Chapter 23

The Evolution of Populations

Key Concepts

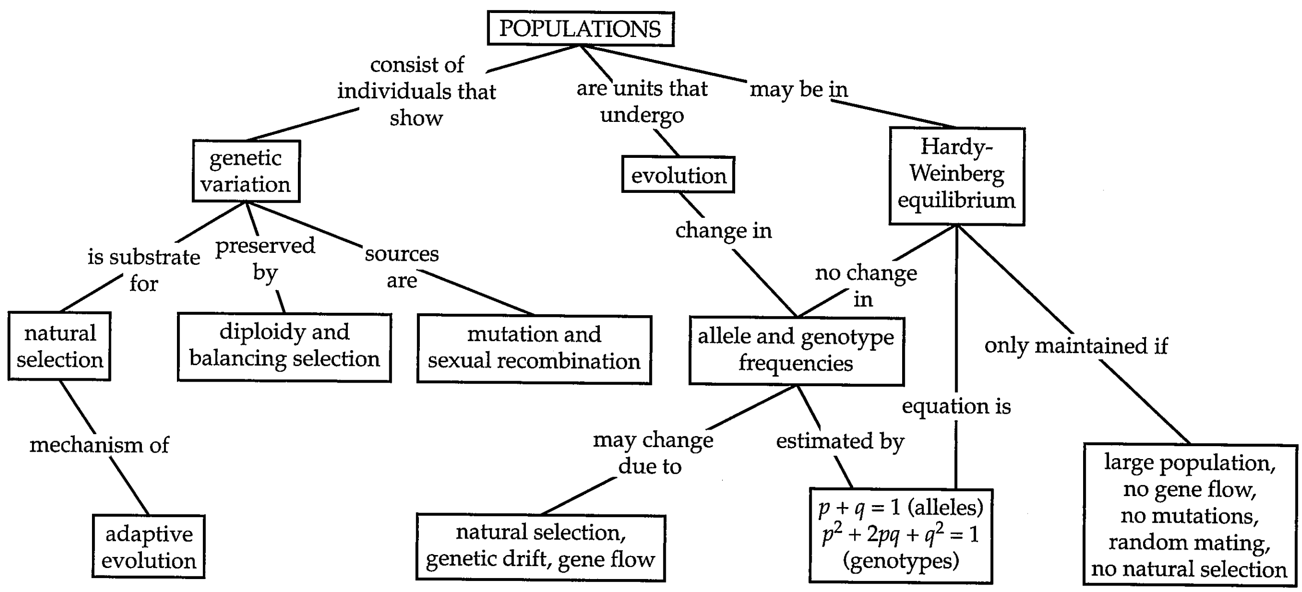
23.1 **Population genetics provides a foundation for studying evolution**

23.2 **Mutation and sexual recombination produce the variation that makes evolution possible**

23.3 **Natural selection, genetic drift, and gene flow can alter a population's genetic composition**

23.4 **Natural selection is the primary mechanism of adaptive evolution**

Framework



Chapter Review

Although it is individuals that are selected for or against by natural selection, it is populations that actually evolve as some characteristics become more common and others less from one generation to the next.

23.1 Population genetics provides a foundation for studying evolution

Microevolution is defined as changes in the genetic makeup of a population from generation to generation. Darwin lacked a genetic model to explain how the heritable variations on which natural selection acts are passed on without blending.

The Modern Synthesis When Mendel's work was rediscovered in the early 1900s, many geneticists believed that Darwin's focus on the inheritance of quantitative traits that vary on a continuum could not be explained by the inheritance of discrete Mendelian traits. The discovery that quantitative characters are influenced by multiple genes that each follow Mendelian inheritance helped to reconcile Darwin's and Mendel's ideas. The field of **population genetics,** which studies genetic change in populations over time, gave rise to a comprehensive theory of evolution, known as the **modern synthesis.** Key ideas of the modern synthesis have included the importance of populations as the units of evolution, the essential role of natural selection, and the gradualness of evolution. This paradigm of evolution, however, continues to evolve.

