21

EVOLUTION AND SPECIATION

STUDY OBJECTIVES

1. To analyze the mechanisms of evolution and speciation 589
2. To investigate the mechanisms of the maintenance of genetic variation in natural populations, both selective and neutral 596
3. To discuss sociobiology, the evolution of social behavior 603

STUDY OUTLINE

The cactus ground-finch (*Geospiza scandens*) from Santa Cruz Island, Galápagos. (© Frans Lanting/ Photo Researchers, Inc.)

Populations change, or evolve, through natural selection and the other forces that perturb the Hardy-Weinberg equilibrium. The merger of population genetics theory with the classical Darwinian view of evolution is known as **neo-Darwinism,** or the "new synthesis." In the two previous chapters, we laid the theoretical groundwork for an understanding of the process of evolution in natural populations. In this chapter, we concern ourselves with long-term evolution and speciation.

DARWINIAN EVOLUTION

Charles Darwin (fig. 21.1) was a British naturalist who published his theory of evolution in 1859 in a book entitled *The Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life.* This book provided overwhelming support for evolution as well as a mechanism for the process. Darwin had been greatly influenced by the writings of the Reverend Thomas Malthus, who is best known for his theory that populations increase exponentially, whereas their food supplies increase arithmetically. Malthus, who proposed his theory in *An Essay on the Principle of Population* in 1798, was referring specifically to human populations and was trying to encourage people to reduce their birthrate rather than let their offspring starve to death. Malthus's writings impressed upon Darwin the realization that under limited resources—the usual circumstance in nature—not all organisms survive. In nature, organisms compete for the resources needed to survive.

Figure 21.1 Charles Darwin (1809–1882). Darwin was an English naturalist who first established the theory of organic evolution by natural selection. (Painting by George Richmond, 1840. Downe House, Downe, Kent. © Archiv/Photo Researchers, Inc.)

Darwin sailed aboard the HMS *Beagle,* a ship that circled the world from 1831 to 1836 with the primary purpose of charting the coast of South America. During his travels on the *Beagle,* Darwin amassed great quantities of observations (especially on South America and the Galápagos Islands) that led him to suggest a theory. Darwin proposed that organisms become adapted to their environment by the process of natural selection. In outline, the process works according to the following principles:

1. *Variation is a characteristic of virtually every group of animals and plants.* Darwin saw variation as an inherent property among individuals of all populations.
2. *Every group of organisms overproduces offspring.* Most populations maintain a relatively constant density over time. Thus, every parent, on average, just replaces itself. Therefore, most of the offspring the individuals of a population produce will die before they reproduce. Hence, in every group of organisms, there is an overabundance of young.
3. *Those that do survive and reproduce will pass on their genes in greater proportion.* This step is the cornerstone and the best-known part of Darwin's theory. Among all the organisms competing for a limited array of resources, only the organisms best able to obtain and utilize these resources survive **(survival of the fittest).** If the favorable characteristics of these individuals are inherited, these traits pass on to the next generation. These organisms then have the greatest reproductive success (box 21.1).

Thus, over time, if advantageous mutations arise, or if the environment changes, the characteristics of a population should change through the process of natural selection (directional or disruptive selection). A particularly well-adapted population in a stable environment may maintain its numbers through the forces of stabilizing selection (see fig. 20.9). Nonrandom mating, genetic drift, and migration may also play a role in population differentiation.

EVOLUTION AND SPECIATION

The term **evolution** describes a change in genotypic frequencies, which usually results in a population of individuals better adapted to the environment than their ancestors were. **Speciation** comes in two different forms. (1) It may be the evolution of a population over time until the current population cannot be classified as

BOX 21.1

Ethics and Genetics

Attacks on Darwinism

From time to time, attacks on neo-Darwinism are mounted, usually by persons who either view evolutionary theory as antireligious or who misunderstand Darwin's theory. One attack, entitled "Darwin's Mistake," by Tom Bethell, was published in *Harper's* magazine in 1976.

Bethell began by pointing out that Darwinian theory is a tautology rather than a predictive theory. (The term *tautology* means a statement that is true by definition.) That is, evolution is the survival of the fittest. But who are the fittest? Obviously, the individuals who survive. Thus, without an independent criterion for fitness other than survival, we are left with the statement that evolution is the survival of the survivors. This, indeed, is a tautology. But it is possible to assign independent criteria for fitness. Darwin wrote extensively about artificial selection in pigeons, in which the breeders' choice was the criterion for fitness. (Many novel breeds of pigeon have been created this way.) Plant and animal breeders have practiced artificial selection extensively. Here, survival is not the criterion for fitness; productivity is.

It is more difficult to establish *a priori* independent criteria of fitness in nature. Often, uncontrolled or unseen vagaries have major impacts on the course of events. Surely the temperature became colder before the mammoths became woolly. Is it then reasonable to predict that elephants would get woolly if the climate became colder in Africa today? The answer is no, for several reasons. First, the elephants might adapt to colder weather in any of a large number of different ways—they could get fatter, they could migrate, and so on. To some extent, adaptation depends not only on the changing environment, but also on the reserve variation within the gene pool of the species. Second, the elephants could become extinct; they might not be able to adapt at all. And third, if the climatic changes were not severe, the elephants might not change at all.

Predicting the exact course of evolution is nearly impossible. To provide independent criteria for fitness in nature is, therefore, very difficult. Some modern evolutionary biologists, although not doubting neo-Darwinism, do worry to some extent about the difficulties in testing modern evolutionary theory. However, lower-level experiments are done to test various aspects of evolution in specific systems. For example, in 1993, B. Grant and P. Grant hypothesized that changes in bill size would occur in the finch *Geospiza fortis* (see fig. 21.6) because of changing food size due to changing weather on the Galápagos Islands. Their proposal seems to be correct. In addition, the support for Darwinism (the fossil

belonging to the same **species** as the original population. This process is known as **anagenesis,** or **phyletic evolution** (*an* is Latin for without, *genesis* is Latin for birth or creation). (2) Speciation may also be the divergence of a population into two distinct forms (species) that exist simultaneously. This branching process is known as **cladogenesis** (*clado* is Greek for branch; fig. 21.2). What do we mean by the term *species?*

Before Darwin's time, **typological thinking** prevailed, and a species was defined as a group of organisms that were morphologically similar. All variants were considered imperfections of the model or type. One of Darwin's greatest contributions to modern biological theory was to treat variation as a normal phenomenon in a group of organisms. The modern **biological species concept** groups together as members of the same species organisms that can potentially interbreed. A species, therefore, is a group of organisms that can mate among themselves to produce fertile offspring.

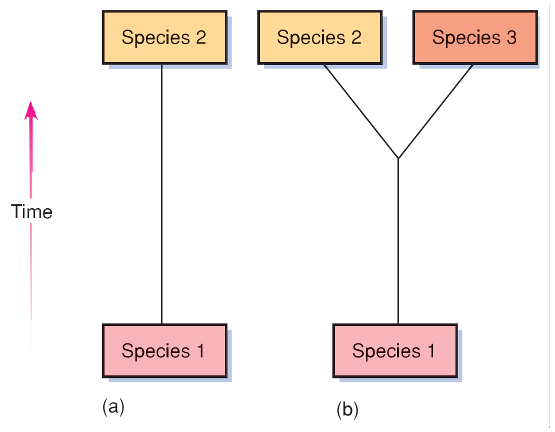


Figure 21.2 Forms of speciation. In anagenesis (*a*), a species changes over time until it is so different from its progenitor that it is classified as a new species. In cladogenesis (*b*), speciation takes place as a branching process wherein one species becomes two or more.

record, embryology, comparative anatomy, geographic distributions, etc.) is so overwhelming that the general nature of evolution is not in doubt. We can clearly trace its path, although we cannot make exact predictions for its future.

From a philosophical point of view, neo-Darwinism is the general paradigm (broad concept) defining "normal" biology. Every scientific endeavor works under the umbrella of a paradigm. When enough inconsistencies appear, a new paradigm is sought to replace the old in what Thomas Kuhn called a "scientific revolution." In physics, relativity overthrew Newtonian principles. In biology, Darwinism overthrew the concept of a recent, biblically described origin of animals and plants. Darwinism became the paradigm because it explained many things in a consistent fashion that a recent origin of all forms of life could not. Neo-Darwinism will remain the current paradigm unless it is overthrown by a better theory that explains previous inconsistencies. To date, no major inconsistencies suggest that neo-Darwinism is not correct.

In his article, Bethell went on to try to refute neo-Darwinism using the following argument: Survival of the fittest can be redefined to mean that some organisms have more offspring than others. Thus, natural selection cannot be a creative force because the only thing it works on is organisms alive now, some having more offspring than others. How, asks Bethell, can this possibly give us tigers and horses from ancestors that did not look like tigers and horses? The answer is that mutation produces variants in the population. The organism best able to compete will leave the most offspring. With an array of different genotypes in a population, natural selection determines which genotypes will increase in future generations. Traits that give the bearer an advantage increase in the population, and evolution takes place. Natural selection was the force behind the evolution from the small Eocene horse to the modern *Equus.*

Misinterpretation of mutation is the basis for other attacks on Darwinism. For example, Darwinian evolution has been attacked as not feasible, since most mutations are deleterious. How, the argument goes, can evolution proceed by a combination of deleterious events? The answer is that although most mutations are deleterious, some are not. This is especially true in changing environments; yesterday's deleterious mutant may be today's favored mutant.

The most recent attacks on Darwinism have been launched by creationists, who have attempted to pass laws in many states requiring schools to teach the biblical version of creation as an alternative to Darwinism. The courts have rejected this position because creationism is not a scientific theory. It does not follow the rules of the scientific method wherein empirical evidence can refute it.

