

## CHAPTER ONE

### Introduction

Of the great principles of truth which the first speculatists discovered, the simplicity is embarrassed by ambitious additions, or the evidence obscured by inaccurate argumentation; and as they descend from one succession of writers to another, like light transmitted from room to room, they lose their strength and splendour, and fade at last in total evanescence. The systems of learning therefore must be sometimes reviewed, complications analyzed into principles, and knowledge disentangled from opinion.

Samuel Johnson, *The Rambler*, 14 September 1751

Natural selection is a major part of the theory of evolution (Darwin 1859; Fisher 1930; Mayr 1963; Ghiselin 1969), yet there is much argument and confusion as to what it is, what it is not, and even whether or not it exists.<sup>1</sup> These disputations have tended to befog the larger questions of mechanisms and even the validity of the theory of evolution (Ghiselin 1969; Wassermann 1981a,b; Gould 1982). It is the purpose of this book to describe natural selection clearly, show that it is neither a tautology nor a metaphysical exercise, discuss the problems of its demonstration and measurement, present the critical evidence for its existence, and place it in perspective. This chapter will define natural selection, relate it to genetic drift and evolution, discuss the restricted meanings the term “natural selection” often takes, and summarize some of its modes.

<sup>1</sup> For differing views and arguments, see Cox 1981; Flew 1981; Gendron 1981; Pearson 1981; Robson 1981; Stephenson 1981; Wasserman 1981a,b.

Throughout this book, lengthy lists of references are given in footnotes, while shorter lists remain parenthetically cited in the text. This dual citation system is not intended to draw any distinction between references, but only to make the text easier to read.

## 1.1. DEFINITION OF NATURAL SELECTION

Natural selection can be defined as a *process* in which:

If a population has:

- a. variation among individuals in some attribute or trait: *variation*;
- b. a consistent relationship between that trait and mating ability, fertilizing ability, fertility, fecundity, and, or, survivorship: *fitness differences*;
- c. a consistent relationship, for that trait, between parents and their offspring, which is at least partially independent of common environmental effects:<sup>2</sup> *inheritance*.

Then:

1. the trait frequency distribution will differ among age classes or life-history stages, beyond that expected from ontogeny;
2. if the population is not at equilibrium, then the trait distribution of all offspring in the population will be predictably different from that of all parents, beyond that expected from conditions *a* and *c* alone.

Conditions *a*, *b*, and *c* are necessary and sufficient for the process of natural selection to occur, and these lead to deductions 1 and 2. As a result of this process, but not necessarily, the trait distribution may change in a predictable way over many generations.<sup>3</sup> The process of natural selection has been called a law (Reed 1981) because if the initial conditions are fulfilled, the conclusions necessarily follow; the principle behind the law is a syllogism. Natural selection probably should not be called a biological law. It proceeds not for biological reasons, but from

<sup>2</sup> The environment common to parents and offspring can yield a correlation between parents and offspring if there is an environmental component to trait variation, the environment is heterogeneous, and there is a physical association between parents and offspring (Falconer 1981).

<sup>3</sup> Modified after Fisher 1930, Falconer 1981, Bulmer 1980, Ewens 1979, Ghiselin 1981, and Williams 1970, 1973.

the laws of probability; conditions *a-c* contain the only biological content.

## 1.2. RELATIONSHIP TO GENETIC DRIFT AND EVOLUTION

Genetic drift is a random sampling process of alleles between generations. The necessary and sufficient conditions for genetic drift (Wright 1931, 1942; Kimura 1983; Lande 1976a, 1980) differ in only two respects from those for natural selection (Table 1.1): (1) condition *b* is absent (by definition), and (2) the effective population size must be small enough to ensure that sampling error is significant. Of course it is perfectly possible for both natural selection and genetic drift to occur simultaneously in small populations. We can divide both processes into phenotypic difference (conditions *a* and *b*) and genetic response (*c*); then the only difference is that the phenotypic difference is consistent (in sign) among generations during natural selection, but randomly varying during genetic drift (Table 1.1). The distinction is blurred where selection varies at random in time.

Evolution may be defined as any net directional change or any cumulative change in the characteristics of organisms or populations over many generations—in other words, descent with modification (after Lincoln et al. 1982). It explicitly includes the *origin* as well as the *spread* of alleles, variants, trait values, or character states. Evolution may occur as a result of natural selection, genetic drift, or both (Figure 1.1); the minimum requirements are those for either process (Table 1.1). Natural selection does not necessarily give rise to evolution, and the same is true for genetic drift.