Gene Pools and Allele Frequencies A **population** is a localized group of individuals that have the ability to interbreed and produce fertile offspring. Populations of a species may be totally isolated or adjoining with their members concentrated in population centers.

The **gene pool** is the term for all the alleles present in a population at any given time. For individuals of a diploid species, the pool includes two alleles for each gene locus. If all individuals are homozygous for the same allele, the allele is said to be *fixed.* More often, two or more alleles are present in the gene pool in some relative proportion or frequency.

■ INTERACTIVE QUESTION 23.1

In a population of 200 mice, 98 are homozygous dominant for brown coat color (*BB*), 84 are heterozygous (*Bb*), and 18 are homozygous recessive (*bb*).

a. The allele frequencies of this population are ________ *B* allele ________ *b* allele.

b. The genotype frequencies of this population are ________ *BB* ________ *Bb* ________ *bb.*

The Hardy-Weinberg Theorem If only Mendelian segregation and recombination of alleles at fertilization are involved, the gene pool of a population will remain constant from one generation to the next. This stasis is formulated as the **Hardy-Weinberg theorem,** named for its originators. The theorem describes how genetic variation is retained in a population, providing the opportunity for natural selection to act.

The allele frequency within a population determines the proportion of gametes that will contain that allele. The random combination of gametes will yield offspring with genotypes that reflect and reconstitute the allele frequencies of the previous generation. If both gamete recombination and mating are random, the population is in **Hardy-Weinberg equilibrium,** and the frequencies of both alleles and genotypes will remain stable from generation to generation.

With the equation for Hardy-Weinberg equilibrium, the frequencies of genotypes within a population can be calculated from the allele frequencies. In a case with two alleles at a particular gene locus, the letters p and q represent the proportions of the two alleles within the population, and their combined frequencies must equal 1: $p + q = 1$. The frequencies of the genotypes in the offspring reflect the probability of each combination of alleles. According to the rule of multiplication, the probability that two gametes containing the same allele will come together is equal to $(p \times p)$ or p^2, or $(q \times q)$ or q^2. A p and q allele can combine in two different ways, depending on which parent contributes which allele; therefore, the frequency of a heterozygous offspring is equal to $2pq$. The sum of the frequencies of all possible genotypes in the population adds up to 1: $p^2 + 2pq + q^2 = 1$.

■ INTERACTIVE QUESTION 23.2

Use the allele frequencies you determined in Interactive Question 23.1 to predict the genotype frequencies of the next generation.

Frequencies of

B (p) = ______ b (q) = ______

$BB = p^2 =$ ______ $Bb = 2pq =$ ______ $bb = q^2 =$ ______

Even if a population is self-fertilizing or does not mate randomly, its allele frequencies will remain constant if gametes are produced at random from the gene pool and no other influences are operating.

Hardy-Weinberg equilibrium is maintained only if all of the following five conditions are met: an extremely large population, no gene flow or transfer of alleles between genetically different populations, no mutations, random mating, and no natural selection. Even though natural populations are rarely in true Hardy-Weinberg equilibrium, the rate of evolutionary change may be so slow that allele and genotype frequencies may be estimated using the Hardy-Weinberg equation.

If the frequency of homozygous recessive individuals is known (q^2), then the frequency of q may be estimated as the square root of q^2 (assuming the population is in Hardy-Weinberg equilibrium for that gene). From our example in Interactive Question 23.2, $q = \sqrt{0.09} = 0.3$. If the frequency of individuals with a recessively inherited disease is known (q^2), then the frequency of carriers of that recessive allele in the population can be calculated.

■ INTERACTIVE QUESTION 23.3

Practice using the Hardy-Weinberg equation so that you can easily determine genotype frequencies from allele frequencies and vice versa.

a. The allele frequencies in a population are $A = 0.6$ and $a = 0.4$. Predict the genotype frequencies for the next generation.

