

Evolution of Phenotypic Traits

If you consider human characteristics, or those of any other species you are familiar with, you will probably be hard pressed to think of a phenotypic feature that displays a single-locus genetic polymorphism with two or three discrete states. Even human eye color doesn't come

just in brown and blue, despite what some elementary biology textbooks might lead you to believe. Instead, variation in most phenotypic characters, such as height or finger length or life span, is continuous, or "quantitative," and it is based on the effects of several or many variable gene loci, as well as those of the environment. At first surmise,



then, it is a bit difficult to see how the one-locus models of evolution described in the previous chapter apply to most of phenotypic evolution.

The field of **quantitative genetics** was developed to analyze quantitative characters, and its methods are used by biologists who study the evolution of morphology, life history characteristics, behavior, and other phenotypic traits.



Artificial selection. Darwin drew on the great changes wrought by artificial selection, such as those between a domesticated basset hound and its ancestor, the wolf, to show that selection can alter characters far beyond the range of variation seen within a species. (Wolf © Painet, Inc.; basset © Lynn M. Stone/naturepl.com.)

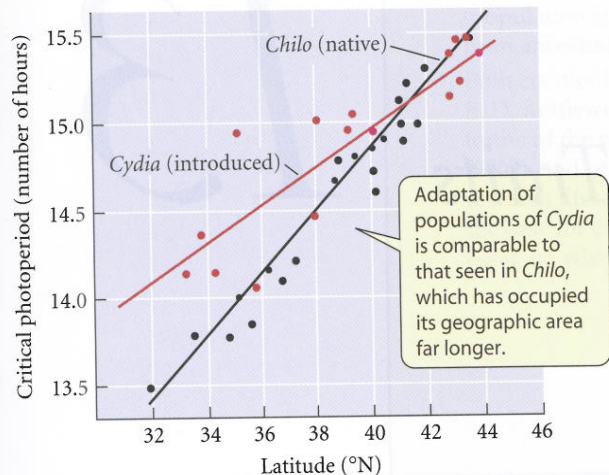


Figure 13.1 Geographic variation in the critical photoperiod for entering diapause in two species of moths at various latitudes. *Chilo suppressalis* is native to Japan. *Cydia pomonella* is an introduced pest in North America, where it has spread within the last 250 years. The two species now occupy the same latitudinal range. (After Tauber et al. 1986.)

southern populations because winter arrives at northern latitudes sooner, when days are still relatively long. The codling moth (*Cydia pomonella*), a major pest of apples, is a European species that was first recorded in New England in 1750, and has since expanded its range over 12 degrees of latitude. Populations have diverged genetically so that they display the same adaptive cline in critical photoperiod as other moth species that have occupied the same latitudinal span for a much longer time (Figure 13.1).

Until the 1950s, German populations of the blackcap (*Sylvia atricapilla*), a European songbird, migrated only to the western Mediterranean region for the winter. Since that time, more and more German blackcaps have overwintered in Britain, migrating northwest rather than southwest to the Mediterranean. When feeling the urge to migrate, a caged bird flutters in the right direction for its migration if it can see the night sky. (Most small birds migrate at night and use star patterns to determine direction.) Peter Berthold and colleagues (1992) used this behavior to show that offspring of blackcaps from populations that overwinter in Britain (who have never made the migratory journey themselves) orient toward the northwest, while offspring from populations that overwinter in the Mediterranean orient toward the southwest. The difference between the populations is genetically based and has evolved in a few decades. The authors suggest that the selective advantage of this change in behavior lies in improved winter weather and other conditions in Britain and in earlier spring return from Britain than from the Mediterranean.

Copper, zinc, and other heavy metals are toxic to plants, but in several species of grasses and other plants, metal-tolerant populations have evolved where soils have been contaminated by mine works that range from over 700 to less than 100 years old (Figure 13.2). In some cases, tolerance has evolved within decades on a microgeographic scale, such as in the vicinity of a zinc fence. Tolerance is based on a variable number of genes, depending on the species and population. When tolerant and nontolerant genotypes of a

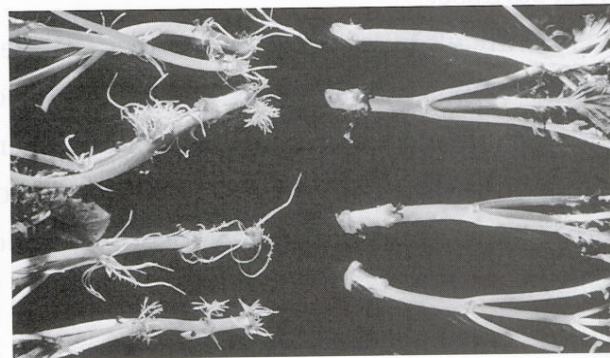
Evolution Observed

In the previous chapter, we encountered a few examples of adaptive change in allele frequencies at a single locus—such as those affecting warfarin resistance in rats—that have been observed in natural populations. However, most observed instances of rapid evolution by natural selection involve quantitative characters that have (or probably have) a polygenic basis. Rapid adaptation, at rates far greater than the average evolutionary rates documented in the fossil record, is most often seen when a species is introduced into a new region or when humans alter features of its environment (Endler 1986; Taylor et al. 1991). The following examples show that rapid evolution has occurred in morphology, physiology, and behavior.

In many insects, the cue for entering diapause, a state of low metabolic activity that is necessary for surviving the winter, is a critical photoperiod (day length). Northern populations are typically genetically programmed to enter diapause at longer day lengths than

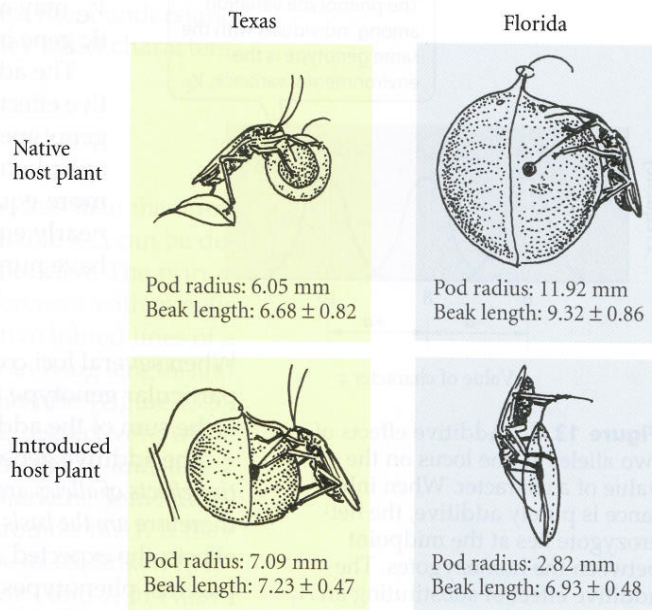
Figure 13.2 Variation in root growth of the monkeyflower *Mimulus guttatus* grown in a copper solution. The plants with the longest roots (left) are more tolerant of copper than those at the right. This variation has a genetic basis, which has enabled some populations of this and other plant species to adapt rapidly to high soil concentrations of copper. (From Macnair 1981; courtesy of M. Macnair.)