By definition, a population at equilibrium has the same trait distribution at each generation; it is not evolving. This may result solely from natural selection, or through a combination of natural selection and other countervailing evolutionary factors. If a population is not at equilibrium, then evolution can proceed, and this was the main interest of Darwin and the other

TABLE 1.1. The relationships among natural selection, genetic drift, and evolution

Property	Natural Selection	Genetic Drift	Evolution <sup>a</sup>
<i>Necessary and Sufficient Conditions</i>			
Condition <i>a</i> (trait variation)	required	required	required
Condition <i>b</i> (fitness differences)	required	absent (by definition)	not required (more likely if present)
Condition <i>c</i> (inheritance)	required	required	required
Small effective population size	not required	required	not required unless condition <i>b</i> is absent
Origin of new variation	not required	not required	required
<i>Other Properties</i>			
Observed differences among phenotypes or age classes (condition <i>b</i> )	consistent in time (deduction 1)	random in time	consistent (or relatively so) in time
Stable equilibrium possible?	yes (part of deduction 2)	yes <sup>b</sup>	no <sup>c</sup> (by definition)
Measure of degree of condition <i>b</i>	fitness <sup>d</sup>	(observed "fitness")	durability <sup>d</sup>

<sup>a</sup> In the sense of any cumulative change in the characteristics of a population over many generations (see text).

<sup>b</sup> Larger populations may appear to be at equilibrium. Also, a stable equilibrium or stationary distribution is possible with mutation and/or gene flow.

<sup>c</sup> A stable equilibrium is possible, but once it is reached, evolution has stopped (by definition) until conditions change.

<sup>d</sup> See Chapter 2 for discussion.

early evolutionists. But if a population is at equilibrium, no evolution is possible (by definition) unless the relationships in conditions *a-c* change, or some other evolutionary factors come into play. Whether or not a population is at equilibrium when studied depends upon its history as well as on current conditions *a-c*.

Population geneticists use a different definition of evolution: a change in allele frequencies among generations. This meaning is quite different from the original; it now includes random as well as directional changes (more than the shaded part of Figure 1.1), but it does not require the origin of new forms. It is roughly equivalent to microevolution (subspecific evolution; macroevolution involves major trends, or transspecific evolution; see Rensch 1959, Mayr 1963). Unfortunately, the use of the population genetics definition often results in an overemphasis on changes in allele frequencies and an underemphasis on (or no consideration of) the *origin* of the different alleles and their properties. Both are important in evolution (see Chapter 8). An

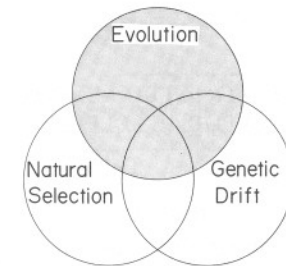


FIGURE 1.1. A Venn diagram, showing the relationship between the necessary and sufficient conditions for natural selection, genetic drift, and evolution. The shaded area results in cumulative changes in genotype frequencies or trait values, and the shaded area outside the domains of natural selection and genetic drift may be due to mutation, meiotic drive, and other processes. See also Table 1.1. The relative sizes and degree of overlap are not meant to imply anything about the relative importance or frequency of these phenomena. Evolution can be regarded either as the shaded area or as the area of all three circles (see text); the former is used in this book.

additional problem is that, for quantitative genetic traits, the frequencies of alleles at many contributing loci can change while the overall mean and variance of the trait remain roughly constant. In this book I will use the older definition of evolution (Lincoln et al. 1982; Figure 1.1, shaded), rather than the population-genetics definition. For either definition, natural selection is sufficient for evolution, but it is neither necessary for nor does it guarantee evolution.

The origin of conditions  $a$ ,  $b$ , and  $c$  is an issue separate from natural selection. Natural selection takes these conditions as given, and it results in consequences 1 and 2. These consequences may or may not affect the conditions for natural selection in the next generation. The conditions are a joint effect of the environment, the genetic system, and the history of the population, and may evolve as a result of many different factors. Thus the origin of conditions  $a$ ,  $b$ , and  $c$  is a function of genetics, evolution and ecology, not necessarily of natural selection. We will return to this in Chapters 2 and 8. Natural selection must not be equated with evolution, though the two are intimately related.

### 1.3. RESTRICTED MEANINGS OF "NATURAL SELECTION"

The term "natural selection" means different things to different people, and this often leads to confusion in the literature. Three restricted meanings are relatively common, and they partially overlap: mortality selection, nonsexual selection, and phenotypic selection. The last two are parts of distinctions which are of very great theoretical importance, and have significantly increased our understanding of natural selection and evolution.

The restricted meanings can be placed in a broader perspective. By the nature of its definition, natural selection can be broken down into various components in two different and independent ways, depending upon alternate subprocesses dif-

fering in dynamics and outcome (Figure 1.2A), or component or sequential subprocesses (Figure 1.2B). The restricted meanings of "natural selection" are parts of these subdivisions: mortality and nonsexual selection are in the first subdivision, while phenotypic selection is in the second.