AA ________ *Aa* ________ *aa* ________

b. What would the allele frequencies be for the generation you predicted above in part a.?

A ________ *a* ________

23.2 Mutation and sexual recombination produce the variation that makes evolution possible

Mutation New alleles and genes originate by **mutation,** changes in the sequence of nucleotides in DNA. Most mutations occur in somatic cells and cannot be passed on to the next generation. Point mutations that occur in noncoding DNA or do not change the amino acid sequence of a protein are harmless. Those mutations that do alter a protein's function or affect a regulatory region of DNA may have serious effects. Rarely, however, a new mutant allele may increase an individual's fitness, or a mutation already present in the population may be selected for when the environment changes.

Chromosomal mutations are most often deleterious. Occasionally, a translocation of a chromosomal piece may bring alleles together that are beneficial in combination. Duplication of smaller DNA segments, introduced by transposons, may provide an expanded genome with extra loci that could eventually take on new functions by mutation. This gene **duplication** provides an important source of variation. The shuffling of exons may also result in new genes.

Mutation rates in animals and plants average about one in every 100,000 genes per generation. Mutation produces genetic variation very rapidly in HIV because of its short generation span and higher rate of mutation in its RNA genome.

Sexual Recombination In a sexually reproducing population, the genetic differences that make adaptation possible arise from the reshuffling of alleles into new combinations (recombination) every generation.

■ INTERACTIVE QUESTION 23.4

a. What is a major source of genetic variation for bacteria and viruses?

b. What is the major source of genetic variation for plants and animals?

c. Explain why your answers to a. and b. are different.

23.3 Natural selection, genetic drift, and gene flow can alter a population's genetic composition

Natural Selection Individuals that are more successful in producing viable, fertile offspring pass their alleles to the next generation in disproportionate numbers. This differential success in reproduction—natural selection—disrupts Hardy-Weinberg equilibrium.

Genetic Drift Chance deviations from expected results are more likely to occur in a small sample. Chance fluctuations in a small population's allele frequencies from one generation to the next are called **genetic drift** and tend to reduce genetic variation in a population.

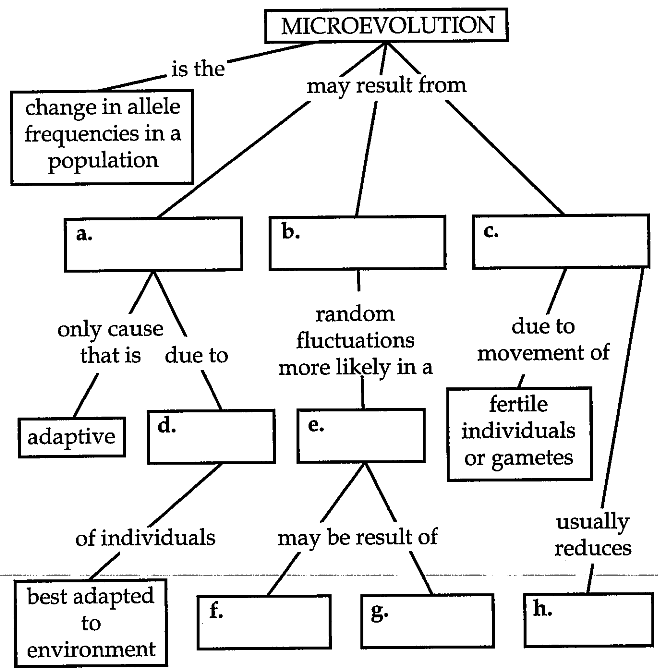
The **bottleneck effect** occurs when some disaster or other factor reduces the population size dramatically, and the few surviving individuals are unlikely to represent the genetic makeup of the original population. Genetic drift will remain a factor until the population grows large enough for chance events to be less significant. A bottleneck usually reduces variability because some alleles are lost from the gene pool.