Higher
copper
tolerance



Less
copper
tolerance

Figure 13.3 Soapberry bugs (*Jadera haematoloma*) and their native and introduced host plants in Texas and Florida, drawn to scale. The bug's beak is the needle-like organ projecting from the head at right angles to the body. The average pod radius of each host species and the average (with standard deviation) beak length of associated *Jadera* populations are given. Beak length has evolved rapidly as an adaptation to the new host plant. (After Carroll and Boyd 1992.)



species are grown in competition with other plant species in the absence of the metal, the relative fitness of the tolerant genotypes is often much lower than that of the nontolerant genotypes, implying a cost of adaptation (Antonovics et al. 1971; Macnair 1981).

Several species of insects, such as the soapberry bug (*Jadera haematoloma*) (Carroll and Boyd 1992; Carroll et al. 1997), have adapted rapidly to new food plants. This insect feeds on seeds of plants in the soapberry family (Sapindaceae) by piercing the enveloping seed pod with its slender beak (Figure 13.3). In Texas, its natural host plant is the soapberry tree, which has a small pod, whereas in Florida it feeds naturally on balloon vine, in which a large spherical capsule envelops the seed. In both regions, some bug populations now feed mostly on introduced plants that have become common only within the last 20 to 50 years. In Texas, the major contemporary host plant is the Asian round-podded golden rain tree (*Koelreuteria paniculata*), which has a larger pod than the native host. In Florida, most bugs feed on the flat-podded rain tree (*Koelreuteria elegans*), also from Asia, which has a flatter, smaller seed pod than the native host. The bugs feed most efficiently if the beak is the right length for reaching seeds. Measurements on museum specimens collected at different times in the past show that the mean beak length of the bugs has changed steadily since the foreign host plants were introduced. Today, the mean beak length of Texan populations that feed on *K. paniculata* is 8 percent longer than that of populations that feed on the native host, and in Florida, beaks are 25 percent shorter where soapberry bugs feed on *K. elegans* than where they still feed on the native balloon vine. These differences have a genetic basis. Adaptation to an altered environment—to new food plants—has resulted in large, rapid changes in morphology.

Components of Phenotypic Variation

In order to discuss the evolution of quantitative traits, we must recall and expand on some concepts introduced in Chapter 9. An important measure of variation is the *variance* (V), defined as the average of the squared deviations of observations from the *arithmetic mean* of a sample. The square root of the variance is the *standard deviation* ($s = \sqrt{V}$), measured in the same units as the observations. If a variable has a normal (bell-shaped) frequency distribution, about 68 percent of the observations lie within one standard deviation on either side of the mean, 96 percent within two standard deviations, and 99.7 percent within three (see Box C in Chapter 9).

The **phenotypic variance** (V_P) in a phenotypic trait is the sum of the variance due to differences among genotypes (the **genetic variance**, V_G) and the variance due to direct effects of the environment and developmental noise (the **environmental variance**, V_E). Thus $V_P = V_G + V_E$. Considering for the moment the effect of only one locus on the phenotype, we may take the midpoint between the two homozygotes' means as a point of reference (Figure 13.4). Then the mean phenotype of A_1A_1 individuals deviates from that midpoint by $+a$, and that of A_2A_2 by $-a$. The quantity a , the **ADDITIVE EFFECT** of an allele, measures how greatly the phenotype is affected by the genotype at this locus. If the inheritance of the phenotype is entirely additive, the heterozygote's phenotype is exactly in between that of the two homozygotes. Such additive effects are responsible for a critically important component of genetic variance, the **additive genetic variance**, denoted V_A . (The genetic variance

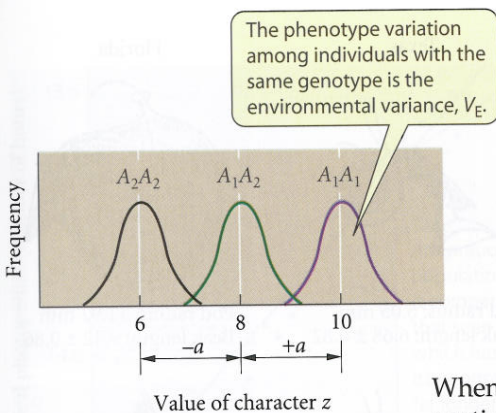


Figure 13.4 Additive effects of two alleles at one locus on the value of a character. When inheritance is purely additive, the heterozygote lies at the midpoint between the homozygotes. The additive effect of substituting an A_1 or an A_2 allele in the genotype is a (in this case, $a = 2$). The magnitude of a affects that of the additive genetic variance, V_A . The phenotypic variation within each genotype is measured by the environmental variance, V_E .

V_G may also include nonadditive components, due to dominance and epistatic gene interactions, that we will not concern ourselves with here.)

The additive genetic variance depends both on the magnitude of the additive effects of alleles on the phenotype and on the genotype frequencies. If one genotype is by far the most common, most individuals are close to the average phenotype, so the variance is lower than if the several genotypes have more equitable frequencies, as they will if the allele frequencies are more nearly equal. When, as in Figure 13.4, two alleles (with frequencies p and q) have purely additive effects, V_A at a single locus is

$$V_A = 2pqa^2$$

When several loci contribute additively to the phenotype, the average phenotype of any particular genotype is the sum of the phenotypic values of each of the loci. Likewise, V_A is the sum of the additive genetic variance contributed by each of the loci.

The additive genetic variance plays a key role in evolutionary theory because *the additive effects of alleles are responsible for the degree of similarity between parents and offspring and therefore are the basis for response to selection within populations*. When alleles have additive effects, the expected average phenotype of a brood of offspring equals the average of their parents' phenotypes.* Evolution by natural selection requires that selection among phenotypically different parents be reflected in the mean phenotype of the next generation. Therefore, V_A enables a **response to selection**—a change in the mean character state of one generation as a result of selection in the previous generation.

The proportion of phenotypic variance that is due to additive genetic differences among individuals is referred to as the character's **heritability in the narrow sense**, h_N^2 . The heritability is determined by the additive genetic variance (V_A), which depends on allele frequencies; and by the environmental variance (V_E), which depends in part on how variable the environmental factors are that affect the development or expression of the character. That is,

$$h_N^2 = V_A / V_P$$

where $V_P = V_G + V_E$ and V_G is the sum of V_A and nonadditive genetic components. Because allele frequencies and environmental conditions may vary among populations, an estimate of heritability is strictly valid only for the population in which it was measured, and only in the environment in which it was measured. Moreover, it is wrong to think that if a character has a heritability of 0.75, the feature is $3/4$ "genetic" and $1/4$ "environmental," as if a character is formed by mixing genes and environment the way one would mix paints to achieve a desired color. It is the *variation* in the character that is statistically partitioned, and even this partitioning is a property of the particular population, not a fixed property of the feature. For evolutionary studies, moreover, the additive genetic variance is often more informative than the heritability (Houle 1992).