Unfortunately, the definition of species on the basis of interbreeding cannot be used in many places, mostly due to the technical problems of applying it. Taxonomists and paleontologists, who often use nonliving specimens (preserved or fossilized), use the **morphological species concept** as a working definition. Under this concept, two organisms are classified as belonging to the same species if they are morphologically similar. They are classified as belonging to two different species if they are as different as two organisms belonging to two recognized species. Other problems arise for taxonomists since speciation is a dynamic process. For example, isolated subgroups of a population may be in various stages of becoming new species; the rate of successful interbreeding among individuals from these subgroups may range from 0 to 100%. How should the in-betweens be classified? There is no correct answer. It depends on the circumstances.

Still other problems make it necessary to turn to the morphological species concept. Haploid and asexual species are hard to classify. Also, two organisms that will not interbreed in nature may do so in a laboratory setting. Thus, the interbreeding test carried out in the laboratory (as is done frequently) is not necessarily an adequate criterion for speciation. Other problems arise in classifying groups that are geographically isolated from each other, such as populations on islands. These individuals are physically isolated, but in many cases they can interbreed freely when brought together with their mainland counterparts. So, although there is a good theoretical definition of a species (potentially interbreeding individuals), more often than not it is necessary for biologists to apply the morphological species concept to determine whether two populations belong to the same species. In some cases, no decision can be made about the species status of a population. It is clear that a population has evolved, but it is not clear whether it has evolved enough to be called a new species. However, this is more of a problem for taxonomists and evolutionary biologists than for the organisms themselves.

Mechanisms of Cladogenesis

Reproductive Isolation

How does one species become two? Basically, **reproductive isolating mechanisms** must evolve to prevent two subpopulations from interbreeding when they come into contact. Reproductive isolating mechanisms are environmental, behavioral, mechanical, and physiological barriers that prevent individuals of two species from producing viable offspring. Following is a modification of the classification system of isolating mechanisms suggested by evolutionary biologist G. L. Stebbins:

1. *Prezygotic mechanisms* prevent fertilization and zygote formation.
    a. Residential—The populations live in the same region, but occupy different habitats.
    b. Seasonal or temporal—The populations exist in the same region, but are sexually mature at different times.
    c. Ethological (in animals only)—The populations are isolated by incompatible premating behavior.
    d. Mechanical—Cross-fertilization is prevented or restricted by incompatible differences in reproductive structures.
2. *Postzygotic mechanisms* affect the hybrid zygotes after fertilization has taken place.
    a. F_1 hybrid breakdown—F_1 hybrids are inviable or weak.
    b. Developmental hybrid sterility—Hybrids are sterile because gonads develop abnormally or because meiosis breaks down before it is completed.
    c. Segregational hybrid sterility—Hybrids are sterile because of abnormal distribution to the gametes of whole chromosomes, chromosome segments, or combinations of genes.
    d. F_2 breakdown—F_1 hybrids are normal, vigorous, and fertile, but the F_2 generation contains many weak or sterile individuals.

Allopatric, Parapatric, and Sympatric Speciation

Reproductive isolating mechanisms are barriers to **gene flow,** the spread of genes between populations. These isolating mechanisms can evolve in three different ways, each of which defines a different mechanism of speciation. Usually, the mode of speciation is dictated by both the properties of the genetic systems of the organisms and stochastic (random) or accidental events. For example, vertebrates tend to have different speciation modes than phytophagous (plant-feeding) insects.

The appearance of a geographic barrier, such as a river or mountain, through the range of a species physically isolates populations of the species. Physical isolation can also occur if migrants cross a particular barrier and begin a new population (founder effect). The physically isolated populations can then evolve independently. If reproductive isolating mechanisms evolve, then two distinct species are formed, and if they come together in the future, they remain distinct species. Speciation that occurs because reproductive isolating mechanisms evolve during physical separation of the populations is called **allopatric speciation** (fig. 21.3). As evolutionary biologist Guy Bush pointed out, "Although examples in nature are difficult to substantiate . . . it [allopatric speciation] has been convincingly demonstrated in frogs . . . and lizards."

Reproductive isolating mechanisms usually originate incidentally to the speciation process. That is, they arise incidentally during the process of evolution in isolated populations rather than being selected for. When isolated populations come together again, incomplete isolating mechanisms may allow hybrids to form. If the hybrids are normal and viable and can freely interbreed with individuals of each parent population, then no speciation has taken place. However, if the hybrids are at a disadvantage, natural selection may favor stronger isolating mechanisms. In this case, organisms that mate with individuals from the other population leave fewer offspring. The result is a more effective barrier to hybridization. Regions in which previously isolated populations come into contact and produce hybrids are called **hybrid zones.**

Until recently, evolutionary biologists believed that allopatric speciation was the general rule. Many now believe that two other modes of speciation may occur frequently in certain groups of organisms. **Parapatric speciation** occurs when a population of a species that occupies a large range enters a new niche or habitat (fig. 21.3). Although no physical barrier arises, the new niche acts as a barrier to gene flow between the population in the new niche and the rest of the species. Here again, reproductive isolating mechanisms evolve to produce two species where there was only one before. Parapatric speciation is believed to have occurred often in relatively nonvagile animals such as snails, flightless grasshoppers, and annual plants. **Sympatric speciation** occurs when a polymorphism, which is the occurrence of alternative phenotypes in the same population, arises within an interbreeding population before a shift to a new niche. This mode of speciation may be common in parasites and phytophagous insects. For example, if a polymorphism arises within a parasitic species that allows an individual with a certain genotype to adapt to a new host, this genotype may be the forerunner of a new species. If the parasite not only feeds on the new host but also mates on the new host, a barrier to gene flow arises, although the parasite may be surrounded by other members of its species with the original genotype. Sympatric speciation can thus occur in the middle of a species range rather than at the edges (fig. 21.3).

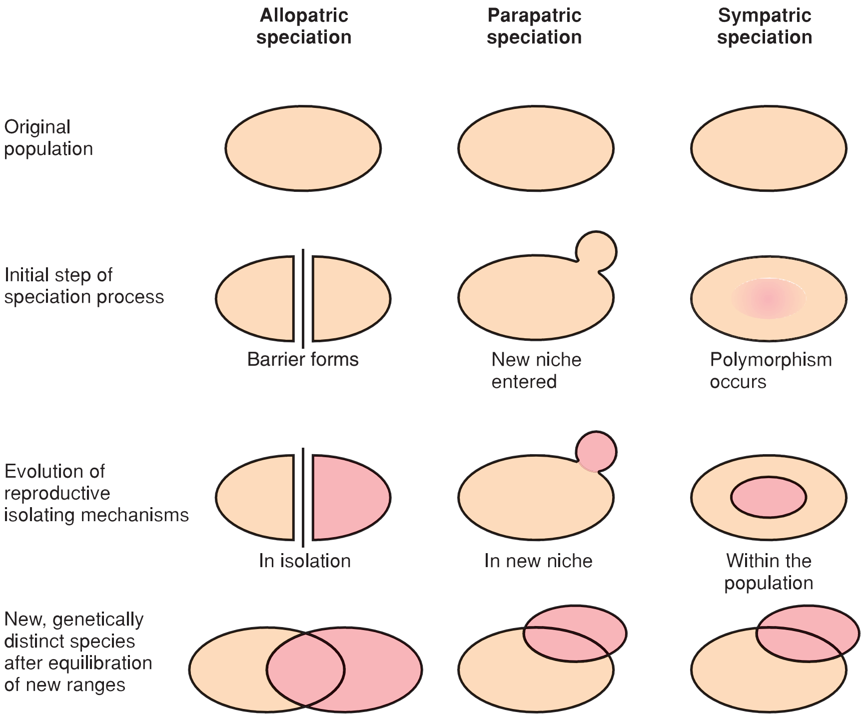


Figure 21.3 The three general mechanisms of speciation. In allopatric speciation, reproductive isolation evolves after the population has been geographically divided. In parapatric speciation, reproductive isolation evolves when a segment of the population enters a new niche. In sympatric speciation, reproductive isolation evolves while the incipient group is still in the vicinity of the parent population.

An example of incipient sympatric speciation has been seen recently in host races of the apple maggot fly (*Rhagoletis pomonella*) in North America (fig. 21.4). This fly was found originally only on hawthorn plants. However, in the nineteenth century, it spread as a pest to newly introduced apple trees. In fact, races are now known on pear and cherry trees and on rose bushes. These races have developed genetic, behavioral, and ecological differences from the original hawthorn-dwelling parent. Evolutionary biologists view this as an opportunity to observe sympatric speciation as it occurs.

Another form of sympatric speciation occurs when cytogenetic changes take place that result in "instantaneous speciation." These cytogenetic changes include polyploidy and translocations. For example, if polyploid offspring cannot produce fertile hybrids with individuals from a parent population, then the polyploid is reproductively isolated. This mechanism is much more common in plants because they can exist vegetatively despite odd ploidy and they usually do not have chromosomal sex-determining mechanisms, which are especially vulnerable to ploidy problems (see chapter 8).

The end result of cladogenesis is the divergence of a homogeneous population into two or more species. One of the classic examples of cladogenesis appears in

Figure 21.4 The apple maggot fly, *Rhagoletis pomonella.* This species has exhibited host range expansion since the nineteenth century from hawthorn to apple, cherry, and roses. Host races are presumably the initial step in sympatric speciation. Magnification 10×. (Source: Jeffrey L. Feder and Guy L. Bush, Zoology Department, Michigan State University.)

the ground finches of the Galápagos Islands. These birds are very well studied not only because they present a striking case of speciation, but also because Darwin studied them and was strongly influenced by them in his views. Figure 21.5 is a map of the Galápagos Islands, and figure 21.6 is a diagram of the species of Darwin's finches.