Genetic drift that occurs when only a few individuals colonize a new area is known as the **founder effect.** Allele frequencies in the small sample are unlikely to be representative of the parent population, and genetic drift will affect the gene pool of the new population until it is larger.

Gene Flow **Gene flow,** the migration of individuals or the transfer of gametes between populations, may change allele frequencies. Differences in allele frequencies between populations tend to be reduced by gene flow.

■ INTERACTIVE QUESTION 23.5

Fill in the following concept map that summarizes three causes of microevolution. Better still, create your own concept map to help you review the ways in which a population's genetic composition may be altered.



23.4 Natural selection is the primary mechanism of adaptive evolution

Genetic Variation Individual variation, the slight differences between individuals as a result of their unique genomes, is the raw material for natural selection. *Discrete characters* vary categorically as distinct phenotypes and usually are determined by a single gene locus. *Quantitative characters,* those that are affected by two or more gene loci, provide most of the heritable variation within a population.

A population is **phenotypically polymorphic** when two or more forms of a discrete character—called *morphs*—are evident in a population. Characters that vary along a continuum are influenced by **genetic polymorphisms** for alleles of the genes involved in determining that character.

Measures of genetic variation look at both gene diversity and nucleotide diversity. The **average heterozygosity** of a population is the average percent of loci that are heterozygous. Nucleotide variability measures the average percent of differences in nucleotide sites between individuals of a population.

Geographic variations are regional genetic differences between populations. These variations may be due to differing environmental selection factors and also to genetic drift. A **cline,** or graded variation within a species along a geographic axis, may parallel an environmental gradient.

■ INTERACTIVE QUESTION 23.6

a. Do humans have more or less genetic variation than most species?

b. Two humans differ by about what percentage of their nucleotide bases?

A Closer Look at Natural Selection **Fitness** is a measure of an individual's relative contribution to the gene pool of the next generation. Population geneticists speak in terms of the **relative fitness** of a genotype as its contribution to the next generation in comparison with the contribution of other genotypes for that locus. The most reproductively successful variants are said to have a relative fitness of 1, whereas the fitness of another genotype is the proportion of offspring it produces compared to the most successful variant.

Natural selection acts on the whole organism. The relative fitness of an allele depends on the entire genetic and environmental context in which it is expressed. Factors that contribute to both survival and fertility determine an individual's evolutionary fitness.

■ INTERACTIVE QUESTION 23.7

a. A gene locus has two alleles, *B* and *b*. The genotype *BB* has a relative fitness of 0.5 and *bb* has a relative fitness of 0.25. What is the relative fitness of the genotype *Bb?*

b. What is the relative fitness of a sterile animal?

The distribution of a trait may be affected by three modes of selection. **Directional selection** occurs most frequently during periods of environmental change, when individuals deviating in one direction from the average for some phenotypic character may be favored. **Disruptive selection** occurs when the environment favors individuals on both extremes of a phenotypic range. **Stabilizing selection** acts against extreme phenotypes and favors more intermediate forms, tending to reduce phenotypic variation.

The Preservation of Genetic Variation The diploidy of most eukaryotes maintains genetic variation by hiding recessive alleles in heterozygotes, enabling them to persist in the population and be selected, should the environment change.

Balancing selection can maintain the frequencies of two of more phenotypes in a population, resulting in **balanced polymorphism.** When individuals heterozygous at a certain gene locus have survival and reproductive advantages, their **heterozygote advantage** tends to maintain two or more alleles at this locus.

In frequency-dependent selection, a morph's reproductive success declines if it becomes too common in the population. Frequency-dependent predation, as predators learn to focus on the more common prey items, may preserve polymorphism in prey populations.

Some of the genetic variation seen in populations may be **neutral variations** that do not confer a selective advantage or disadvantage. In **pseudogenes,** which have become inactivated by mutations, variations are not affected by natural selection and will change randomly by genetic drift. There is no consensus on how much variation is truly neutral.