The additive genetic variance is estimated from resemblances among relatives. In order to achieve accurate estimates, it is important that relatives not develop in more similar environments than nonrelatives; otherwise, it may not be possible to distinguish similarity due to shared genes from similarity due to shared environments.

The narrow-sense heritability (h_N^2) of a trait equals the slope (b) of the *regression* of offspring phenotypes (y) on the average of the two parents of each brood of offspring (x) (see Figure 13.8 below; see also Figure 9.20). The slope of this relationship is calculated so as to minimize the sum of the squared deviations of all the values of y from the line. As the correspondence between offspring and parents is reduced, the slope of the regression declines (compare parts A and B of Figure 13.8). Therefore, anything that reduces the similarity between parents and their offspring (such as environmental effects on phenotype, or dominance) reduces heritability. There are also ways of estimating V_A and other components of genetic variance from similarities among other relatives, such as siblings ("full sibs") or half sibs (individuals that have only one parent in common).

*The correlation between parent and offspring phenotypes is lower if there is dominance at a locus.

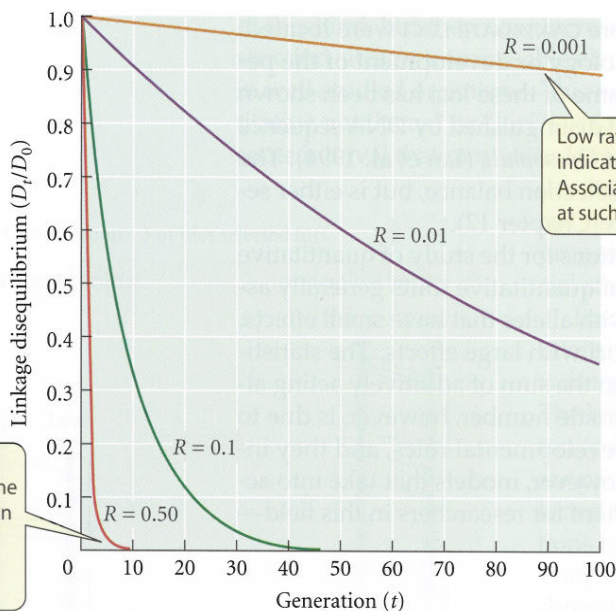


Figure 13.7 The decrease in linkage disequilibrium (D) over time, relative to its initial value (D_0), for pairs of loci with different recombination rates (R). $R = 0.50$ if loci are unlinked. (After Hartl and Clark 1989.)

When $R = 0.5$, loci are unlinked, and the association between alleles on different loci rapidly approaches zero.

Low rates of recombination indicate strongly linked loci. Association between alleles at such loci declines slowly.

- When a new mutation arises, the single copy is necessarily associated with specific alleles at other loci on the chromosome, and therefore is in linkage disequilibrium with those alleles. The copies of this mutation in subsequent generations will retain this association until it is broken down by recombination.
- The population may have been formed recently by the union of two populations with different allele frequencies, and linkage disequilibrium has not yet decayed.
- Recombination may be very low or nonexistent. Chromosome inversions and parthenogenesis (asexual reproduction) have this effect.
- Linkage disequilibrium may be caused by genetic drift. If the recombination rate is very low, the four gamete types in the example above may be thought of as if they were four alleles at one locus. One of these "alleles" may drift to high frequency by chance, creating an excess of that combination relative to others.
- Natural selection may cause linkage disequilibrium if two or more gene combinations are much fitter than recombinant genotypes.

Evolution of Quantitative Characters

Genetic variance in natural populations

Heritable variation has been reported for the great majority of traits in which it has been sought, in diverse species (Lynch and Walsh 1998). Not all characters are equally variable, however. For example, characters strongly correlated with fitness (such as fecundity) tend to have lower heritability than characters that seem unlikely to affect fitness as strongly (Mousseau and Roff 1987). However, the low h^2_N of fitness components arises from the greater magnitude of other variance components, especially V_E , in the denominator of the expression $h^2_N = V_A/V_P$. The additive genetic variance (V_A) of components of fitness is actually higher than that of morphological and other traits, probably because many physiological and morphological characteristics affect fitness (Houle et al. 1996).

In some cases, traits do not appear to be genetically variable at all. The paucity of genetic variation would then be a genetic constraint that could affect the direction of evolution (for example, an insect might adapt to some species of plants rather than to others) or prevent adaptation altogether. For instance, in sites near mines where the soil concentration of copper or zinc is high, a few species of grasses have evolved tolerance for these toxic metals (see Figure 13.2), but most species of plants have not. Populations of various species of grasses growing on normal soils were screened for copper tolerance by sowing large numbers of seeds in copper-impregnated soil. Small numbers of tolerant seedlings were found in those species that had evolved tolerance in other locations, but no tolerant seedlings were found in most of the species that had not formed tolerant populations (Macnair 1981; Bradshaw 1991). Genetic variation that might enable the evolution of copper tolerance seems to be rare or absent in those species.

Response to selection

In the simplest model of the effect of selection on a quantitative trait z , such as the tail length of rats, we assume that z has a normal frequency distribution in a population. (A roughly normal distribution is expected if a large number of loci, all with relatively small effects on the character, freely recombine.) Suppose an experimenter imposes selection for greater tail length by breeding only those rats in a captive population with tails longer than a certain value. This form of selection is called **truncation selection**. The mean tail length of the selected parents differs from that of the population from which they were taken (\bar{z}) by an amount S , the **selection differential** (Figure 13.8A). The average tail length (\bar{z}') among the offspring of the selected parents differs from that of the parental generation as a whole (\bar{z}) by an amount R , the **response to selection** (Figure 13.8A, right-hand graph). The magnitude of R is proportional to the heritability of the trait (compare graphs