An original flock of finches somehow reached the Galápagos Archipelago from South America, 700 miles away, and with time spread to the various islands of the Galápagos Archipelago. Given the limited ability of the birds to get from island to island, allopatric speciation took place. On each island, the finch population evolved reproductive isolating mechanisms while evolving to fill certain niches not already filled on the islands. For example, in South America, no finches have evolved to be like woodpeckers because many woodpecker species already live there. But the Galápagos Islands, being isolated from South America, have what is called a **depauperate fauna,** a fauna lacking many species found on the mainland. The islands lacked woodpeckers, and a very useful food resource for birds—insects beneath the bark of trees—was going unused. Finches that could make use of this resource would be at an advantage and would thus be favored by natural selection. On one island, a finch did evolve to use this food resource. The woodpecker finch acts like a woodpecker by inserting cactus needles into holes in dead trees to extract insects. Darwin wrote: "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."

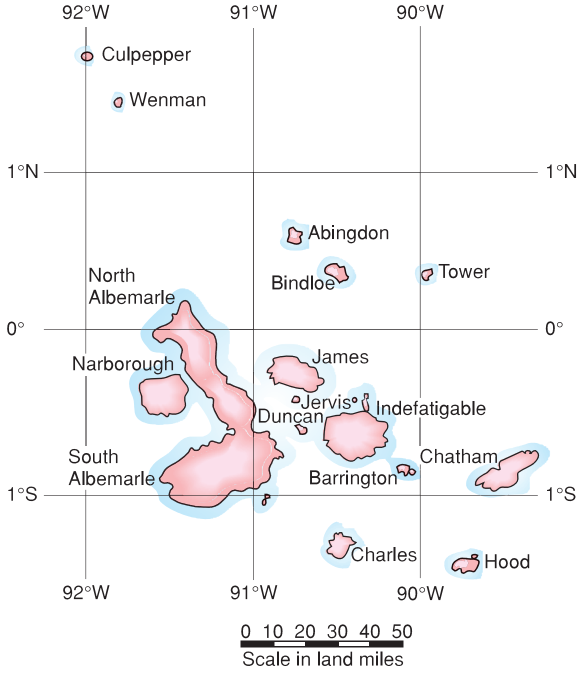
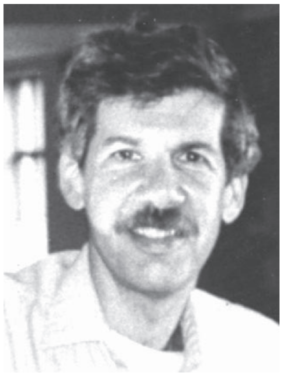


Figure 21.5 The Galápagos Archipelago is located about 700 miles west of Ecuador. This isolated chain of islands is a natural laboratory for the study of evolutionary processes. (From David Lack, *Darwin's Finches.* Copyright © 1947 by Cambridge University Press, New York, NY. Reprinted by permission.)

Phyletic Gradualism Versus Punctuated Equilibrium

Darwin visualized cladogenesis as a gradual process, which we refer to as **phyletic gradualism.** However, an alternative view arose in 1972, when N. Eldredge and S. J. Gould suggested that speciation itself, and the morphological changes accompanying speciation, occur rapidly, separated by long periods of time when little change occurs (*stasis*). They called their model **punctuated equilibrium** (periods of stasis punctuated by rapid evolutionary change). Although figure 21.7 presents what appear to be two clear alternatives, in practice the models are very hard to tell apart. They both start with the same ancestral species and predict the same number of modern species. Allopatric, parapatric, and sympatric speciation mechanisms apply to both punctuated equilibrium and phyletic gradualism. The only major difference between the models is the rate of change, and this can only be discovered from an almost complete fossil record. The punctuated equilibrium model has brought much excitement to modern evolutionary biology. We await a time in the near future when we can decide which model has predominated in evolutionary history.



Stephen J. Gould (1943–). (Courtesy of Dr. Stephen J. Gould and the Harvard University News Office.)

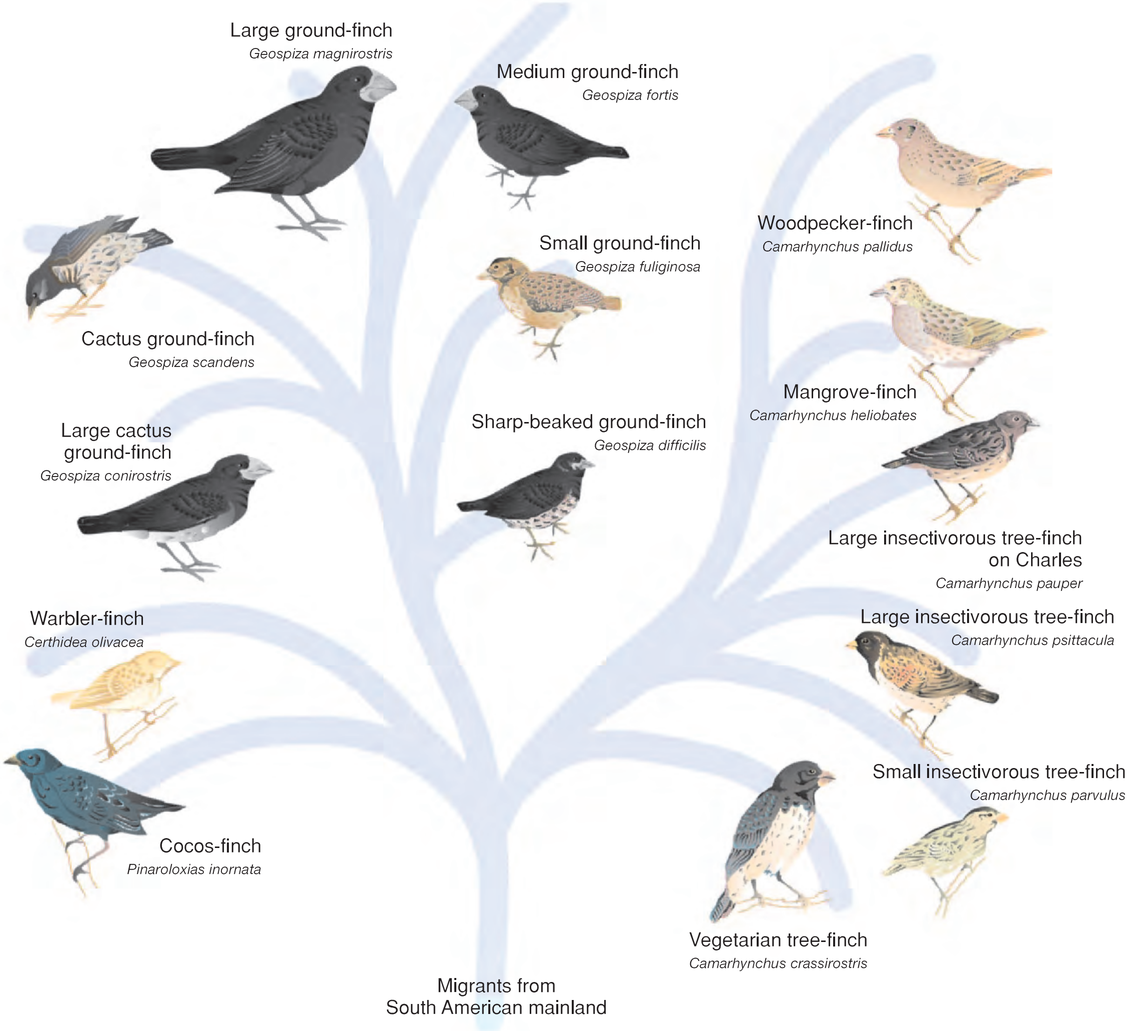


Figure 21.6 Species of Darwin's finches. These birds apparently evolved from a single group of migrants from the South American mainland. Isolated on the different islands, the birds evolved to fill many vacant niches.

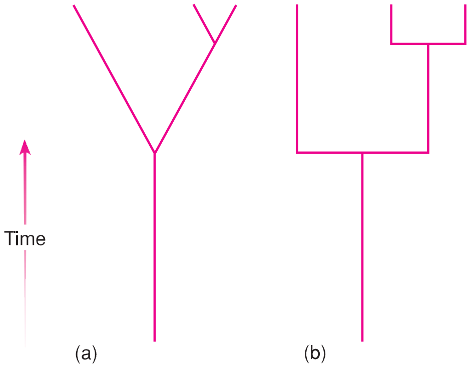


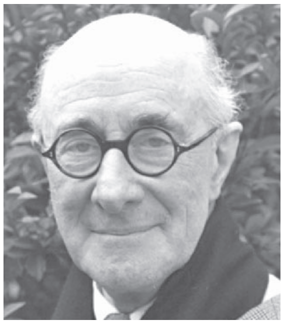
Figure 21.7 Diagrammatic interpretation of cladogenesis. (*a*) Phyletic gradualism is depicted as a gradual divergence over time. (*b*) Punctuated equilibrium is depicted as a rapid divergence of two groups after long periods of no change. The horizontal axis is some arbitrary measure of species differences.

GENETIC VARIATION

Darwinian evolution depends on the variation within a population. E. B. Ford, a British evolutionary biologist, applied the term **genetic polymorphism** to the occurrence of more than one allele at a given locus. Usually, we consider a locus polymorphic if a second allele occurs in the population at a frequency of 5% or more. Before the mid-1960s, the general belief was that only a few loci were polymorphic in any individual or any population.

In 1966, two researchers found a way to sample the genome in what they perceived was a random manner. R. C. Lewontin and J. L. Hubby used acrylamide-gel electrophoresis (see chapter 5) to investigate variability in a fruit fly species, *Drosophila pseudoobscura.* (H. Harris reported independent, similar work with human DNA.) Lewontin and Hubby reasoned that choosing enzymes and general proteins that are amenable to separation by electrophoresis, is, in fact, choosing a random sample of the genome of the fruit fly. If this is the case, then the degree of polymorphism found by electrophoretic sampling would provide an estimate of the amount of variability occurring in the individual organism and in the population. Their results were startling.