■ INTERACTIVE QUESTION 23.8

a. Why is the highly deleterious sickle-cell allele still present in the gene pool of the U.S. population?

b. Why is this allele at such a relatively high frequency in the gene pool of some African populations?

Sexual Selection **Sexual dimorphism** is the distinction between males and females on the basis of secondary sexual characteristics. Sexual selection is the selection for traits that may not be adaptive to the environment but do enhance reproductive success. Such traits may increase an individual's success in competing for **(intrasexual selection)** or attracting **(intersexual selection)** a mate. Also called mate choice, intersexual selection may be based on showy traits that reflect the general health of the male and, thus, the fitness of his alleles.

The Evolutionary Enigma of Sexual Reproduction From a reproductive output standpoint, asexual reproduction is far superior, and sexual reproduction should, in theory, be selected against. One explanation for how sexual reproduction is maintained by natural selection is the selective advantage of genetic variation in disease resistance. For example, maintaining high variation in the cell surface molecules helps a population's offspring resist pathogens such as viruses and bacteria that key in on such receptor molecules. The coevolutionary race between host and rapidly evolving parasites is known as a "Red Queen race."

Why Natural Selection Cannot Fashion Perfect Organisms There are at least four reasons evolution does not produce perfect organisms. First, each species has evolved from a long line of ancestral forms, many of whose structures have been coopted for new situations. Second, adaptations are often compromises between the need to do several different things, such as swim and walk, or be agile and strong. Third, chance events affect a population's evolutionary history. Fourth, natural selection can act only on variations that are available; new alleles do not arise as they are needed.

Word Roots

inter- = between (*intersexual selection:* individuals of one sex are choosy in selecting their mates from individuals of the other sex, also called mate choice)

intra- = within (*intrasexual selection:* a direct competition among individuals of one sex for mates of the opposite sex)

micro- = small (*microevolution:* a change in the gene pool of a population over a succession of generations)

muta- = change (*mutation:* a change in the DNA of genes that ultimately creates genetic diversity)

poly- = many; **morph-** = form (*polymorphism:* the coexistence of two or more distinct forms of individuals in the same population)

Structure Your Knowledge

1. **a.** What is the Hardy-Weinberg theorem?
   b. Define the variables of the equation for Hardy-Weinberg equilibrium. Make sure you can use this equation to determine allele frequencies and predict genotype frequencies.
2. It seems that natural selection would work toward genetic unity; the genotypes that are most fit produce the most offspring, increasing the frequency of adaptive alleles and eliminating less beneficial alleles from the population. Yet there remains a great deal of variability within populations of a species. Describe some of the factors that contribute to this genetic variability.

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Which of the following determines an organism's fitness?
a. survival
b. number of matings
c. adaptation to the environment
d. successful competition for resources
e. number of viable offspring

2. According to the Hardy-Weinberg theorem,
a. the allele frequencies of a population should remain constant from one generation to the next if the population is large and only sexual recombination is involved.
b. only natural selection, resulting in unequal reproductive success, will cause evolution.
c. the square root of the frequency of individuals showing the recessive trait will equal the frequency of p.
d. genetic drift, gene flow, and mutations are always maladaptive.
e. all of the above are correct.

3. If a population has the following genotype frequencies, $AA = 0.42$, $Aa = 0.46$, and $aa = 0.12$, what are the allele frequencies?
a. $A = 0.42$ $a = 0.12$
b. $A = 0.6$ $a = 0.4$
c. $A = 0.65$ $a = 0.35$
d. $A = 0.76$ $a = 0.24$
e. $A = 0.88$ $a = 0.12$

4. In a population with two alleles, B and b, the allele frequency of b is 0.4. What would be the frequency of heterozygotes if the population is in Hardy-Weinberg equilibrium?
a. 0.16
b. 0.24
c. 0.48
d. 0.6
e. You cannot tell from this information.