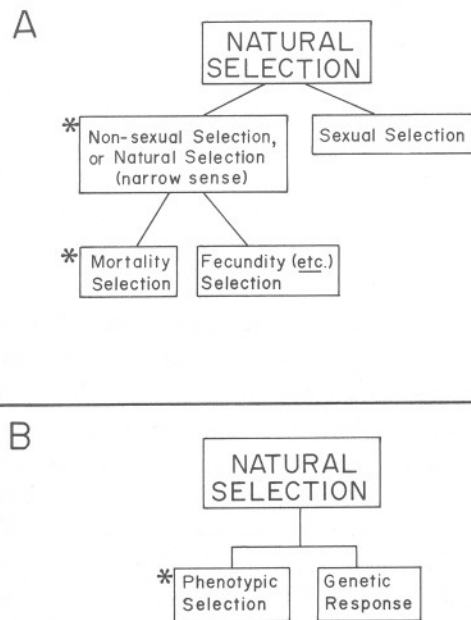


FIGURE 1.2. Two logical and independent subdivisions of natural selection, illustrating the restricted meanings that "natural selection" often takes in the literature. *A*, subdivision by alternate subprocesses; *B*, subdivision by sequential subprocesses. The subprocesses in *A* are distinguished with respect to condition  $b$  (fitness differences) and implicitly contain conditions  $a$  (trait variance) and  $c$  (inheritance) for natural selection; each is necessary and sufficient for natural selection to occur. Each does not guarantee evolution because conditions  $a$ ,  $b$ , and  $c$  can result in a stable equilibrium. The subprocesses in *B* are separated on the basis of the three conditions for natural selection: phenotypic selection requires conditions  $a$  and  $b$ , while the genetic response requires condition  $c$ . Neither is sufficient by itself for the process of natural selection, though both together are necessary and sufficient. Asterisks indicate the subprocesses that are frequently called "natural selection" in the literature.

### 1.3.1. Mortality Selection

Natural selection is sometimes used to refer only to the effects of consistent phenotype-specific mortality (discussed in Fisher 1930 and Ghiselin 1969; see Figure 1.2A); examples are Hailman (1982) and Darlington (1983). Consider an expanding population consisting of two genotypes, one of which is increasing faster than the other. Some researchers do not consider this a case of natural selection because there is no mortality (Hailman 1982; pers. comm. 1983). Restriction to mortality selection in the literature depends, in part, on equating natural selection with "survival of the fittest." It also depends upon a singular interpretation of what Darwin meant by natural selection. Three quotes from Darwin (1859) give slightly different impressions:

Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection. (p. 61)

I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. (p. 62)

If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that

individuals having any advantage, however slight, over others, would have the best chance of surviving and procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. (pp. 80–81)

These definitions might be understood to indicate only mortality effects, but they are easier to interpret as including other components such as fecundity and fertility. Further reading of Darwin (1859 and 1871) suggests that he thought natural selection included more than mortality. Mortality selection is clearly a special case of natural selection (Figure 1.2A); it is too restricted to be useful except in special cases, although natural selection will proceed with mortality selection alone.

### 1.3.2. Sexual and Nonsexual Selection

Darwin (1859, p. 88; 1871) made a careful distinction between natural selection and sexual selection (Figure 1.2A): sexual selection is a result of differential mating success, including fertilization and pairing. The distinction was made because traits favored by sexual selection may sometimes be disadvantageous, or opposed by other components of natural selection (Darwin 1871; Ghiselin 1974; Wade and Arnold 1980). Thus the outcome, as well as the dynamics, can be quite different from what Darwin and many biologists would regard as "natural selection" (Fisher 1930; Lande 1981; Kirkpatrick 1982; Arnold 1983a). Explicit as well as implicit differences of opinion abound on whether or not sexual selection is a subset of natural selection; in addition, to add to the confusion, other aspects of differential reproductive success (such as fertility) have often also been included with sexual selection. Because the consequences of mating success are so distinct, it is best to restrict "sexual selection" to its original meaning and its application

to differential mating success, rather than to include all aspects of reproductive success (Ghiselin 1974; Wade and Arnold 1980; Arnold 1983a).

As defined in this book, sexual selection is a logical subset of the process of natural selection. This is true because (1) mating ability is one of several alternatives in condition *b*, and (2) the definition of the process takes no account of the details of its outcome; it merely states that the trait frequency distribution may change if conditions *a*, *b*, and *c* are met. In fact there is no difference between sexual and nonsexual selection in the methods of demonstration or measurement (see Chapter 6 and Arnold and Wade 1984a,b). In addition, other components of natural selection can oppose one another. In the very general sense, sexual selection is a subset or aspect of natural selection, but at a lower level (considering their dynamics and outcomes) they are very distinct. Perhaps we should use the term "organic selection" for the general process, sexual selection for processes involving mating success, and natural selection (narrow sense) for the remainder. However, for simplicity in this book the term "natural selection" will be used for the general process, and nonsexual selection and sexual selection will be used for the specific subprocesses. Note that mortality selection is a special case of nonsexual selection (Figure 1.2A), and, like mortality selection, sexual and nonsexual selection are sufficient by themselves for natural selection to proceed.