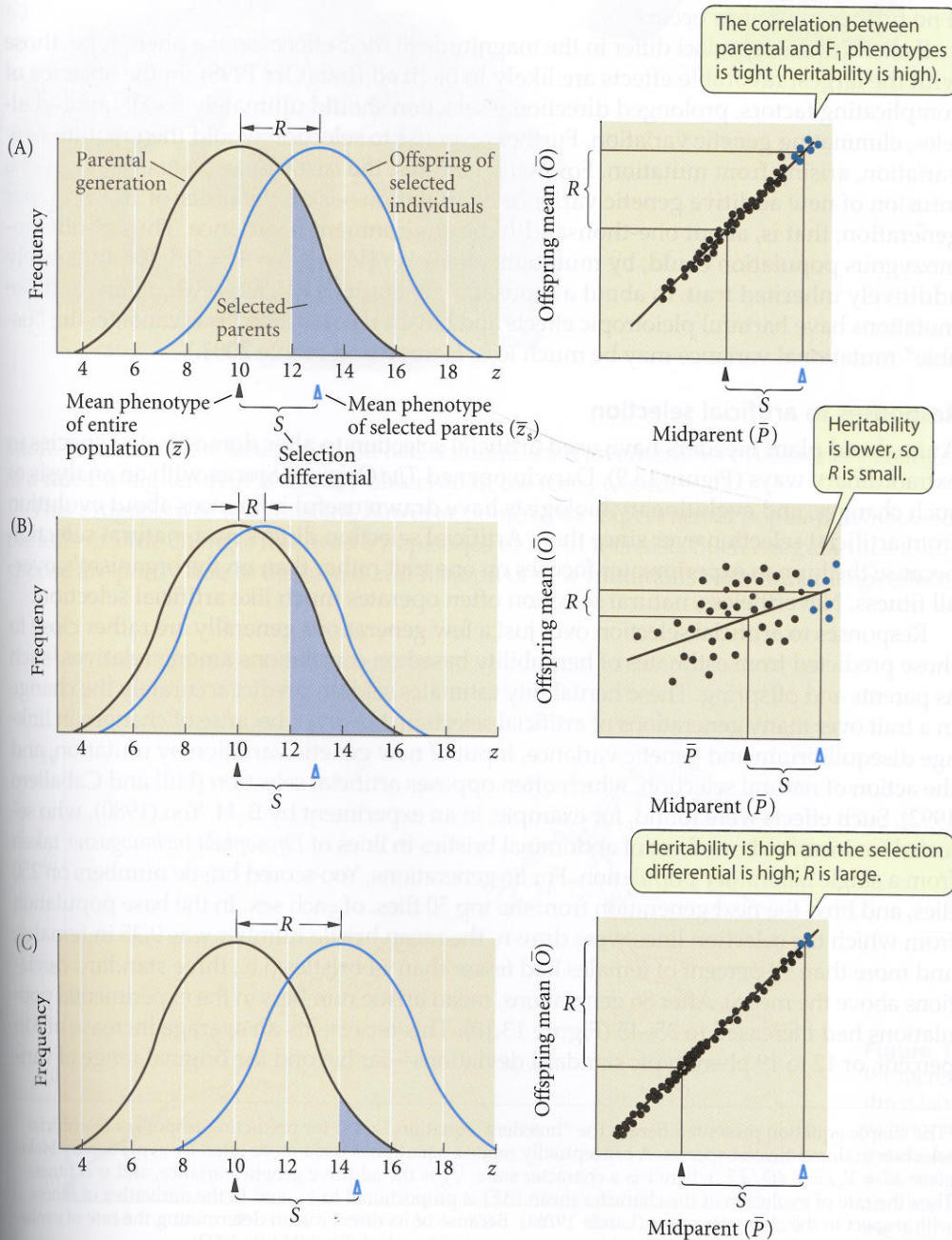


Figure 13.8 The response of a quantitative character to selection depends on the heritability of the character and the selection differential. (A) The black curve shows a normally distributed trait, z , with an initial mean of 10. Truncation selection is imposed, such that individuals with $z > 12$ reproduce. The graph at the right shows a strong correspondence between the average phenotype of pairs of selected parents (\bar{P}) and that of their broods of offspring (\bar{O}), i.e., high heritability. Blue circles represent the selected parents and offspring, black circles the rest of the population (were it to have bred). Because heritability is high, the selection differential S results in a large response to selection (R). The blue curve is the distribution of z in the next generation, whose mean lies R units to the right of the mean of the parental generation. (B) The circumstances are the same, but the relationship between phenotypes of parents and offspring is more variable and has a lower slope in the graph at the right, i.e., lower heritability. Consequently, the selection differential S translates into a smaller response (R). The frequency distribution of offspring (blue curve) shifts only slightly to the right. (C) Here the heritability is very high, as in part A, but the selected parents have $z > 14$. Thus the selection differential S is larger, resulting in a greater response to selection (R).

A and B in Figure 13.8) and to the selection differential S (compare graphs A and C).^{*} In fact, the change in mean phenotype in offspring, R , due to selection of parents, S , can be read directly from the regression line as

$$R = h^2_N S$$

Since this equation can be rearranged as $h^2_N = R/S$, heritability can be estimated from a selection experiment in which S (which is under the experimenter's control) and R are measured. Such an estimate of h^2_N is called the **realized heritability**. This is how (as you may recall from Chapter 9) Dobzhansky and Spassky estimated that the heritability of phototaxis in *Drosophila pseudoobscura* was about 0.09 (see Figure 9.21).

As selection proceeds, it increases the frequencies of those alleles that produce phenotypes closer to the optimum value. As those frequencies increase, multilocus genotypes (combinations of alleles at different loci) that had been extremely rare become more common, so phenotypes arise that had been effectively absent before. *Thus the mean of a polygenic character shifts beyond the original range of variation as directional selection proceeds, even if no further mutations occur.*

If alleles at different loci differ in the magnitude of their effects on the phenotype, those with the largest favorable effects are likely to be fixed first (Orr 1998). In the absence of complicating factors, prolonged directional selection should ultimately fix all favored alleles, eliminating genetic variation. Further response to selection would then require new variation, arising from mutation. For many features, the **MUTATIONAL VARIANCE**, V_m —the infusion of new additive genetic variance by mutation—is on the order of $10^{-3} \times V_E$ per generation; that is, about one-thousandth the environmental variance. Thus a fully homozygous population could, by mutation, attain $V_A/(V_A + V_E) = h^2 = 0.5$, for an entirely additively inherited trait, in about a thousand generations. (If, however, many of these mutations have harmful pleiotropic effects and have a net selective disadvantage, the “usable” mutational variance may be much less; Hansen and Houle 2004.)

Responses to artificial selection

Animal and plant breeders have used artificial selection to alter domesticated species in extraordinary ways (Figure 13.9). Darwin opened *The Origin of Species* with an analysis of such changes, and evolutionary biologists have drawn useful inferences about evolution from artificial selection ever since then. Artificial selection differs from natural selection because the human experimenter focuses on one trait rather than on the organism's overall fitness. Nevertheless, natural selection often operates much like artificial selection.

Responses to artificial selection over just a few generations generally are rather close to those predicted from estimates of heritability based on correlations among relatives, such as parents and offspring. These heritability estimates seldom predict accurately the change in a trait over many generations of artificial selection, however, because of changes in linkage disequilibrium and genetic variance, input of new genetic variation by mutation, and the action of natural selection, which often opposes artificial selection (Hill and Caballero 1992). Such effects were found, for example, in an experiment by B. H. Yoo (1980), who selected for increased numbers of abdominal bristles in lines of *Drosophila melanogaster* taken from a single laboratory population. For 86 generations, Yoo scored bristle numbers on 250 flies, and bred the next generation from the top 50 flies, of each sex. In the base population from which the selection lines were drawn, the mean bristle number was 9.35 in females, and more than 99 percent of females had fewer than 14 bristles (i.e., three standard deviations above the mean). After 86 generations, mean bristle numbers in the experimental populations had increased to 35–45 (Figure 13.10). This represents an average increase of 316 percent, or 12 to 19 phenotypic standard deviations—far beyond the original range of vari-

^{*}The simple equation presented here is the “breeders’ equation,” used for predicting responses to artificial selection in domesticated species. A conceptually related equation is used more often by evolutionary biologists: $\Delta\bar{z} = V_A/\bar{w} \times d\bar{w}/d\bar{z}$, where z is a character state, V_A is the additive genetic variance, and w is fitness. Thus the rate of evolution of the character mean ($\Delta\bar{z}$) is proportional to V_A and to the derivative of fitness with respect to the character value (Lande 1976a). Because of its direct role in determining the rate of evolution, V_A is better than the heritability, h^2_N , as a measure of “evolvability” (Houle 1992).

