whose effects may be additive, complementary, or modifying.

A number of factors can affect variation in a population. The ultimate source of natural variation is mutations. Mutations are thought to exert a relatively weak force on variation in nature. Random variations in fecundity or mortality may also affect variation in populations, particularly small ones—a phenomenon called genetic drift (see Chapter 14). A third factor affecting variation is immigration and emigration. **Assortative mating** may also change allele frequencies in populations. Assortative mating simply means that mates are chosen nonrandomly with respect to genotypes. Like mating with like, which could include inbreeding, is referred to as **positive assortative mating;** a tendency for mates to differ genetically is referred to as **negative assortative mating.** Positive assortative mating (for example, $A_1A_1 \times A_1A_1$) tends to reduce the proportion of heterozygotes in the population, whereas the opposite results from negative assortative mating ($A_1A_1 \times A_2A_2$). Thus, the expression of recessive alleles, including rare and harmful genes, increases with positive assortative mating. Finally, and most importantly, natural selection may affect variation.

It is the action of natural selection that will command most of our attention in this part of the book. When selection is applied to some traits, such as the amount of black pigment in the wing scales of peppered moths, a single gene locus or a few gene loci are affected. Selection upon other traits, such as body shape or patterns of social behavior, may affect numerous genes responsible for producing the trait, many of which in turn influence other characteristics of the phenotype.

The Hardy-Weinberg Model

The evolutionary mechanics of selection and genetic responses are the subject of **population genetics** (Crow and Kimura 1970, Hartl and Clark 1989, Tamarin 1993). A primary task of population geneticists since the late 1920s has been to develop quantitative predictions of changes in gene frequencies in response to selection. While population genetic models are often extremely complex, the essence of natural selection may be understood using a very simple genetic model, which was discovered independently in 1908 by G. H. Hardy and W. Weinberg. The purpose of the model was to show how genetic variation is retained in Mendelian inheritance. The model, called the **Hardy-Weinberg law,** demonstrates that the frequencies of alleles and genotypes remain constant from generation to generation in large populations in which there is random mating (each zygote is formed from the random combination of any two gametes), no selection, no mutation, and no migration to or from the population. This model may be used as a point of comparison for studying the effects of natural selection. If selection is applied to a reasonably large closed population having random mating and no mutation, then changes in the frequencies of the alleles in that population over several generations may be attributed to selection. Let us examine the Hardy-Weinberg law in more detail and show how it can be used to demonstrate the effects of selection.

When a population exists at Hardy-Weinberg equilibrium, the proportions of homozygotes and heterozygotes take on equilibrium values, which we can calculate from the proportions of each allele in the population. Thus, two alleles A_1 and A_2 of the locus A might occur in the population with frequencies p and q respectively ($p + q = 1$, and therefore $q = 1 - p$). The three possible genotypes in the population are the two homozygotes A_1A_1 and A_2A_2 and the heterozygote A_1A_2, which, in a population at Hardy-Weinberg equilibrium, will occur with frequencies p^2, q^2, and $2pq$, respectively. Because of random mating, $p^2 + 2pq + q^2 = 1$. If alleles A_1 and A_2 occur with frequencies 0.7 and 0.3 respectively in the population, than the proportion of A_1A_1 genotypes in the population is $0.7^2 = 0.49$ (49%), if all the assumptions of the Hardy-Weinberg law are met. In the same manner, we see that 42% of the genotypes will be A_2A_2 and 9% will be the heterozygote A_1A_2.

We may use the Hardy-Weinberg law to evaluate relative fitness. Suppose genotype A_1A_1 has a fitness of 1. If A_1 is dominant over A_2, then the genotype A_1A_2 will also have a fitness of 1. Let genotype A_2A_2 have a lower fitness by some fraction s, which we denote $1 - s$. Prior to selection, the frequencies of the genotypes A_1A_1, A_1A_2, and A_2A_2 are p^2, $2pq$, and q^2 respectively, according to the Hardy-Weinberg law (Table 30-1). How much will the frequency of each allele change in the course of one generation of selection? For each generation, the frequencies of the genotypes are multiplied by their respective fitness values to obtain the relative number of their descendants in the next generation. If the fitnesses of the A_1A_1 and A_2A_2 phenotypes are 1 and $1 - s$ respectively, the relative numbers of progeny of each of the genotypes are p^2, $2pq$, and $(1 - s)q^2$. By counting up the relative numbers of A_1 and A_2 alleles in the progeny, we can calculate the change in frequency of the A_2 allele caused by selection against homozygous genotypes (Table 30-1).