### 1.2.3. Phenotypic Selection and Response

This subdivision of natural selection is independent of the previous ones (Figure 1.2B). Quantitative geneticists and animal breeders decompose the process of natural selection into phenotypic selection and genetic (or "evolutionary") response (Fisher 1930; Haldane 1954; Falconer 1981; Lande and Arnold 1983). Phenotypic selection is the *within-generation* change in the trait distribution among cohorts (or the difference between the actual number of mates and the effective number of mates in

the case of sexual selection), and is independent of any genetic system or genetic determination. In terms of the definition of natural selection, phenotypic selection requires conditions *a* and *b*. The response is the genetic change that occurs as a result of phenotypic selection in combination with the genetic system, which requires condition *c*. This is a very important and useful distinction (see Falconer 1981).

If there is no inheritance (condition *c*) the process of natural selection cannot occur. In spite of this, phenotypic selection is sometimes called "natural selection" (for example, Lande and Arnold 1983). One good reason for this is that natural selection works on phenotypes and not on genotypes (Mayr 1963; Lewontin 1974). But natural selection is the differential survival and perpetuation of phenotypes, and perpetuation requires inheritance. Phenotypic selection determines the distribution of traits during reproduction, but inheritance is required to transform the distribution into the next generation. To say that natural selection is synonymous with phenotypic selection is to trivialize it—this is tantamount to saying that there are differences among different phenotypes, which can easily lead to tautology (Chapter 2).

The restriction of natural selection to phenotypic selection results at least in part from an inconsistent distinction between evolution, natural selection, and genetic drift. It also accounts for the occasional use of the term "evolutionary response" for "genetic response." "Evolutionary response" is an unfortunate usage because natural selection does not necessarily result in evolution—at equilibrium there can be a genetic response to phenotypic selection every generation, but no change in trait distributions, that is, no evolution (Table 1.1). Random genetic drift can also yield differences among age classes, which will appear to be phenotypic selection if only a few generations are examined. This apparent phenotypic selection will be followed by a genetic response as the random within-generation change is transformed into the next generation through the hereditary



process, but that is not natural selection! It is condition *b* and not *c* that distinguishes natural selection from genetic drift (Table 1.1); merely splitting off *c* is insufficient. To be logically consistent, we must either include genetic response as part of the process of natural selection (as in the definition in this book), or distinguish *three* processes: (1) phenotypic (“natural”) selection; (2) genetic response; and (3) cumulative genetic change (evolution). Phenotypic selection and genetic response should be regarded as subprocesses of natural selection. This also appears to be closer to what Darwin intended:

But if variations useful to any organic being do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection. (Darwin 1859, p. 127)

Natural selection can preserve differences; this is impossible without condition *c*. An additional reason for including *c* as a requirement for natural selection is that its separation from *a* and *b* has been a major contributing factor in keeping the fields of ecology and genetics separate.

To put this usage into a broader perspective, those who restrict “natural selection” to phenotypic selection also call natural selection, as defined in this book, “evolution”; those who are more careful call it “evolution by natural selection.” But evolution is more than merely a change in trait distributions or allele frequencies; it also includes the *origin* of the variation. I will return to this in Chapter 8. For these reasons, the distinctions between natural selection, genetic drift, and evolution as shown in Table 1.1 will be used in this book.

As with the distinction between sexual and nonsexual selection, the distinction between phenotypic selection and genetic

response is an important and useful one, and is based upon a subdivision of the process of natural selection (Figure 1.2B), but unlike the first subdivision (Figure 1.2A), phenotypic selection (conditions *a* and *b*) and genetic response (condition *c*) are not by themselves sufficient for the *process* of natural selection.

To reiterate, natural selection may be broken down into two orthogonal subdivisions (Figure 1.2), and the restricted meanings emphasize these subdivisions. The first subdivision (Figure 1.2A) breaks the process into complete components, differing only in the details of condition *b*; natural selection can occur for any one of the subprocesses in this subdivision. On the other hand, the second subdivision (Figure 1.2B) breaks the process sequentially into one containing conditions *a* and *b* and one with *c*; natural selection cannot occur without both subprocesses of the second subdivision. Mortality and nonsexual selection are components of the first subdivision, while phenotypic selection is a component of the second; of the three restricted meanings, only phenotypic selection is insufficient by itself for natural selection to proceed. If mortality, nonsexual, or phenotypic selection must be called “natural selection,” one must make it absolutely clear precisely which restricted meaning one intends. In this book, I will use the general meaning of “natural selection” rather than the restricted meanings.

#### 1.4. MODES OF SELECTION

Natural selection may affect populations in a number of different ways or modes. There are basically six classes of modes, each emphasizing different aspects of the process. They relate to differences in (1) trait mean, variance, and covariance; (2) number of equivalent phenotypes; (3) effects of other phenotypes; (4) habitat diversity and habitat choice; (5) levels of selection; and (6) mode of inheritance. These are independent, and several may happen simultaneously in the same population.