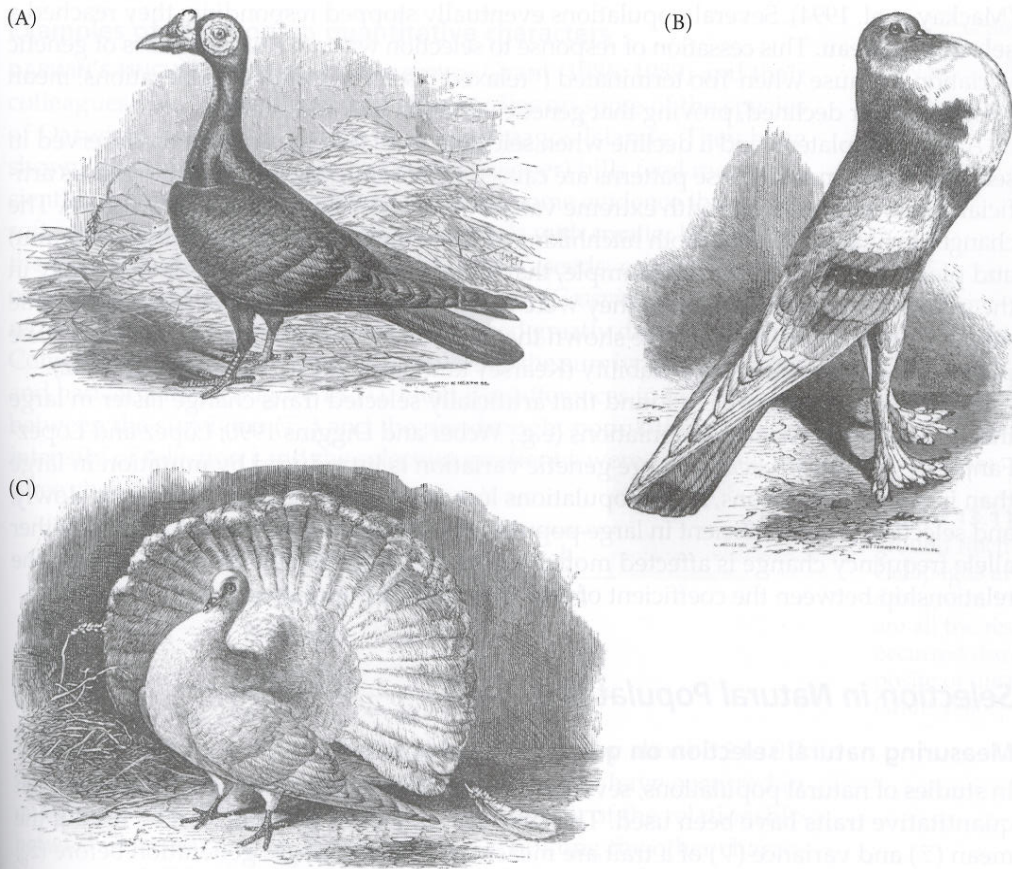


Figure 13.9 Results of artificial selection: domesticated breeds of pigeons, all developed from the wild rock pigeon by selective breeding. Each breed has features quite unlike the wild ancestor, such as (A) the long bill and large featherless region surrounding the eye of the English carrier; (B) the greatly inflated esophagus, erect stance, elongated body and legs, and feathered toes of the English pouter; and (C) the tail of the fantail with its 32 (or more) feathers. The fantail is remarkable because the tails of all species in the pigeon family (and in most other families of birds) normally have 12 feathers. These drawings are from Darwin's book *The Variation of Animals and Plants under Domestication* (1868). Darwin kept pigeons, studied pigeon breeds extensively, and used information from pigeons and other domesticated species in developing his argument for evolution.

ation. In a very short time, selection had accomplished an enormous evolutionary change, at a rate far higher than is usually observed in the fossil record.

This progress was not constant, however. Some of the experimental populations showed periods of little change, followed by episodes of rapid increase. Such irregularities in response are partly due to the origin and fixation of new mutations with rather large effects

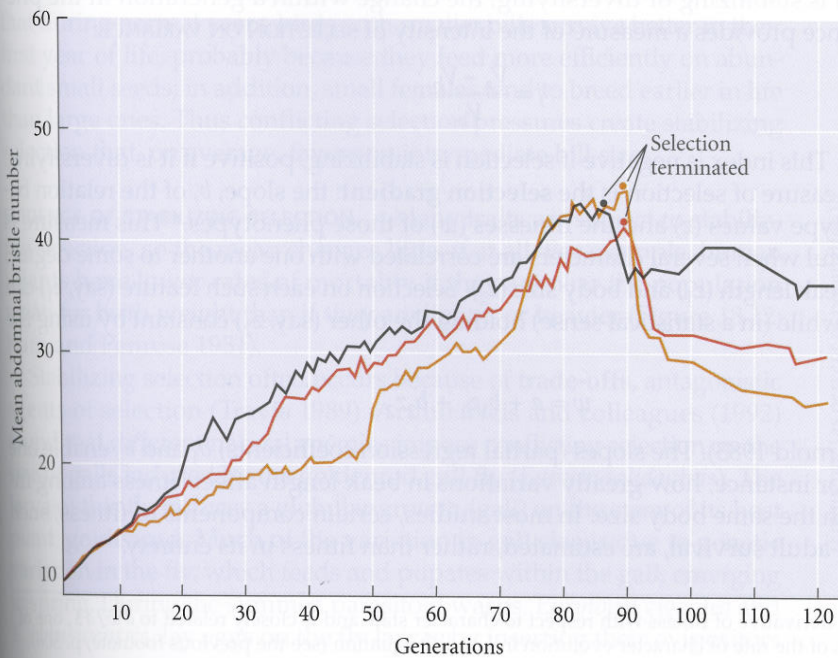


Figure 13.10 Responses to artificial selection for increased numbers of abdominal bristles in three laboratory populations of *Drosophila melanogaster*. After about 86 generations, the means had increased greatly. Selection was terminated at the points indicated by colored circles and bristle number declined thereafter, indicating that genotypes with fewer bristles had higher fitness. (After Yoo 1980.)

(Mackay et al. 1994). Several populations eventually stopped responding: they reached a **selection plateau**. This cessation of response to selection was not caused by loss of genetic variation, because when Yoo terminated ("relaxed") selection after 86 generations, mean bristle number declined, proving that genetic variation was still present.

A selection plateau and a decline when selection is relaxed are commonly observed in selection experiments. These patterns are caused by natural selection, which opposes artificial selection: genotypes with extreme values of the selected trait have low fitness. The changes in fitness are due to both hitchhiking of deleterious alleles (linkage disequilibrium) and pleiotropy. Yoo found, for example, that lethal alleles had increased in frequency in the selected populations because they were closely linked to alleles that increased bristle number. Other investigators have shown that some alleles affecting bristle number have pleiotropic effects that reduce viability (Kearsey and Barnes 1970; Mackay et al. 1992).