Lewontin and Hubby found that the species was polymorphic at 39% of eighteen loci examined, the average population was polymorphic at 30% of its loci, and the average individual was heterozygous at 12% of its loci. The high rate of polymorphism sparked two interrelated controversies. The first was whether electrophoresis does, in fact, randomly sample the genome. The second was whether most electrophoretic alleles are maintained in the population by natural selection. Let us return to the arguments after looking at ways in which genetic polymorphisms could be maintained in natural populations.



Edmund Brisco Ford (1901–1988). (Courtesy of Professor Edmund Brisco Ford.)

Richard C. Lewontin (1929–). (Courtesy of Dr. Richard C. Lewontin.)

Maintaining Polymorphisms

Heterozygote Advantage

When selection acts against both homozygotes, an equilibrium is achieved, dependent solely on the selection coefficients, that maintains both alleles (see chapter 20). The classic example of heterozygote advantage in human beings is sickle-cell anemia. Sickle-cell hemoglobin (Hb^S) differs from normal hemoglobin (Hb^A) because it has a valine in place of a glutamic acid in position number 6 of the beta chain of the globin molecule. When the availability of oxygen is reduced, the erythrocytes containing sickle-cell hemoglobin change from round to sickle-shaped cells (see fig. 2.28). There are two unfortunate consequences: (1) sickle-shaped cells are rapidly broken down, which causes anemia as well as hypertrophy of the bone marrow, and (2) the sickle cells clump, which blocks capillaries and produces local losses of blood flow that result in tissue damage.

This condition of reduced fitness would lead one to predict that the sickle-cell allele would be selected against in all populations and, therefore, would be rare. But this is not the case. The sickle-cell allele is common in many parts of Africa, India, and southern Asia. What could possibly maintain this detrimental allele? In the search for an answer to this question, biologists discovered that the distribution of the sickle-cell allele coincided well with the distribution of malaria. The following facts have now been uncovered. The sickle-cell homozygote (Hb^SHb^S) almost always dies of anemia. The sickle-cell heterozygote (Hb^AHb^S) is only slightly anemic and has resistance to malaria. The normal homozygote (Hb^AHb^A) is not anemic and has no resistance to malaria. Thus, in areas where malaria is common, the most fit genotype of the three appears to be the sickle-cell heterozygote, which has resistance to malaria and only a minor anemia.

This conclusion is supported by the changes in allelic frequencies that occur when a population from a malarial area moves to a nonmalarial area. Since the normal homozygote is no longer at risk for malaria, selection acts mainly on the sickle-cell homozygote and, to a slight extent, on the heterozygote. Table 21.1 shows data for African blacks versus African Americans. The African population is, of course, under malarial risk, whereas the American population is not. The sickle-cell hemoglobin allele (Hb^S) is reduced in frequency in African Americans.

Heterozygote advantage is an expensive mechanism for maintaining a polymorphism. Losses must occur in both homozygous groups in order for the polymorphism to exist. Thus, part of the reproductive output of a population is lost each generation to maintain each polymorphism under heterozygote advantage. In the case of sickle-cell anemia, this means a tragic loss of human life due to either anemia or malaria. (The loss of individuals

Table 21.1 **Sickle-Cell Anemia Frequencies in African Blacks and African Americans**

	Percentage of Homozygotes (Hb^AHb^A)	Percentage of Heterozygotes (Hb^AHb^S)	Frequency of Hb^S (q)
African Blacks (Midcentral Africa)	82	18	0.09
African Americans	92	8	0.04

to maintain genetic variation at a particular locus is called **genetic load.** In the sickle-cell case, it is due to the segregation of individuals with lowered fitness and is therefore called **segregational load.**) Very few other examples of heterozygote advantage have been documented.

Frequency-Dependent Selection

All the selection models discussed so far (chapter 20) have had selection coefficients that were constants. This is not always the case. For example, L. Ehrman has shown that when a female fruit fly has a choice between mates with different genotypes, the female fly chooses to mate with a male with a rare genotype. **Frequency-dependent selection** is selection in which the fitnesses of genotypes change according to their frequencies in the population.

The population geneticist Bruce Wallace has coined the terms *hard selection* and *soft selection* to deal with cases of frequency and density dependence. (Density-dependent selection exists when the fitness of a genotype changes as population density changes. We will not deal with that here.) Wallace defined soft selection as selection in which the selection coefficients depend on the frequency and density of genotypes. Hard selection is selection that is independent of both frequency and density. For example, the low fitness of sickle-cell anemia homozygotes involves hard selection because of the objectively deleterious effects of the anemia. Soft selection could be envisioned as selection that might act on aggressive behavioral genotypes in some lemming and field mouse species. When population density and frequency of the genotypes are low, these animals survive and reproduce. As population density increases, there can be a selection for more aggressive genotypes because they may be more successful in obtaining resources. As density increases further and the frequencies of the aggressive genotypes increase, they may be selected against because of the preoccupation of these aggressive individuals with territory defense under crowded conditions. This has been suggested as a mechanism of wildlife's "lemming cycle," rapid declines in the density of lemming and field mouse populations every three to five years.

Lee Ehrman (1935–). (Courtesy of Dr. Lee Ehrman. Photo by Jan Robert Factor.)

A model for frequency-dependent selection can be constructed by assigning fitnesses that are not constants. One way to do this is to assign fitnesses that are a function of allelic frequencies. Thus, the assigned fitnesses for one locus with two alleles could be $(1.5 - p)$, 1, and $(1.5 - q)$ for the *AA*, *Aa*, and *aa* genotypes, respectively (table 21.2). An interesting outcome of this model is that at $p = q = 0.5$, the system is in equilibrium, and no selection takes place because all the fitnesses are equal to 1.

Another way of looking at frequency-dependent selection is to look at the situation in which each genotype exploits a slightly different resource. As a genotype becomes rare, competition for the resource that genotype uses will likely decrease, and the genotype will thus have an advantage over the common genotypes, which are competing for resources. This type of selection is probably very common.

Transient Polymorphism

A genetic polymorphism can result when an allele is being eliminated either by random or selective mechanisms. If a population starts out homozygous for the *a* allele, for example, and a mutation brings in a more favored *A* allele, the population gradually becomes all *A* through directional selection. However, during the process of replacement, both alleles are present.

Other Systems

Selection at one stage in the life cycle of an organism can balance a different form of selection at another stage in the life cycle. For example, an allele can be favored in a

Table 21.2 Selection Model of Frequency-Dependent Selection: The *A* Locus with the *A* and *a* Alleles

	Genotype			
	AA	***Aa***	***aa***	**Total**
Initial genotypic frequencies	p^2	$2pq$	q^2	1
Fitness (W)	$1.5 - p$	1	$1.5 - q$	
Ratio after selection	$p^2(1.5 - p)$	$2pq$	$q^2(1.5 - q)$	$\overline{W} = 0.5 + 2pq$
Genotypic frequencies after selection	$\frac{p^2(1.5 - p)}{\overline{W}}$	$\frac{2pq}{\overline{W}}$	$\frac{q^2(1.5 - q)}{\overline{W}}$	1

larva but selected against in an adult. There can also be a balance of selection in different parts of the habitat in a heterogeneous environment. For instance, an allele can be favored in a wet part of the habitat but selected against in a dry part.

Maintaining Many Polymorphisms

In summary, allelic polymorphisms in a population were classically accounted for by heterozygote advantage, frequency-dependent selection, or, infrequently, some other mechanism. Until Lewontin and Hubby did their work, heterozygote advantage was considered the most common method of maintaining a polymorphism at a given locus. The maintenance of an allele by heterozygote advantage costs the population a certain number of its offspring due to the mortality (or sterility) of the homozygotes. Most populations can afford the loss if polymorphisms are maintained at only a few loci. After Lewontin and Hubby reported that polymorphisms seemed to exist at a large proportion of loci, new explanations were needed to account for them. Three explanations were considered:

1. Electrophoresis (the technique used in Lewontin and Hubby's research) does not randomly sample the genome, and thus the large amount of variability they found does not really exist.
2. New population genetic models can be derived that explain how natural selection maintains this large amount of variability.
3. Electrophoretic alleles are not under selective pressure. That is, allozymic forms of an enzyme all perform the function of the enzyme equally well. This idea is called the **neutral gene hypothesis.**

Sampling the Genome

Does electrophoresis randomly sample the genome? Since, on the basis of DNA content, the genome of higher organisms has the potential to contain half a million genes, this question may be difficult to resolve. Since the original reports of Lewontin and Hubby and Harris, numerous studies on many different organisms agree, for the most part, on the high amount of polymorphism in natural populations (table 21.3). However, several lines of evidence suggest that the results from electrophoresis are actually underestimates of the true amount of genetic variability present in a population.

The majority of amino acid substitutions, for example, do not change the charge of the protein. Thus, what appear to be single bands on an electrophoretic gel could actually be heterogeneous mixtures of the products of several alleles. Also, we now know that glycolytic enzymes are less polymorphic than other enzymes. Since glycolysis is a limited process in which most enzymes are not involved, it follows that the average heterozygosity over all loci should be slightly higher than the original estimates that included glycolytic enzymes. Recent technical advances of multidimensional electrophoresis and DNA sequencing support the hypothesis that electrophoresis does randomly sample the genome. However, DNA sequencing studies have shown that abundant variation exists, especially in the third (wobble) position of codons, and in parts of introns. Heterozygosity at the DNA sequence level seems to approach 100%.