## 1.4.1. Mean, Variance, and Covariance

Natural selection is a process that affects the frequency distributions of heritable traits of a population. Traits may vary continuously or discontinuously (Figure 1.3). Continuously varying traits are often called quantitative (or morphometric) traits, and discontinuously varying traits are often called polymorphic

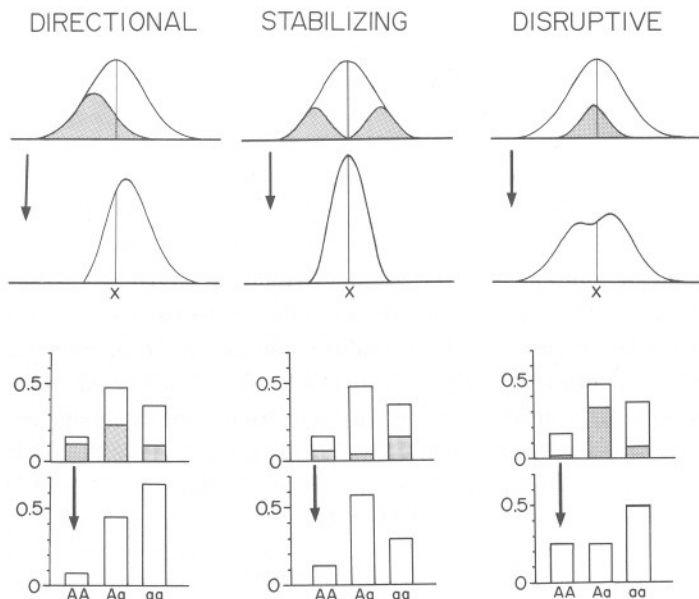


FIGURE 1.3. Three modes of selection for quantitative (upper row) and polymorphic (lower row) traits. In each case the vertical axis is the proportion of individuals, and the area under the curve, or the set of 3 bars, represents the total number of individuals. The individuals in the shaded portion are at a relative disadvantage compared to the individuals in the unshaded portion of the population. The arrows point to the offspring distribution after selection.  $X$  marks the mean of the distribution of quantitative trait values before selection, and the labels  $AA$ ,  $Aa$ , and  $aa$  refer to three genotypes at a single polymorphic locus. In truncation selection (not shown) individuals above or below a threshold value  $x$  would be at an advantage, rather than have the more probabilistic relationships shown here.

traits. A third class of traits, quantitative threshold traits, has so far received virtually no attention in natural populations. These traits are phenotypically expressed in discrete classes, and so appear polymorphic. But they are inherited as though they were determined by an underlying quantitative variable with thresholds; the thresholds determine to which discontinuous phenotypic class an individual belongs. See Falconer (1981) for a fascinating discussion of this subject. In this book, the term "quantitative trait" will refer to quantitative threshold traits as well as ordinary continuous traits. In actual practice, the means and variances of the underlying continuous variables of threshold traits will have to be worked out by genetic analysis.

Natural selection affects these trait classes in somewhat similar ways, though their associated theories are quite different. A major difference is that quantitative trait theory explicitly includes the effects of environment on phenotype (Falconer 1981; Bulmer 1980), whereas polymorphic trait theory (Ewens 1979; Wallace 1981) assumes that, except for simple dominance, phenotypic variation is the same as genotypic variation. See Milkman (1982), Kimura and Crow (1978), Crow and Kimura (1979), and Lynch (1984) for more discussion of the relationships between selection of polymorphic and quantitative traits.

Simpson (1944) and Mather (1953) were the first to point out three ways in which natural selection can affect frequency distributions; this applies to both quantitative and polymorphic traits (Figure 1.3). In *directional* selection individuals toward one end of the distribution are favored. The mean will change, and the variance may decrease. In *stabilizing* selection intermediate individuals do better than the extremes; there is an intermediate optimum value. The variance will decrease, but the mean will not change unless there is a significant difference between the population mean and the mean selective value or optimum. In *disruptive* (or *diversifying*) selection extreme individuals do better than those with more intermediate characteristics. One possible reason for this is density-dependent or



frequency-dependent selection; individuals with phenotypes closer to the mean will be more common and hence will be at a relative disadvantage. Another form of disruptive selection results when two different optimum values (or niches) are present and independent of the current trait distribution. In both forms of disruptive selection the variance will increase, but the mean will not change unless there is a significant difference between the population mean and the optimum or the mean of both optima. Note that these predictions only work if one form of selection affects the trait. It is quite possible for more than one mode to occur simultaneously; this will depend upon the trait distribution relative to the environment (Figure 1.4). Natural selection does not necessarily result only in a change in the mean and should therefore be described as well as defined

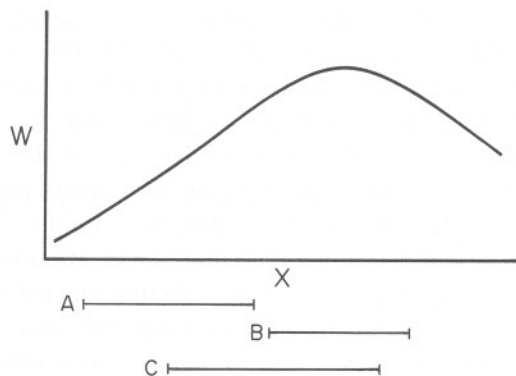


FIGURE 1.4. Selection mode and population variability. Consider a species that can vary in trait value  $X$ . For biophysical or physiological reasons, the fitness of an individual  $W$  varies with  $X$  as shown, no matter what part of the species geographic range we consider. A population showing the range of  $X$  values marked  $A$  will experience "pure" directional selection, while population  $B$  will experience "pure" stabilizing selection. Population  $C$  will experience a mixture of directional and stabilizing selection. The mode of selection depends upon the range of a population's variability as well as the fitness function.

in terms of the entire trait frequency distribution and the particular environmental conditions.