Several investigators have found that artificially selected traits change faster in large than in small experimental populations (e.g., Weber and Diggins 1990; López and López-Fanjul 1993). This is because more genetic variation is introduced by mutation in large than in small populations, large populations lose variation by genetic drift more slowly, and selection is more efficient in large populations. (Recall from Chapter 12 that whether allele frequency change is affected more by selection or by genetic drift depends on the relationship between the coefficient of selection and the population size.)

Selection in Natural Populations

Measuring natural selection on quantitative characters

In studies of natural populations, several measures of the strength of natural selection on quantitative traits have been used. The simplest indices of selection can be used if the mean (\bar{z}) and variance (V) of a trait are measured within a single generation before (\bar{z}_b, V_b) and then again after (\bar{z}_a, V_a) selection has occurred. (For instance, these measurements may be made on juveniles and then on those individuals that successfully survive to adulthood and reproduce.) Then, if selection is directional, an index of the **intensity of selection** is

$$i = \frac{\bar{z}_a - \bar{z}_b}{\sqrt{V_p}}$$

where V_p is the phenotypic variance.

If selection is stabilizing or diversifying, the change within a generation in the phenotypic variance provides a measure of the intensity of SELECTION ON VARIANCE:

$$j = \frac{V_a - V_b}{V_b}$$

(Endler 1986). This index is negative if selection is stabilizing, positive if it is diversifying.

Another measure of selection is the **selection gradient**: the slope, b , of the relation between phenotype values (z) and the fitnesses (w) of those phenotypes.* This measure is especially useful when several characters are correlated with one another to some degree, such as, say, beak length (z_1) and body size (z_2). Selection on each such feature (say, z_1) can be estimated while (in a statistical sense) holding the other (say, z_2) constant by using the equation

$$w = a + b_1 z_1 + b_2 z_2$$

(Lande and Arnold 1983). The slopes (partial regression coefficients) b_1 and b_2 enable one to estimate, for instance, how greatly variations in beak length affect fitness among individuals with the same body size. In most studies, certain components of fitness, such as juvenile-to-adult survival, are estimated, rather than fitness in its entirety.

*The slope is the derivative of fitness with respect to character state and is closely related to $d\bar{w}/d\bar{z}$, one of the determinants of the rate of character evolution in Lande's equation (see the previous footnote, p. 306).

Examples of selection on quantitative characters

DARWIN'S FINCHES. Peter and Rosemary Grant (1986, 1989) and their colleagues have carried out long-term studies on some of the species of Darwin's finches on certain of the Galápagos Islands. They have shown that birds with larger (especially deeper) bills feed more efficiently on large, hard seeds, whereas there is some evidence that small, soft seeds are more efficiently utilized by birds with smaller bills. When the islands suffered a severe drought in 1977, seeds, especially small ones, became sparse, medium ground finches (*Geospiza fortis*) did not reproduce, and their population size declined greatly due to mortality. Compared with the pre-drought population, the survivors were larger and had larger bills (Figure 13.11). From the differences in morphology between the survivors (\bar{z}_a) and the pre-drought population (\bar{z}_b), the intensity of selection i and the selection gradient b were calculated for three characters:

Character	i	b
Weight	0.28	0.23
Bill length	0.21	-0.17
Bill depth	0.30	0.43

The values of i show that each character increased by about 0.2 to 0.3 standard deviations, a very considerable change to have occurred in one generation. The values of b show the strength of the relationship between survival and each character while holding the other characters constant. Selection strongly favored birds that were larger and had deeper bills because they could more effectively feed on large, hard seeds, virtually the only available food. The negative b values show that selection favored shorter bills. Nevertheless, bill length increased, in opposition to the direction of selection, because bill length is correlated with bill depth. Thus a feature can evolve in a direction opposite to the direction of selection if it is strongly correlated with another trait that is more strongly selected. (We will soon return to this theme.)

Why don't these finches evolve ever larger bills? The Grants found that during normal years, birds with smaller bills survive better in their first year of life, probably because they feed more efficiently on abundant small seeds; in addition, small females tend to breed earlier in life than large ones. Thus conflicting selection pressures create stabilizing selection that, on average, favors an intermediate bill size.

EVIDENCE OF STABILIZING SELECTION. Many traits are subject to stabilizing selection, so the mean changes little, if at all. For example, human infants have lower rates of mortality if they are near the population mean for birth weight than if they are lighter or heavier (Figure 13.12; Karn and Penrose 1951).

Stabilizing selection often occurs because of **trade-offs**, antagonistic agents of selection (Travis 1989). Arthur Weis and colleagues (1992) found that different natural enemies impose conflicting selection on the size of galls induced by the goldenrod gall fly (*Eurosta solidaginis*). The larva of this fly induces a globular growth (gall) on the stem of its host plant, goldenrod. Much of the variation in gall size is due to genetic variation in the fly, which feeds and pupates within the gall, emerging in spring. During the summer, parasitoid wasps, *Eurytoma gigantea* and *E. obtusiventris*, lay eggs on the fly larvae by inserting their ovipositors

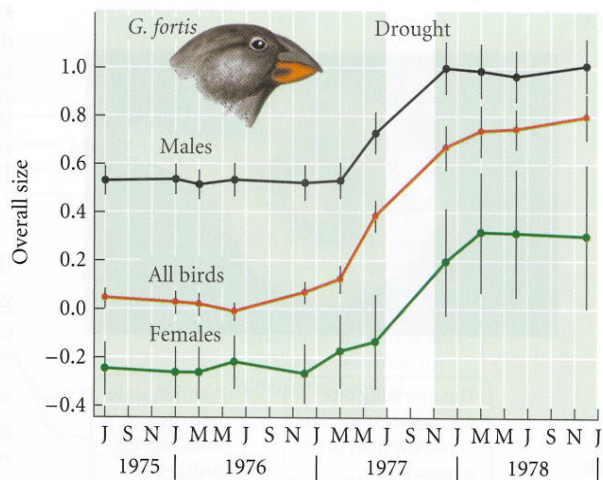
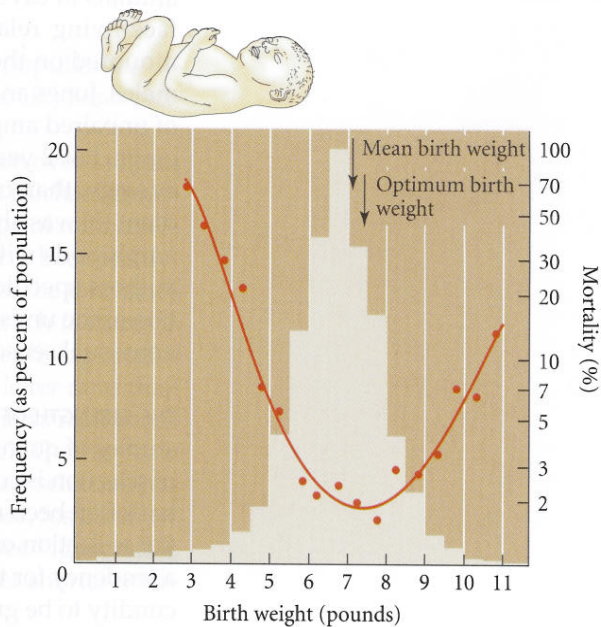


Figure 13.11 Changes in the mean size of the ground finch *Geospiza fortis* on Daphne Island in the Galápagos archipelago due to mortality during a drought in 1977. Changes occurring in 1977 and 1978 are all the result of mortality; no reproduction occurred during this period. "Overall size" is a composite of measurements of several characters. (After Grant 1986.)