Multilocus Selection Models

Can standard genetic models account for the high degree of variability in natural populations? If each locus is considered independently, then for each polymorphic locus, offspring in a population lost to maintain that polymorphism by heterozygote advantage are independent of offspring lost due to selection at other loci. The losses would soon outstrip the reproductive capacity of any species. Models proposed since Lewontin and Hubby's report have suggested that natural selection favors the individuals that are the most heterozygous overall. Individuals selected against because of their homozygosity would be individuals with many homozygous loci. In other words, natural selection acts on the entire genome, not on each locus separately. We can show algebraically that the large

Table 21.3 Survey of Genic Heterozygosity

Species	Number of Populations	Number of Loci	Proportion of Loci Polymorphic per Population	Heterozygosity per Locus	Standard Error of Heterozygosity
Homo sapiens	1	71	0.28	0.067	0.018
Mus musculus musculus	4	41	0.29	0.091	0.023
M. m. brevirostris	1	40	0.30	0.110	—
M. m. domesticus	2	41	0.20	0.056	0.022
Peromyscus polionotus	7 (regions)	32	0.23	0.057	0.014
Drosophila pseudoobscura	10	24	0.43	0.128	0.041
D. persimilis	1	24	0.25	0.106	0.040
D. obscura	3 (regions)	30	0.53	0.108	0.030
D. subobscura	6	31	0.47	0.076	0.024
D. willistoni	2–21	28	0.86	0.184	0.032
	10	20	0.81	0.175	0.039
D. melanogaster	1	19	0.42	0.119	0.037
D. simulans	1	18	0.61	0.160	0.052
Limulus polyphemus	4	25	0.25	0.061	0.024

Source: The Genetic Basis of Evolutionary Change by R. C. Lewontin, (New York: Columbia University Press, 1974). Reprinted with permission of the publisher.

Note: See source (Lewontin, 1974) for individual references.

number of polymorphisms that exist in natural populations could be maintained according to these models.

Neutral Alleles

The high incidence of polymorphism that electrophoresis reveals may not be important from an evolutionary point of view. If all or most electrophoretic alleles are neutral (i.e., if no allele is more fit than its alternative) or only very slightly deleterious, there is virtually no selection at these loci, and the variation observed in the population is merely a chance accumulation of a combination of mutation and genetic drift. This model, proposed by M. Kimura of Japan, is an alternative to the natural selection model.


Motoo Kimura (1924–1994). (Courtesy of Dr. Motoo Kimura.)

Which Hypothesis Is Correct?

Researchers who favor the concept that most electrophoretic alleles are neutral do not deny that selection exists. They do not hold that evolution is non-adaptive, but say merely that most of the molecular variation (electrophoretic) found in nature is not related to fitness—it is neutral. Thus, the demonstration that selection actually exists, in electrophoretic systems or otherwise, is not proof against the neutralist view. No one denies the explanation for the maintenance of sickle-cell anemia. Selection at several other electrophoretic systems is also known.

For example, R. Koehn showed that different alleles of an esterase locus in a freshwater fish in Colorado produced proteins with different enzyme activities at different water temperatures. Koehn then showed that the alleles were distributed as one would predict on the basis of the water temperature. In other words, the distribution of alleles correlated with the distribution of water temperature. The enzyme produced by the *ES-1*^{a} allele functioned best at warm temperatures, whereas the enzyme produced by the *ES-1*^{b} allele functioned best at cold temperatures. The cold-adapted enzyme was prevalent in the fish in colder waters (higher latitudes), and the warm-adapted enzyme was prevalent in the fish in warmer waters (lower latitudes; fig. 21.8).

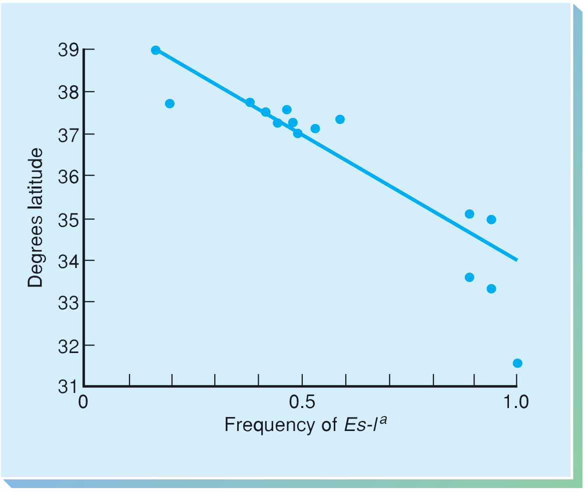


Figure 21.8 Relation of latitude and frequency of the warm-adapted esterase allele *Es-I*^{a} in populations of the fish *Catostomus clarki.* Note how the frequency of the allele increases as latitude decreases (warmer water). (From Richard Koehn, "Functional and evolutionary dynamics of polymorphic esterases in catostomid fishes," *Transactions of the American Fisheries Society,* 99:223. Copyright © 1970 American Fisheries Society, Bethesda, MD.)

Isolated instances of selection, however, do not adequately prove the case for maintaining variation by means of natural selection or disprove the case for maintaining variation of neutral alleles. Both theories recognize natural selection as the guiding force in producing adapted organisms. What is needed is proof that the majority of polymorphic loci are either being selected or are neutral. For this proof, many loci must be examined independently—a very difficult undertaking—or some grand pattern must emerge supporting one hypothesis or the other.

Grand Patterns of Variation

Clinal Selection

Data on the geographic distribution of alleles fail to adequately support either theory. Often, a single allele predominates over the range of a species (fig. 21.9). Changes in allelic frequency from one geographic area to another can often be attributed to **clinal selection,** selection along a geographic gradient, in which allelic frequencies change as altitude, latitude, or some other geographic attribute changes. Note in figure 21.9 the general increase in the *Es-5*^{b} frequency from west to east in the southern United States. But, in line with the neutralist view, geographic patterns similar to those in figure 21.9 can also be produced by neutral alleles with a very low level of migration, as little as one individual per one thousand per generation.

Molecular Evolutionary Clock

The advancing technology that made it possible to detect the sequence of amino acids in a protein also made it possible to discover how much the proteins and DNA of various species differ. In chapter 17, we discussed the use of mitochondrial DNA (mtDNA) to determine evolutionary relationships. Currently, protein, nuclear DNA, and mtDNA clocks are being studied.

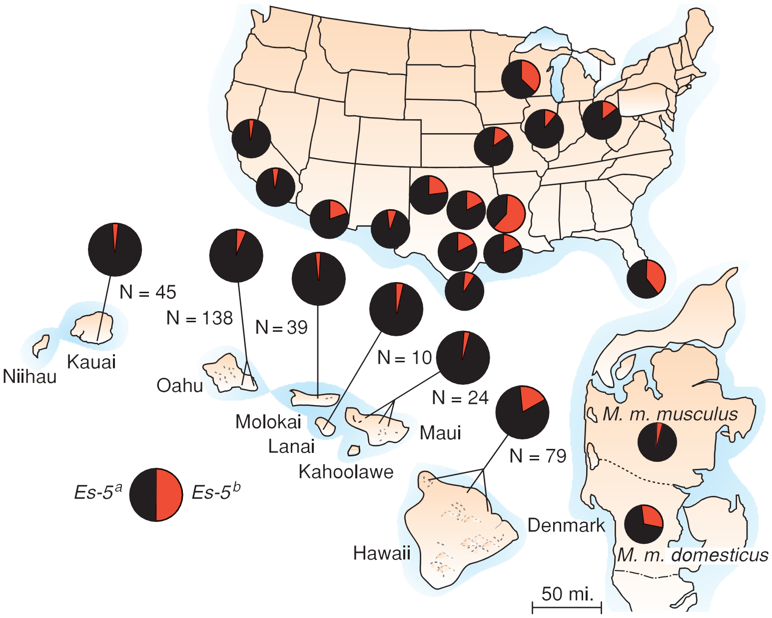


Figure 21.9 Frequency distribution of the *Es-5* alleles of an esterase locus in house mice. Each *circle* represents allelic frequencies at that geographic location. Note the general tendency for the *Es-5*^{b} allele to increase from west to east in the continental United States. (From L. Wheeler and R. Selander, "Genetic Variation in Populations of the House Mouse, Mus musculus, in the Hawaiian Islands," *Studies in Genetics,* VII, 1972. University of Texas Publication 7213. Reprinted with permission of M. R. Wheeler.)

Knowledge of the changes in amino acid sequences can be used to estimate the rate of evolutionary change. That is, the data show how many amino acid substitutions have occurred between two known groups of organisms. The genetic code dictionary allows us to estimate the minimum number of nucleotide substitutions required for this change. For example, if one protein contains a phenylalanine in position 7 (codons UUU, UUC), and the same protein in a different species has an isoleucine in the same position (AUU, AUC, AUA), we can see that the minimum number of substitutions to convert a phenylalanine codon to an isoleucine codon is one (UUU → AUU). When we know the minimum number of substitutions, we can calculate molecular **evolutionary rates,** nucleotide substitutions per million years. In a sense, these rates provide us with a **molecular evolutionary clock** that measures evolutionary time in nucleotide substitutions.

Many studies of the rate of amino acid and nucleotide substitutions have been done on hemoglobin, on cytochrome *c*, on a class of proteins involved in blood clotting called fibrinopeptides, and on many others. Figure 21.10 shows the way in which an amino acid sequence differs among species. From comparisons of this type, we can calculate the actual number of amino acid differences, as well as percentage differences. Table 21.4 is a compilation of percentage differences between various species based on the cytochrome *c* protein. This type of information can be used two ways.

First, we can construct a **phylogenetic tree** that tells us the evolutionary history of the species under consideration (fig. 21.11). This tree can be compared with phylogenetic trees constructed by more classical means using fossil evidence and evidence from morphology, physiology, and development. From the comparisons, we can look at areas of disagreement in an attempt to find out the best way to create phylogenetic trees. In addition, molecular phylogenies can give us information unattainable in any other way, as, for example, when the fossil record is incomplete or ambiguous.

A second use of DNA or amino acid difference data is to determine average rates of substitution. Once we know the current amino acid differences in the proteins of two species, it is possible to estimate the actual number of nucleotide substitutions that have taken place over evolutionary time using the statistical Poisson distribution, which deals with rare events. The index, K, is the average number of amino acid substitutions, per site, between two proteins:

$$K = -\ln(1 - p)$$

in which ln is the natural logarithm (to the base e), and $p = d/n$ in which d is the number of amino acid differences and n is the total number of amino acid sites being compared. For example, in figure 21.10, $n = 8$ and $d = 3$ between the dog and chicken. Thus

$$K = -\ln(1 - 0.375) = 0.47$$

Therefore, the average number of amino acid substitutions, per site, between dog and chicken is 0.47.