These predictions may also be affected if there are effects of selection for phenotypically correlated traits (Lande and Arnold 1983). If another trait is phenotypically correlated with the trait studied, and the other trait is subject to directional, stabilizing, or disruptive selection, then the apparent selection on the first trait may appear very different from the actual model of selection. The observed pattern of selection may be further modified by the presence of an additional mode, *correlational selection*. In correlational selection certain combinations of traits or alleles are favored at the expense of other combinations (Figure 1.5). This will result in patterns of gametic phase ("linkage") disequilibrium for suites of polymorphic traits (Ewens 1979), and patterns of phenotypic correlations for quantitative traits (Lande and Arnold 1983; Arnold et al. 1986). Correlational selection may not necessarily change the distribution of each trait considered by itself (Figure 1.5A), and so may not be detectable if only one trait is studied. Correlational selection may also give false evidence for other modes of selection, just as selection of certain traits can cause apparent directional or stabilizing selection in phenotypically correlated traits; we will return to this in Chapters 3 and 6. Once again, we must know as much as possible about the trait distributions and environmental parameters to understand natural selection.

Since natural selection does not necessarily result in a change in trait distributions among generations, nothing may be detectable if the population is at or near a stable equilibrium. An equilibrium can result from some form of stabilizing selection, a balance between directional selection and gene flow, or a balance between directional selection and a genetic bias such as meiotic drive. If a population is at or near equilibrium, then no change will be detected if the trait distributions are examined in successive generations at the same age classes, though there

will be a consistent difference among the age classes. If there is directional selection, then differences will be seen among age classes and generations. For this reason the deductions from the three conditions for natural selection are stated in terms of differences among age classes, and the second deduction is conditional.

Natural selection may effect the distribution of trait values either as a smooth function of value, as in Figure 1.3, or with respect to a threshold. Truncation selection is a special form of directional selection in which individuals with trait values above (or below) a critical value survive or reproduce while

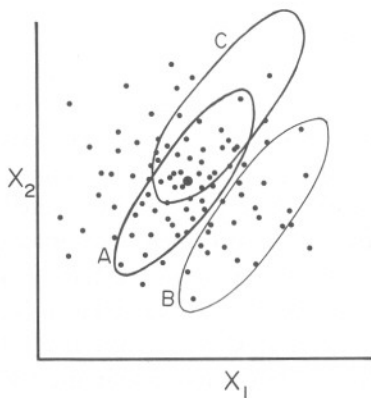


FIGURE 1.5. Correlational selection. Consider a species with two traits 1 and 2 which vary as shown: a single point represents an individual with trait values  $X_1$  and  $X_2$ . The large dot is the population mean of both traits. The three ellipses *A*, *B*, and *C* indicate three possible results of selection, where the individuals within an ellipse are those that survived or bred successfully. *A*, "pure" correlational selection: here the means of  $X_1$  and  $X_2$  do not change during selection. *B*, correlational and directional selection: here directional selection strongly effects trait 1 and weakly effects trait 2. *C*, correlation and directional selection: here directional selection effects both traits equally. In all three cases the correlational selection favors similar combinations of trait values, and there is also some stabilizing selection. As with Figure 1.4, a complete knowledge of the distributions and environment is very important.

those on the other side of the threshold do not. Truncation selection is more efficient than gradual directional selection; the relationship between the two is discussed by Crow and Kimura (1979).

#### 1.4.2. Number of Equivalent Phenotypes

In studies of natural selection, it is often assumed that all genotypes, phenotypes, or trait values are selectively different. But this is unrealistic. The distinctions we perceive between phenotypes may be different from how phenotypes are affected by natural selection. It is quite possible for a group of individuals of two or more phenotypes to be selectively neutral with respect to a particular environment, selectively advantageous relative to a second such group in the same environment, but disadvantageous to the second group in another environment (Endler 1978; Milkman 1982). In other words, there are multiple genetic "solutions" or outcomes to the same environmental factors or "problems" (Bock 1959; Gould and Lewontin 1979). I will refer to the selectively equivalent phenotypes within groups as "equivalent phenotypes." There may be no differences in condition *b* (fitness) or in the effects of natural selection among individuals within a group of equivalent phenotypes, but only among individuals of different groups.

