

Natural Selection in the Wild

JOHN A. ENDLER

Natural Selection in the Wild

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JOHN A. ENDLER

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TO
Arthur J. Cain

AND
Bryan C. Clarke

THIS BOOK IS AFFECTIONATELY
DEDICATED

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Preface

This is a book on natural selection for those who are interested in both the evolution and ecology of natural populations of organisms. Natural selection is an immense and important subject, yet there have been few attempts to summarize its effects on natural populations, and fewer still that are concerned with the methods and problems of working with natural selection in the wild. This book attempts to permeate this void. Theoreticians will find nothing that is new in this book, and those who primarily work with laboratory populations will look in vain for their favorite examples. Laboratory populations serve as models of nature, and help to test specific predictions or conjectures about the way nature works; but without extensive knowledge of natural selection in the wild, we have no idea how relevant experiments or theory are to the evolution of natural populations. This is meant to be a field guide rather than a textbook or manual, so common methods will not be given in detail (major references are always provided).

Although this book is not meant to be a eulogy to Eris, I expect that nobody will find it wholly satisfactory. Among the many people who have read it in manuscript, some find parts exceedingly helpful, while others find the very same parts boring or superfluous. To many, the most irritating parts will probably be found in Chapters 1, 2, and 8 because they attempt to put the various points-of-view, definitions, and meanings of natural selection in perspective, and everyone thinks that his own emphasis is most important. A typical reaction is: "I find it fascinating that more than 100 years after the *Origin* and Mendel

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there can be two major positions on this everyday phrase"; actually there are more than two (Figure 1.2).

A major problem in this subject is that there is a multiplicity of meanings for the same terms, and the same terms mean different things to different people. This complexity and our understanding of natural selection may benefit from my crude attempt at standardization. I hold no hope of convincing those who are used to a particular meaning of a word to conform to the suggested standardization. For example, in another book (Endler 1977), I clearly distinguished migration, dispersal, and gene flow—terms that had a similar mix-up with, say, fitness and adaptation (Chapter 2). Migration can have nothing to do with gene flow, and has a meaning entirely different to ecologists and ethologists compared to population geneticists, yet the latter insist on calling gene flow "migration." This is perfectly clear if one is sufficiently narrow to read only the literature within a minutely circumscribed field. However, it is a source of serious confusion to those with more catholic tastes and to beginning students. That the need for standardization is urgent is shown by the latest example of synonymy in name only: selection gradients. In 1973 I used the term "selection gradient" to denote a geographic gradient in natural selection, and this followed general usage going back to Huxley and others in the 1930s (references in Endler 1977). More recently Lande and others (for example, Lande and Arnold 1983) used "selection gradient" in a completely different sense: the rate of change of fitness with trait value. This comes from a mathematical model of natural and artificial selection of multiple traits, which can be regarded as a surface with a gradient in value. This is a perfectly correct usage of the term "selection gradient" and would be fine if the word had not already been used for geographically varying selection for the past fifty years! This is a potentially serious problem for the unwary because a cline may be associated with both kinds of "selection gradients." We need some sort of rule of priority, analogous to that in systematics,

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which states that the earlier meaning of the word should stand, and another word should be used for the new meaning. However, human nature being what it is, this rule will probably be ignored. I therefore present the standardization attempt (Chapters 1 and 2) primarily as a guide for students and others who read the literature outside a narrow field of specialization. The main purpose of this book is not to argue about words, but to summarize natural selection as it can be seen in natural populations.

I thank Ric Charnov for encouraging me to write, and to finish, this book. Elliott Sober very kindly let me read his splendid book (1984) before publication. I am grateful for discussions and comments on all or parts of the manuscript from Steve Arnold, Robert Brandon, Arthur Cain, Ric Charnov, Bryan Clarke, Blaine Cole, Jim Crow, Monica Geber, Michael Ghiselin, Peter Grant, Paul Harvey, Lynn Jorde, Mark Kirkpatrick, Russ Lande, Yan Linhart, Jim Mallett, Bob May, Tracy McLellan, Trevor Price, Sam Skinner, Elliott Sober, Bill Stubblefield, Sam Sweet, and David Temme. They certainly have not always agreed with my observations and conclusions.

December 1984

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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.¹ 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.

¹ 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.

INTRODUCTION

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:² *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.³ 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

² 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).

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

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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 ^a
<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 ^b	no ^c (by definition)
Measure of degree of condition <i>b</i>	fitness ^d	(observed "fitness")	durability ^d

^a In the sense of any cumulative change in the characteristics of a population over many generations (see text).

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

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

^d See Chapter 2 for discussion.

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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

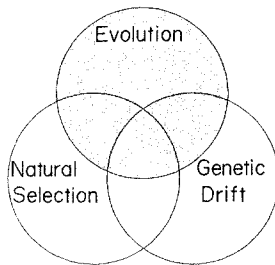


FIGURE 1.1. A Venn diagram, showing the relationship between the necessary and sufficient conditions for natural selection, genetic drift, and evolution. The shaded area results in cumulative changes in genotype frequencies or trait values, and the shaded area outside the domains of natural selection 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.