5. In a population that is in Hardy-Weinberg equilibrium for two alleles, C and c, 16% of the population show a recessive trait. Assuming C is dominant to c, what percent show the dominant trait?
a. 36%
b. 48%
c. 60%
d. 84%
e. 96%

6. Genetic drift is likely to be seen in a population
a. that has a high migration rate.
b. that has a low mutation rate.
c. in which natural selection is occurring.
d. that is very small.
e. for which environmental conditions are changing.

7. Gene flow often results in
a. populations that move to better environments.
b. an increase in randomness in the genetic composition of the next generation.
c. adaptive microevolution.
d. a decrease in allele frequencies.
e. a reduction of the allele frequency differences between populations.

8. The existence of two distinct phenotypic forms in a species is known as
a. geographic variation.
b. stabilizing selection.
c. heterozygote advantage.
d. polymorphism.
e. directional selection.

9. The average heterozygosity of *Drosophila* is estimated to be about 14%, which means that
a. 86% of fruit fly genes are identical.
b. on average, 14% of a fruit fly's gene loci are heterozygous.
c. only 14% of nucleotide sites differ between individuals.
d. nucleotide variability must be very great between individuals.
e. the fruit fly population never experienced a bottleneck effect.

10. Mutations are rarely the cause of microevolution in eukaryotes because
a. they are most often harmful and do not get passed on.
b. they do not directly produce most of the genetic variation present in a diploid population.
c. they occur very rarely.
d. they are only passed on when they occur in gametes.
e. of all of the above.

11. In a study of a population of field mice, you find that 48% of the mice have a coat color that indicates that they are heterozygous for a particular gene. What would be the frequency of the dominant allele in this population?
    a. 0.2.4
    b. 0.48
    c. 0.50
    d. 0.60
    e. You cannot estimate allele frequency from this information.

12. In a random sample of a population of shorthorn cattle, 73 animals were red (C^RC^R), 63 were roan, a mixture of red and white (C^RC^r), and 13 were white (C^rC^r). Estimate the allele frequencies of C^R and C^r, and determine whether the population is in Hardy-Weinberg equilibrium.
    a. $C^R = 0.64$, $C^r = 0.36$; because the population is large and a random sample was chosen, the population is in equilibrium.
    b. $C^R = 0.7$, $C^r = 0.3$; the genotype ratio is not what would be predicted from these frequencies and the population is not in equilibrium.
    c. $C^R = 0.7$, $C^r = 0.3$; the genotype ratio is close to what would be predicted from these frequencies and the population is in equilibrium.
    d. $C^R = 1.04$, $C^r = 0.44$; the allele frequencies add up to greater than 1 and the population is not in equilibrium.
    e. You cannot estimate allele frequency from this information.

13. A scientist observes that the height of a certain species of asters decreases as the altitude on a mountainside increases. She gathers seeds from samples at various altitudes, plants them in a uniform environment, and measures the height of the new plants. All of her experimental asters grow to approximately the same height. From this she concludes that
    a. height is not a quantitative trait.
    b. the cline she observed was due to genetic variations.
    c. the differences in the parent plants' heights were due to directional selection.
    d. the height variation she initially observed was an example of nongenetic environmental influence.
    e. stabilizing selection was responsible for height differences in the parent plants.

14. Sexual selection will
    a. select for traits that enhance an individual's chance of mating.
    b. increase the size of individuals.
    c. result in individuals better adapted to the environment.
    d. produce more offspring.
    e. result in a relative fitness of more than 1.

15. The greatest source of genetic variation in plant and animal populations is from
    a. mutations.
    b. sexual recombination.
    c. selection.
    d. polymorphism.
    e. recessive masking in heterozygotes.

16. A plant population is found in an area that is becoming more arid. The average surface area of leaves has been decreasing over the generations. This trend is an example of
    a. a cline.
    b. directional selection.
    c. disruptive selection.
    d. gene flow.
    e. genetic drift.