Examples of equivalent phenotypes are known for variation in secondary compounds in plants, which affect palatability to herbivores; many different combinations of secondary compounds yield the same degree of unpalatability (Cook et al. 1971; Simons and Marten 1971; Sturgeon 1979). Other examples are found in seed color and survival (Brayton and Capon 1980), life-history patterns in *Corythucha* and *Gargaphia* lacebugs (Tallamy and Denno 1981), and color patterns in fishes (Endler 1978, 1980, 1983). For example, guppies (*Poecilia reticulata*) with many different combinations of genetically determined spots of particular sizes, colors, and brightnesses can be equally

cryptic on a given background but conspicuous on another background. Another group of guppies with different phenotypes will be conspicuous on the first background, but cryptic on the second. There is nothing about selection that necessarily favors a *single* best genotype, phenotype, or phenotypic value, though it may happen briefly in a single locality.

#### 1.4.3. *Effects of Other Phenotypes*

The mode of selection may or may not depend upon phenotypic composition of the population. In frequency-dependent selection, condition *b* (fitness differences) depends upon the relative frequency of similar phenotypes, and in density-dependent selection it depends on the relative as well as absolute numbers of phenotypes. (In some density-dependent models fitness may depend only on total numbers.) Wallace (1981) also makes a distinction between "hard" and "soft" selection. In "hard" selection successful phenotypes are better than an absolute criterion value; the presence of other phenotypes does not affect their relative success rate. Ground squirrels above a critical size may be the only ones to survive a severe winter, no matter what the size of their neighbors. This may result in the extirpation of some populations with very small mean sizes. On the other hand, in "soft" selection, success depends upon which other phenotypes are present, and it may depend upon relative or a combination of relative and absolute criteria. The larger squirrels in each population may have more offspring because they are better able to defend territories or to escape predators. Thus in summer the successful squirrels in populations of small squirrels will be smaller than equally successful squirrels in populations of large squirrels. As we can see, there is no simple one-to-one relationship between "hard" or "soft" selection and density-independent or density-dependent selection (for further discussion, see Wallace 1981, Walsh 1984, and references therein). Clearly, the dynamics and outcome of selection will depend

upon the interactions among phenotypes as well as the interactions of phenotypes and their environment.

#### 1.4.4. *Habitat Diversity and Choice*

There is no reason for the mode of natural selection to be the same throughout the geographic range of a species, and most species ranges contain many different habitats. Geographic variation in selection, along with gene flow, can cause geographic variation in gene frequencies and trait values, and maintain variation in a way that would appear impossible if only one locality were analyzed (reviewed in Endler 1977). Spatial variation in selection on a scale equal to or smaller than a deme or neighborhood can also maintain variation, though the conditions are more stringent for these "multiple-niche polymorphisms" (Ewens 1979; Maynard Smith and Hoekstra 1980; Hedrick 1983). If there is any tendency for different phenotypes to actively choose microhabitats in which they are favored, then the conditions are less stringent (Jones and Probert 1980; Maynard Smith and Hoekstra 1980). Though there is much theoretical work on the subject, virtually no work has been done to these ideas in natural populations. This would repay further study.

#### 1.4.5. *Levels of Selection*

It is theoretically possible for selection to have different effects at levels other than the individual phenotype—for example on genes, genotypes, groups, populations, species, or even self-replicating molecules (Dawkins 1976, 1982; Sober 1984). Sober (1984) provides a superb discussion of the units of selection problem. In his discussion of the difference between "units" and "levels" of selection, Brandon (1982) presents an interesting method to help decide at what level (or levels) natural selection should be considered:

Natural selection occurs at a given level if and only if:

1. Conditions *a*, *b*, and *c* [see section 1.1] hold at that level.

2. The expected fitness of those entities screen off the expected fitness of entities at every other level from that at the given level. (Rephrased from Brandon 1982.)

“Screening off” is a method of statistical inference, devised by Salmon and Reichenbach to attempt to assign primary cause in a complex cause-effect relationship (Salmon 1971). For the moment, we will define fitness as the differences expressed in condition *b*; this will be discussed further in Chapter 2. Following Brandon’s discussion: If *A* renders *B* statistically irrelevant with respect to outcome *C*, but not vice versa, then *A* is a better causal explainer of *C* than is *B*; *A* screens off *B* from *C*. In other words:

$$P(C|A \cdot B) = P(C|A) \neq P(C|B). \quad (1.1)$$

[ $P(C|A \cdot B)$  is the probability of *C*, given *A* and *B*.] More remote causes are screened off by more immediate causes. Brandon’s examples are quite revealing: (1) A sudden drop in atmospheric pressure (*A*) screens off a drop in barometer reading (*B*) from the occurrence of a storm (*C*); (2) phenotypes (*A*) screen off genotypes (*B*) (and genes) from differential reproduction (*C*). “Tampering with the phenotype without changing the genotype can affect reproductive success (as my castrated cat testifies), while tampering with the genotype without changing the phenotype cannot affect reproductive success” (Brandon 1982, p. 317). The latter is another restatement of Mayr’s (1963) argument that phenotypes, rather than genotypes or genes, are affected by natural selection. One major problem with this method is that it is not always clear that what seems to be the most proximal cause is indeed the primary cause; this is the fundamental problem of distinguishing cause-effect from correlation.<sup>4</sup>

<sup>4</sup> For further discussion, including a good one of group selection, see Williams 1966; Brandon 1982; and especially Sober 1981, 1984. A collection of important papers on the levels and units of the selection problem is reprinted in Brandon and Burian 1984.