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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-

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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.

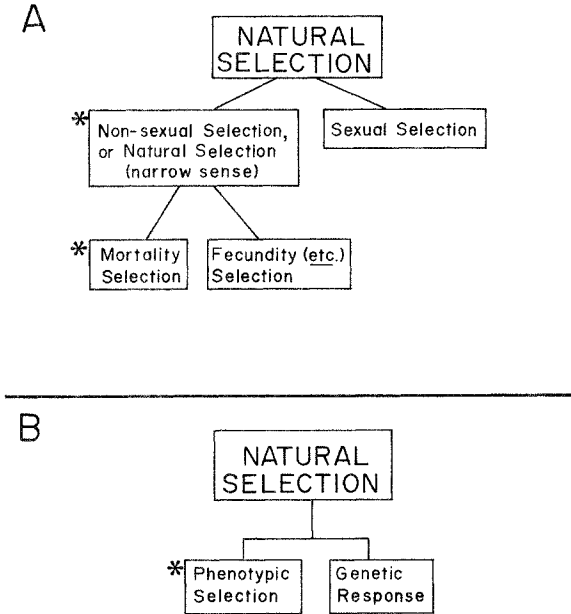


FIGURE 1.2. Two logical and independent subdivisions of natural selection, illustrating the restricted meanings that “natural selection” often takes in the literature. *A*, subdivision by alternate subprocesses; *B*, subdivision by sequential subprocesses. The subprocesses in *A* are distinguished with 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.

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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

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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

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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

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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

INTRODUCTION

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

INTRODUCTION

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.

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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

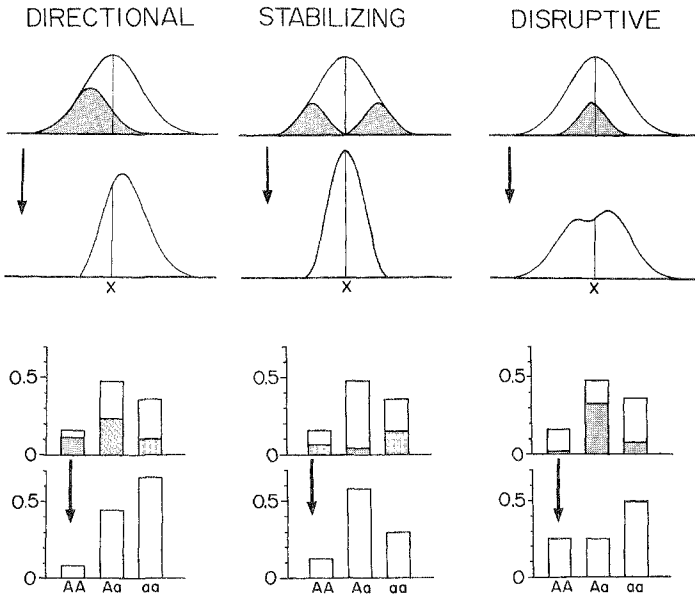


FIGURE 1.3. Three modes of selection for quantitative (upper row) and polymorphic (lower row) traits. In each case the vertical axis is the proportion of individuals, and the area under the curve, or the set of 3 bars, represents the total number of individuals. The individuals in the shaded portion 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. $\bar{X}$ 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.

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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

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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

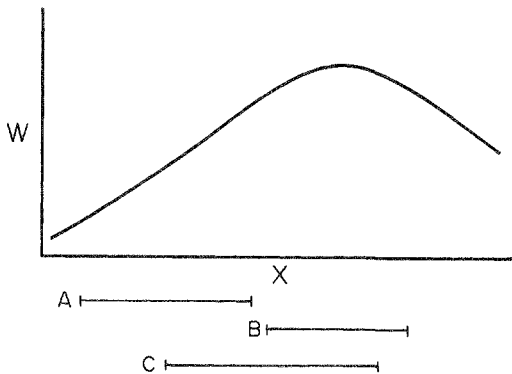


FIGURE 1.4. Selection mode and population variability. Consider a species that can vary in trait value X . For biophysical or physiological reasons, the fitness of an individual W varies with X as shown, no matter what part of the species geographic range we consider. A population showing the range of 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.

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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

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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

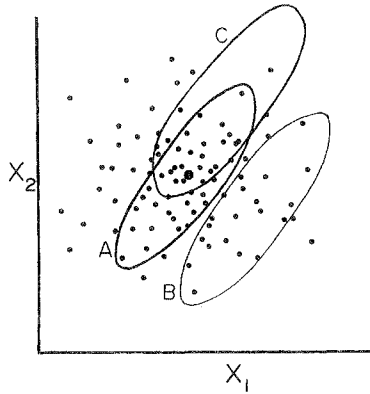


FIGURE 1.5. Correlational selection. Consider a species with two traits 1 and 2 which vary as shown: a single point represents an individual with trait values X_1 and X_2 . The large dot is the population mean of both traits. The three ellipses A , B , and C indicate three possible results of selection, 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.