founder effect and the bottleneck effect.

Chapter Summary

- Macro-evolution is evolution on a grand scale; a large evolutionary change. (20.1)
- Micro-evolution is the change in the gene frequencies within a population over time. (20.1)
- The Hardy-Weinberg equation is $p^2 + 2pq + q^2 = 1$. (20.2)
- The five conditions required to maintain a population in Hardy-Weinberg equilibrium are random mating, no mutations, isolation, large population size, and no natural selection. (20.2)
- Mutations may provide new alleles in a population and, as a result, may provide the variation required for evolution to occur. (20.3)
- The five causes of micro-evolution are natural selection, gene flow, genetic drift, non-random mating, and mutation. (20.3)
- The bottleneck effect and founder effect lead to genetic drift. (20.3)
- Three ways in which natural selection can affect genetic variation are stabilizing selection, directional selection, and disruptive selection. (20.3)

Language of Biology

Write a sentence including each of the following words or terms. Use any six terms in a concept map to show your understanding of how they are related.

- macro-evolution
- micro-evolution
- mutation
- modern synthesis
- allele
- locus
- homozygous
- heterozygous
- dominant allele
- recessive allele
- genotype
- phenotype
- incomplete dominance
- co-dominant
- population
- polymorphic
- fixed
- electrophoresis
- polymerase chain reaction (PCR)
- frequency
- genetic structure
- Hardy-Weinberg principle
- Hardy-Weinberg equilibrium
- genetic drift
- bottleneck effect
- founder effect
- gene flow
- inbreeding
- non-random mating
- assortative mating
- stabilizing selection
- directional selection
- disruptive (diversifying) selection
- sexual dimorphism
- sexual selection

UNDERSTANDING CONCEPTS

1. Differentiate between (a) dominant and recessive, and (b) gene and allele.

2. Explain the relationship between population size and the frequency of change in gene pools.

3. If a person gets his straight hair permed, explain whether this affects his (a) genotype; (b) phenotype.

4. Describe the possible fates of a mutation and the effects a mutation may have on a population.

5. A fly has a mutation that allows it to survive being sprayed by an insecticide. Is the mutation alone an example of micro-evolution? Explain your answer.

6. Are sex characteristics such as antlers adaptive in any way? Explain your answer and describe how sexual selection may affect the frequency of particular alleles in a population.

7. A species of toad commonly selects mates that are similar in size. How does this behaviour affect micro-evolution?

8. Give five examples of ways in which populations deviate from the Hardy-Weinberg equilibrium.

9. Choose an organism introduced in this unit and explain how two of the five situations that result in micro-evolution affect this population.

10. Describe how the work of Mendel and Darwin were blended to help develop the modern synthesis of the theory of evolution.

11. In pea plants, yellow peas are dominant over green peas. Predict the phenotypes and genotypes of the offspring of a cross between a plant heterozygous for yellow peas (Yy) and a plant homozygous for green peas (yy).

12. Describe the genotype of the parents and offspring in the following situations:

(a) A black mouse is crossed with a white mouse. There are 16 offspring, of which 75 percent are black and 25 percent are white.

(b) A bean with speckled seeds is crossed with a bean heterozygous for this characteristic. All offspring have speckled seeds.

(c) A tall dog and a short dog have two tall pups.

13. If a population has two alleles for a particular locus, B and b, and if the allele frequency of B is 0.7, calculate the frequency of heterozygotes if the population is in Hardy-Weinberg equilibrium.

14. If 16 percent of individuals in a population have a recessive trait, calculate the frequency of the dominant allele in the population. Assume the population is in Hardy-Weinberg equilibrium.

15. Describe three situations that might result in a bottleneck effect in a population.

16. Describe four situations that might result in gene flow in a population.

17. Explain why most mating is *not* random. Give an example of non-random mating in plants and in animals.

18. Describe assortative mating and provide an example.

19. Identify whether each of the following is an example of stabilizing, directional, or disruptive selection.

- **(a)** a population has only very large and very small snails
- **(b)** a population of ducks lays eggs of intermediate weight
- **(c)** in different parts of Africa, the colour pattern of the butterfly *Papilio dardanus* is dramatically different
- **(d)** most individuals in a population of hummingbirds have long beaks
- **(e)** a population has only medium-sized spiders
- **(f)** a population shifts from being primarily black moths to being primarily flecked moths