There has been considerable interest in the possibility of group selection, or natural selection resulting from the differential proliferation or extinction of groups of individual organisms (Dawkins 1976; Wade 1978; Wilson 1983; Sober 1984). Nunney (1985) provides a very useful discussion of the various meanings of the term, and the conceptual difficulties are lucidly discussed by Sober (1984). Wade (1978) makes a fine review of the literature and has provided the only critical evidence for its existence—in the laboratory. The conditions for group selection are rather stringent (Wade 1978), suggesting that it may not be common in nature. The only evidence for group selection in natural populations is indirect and comes from successful prediction of sex ratios in the presence of local mate competition (summarized in Charnov 1982). In any case, there is no question that population structure affects the outcome and mode of natural selection (Wade 1978; Wilson 1983; Sober 1984; Nunney 1985). Another possibility is species selection (Stanley 1979; Gould 1982; Sober 1984). It is based upon the assumption—for which there is some evidence (Jablonski and Lutz 1983)—that certain kinds of species tend to speciate, and go extinct, more often than others. Since the evidence is weak or incomplete, group and species selection will not be discussed further in this book. See Sober (1984) for a thoughtful discussion.

#### 1.4.6. *Mode of Inheritance*

The definition of natural selection does not necessarily apply only to strictly genetic traits. In social animals that transmit information from parents to offspring, or more generally between a group of parents and all their offspring, condition *c* (inheritance) is met. Given also conditions *a* (variation) and *b* (fitness differences), natural selection of cultural traits will result. Good examples include the spread of milk-bottle cap opening behavior in British *Parus* (Sherry and Galef 1984), and agriculture in man (Ammerman and Cavalli-Sforza 1984). Cultural selection may also have interesting side ef-

fects on "regular" genetic inheritance (Cavalli-Sforza and Feldman 1981; Ammerman and Cavalli-Sforza 1984). See Dawkins (1976, 1982), and especially Cavalli-Sforza and Feldman (1981), for reviews of cultural inheritance. Common-environment effects (footnote 2) may also yield apparently heritable effects for several generations, blurring the distinction between genetic and cultural inheritance. An example is found in red deer: accidental differences in a deer's food and conditions can have significant effects on the fitness of its children and grandchildren (Clutton-Brock et al. 1982).

### 1.5. SUMMARY

Natural selection is a process that results from biological differences among individuals, and which may give rise to cumulative genetic change or evolution, but does not guarantee it. The process is derived from a syllogism; given three conditions for natural selection (*a*, variation; *b*, fitness differences; *c*, inheritance), two conclusions necessarily follow: (1) differences in trait distributions among age classes or life history stages; and (2) if the population is not at equilibrium, a predictable difference among generations. By the nature of its definition, natural selection can be broken down into various components, either by separation into alternative (sexual and nonsexual selection) or sequential subprocesses (phenotypic selection and genetic response). These components are all parts of the same process, but restricted meanings of the term "natural selection" to one or more of its components are confusing when the restriction is not made explicit. Natural selection may occur in various modes, and the diversity of mode classifications represent different aspects of the process.

## Philosophical Comments

It is one of the maxims of the civil law that definitions are hazardous. Things modified by human understandings, subject to varieties of complication, and changeable as experience advances knowledge, or accident influences caprice, are scarcely to be included in any standing form of expression, because they are always suffering some alteration of their state.

Samuel Johnson, *The Rambler*, 28 May 1751

Although it is a relatively simple concept, natural selection is associated with quite a few philosophical problems. Arguments about the existence and logical status of natural selection have crossed many fields, and have involved philosophers, biologists, phylogenetic systematists and others.<sup>1</sup> Disputes have resulted from incomplete understanding, including confusion between cause and effect, and historical accident. In addition, many problems are due to progressive modification of concepts without modification of terminology: the same words have completely different meanings to different people. We have already had an example of this in the discussion of restricted meanings of natural selection (Figure 1.2), but problems of nonstandard terminology are deeper than this. It is the purpose of this chapter to summarize briefly some of these problems, suggest some solutions, and offer some suggestions for standardization in order to

<sup>1</sup> *Philosophers*: Reed 1981; Hull 1980; Popper 1963, 1972, 1974, 1978; Mackie 1978; Ruse 1977; Caplan 1977; Sober 1984; Urbach 1978; Wasserman 1978, 1981; M. B. Williams 1970, 1973. *Biologists*: Ghiselin 1969; Lewontin 1974; Gould 1982; Gould and Lewontin 1979; Peters 1976; Castrodeza 1977; Stebbins 1977; Stern 1970; G. C. Williams 1966. *Phylogenetic systematists* ("cladists"): Eldredge and Cracraft 1980; Platnick 1977; Rosen 1978; Rosen and Buth 1980. *Others*: Macbeth 1971; Bethell 1976.