17. Mice that are homozygous for a lethal recessive allele die shortly after birth. In a large breeding colony of mice, you find that a surprising 5% of all newborns die from this trait. In checking lab records, you discover that the same proportion of offspring have been dying from this trait in this colony for the past three years. (Mice breed several times a year and have large litters.) How might you explain the persistence of this lethal allele at such a high frequency?
    a. Homozygous recessive mice have a reproductive advantage.
    b. A large mutation rate keeps producing this lethal allele.
    c. There is some sort of heterozygote advantage and perhaps selection against the homozygous dominant trait.
    d. Genetic drift has kept the recessive allele at this high frequency in the population.
    e. Since this is a diploid species, the recessive allele cannot be selected against when it is in the heterozygote.

18. In breeding experiments with *Drosophila*, you count the offspring produced by each of three different genotypes and determine that flies with the genotype *AA* have a relative fitness of 1. What does that mean?
    a. *AA* flies have a lower fitness than do flies that are *Aa* or *aa*.
    b. *AA* flies produce more viable offspring than do *Aa* or *aa* flies.
    c. This fly population must be in Hardy-Weinberg equilibrium.
    d. *AA* flies live longer than do *Aa* or *aa* flies.
    e. The *A* and *a* alleles must both have a frequency of 0.5.

19. All of the following would tend to maintain balanced polymorphism in a population *except*
    a. balancing selection.
    b. directional selection.
    c. diversifying selection.
    d. heterozygote advantage.
    e. frequency-dependent selection.

20. Genetic analysis of a large population of mink inhabiting an island in Michigan revealed an unusual number of loci where one allele was fixed. Which of the following is the most probable explanation for this genetic homogeneity?
    a. The population exhibited nonrandom mating, producing homozygous genotypes.
    b. The gene pool of this population never experienced mutation or gene flow.
    c. A very small number of mink may have colonized this island, and this founder effect and subsequent genetic drift could have fixed many alleles.
    d. Natural selection has selected for and fixed the best adapted alleles at these loci.
    e. The colonizing population may have had much more genetic diversity, but genetic drift in the last year or two may have fixed these alleles by chance.

21. Directional selection would be most likely to occur when
    a. a population's environment has undergone a change.
    b. a population's environment has two very different habitats.
    c. frequency-dependent selection is acting on a population.
    d. a population's environment is very harsh.
    e. a population is small and its environment is stable.

22. If an allele is recessive and lethal in homozygotes,
    a. the allele is present in the population at a frequency of 0.001.
    b. the allele will be removed from the population by natural selection in approximately 1,000 years.
    c. the relative fitness of the homozygous recessive genotype is 0.
    d. the allele will most likely remain in the population at a low frequency because it cannot be selected against when in a heterozygote.
    e. Both c and d are correct.

23. Sexual reproduction may be maintained by natural selection because
    a. it produces the greatest number of offspring.
    b. intrasexual selection produces the strongest males.
    c. intersexual selection allows females to choose their mates.
    d. maintaining a high variability in a population for traits such as cell surface markers protects against pathogens such as viruses and bacteria.
    e. it maintains high genetic variability in a population's gene pool so that the population can adapt should environmental conditions change.

24. Humans have an estimated 1,000 olfactory receptor genes. This is most likely an example of
    a. gene flow.
    b. frequency-dependent selection.
    c. gene duplication.
    d. neutral variation.
    e. a quantitative character.

25. Which of these types of selection is mismatched with its example?
    a. disruptive—a population of black-bellied seedcrackers consists of birds with either small bills (more effective at eating soft seeds) or large bills (able to crack hard seeds)
    b. Intrasexual—elephant seal males are more than four times larger than females; males fight over areas of beach where females congregate during breeding season
    c. Intersexual—female zebra finches chose males with the brightest bills; bill color correlates with high levels of carotenoids (antioxidants)
    d. frequency-dependent—as fish of one coloration become more numerous, predator fish form a "search image" and preferentially feed on them
    e. stabilizing—the frequency of A, B, AB, and O blood groups remains constant in a population