Figure 13.12 Stabilizing selection for birth weight in humans. The rate of infant mortality is shown by the points and the line fitting them. The histogram shows the distribution of birth weights in the population. (After Cavalli-Sforza and Bodmer 1971.)



(Mackay et al. 1994). Several populations eventually stopped responding: they reached a **selection plateau**. This cessation of response to selection was not caused by loss of genetic variation, because when Yoo terminated ("relaxed") selection after 86 generations, mean bristle number declined, proving that genetic variation was still present.

A selection plateau and a decline when selection is relaxed are commonly observed in selection experiments. These patterns are caused by natural selection, which opposes artificial selection: genotypes with extreme values of the selected trait have low fitness. The changes in fitness are due to both hitchhiking of deleterious alleles (linkage disequilibrium) and pleiotropy. Yoo found, for example, that lethal alleles had increased in frequency in the selected populations because they were closely linked to alleles that increased bristle number. Other investigators have shown that some alleles affecting bristle number have pleiotropic effects that reduce viability (Kearsey and Barnes 1970; Mackay et al. 1992).

Several investigators have found that artificially selected traits change faster in large than in small experimental populations (e.g., Weber and Diggins 1990; López and López-Fanjul 1993). This is because more genetic variation is introduced by mutation in large than in small populations, large populations lose variation by genetic drift more slowly, and selection is more efficient in large populations. (Recall from Chapter 12 that whether allele frequency change is affected more by selection or by genetic drift depends on the relationship between the coefficient of selection and the population size.)

Selection in Natural Populations

Measuring natural selection on quantitative characters

In studies of natural populations, several measures of the strength of natural selection on quantitative traits have been used. The simplest indices of selection can be used if the mean (\bar{z}) and variance (V) of a trait are measured within a single generation before (\bar{z}_b, V_b) and then again after (\bar{z}_a, V_a) selection has occurred. (For instance, these measurements may be made on juveniles and then on those individuals that successfully survive to adulthood and reproduce.) Then, if selection is directional, an index of the **intensity of selection** is

$$i = \frac{\bar{z}_a - \bar{z}_b}{\sqrt{V_P}}$$

where V_P is the phenotypic variance.

If selection is stabilizing or diversifying, the change within a generation in the phenotypic variance provides a measure of the intensity of SELECTION ON VARIANCE:

$$j = \frac{V_a - V_b}{V_b}$$

(Endler 1986). This index is negative if selection is stabilizing, positive if it is diversifying.

Another measure of selection is the **selection gradient**: the slope, b , of the relation between phenotype values (z) and the fitnesses (w) of those phenotypes.* This measure is especially useful when several characters are correlated with one another to some degree, such as, say, beak length (z_1) and body size (z_2). Selection on each such feature (say, z_1) can be estimated while (in a statistical sense) holding the other (say, z_2) constant by using the equation

$$w = a + b_1 z_1 + b_2 z_2$$

(Lande and Arnold 1983). The slopes (partial regression coefficients) b_1 and b_2 enable one to estimate, for instance, how greatly variations in beak length affect fitness among individuals with the same body size. In most studies, certain components of fitness, such as juvenile-to-adult survival, are estimated, rather than fitness in its entirety.

*The slope is the derivative of fitness with respect to character state and is closely related to $d\bar{w}/d\bar{z}$, one of the determinants of the rate of character evolution in Lande's equation (see the previous footnote, p. 306).

Examples of selection on quantitative characters

DARWIN'S FINCHES. Peter and Rosemary Grant (1986, 1989) and their colleagues have carried out long-term studies on some of the species of Darwin's finches on certain of the Galápagos Islands. They have shown that birds with larger (especially deeper) bills feed more efficiently on large, hard seeds, whereas there is some evidence that small, soft seeds are more efficiently utilized by birds with smaller bills. When the islands suffered a severe drought in 1977, seeds, especially small ones, became sparse, medium ground finches (*Geospiza fortis*) did not reproduce, and their population size declined greatly due to mortality. Compared with the pre-drought population, the survivors were larger and had larger bills (Figure 13.11). From the differences in morphology between the survivors (\bar{z}_a) and the pre-drought population (\bar{z}_b), the intensity of selection i and the selection gradient b were calculated for three characters:

Character	i	b
Weight	0.28	0.23
Bill length	0.21	-0.17
Bill depth	0.30	0.43

The values of i show that each character increased by about 0.2 to 0.3 standard deviations, a very considerable change to have occurred in one generation. The values of b show the strength of the relationship between survival and each character while holding the other characters constant. Selection strongly favored birds that were larger and had deeper bills because they could more effectively feed on large, hard seeds, virtually the only available food. The negative b values show that selection favored shorter bills. Nevertheless, bill length increased, in opposition to the direction of selection, because bill length is correlated with bill depth. Thus a feature can evolve in a direction opposite to the direction of selection if it is strongly correlated with another trait that is more strongly selected. (We will soon return to this theme.)

Why don't these finches evolve ever larger bills? The Grants found that during normal years, birds with smaller bills survive better in their first year of life, probably because they feed more efficiently on abundant small seeds; in addition, small females tend to breed earlier in life than large ones. Thus conflicting selection pressures create stabilizing selection that, on average, favors an intermediate bill size.

EVIDENCE OF STABILIZING SELECTION. Many traits are subject to stabilizing selection, so the mean changes little, if at all. For example, human infants have lower rates of mortality if they are near the population mean for birth weight than if they are lighter or heavier (Figure 13.12; Karn and Penrose 1951).