From Table 30-1, we see that the relative proportion of the A_2 allele in the descendant population (q') is the ratio of the A_2 alleles to the total, or

$$q' = \frac{pq + (1 - s)q^2}{p^2 + pq + (1 - s)q^2}, \qquad (30\text{-}1)$$

TABLE 30-1 Rate of change of allele frequencies under selection

	Genotype		
	A_1A_1	A_1A_2	A_2A_2
Initial genotype frequency	p^2	$2pq$	q^2
Reproductive success (fitness)	1	1	$(1 - s)$
Relative proportion of descendants	p^2	$2pq$	$(1 - s)q^2$
Relative proportion of A_1 alleles in the descendant population	p^2	pq	
Relative proportion of A_2 alleles in the descendant population		pq	$(1 - s)q^2$

which may be simplified to

$$q' = \frac{q(1 - sq)}{1 - sq^2}. \qquad (30\text{-}2)$$

The change in allele frequency from one generation to the next, Δq, is $q' - q$, which, with a little algebra, can be rearranged to give

$$\Delta q = \frac{-sq^2(1 - q)}{1 - sq^2}. \qquad (30\text{-}3)$$

When the recessive homozygote is lethal ($s = 1$), the equation above simplifies to $\Delta q = -q^2/(1 + q)$. That is, the change in the frequency of allele A_2 is entirely dependent on the proportion of A_2 in the population. When selection is very weak (s is very small, perhaps less than 0.01, or 1%), the equation becomes approximately $\Delta q = -sq^2(1 - q)$.

These equations show that selection against the A_2A_2 genotype always causes a decrease in the frequency of the A_2 allele. Additionally, the rate of change in q depends on both the selective pressure on a population and the frequency of the A_2 allele. For example, change in q is fastest when q is relatively large because a larger proportion of the A_2 alleles are exposed in homozygous form (Figure 30-1). Also, evolution stops ($\Delta q = 0$) only when q is equal to either 0 or 1, in which case either the A_1 or the A_2 allele is fixed in the population, and there is no longer any genetic variation for selection act upon.

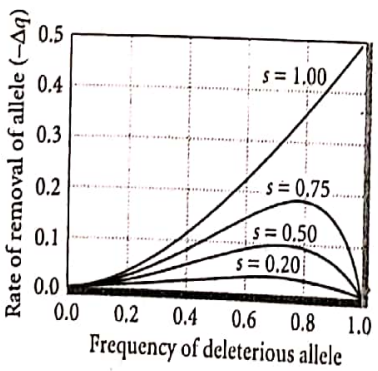

FIGURE 30-1 Rate of change in the frequency of a recessive, harmful allele as a function of allele frequency and strength of selection.

Rates of Evolution

The models above predict the change in a single gene with one allele dominant over the other. Equations that predict the change in allele frequencies resulting from one generation of selection can be used to show how a population evolves over many generations of continued selection and to predict how rapidly a population can respond genetically to a change in its environment.

The time required for a dominant allele to replace a recessive allele depends on its initial frequency in the population and on the strength of selection. To illustrate this, let us take another look at the peppered moth (*Biston betularia*) that inhabits woodland areas of England, where it rests on lichen-covered trees during the daytime. Recall from Chapter 1 that early in the nineteenth century, occasional dark or melanistic specimens of this common moth were collected, and subsequently, over period of about 100 years, the dark form, referred to as *carbonaria*, became increasingly common in forests near heavily industrialized regions of England. It appeared that environmental conditions had somehow been altered to give the dark forms a survival advantage over the light forms, and natural selection led to the replacement of typical light individuals with *carbonaria* individuals. To test this hypothesis, the English biologist H. B. D. Kettlewell measured the relative fitnesses of the two forms independently of the fact that the frequency of one had increased over that of the other.

From the results of Kettlewell's experiments, we can estimate that the fitness of the recessive homozygous genotype for typical (light) coloration was only 47% that of the *carbonaria* genotype in woods affected by industrial pollution; hence the fitness differential, or strength of selection against the typical