20. Compare natural selection with sexual selection.

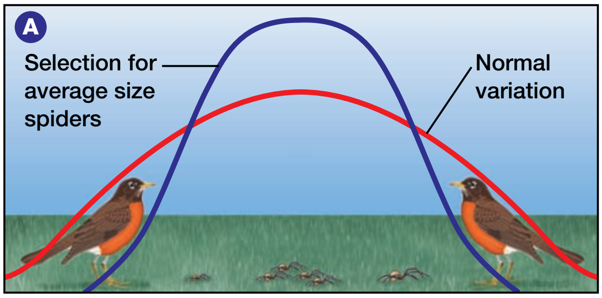
INQUIRY

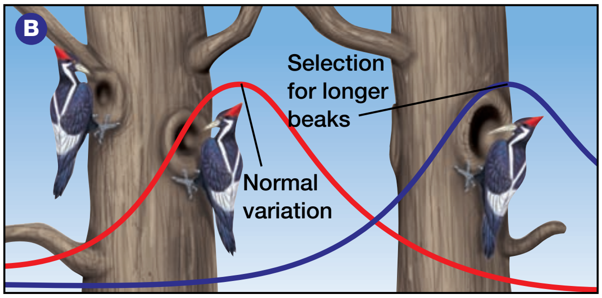
21. Plan an experiment or model that explains gene flow.

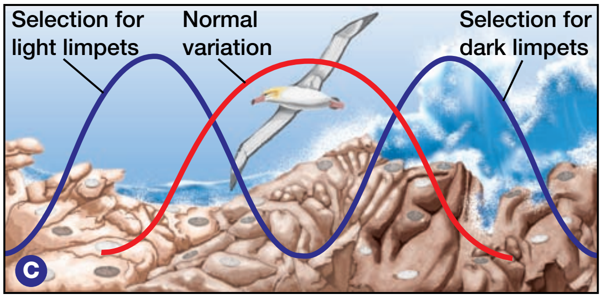
22. Devise a demonstration using coins, poker chips, or another item of your choice to explain how the founder effect works.

23. Create a demonstration, game, or other activity that explains one way in which populations can change over time.

24. The diagrams on the right illustrate different types of natural selection. The red bell-shaped curves indicate a trait's variation in a population. The blue bell-shaped curves indicate the effect of natural selection. Determine the type of selection occurring in each illustration and provide an explanation for how and/or why that type of selection might be occurring.







25. Using the data given below on the peppered moths (which you read about in Chapter 19, section 19.1), create bell-shaped curves that illustrate the natural selection of peppered moths from a polluted environment (in 1959) to a less polluted environment (in 1985 and 1989). Explain what is happening from 1959 to 1989 in the peppered moth population.

Year	In the region near Manchester
1959	9 out of 10 peppered moths were black
1985	5 out of 10 peppered moths were black
1989	3 out of 10 peppered moths were black

COMMUNICATING

26. Create a diagram that shows how non-random mating can increase the frequency of homozygous individuals in a population.

27. Explain the conditions in which a seemingly neutral mutation present in a small portion of a population may become quickly perpetuated in, and advantageous to, the population.

28. Theodosius Dobzhansky, a pioneer in the field of population genetics and one of the architects of the modern synthesis, said "Nothing in biology makes sense except in light of evolution." Explain your understanding of this statement.

29. You are a biologist who has been asked to explain evidence for micro-evolution to a class. Prepare your talk in point form. Provide examples of micro-evolution in action and of ways in which biologists study micro-evolution.

30. Summarize the three ways in which natural selection can shift the traits in a population's gene pool over time. Use diagrams to illustrate your summaries.

31. Scientists have used various types of biochemical and genetic analyses to determine the relatedness among the giant panda, the red panda, bears (such as polar bear, brown bear, black bear), and the raccoon. Results showed that the giant panda has DNA that more closely resembles the DNA of bears, and the red panda has DNA that more closely resembles the DNA of the raccoon. Draw a phylogenetic tree that shows these relationships.

32. You are a doctor who often prescribes antibiotics. Make a list of criteria for your patients explaining why they must take antibiotics only as prescribed.

MAKING CONNECTIONS

33. Why might a plant breeder be interested in knowing how certain traits are inherited?

34. Suppose paleontologists unearth a human skeleton that has been partially mummified and has had some of its hair preserved. What techniques could scientists use to gather more information from this discovery that would add to our understanding of evolutionary history? What are the limitations of the data and the techniques?

35. You are a biologist studying an endangered species of fox. Explain how you might use your understanding of population genetics in your work.

36. Describe different ways in which plant or animal biologists working with endangered species try to enhance genetic variation in populations.

37. What would happen to the conservation efforts if a number of alleles were eliminated from the current whooping crane population?

38. Sickle cell disease is caused by a recessive allele. Explain why the fact that we are diploid organisms keeps this allele at lower frequencies in the population. Imagine that a population of 20 individuals, three of whom carried the recessive allele for sickle cell disease, colonized a deserted island 200 years ago. The descendents of these individuals still live on this island. Predict the incidence of sickle cell disease on the island compared with the incidence of the disease in the human population at large.

39. Do you think that antibiotics should be available without a prescription? Give reasons for your opinion.