We can take this calculation one step further by determining the per-year rate:

$$k = K/2T$$

in which k is the amino acid substitution rate per site per year, and T is the number of years since the two species diverged from a common ancestor. We divide by $2T$ because each side of the tree has evolved independently for T years. When k's are calculated for many proteins over many species, they cluster around 10^{-9} (table 21.5). In fact, Kimura has suggested the unit of a *pauling* to be equal to 10^{-9} amino acid substitutions per year per site in

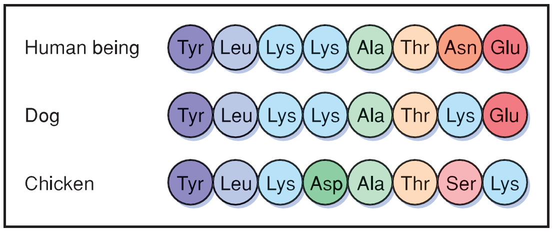


Figure 21.10 The amino acids making up the terminal portion of cytochrome *c* in three species. Note the similarities and differences.

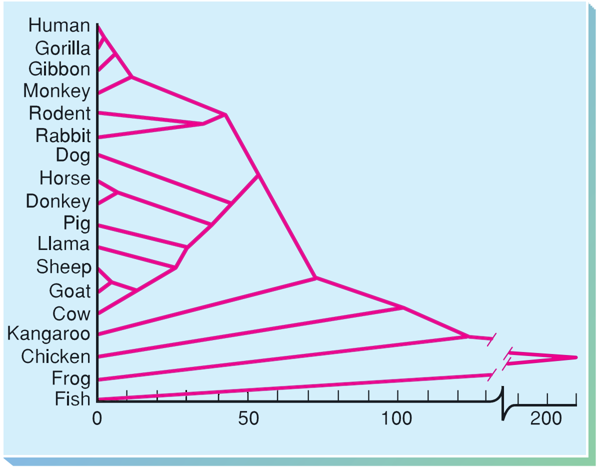


Figure 21.11 Composite evolution of hemoglobin, cytochrome *c*, and fibrinopeptide A. The total number of nucleotide substitutions appears on the horizontal axis. Note how the tree groups similar organisms and generally agrees with classical systematics. (From C. H. Langley and W. M. Fitch, "An examination of the constancy of the rate of molecular evolution," *Journal of Molecular Evolution,* 3:168. Copyright © 1974 Springer-Verlag, Heidelberg. Reprinted by permission.)

Table 21.4 **Amino Acid Differences (By Percentage) in Cytochrome *c* Between Different Organisms**

	Human being	Pig	Horse	Chicken	Turtle	Bullfrog	Tuna	Carp	Lamprey	Fruit fly	Screwworm	Silkworm	Sesame	Sunflower	Wheat	*C. krusei*	Yeast	*N. crassa*	*R. rubrum*
Human being	0	10	12	13	14	17	20	17	19	27	25	29	35	38	38	46	41	44	65
Pig, bovine, sheep		0	3	9	9	11	16	11	13	22	20	25	38	40	40	45	41	43	64
Horse			0	11	11	13	18	13	15	22	20	27	39	41	41	46	42	43	64
Chicken, turkey				0	8	11	16	14	17	23	21	26	40	41	41	45	41	44	64
Snapping turtle					0	10	17	13	18	22	22	26	38	39	41	47	44	45	64
Bullfrog						0	14	13	20	20	20	27	41	42	43	46	43	45	65
Tuna							0	8	18	23	22	30	42	43	44	43	43	45	65
Carp								0	12	21	20	25	40	41	42	45	42	43	64
Lamprey									0	27	26	30	44	44	46	50	45	47	66
Fruit fly										0	2	14	42	41	42	43	42	38	65
Screwworm fly											0	13	41	40	40	43	42	38	64
Silkworm moth												0	39	40	40	43	44	44	65
Sesame													0	10	13	47	44	48	65
Sunflower														0	13	47	43	49	67
Wheat															0	45	42	48	66
Candida krusei																0	25	39	72
Baker's yeast																	0	38	69
Neurospora crassa																		0	69
Rhodospirillum rubrum																			0

Source: From M. O. Dayhoff, ed., Atlas of Protein Sequence and Structure," National Biomedical Research Foundation, Washington, D.C., 1972. Reprinted with permission.

honor of Linus Pauling, who, along with E. Zuckerkandl, first proposed the concept of a molecular clock in 1963. If the values of k (such as those in table 21.5) form a normal distribution around 10^{-9}, then 10^{-9} would be the rate of "the" molecular evolutionary clock. So far, the data have been too limited to determine the distribution.

Although controversy still exists, the neutralists have interpreted the relative constancy of the molecular evolutionary clock as strong evidence in support of the neutral gene hypothesis. A constant rate of molecular evolution over many groups of organisms over many different time intervals implies that the substitution rate is a stochastic or random process rather than a directed or selectional process. This is not to say that no adapted changes occur in proteins or that there are no constraints. In fact, the evidence suggests that three classes of amino acids can be grouped in terms of substitution rate: invariant, moderately variant, and hypervariant. It seems possible that virtually no substitutions of amino acids will occur in and around the active site of the enzyme since any amino acid change in that area might be deleterious or lethal. For example, a segment of cytochrome *c* that runs from amino acids 70 to 80 is invariant in all organisms tested. This area includes a binding site of the protein.

DNA Variation

If the neutralist view of molecular evolution is correct, we should be able to make some predictions about rates of change in DNA. For example, we predict that DNA under greater constraint should amass fewer base changes than DNA under lesser constraint. We could test this by looking at the accumulation of mutations in the three positions of the codon, or we could look at DNA that is not directly translated, such as pseudogenes (see chapter 15) or introns, which are probably under lesser constraint. Let us first look at the three positions of the codon.

A reexamination of the codon dictionary (see table 11.4) shows that the third, or wobble, position of the codon should be under less constraint. Eight amino acids belong to unmixed families; their amino acids are defined by the first and second positions coupled with any of the

Table 21.5 **Evolutionary Rates (k) as 10^{-9} Substitutions Per Amino Acid Site Per Year for Various Proteins**

Protein	k
Fibrinopeptide	8.3
Pancreatic ribonuclease	2.1
Lysozyme	2.0
Hemoglobin alpha	1.2
Myoglobin	0.89
Insulin	0.44
Cytochrome *c*	0.3
Histone H4	0.01

Source: From M. Kimura, *The Neutral Theory of Molecular Evolution*, Cambridge University Press, 1983. Reprinted with the permission of Cambridge University Press.

four bases in the third position of the codon. The remaining amino acids belong to mixed families; the first two positions and the purine or pyrimidine nature of the third position in their codons is important. Hence, the wobble (third) position of the codon is under the least constraint and should build up the most neutral or near-neutral mutations.

In addition, analysis of changes in the first and second positions indicates that more drastic change takes place by mutation of the second rather than the first position of the codon. Thus, we predict that evolutionary distance, as measured by base substitutions, should be greatest for the third codon position and least for the second position. This turns out to be generally true (table 21.6).

It should be clear that a major problem facing those who study evolutionary clocks is how to calibrate them. Are average changes uniform throughout lineages? Do clocks speed up, slow down, or show other unpredictable changes through time? There is evidence, for example, that both the nuclear and mitochondrial DNA clocks have slowed down in the hominid lineage as compared with old world monkeys. If the clocks change speed in different lineages, at different times, and for different parts of the genome, there will be errors in interpreting lineages and errors in using averages to understand the general patterns of change.

Table 21.6 **Evolutionary Distance of Codons, Measured in Base Substitutions Per Nucleotide Site**

	Codon Site		
	2	1	3
Beta globin, human being vs. mouse	0.13	0.17	0.34
Beta globin, chicken vs. rabbit	0.19	0.30	0.64
Rabbit, alpha vs. beta globin	0.44	0.54	0.90

Source: From M. Kimura, *The Neutral Theory of Molecular Evolution*, Cambridge University Press, 1983. Reprinted with the permission of Cambridge University Press.

At this point, it is probably safe to say that while natural selection acts to create organisms that are adapted to their environments (see box 21.2 on mimicry), many nucleotide and amino acid changes may not have measurable effects on the fitness of the organism, and hence their frequencies may be determined by the stochastic processes of mutation and genetic drift. Adaptation is by natural selection, but neutral variation most certainly also occurs in organisms.

SOCIOBIOLOGY

We close this chapter by looking at a level of evolution only recently addressed. In 1975, E. O. Wilson published a mammoth tome entitled *Sociobiology: The New Synthesis.* This book has been at the center of major controversies that have spread to the fields of sociology, psychology, anthropology, ethology, and political science. The basic premise of the book is that social behavior is under genetic control. Although Wilson's book contains twenty-six chapters concerned with the animal kingdom, controversies have arisen because of the one chapter that applies the theory to human beings.

Altruism

V. C. Wynne-Edwards published a book in 1962 entitled *Animal Dispersion in Relation to Social Behavior.* In it, he suggested that animals regulate their own population density through altruistic behavior. For example, under crowded conditions, many birds cease reproducing. The interpretation of this phenomenon was that these birds were being altruistic: Their failure to breed was for the ultimate good of the species. (**Altruism** means risking loss of fitness in an act that could improve the fitness of another individual.) Wynne-Edwards suggested a mechanism called **group**

Edward O.Wilson (1929–). (Courtesy of Dr. Edward O. Wilson. Photo by Pat Hill/OMNI Publications International, Ltd.)

BOX 21.2

Experimental Methods

Mimicry

Mimicry is a phenomenon whereby an individual of one species gains an advantage by resembling an individual of a different species. There are at least two types of mimicry.