Stabilizing selection often occurs because of **trade-offs**, antagonistic agents of selection (Travis 1989). Arthur Weis and colleagues (1992) found that different natural enemies impose conflicting selection on the size of galls induced by the goldenrod gall fly (*Eurosta solidaginis*). The larva of this fly induces a globular growth (gall) on the stem of its host plant, goldenrod. Much of the variation in gall size is due to genetic variation in the fly, which feeds and pupates within the gall, emerging in spring. During the summer, parasitoid wasps, *Eurytoma gigantea* and *E. obtusiventris*, lay eggs on the fly larvae by inserting their ovipositors

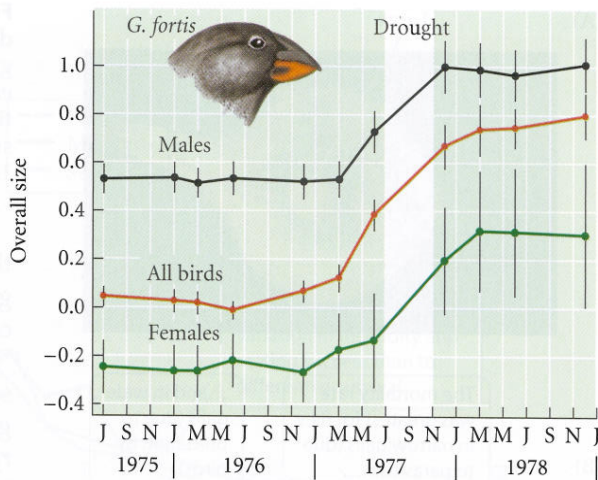
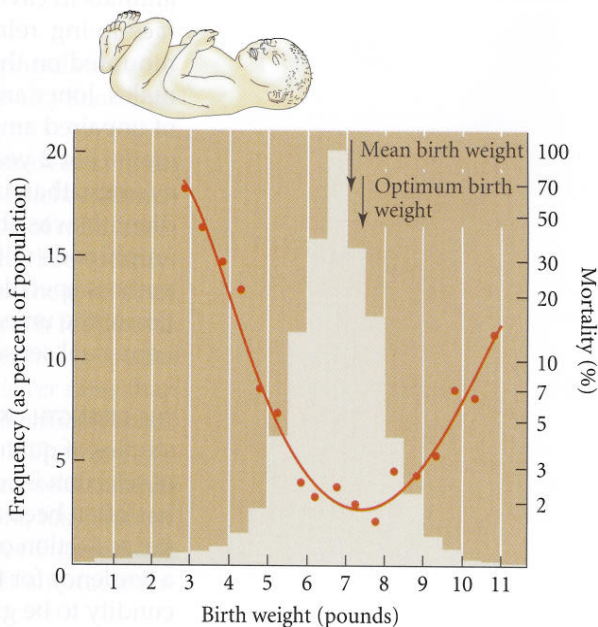


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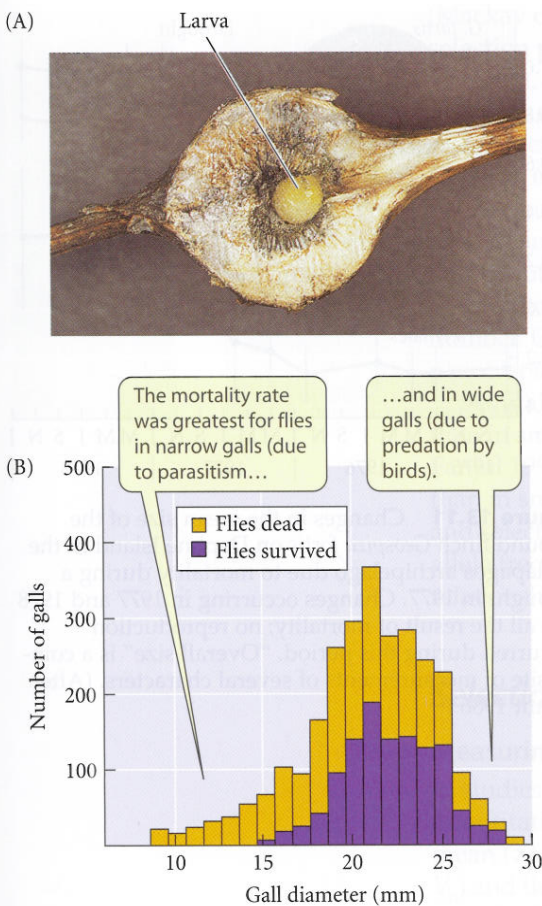


Figure 13.13 (A) Larva of the gall fly (*Eurosta solidaginis*), shown inside the dissected stem gall of a goldenrod plant. (B) Stabilizing selection on the size of galls made by *E. solidaginis*. The height of each bar shows the proportion of each plant gall size in the population, and the blue portion shows the proportion of fly larvae that survived. Flies in intermediate-sized galls had the highest survivorship. (A © Scott Camazine/Photo Researchers, Inc.; B after Weis et al. 1992.)

through the gall wall. During winter, woodpeckers and chickadees open galls and feed on the fly pupae. Mortality caused by parasitoids and birds can be determined by examining galls in the spring.

The researchers found that the parasitoid *E. gigantea* very consistently selected for wide galls (i.e., mortality was greatest for fly larvae in narrow galls) because the wasp's ovipositor cannot penetrate thick gall tissue. *Eurytoma obtusiventris* generally selected for intermediate-sized galls, whereas birds most frequently attacked wide galls, selecting for narrower gall diameter. Taken together, these enemies imposed rather strong stabilizing selection ($j = -0.30$), but because selection by parasitoids was weaker than selection by birds, a directional component ($i = 0.34$) was detected as well (Figure 13.13).

VESTIGIAL FEATURES IN CAVE ORGANISMS. A long-standing puzzle is why, over the course of evolution, features that have no function become vestigial and are ultimately lost. For instance, snakes have vestigial legs or none at all; many flowers have only female or male function and possess vestigial stamens or pistil.

The Lamarckian explanation, whereby organs are maintained or lost as a result of use or disuse, has long since been rejected. Neo-Darwinian theory offers two possible explanations: either mutations that cause degeneration of an unused character become fixed by genetic drift because variations in the character are selectively neutral, or there is selection against an unused organ, perhaps because it interferes with some important function or requires energy and materials that could better be used for other purposes. In addition, selection could indirectly reduce an unused organ if, due to pleiotropy, it were negatively correlated with another feature that increased due to selection (Fong et al. 1995).

Cave-dwelling populations of the amphipod crustacean *Gammarus minus*, like many animals in caves, have eyes that are highly reduced compared with those of their surface-living relatives. The heritability of eye size is high. Male amphipods remain mounted on their mates for a week or two after mating, guarding them against other males. Jones and Culver (1989) compared the eye sizes of paired amphipods with those of unpaired amphipods, which were assumed to have lower reproductive success on average. For 2 years in succession, mating individuals of both sexes had smaller eyes, on average, than unmated individuals. The investigators estimated that the selection gradient (b) was about -0.30 , indicating that selection for small eyes was quite strong. Why amphipods with reduced eyes should have higher mating success is not clear, but the authors speculated, based on neurobiological studies by other researchers, that reduction of the unused visual system might free more of the central nervous system to process nonvisual sensory input.

THE STRENGTH OF NATURAL SELECTION. The strength of selection has been estimated in many studies of quantitative traits in natural populations (Kingsolver et al. 2001). The strength of selection is commonly quite modest, although strong selection (b greater than, say, 0.25) has often been recorded (Figure 13.14A). Stabilizing selection and diversifying selection (i.e., selection on variance) appear to be about equally common (Figure 13.14B). There is a tendency for the strength of selection due to variation in mating success and female fecundity to be greater, on average, than that of selection due to differences in survival.