In **Mülerian mimicry,** named after F. Müller, several groups of organisms gain an advantage by looking like one another. This mimicry occurs among organisms in which all the mimetic species are offensive and obnoxious. The classic example is the general similarity among bees, wasps, and hornets.

In **Batesian mimicry,** named after H. W. Bates, a vulnerable organism (mimic) gains a selective advantage by looking like a dangerous or distasteful organism (model). The classic example of Batesian mimicry was, until 1991, the monarch (*Danaus plexippus*) and viceroy (*Limenitis archippus*) butterflies (fig. 1). Although the viceroy is smaller and, on close examination, looks different from the monarch, the resemblance is striking at first glance. Monarch butterflies feed on milkweed plants, obtaining noxious chemicals called cardiac glycosides, which the monarchs store in their bodies. When a bird tries to eat a monarch, it becomes sick and regurgitates what it has eaten. Thereafter, the bird will not only avoid eating monarchs, but it will also avoid eating any butterflies that look anything like monarchs. Previously it was believed that the mimetic viceroy butterfly gained a selective advantage by looking like the monarch and fooling bird predators into thinking that the viceroy was bad to eat. However, D. Ritland and L. Brower demonstrated a previously unrealized fact: The viceroys taste as bad as the monarchs to birds. This fact changes the mimicry of these two species from Batesian to Müllerian mimicry.

Examples of Batesian mimicry do occur in numerous butterfly species. For example, in West Africa, *Pseudacraea* species mimic species of the genus *Bematistes* (fig. 2). These species are primarily black and white or black and orange, and in some the sexes differ, each having a different mimic. Upwards of twenty species can be involved in these mimicry complexes in one area. Both forms of mimicry depend on the selective pressure generated by predation. Certain requirements must be met for each system to work properly. Batesian mimicry has the following requirements:

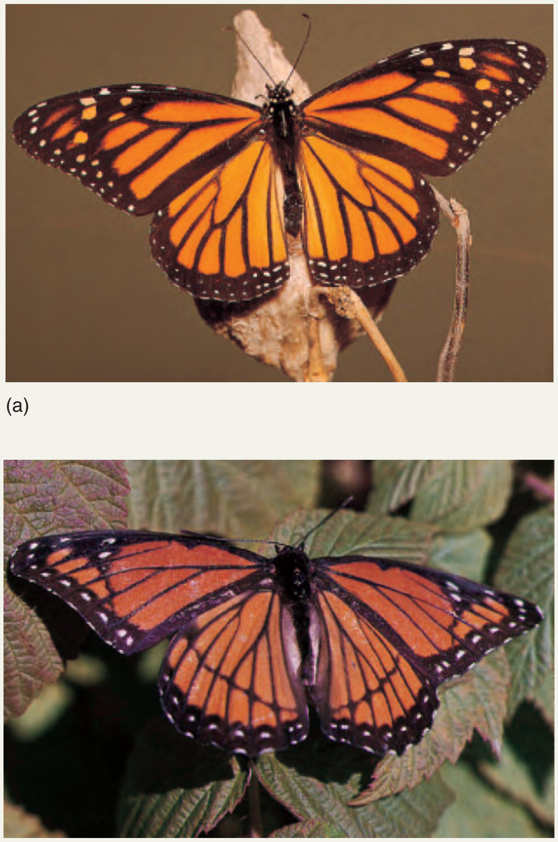
1. The model species must be conspicuous and inedible or dangerous.
2. Both model and mimic species must occur in the same area, with the model being very abundant. If the model is rare, predators do not have sufficient opportunity to learn that its pattern is associated with a bad taste. In fact, the reverse can happen; the model can be at a selective disadvantage if it is rare because the predators will learn from the mimic that the pattern is associated with something good to eat.
3. The mimic should be very similar to the model in the morphological characteristics predators perceive but not necessarily similar in other traits. The mimic is not evolving to *be* the model, only to look like it.

Müllerian mimicry requires that all the species be similar in appearance and distinctly colored. They can, however, be equally numerous. And, as the British geneticist P. M. Sheppard pointed out, the resemblance among Müllerian mimics need not be as good as between the mimic and model of a Batesian pair because Müllerian mimics are not trying to deceive a predator, only to remind the predator of the relationship.

Although there have been some critics of mimicry theory, especially critics of the way in which the system could evolve, the general model put forth by population geneticist and mathematician R. A. Fisher is generally accepted. According to Fisher, any new mutation that gave a mimic any slight advantage would be selected for. As time proceeded, other loci that might favorably modify the expression of mimetic genes would also be selected for in order to increase the similarity of mimic and model. This mechanism surmounts the criticism that a single mutation could not produce a mimic that so closely resembled its model.

selection: groups that had altruistic behavior would have a survival advantage over groups that did not.

In 1966, G. Williams, in his book *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought,* refuted the altruistic view with the charge that individuals that performed altruistic acts would be selected against. In other words, organisms not performing altruistic acts would have a higher degree of fitness. Williams held that apparent altruism had to be interpreted on the basis of benefits accruing to the individual performing the altruistic act. After his book, the idea of doing something for the good of the species became passé. How, then, can apparent altruism be accounted for? How can we explain why ground squirrels appear to put themselves at risk to predators by giving alarm calls, and why female workers in ant, wasp, and bee colonies


(a)

(b)

Figure 1 Müllerian mimicry. (*a*) Monarch butterfly and (*b*) viceroy butterfly. Both have similar colors (*orange* and *black*) and a generally similar color pattern. ([*a*] © Robert Finke/Photo Researchers, Inc. [*b*] © Richard Parker/Photo Researchers, Inc.)


Figure 2 Batesian mimicry seen in West African butterflies that live in the same places. Those on the *left* are species belonging to the genus *Bematistes*. Those on the *right* that mimic them are different species belonging to the genus *Pseudacraea*. (© J. A. L. Cooke/Oxford Scientific Films/Animals, Animals.)

forsake reproduction in order to work for the colony? **Sociobiology,** the study of the evolution of social behavior, attempts to answer these questions.

Kin Selection and Inclusive Fitness

In 1964, W. D. Hamilton developed concepts that explained altruistic acts without resorting to group selection. Starting with the known fact that relatives have alleles in common, Hamilton suggested that natural selection would favor an allele that promoted altruistic behavior toward relatives because the result might be an increase in copies of that allele in the next generation. The proportion of alleles shared by two individuals can be defined as a **coefficient of relationship, *r*.** If an individual has a certain allele, the probability that a particular relative also has that allele is *r.* Siblings have an $r = 1/2$. A squirrel is likely to have virtually all its alleles still viable if it sacrifices itself for two or more siblings. In fact, natural selection should definitely favor altruism of an individual toward three siblings because, in a sense, natural selection is weighing 1 copy of an individual's alleles (the individual itself) versus 1.5 copies (three siblings).

This sort of reasoning has been termed the **calculus of the genes.** It does not imply that individuals actually think these things out; rather, natural selection has favored the individuals that behave this way. Hamilton referred to the sum of an individual's fitness plus the fitness effects of alleles that relatives share as **inclusive fitness.** He referred to the way natural selection acts on inclusive fitness as **kin selection.**

Hamilton applied his ideas of inclusive fitness and kin selection to explain sterile castes in the eusocial (truly social) hymenoptera (bees, ants, and wasps). The workers in these colonies are sterile females. Why do they forsake their ability to reproduce in order to help maintain the hive or colony? The answer seems to come from **haplodiploidy,** the unusual sex-determining mechanism of these species. In the eusocial hymenoptera with sterile castes, fertilized eggs produce diploid females, whereas unfertilized eggs produce haploid males (drones). The difference between a reproductive queen and a sterile worker in bees is larval nutrition: larvae fed "royal jelly" can become queens. Hamilton showed that since a worker is more closely related to her sisters than to her own potential offspring, kin selection could favor a worker who helps her sisters at the expense of her own reproduction.

Figure 21.12 shows a queen (female) with alleles A_1 and A_2 at the A locus and a haploid drone (male) with the A_3 allele. A daughter will have either the A_1A_3 or A_2A_3 genotype. If we compare one of these daughters with her sisters, we see that the average $r = 0.75$—half of the time, $r = 1.0$, and the other half of the time, $r = 0.5$. A queen and her daughters have an $r = 0.5$. Thus, we see that workers (females) are more closely related to their sisters, and hence are at a reproductive advantage by raising them rather than their own young. Wilson has pointed out that sterile caste systems have evolved among insects in only one other group beside the eusocial hymenoptera, the termites. Although eusocial hymenoptera make up only 6% of insects, sterile castes have independently evolved at least eleven times. This is compelling evidence for the validity of Hamilton's analysis. Only one noninsect example of a caste has been discovered: the naked mole rat, a small subterranean rodent living in Africa, has this type of social system.

Many studies concerned with apparently altruistic acts have provided a large body of support for Hamilton's theory of kin selection and inclusive fitness. P. Sherman, working with ground squirrels, for example, has observed that the individuals that make the alarm calls have the most to gain from the standpoint of inclusive fitness; these individuals are resident females surrounded by kin.

One other explanation for altruism is also consistent with benefits to individual fitness. It is that many apparently altruistic acts are in reality selfish—they just look altruistic. To be altruistic, an individual must risk reducing its fitness to potentially benefit the fitness of others. We may, in fact, misinterpret some acts as altruistic that simply are not.

This turnaround in thought, from group selection to individual selection, has been an intellectual revolution in modern evolutionary biology. Before this revolution, many of the behaviors in nature that involved apparent altruism were difficult to explain. Now sociobiological reasoning provides an explanation.

The reason so much controversy has sprung up over the theory of genetic control of social behavior is because of the implications the theory has for human social, political, and legal issues. Human husband-wife, parent-child, and child-child conflicts, for example, may be built into the genes. Altruism, our highest form of nobility, may be mere selfishness. Many critics fear that sociobiological concepts can be used to support sexism and racism. For human beings, the alternative to the theory of sociobiology is the theory that most human behavior, including cultural learning, is determined by the environment. At present, although much evidence remains to be gathered, the sociobiology concept is compelling to many evolutionists.

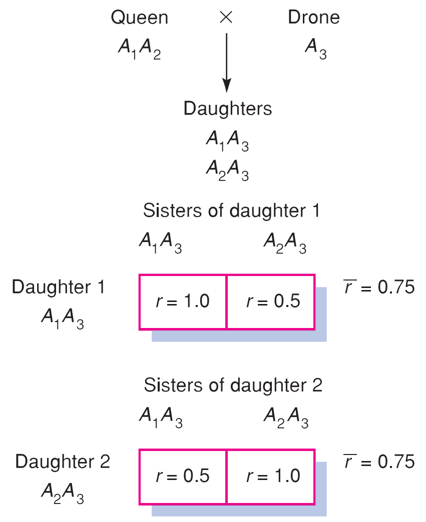


Figure 21.12 Haplodiploidy in eusocial hymenoptera produces sisters with an average r of 0.75. Because drones (males) are haploid, queens produce daughters of only two genotypes at any locus. A given daughter has an r of 1.0 with sisters of identical genotype and an r of 0.5 with sisters of the other genotype, for an average r of 0.75. In other words, females have a 75% genetic similarity with their sisters but only a 50% similarity with their own offspring.

SUMMARY

STUDY OBJECTIVE 1: To analyze the mechanisms of evolution and speciation 589–595

The theory of evolution by natural selection was put forward by Charles Darwin, who recognized the natural variation among individuals within a population of similar organisms. He noted also that offspring are overproduced in nature, and this overproduction inevitably leads to competition for scarce resources. Darwin assumed that, when competition occurs, the most fit will survive; through time, then, a population will become better adapted to its environment through the process of natural selection. Applying the algebra of population genetics to this theory leads to the modern concept of evolution, neo-Darwinism.

Cladogenic speciation occurs when reproductive isolating mechanisms arise, usually after gene flow in a population is blocked. Different populations of a species can then evolve independently. When individuals from the isolates can no longer interbreed, speciation has taken place. If the isolates then come in contact again, they will remain as separate species. Speciation may occur gradually or in a punctuated manner; it can be by allopatric, parapatric, or sympatric mechanisms.

STUDY OBJECTIVE 2: To investigate the mechanisms of the maintenance of genetic variation in natural populations, both selective and neutral 596–603

Evolution depends on variation. In 1966, Lewontin and Hubby, using electrophoresis, showed that a tremendous amount of heterozygosity occurred in natural populations. Attempts to explain this variation have led to two major competing theories: (1) variation is maintained selectively and (2) variation is not under selective pressure, but is instead neutral. Two areas of evidence support the neutralist view.

First, the molecular evolutionary clock (the per-year, per-amino acid, substitution rate) appears to be fairly constant at 10^{-9}. This constancy implies that the majority of amino acid changes are the result of stochastic processes. Second, there have been greater numbers of nucleotide substitutions in DNA under lesser constraint than in DNA under greater constraint. For example, the third, or wobble, position of the codon has accumulated more mutations than the other two positions. We conclude that natural selection creates adapted organisms, but the majority of base and amino acid changes may be neutral.

STUDY OBJECTIVE 3: To discuss sociobiology, the evolution of social behavior 603–606

Sociobiology is another term for evolutionary behavioral ecology. It attempts to provide evolutionary explanations for social behaviors. Apparent altruistic behavior can be explained either as kin selection or as selfishness. Sterile insect castes have come about because of the unusual haplodiploid sex-determining mechanism in the eusocial hymenoptera. There is much controversy about and little information for applying sociobiological principles to human behavior.

SOLVED PROBLEMS

PROBLEM 1: What are the roles of reproductive isolating mechanisms in the process of evolution?

Answer: Reproductive isolating mechanisms prevent individuals in two populations from mating with each other or producing viable offspring. These mechanisms can be prezygotic or postzygotic. They usually evolve while populations are isolated from each other, either physically or during parapatric or sympatric speciation. For example, if a species is split by a new river, the populations on either side of the river can evolve in isolation from each other. Reproductive isolating mechanisms usually evolve irrespective of the other facets of evolution taking place. Thus, if, after time, the two populations come into contact (the river dries up), reproductive isolating mechanisms may have evolved to prevent mating. If weak reproductive isolating mechanisms have evolved, natural selection usually favors strengthening them by selecting against hybrids and against any mating behavior that leads to the formation of hybrids.

PROBLEM 2: What is our modern evolutionary concept of altruism?

Answer: An altruistic act is one in which an individual risks the loss of fitness in order to benefit another individual. Human beings value these "selfless" acts; however, they are not favored in natural animal populations, except under very specific circumstances, because altruistic acts should be selected against. In other words, all other things being equal, an individual that did not do altruistic acts would have a higher fitness than one that did do these acts. Therefore, fitness is higher for "selfish" individuals. Altruistic acts, however, are expected if the beneficiary of the acts shares genes in common with the benefactor performing the acts. Generally, altruism can be expected among relatives, following the rules of kin selection.

EXERCISES AND PROBLEMS*

DARWINIAN EVOLUTION

1. Outline the Darwinian mechanism of the process of evolution. What is meant by neo-Darwinism?

EVOLUTION AND SPECIATION

2. Population geneticist Hampton Carson has defined a "population flush" as a period of reduced selection during population increase. Why should there be reduced selection during a flush?

3. Describe how the processes of allopatric, parapatric, and sympatric speciation could take place.

4. Can information on evolutionary rates gained from molecular techniques shed light on the punctuated equilibrium-phyletic gradualism controversy? What additional data are needed to decide this controversy?

5. What is meant by "constraint" in the molecular evolution of DNA and proteins?

6. Recently, a vial of bull semen was stolen from an artificial insemination facility. Your friend is about to undergo artificial insemination and is concerned she may give birth to a Minotaur, or a cow-human hybrid. Provide two explanations for why she should not worry about this possibility.

7. In *Drosophila,* females in populations A and B produce an average of 250 offspring each. When the two populations are crossed, AB females produce only about 100 offspring each. Are populations A and B in the process of becoming different species?

8. A few plants of species Q ($2n = 14$) suddenly double their chromosomes ($2n = 28$) and immediately become a new species, R. Why are QR hybrids sterile?

9. One of the arguments creationists use to refute evolution is the presence of gaps in the fossil record. How can you explain the gaps from an evolutionary standpoint?

GENETIC VARIATION

10. The following electrophoretic data are from a sample of one hundred field mice for their salivary amylase-1 genotypes. The two alleles are *F* and *S,* for fast and slow migration in an electric field: *FF,* forty-three, *FS,* fifty-four, and *SS,* three. Is selection acting? What would you look for in data to determine whether frequency-dependent selection, heterozygote advantage, or transient polymorphism is at work?

11. What mechanisms permit the maintenance of genetic variability in natural populations? Give examples where possible.

12. Discuss the "neutral gene hypothesis." What are its alternatives? What data are needed to distinguish among these views?

13. Koehn showed that differently functioning alleles of an esterase system in fish correlated with water temperature. What sorts of selection can you imagine that could affect the same type of alleles in mammals, which are homeothermic (warm-blooded) and hence maintain a relatively constant internal temperature?

14. P. Niemalä and J. Tuomi have suggested that the irregular leaf outlines in some plant species are a form of mimicry. What would the leaves be mimicking? What form of mimicry might this be?

15. From figure 21.10, what is K (the average number of amino acid substitutions per site) between human beings and chickens? between dogs and human beings? Do all three possible comparisons support known evolutionary relationships?

16. How does the acceptance of the neutral mutation theory change our basic view of neo-Darwinism?

17. In a given population, the frequencies of *AA, Aa,* and *aa* genotypes are 0.36, 0.48, and 0.16, respectively. If the assigned fitnesses are $1.5 - p$, 1.0, and $1.5 - q$, what will the genotypic frequencies be after one generation of selection?

18. If the rate of amino acid substitution per site per year is 2×10^{-9}, and the average number of amino acid substitutions per site is 0.2, how long has it been since the two species diverged?

19. Scientists have examined one thousand amino acids in the proteins of human beings and chimps and have found a difference in twenty-three. Calculate the average number of amino acid substitutions per site.

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*Answers to selected Exercises and Problems are on page A-24.

20. Scientists are now using DNA sequences to show phylogenetic relationships between or among species. In many cases, cDNA is made from isolated mRNA and then sequenced. Is the method a reasonable approach to show evolutionary relationships?

21. In which codon position should the greatest abundance of variation occur? Why?

SOCIOBIOLOGY

22. What are the differences among individual selection, group selection, and kin selection? How could each type of selection explain altruistic acts?

23. If the "calculus of the genes" suggests sacrificing oneself for two siblings, for how many first cousins should one sacrifice oneself?

24. In certain animal populations, infanticide is practiced by one or more males. Do you think this infanticide is random, or would you expect specific individuals to be eliminated?

CRITICAL THINKING QUESTIONS

1. The peppered moth (*Biston betularia*) has two phenotypic forms, melanic (dominant) and peppered (recessive). The moths face predation by birds, and the predation is selective against different-colored tree trunks. In an industrialized area, one in which the tree trunks are dark like the melanic form (and thus "hide" the melanic forms from the birds), a sample of moths indicated that the frequency of the allele for peppering was 0.6; the next year, it was 0.5. What is the fitness of the peppered genotype under this circumstance?

2. V. C. Wynne-Edwards suggested that birds form flocks so that they can assess their population numbers. When they assess that their numbers are high, they decide not to breed for the good of the species, so that they do not exhaust their resources. Edwards called this process *group selection.* Why can't this mechanism work, given that it involves behavior that is for the good of the species?

Suggested Readings for chapter 21 are on page B-20.