ROBERT N. BRANDON

Adaptation and Environment

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ADAPTATION AND ENVIRONMENT

PREFACE

In this book I explore a tightly interconnected set of questions within evolutionary biology whose common thead is the phenomenon of adaptation. I emphasize that the process of adaptation, and the products of that process, cannot be fully understood without an analysis of the notion of environment as it is relevant to the theory of evolution by natural selection. That theory is our only general and scientifically legitimate theory of adaptation. I argue that natural selection is the process of differential reproduction that is due to differential adaptedness to a common selective environment. Although this characterization of natural selection is relatively uncontroversial, I believe it is not well understood. I present the characterization in terms of two basic concepts: relative adaptedness (what many call "relative fitness"), and common selective environments. The former has received extensive attention from both philosophers and biologists interested in evolution, but the latter has been virtually ignored. When properly understood, the concept of common selective environments and the characterization of natural selection given in terms of it have surprising implications.

In chapters 1 and 2 I define the basic concepts. Chapter 1 is an overview of the concept of relative adaptedness, including the process of adaptation and the products of that process. I defend a version of what has come to be known as the propensity interpretation of adaptedness (or of fitness), while also reviewing the major rival interpretations, exposing the weaknesses of each. In chapter 2 I propose that in biology (or more accurately, within population biology) one can distinguish at least three different notions of environment: the *external environment*, the *ecological environment*, and the *selective environment*. There are interesting interrelations among these three sorts of environments, the most prominent among them being that the selective environment is decoupled from the external environment in the sense that variation in the external environment is neither a necessary nor a sufficient condition for variation in selective environments. I argue that it is the selective environment that is relevant to the theory of evolution by natural selection. This assertion has direct implications for both the theoretical and experimental study of some of the major questions of evolutionary biology, that is, those dealing with selection in heterogeneous environments. For instance, sexual reproduction and phenotypic plasticity, both pervasive biological phenomena, are thought to be selectively advantageous in heterogeneous environments.

In chapters 3, 4, and 5 I explore some of the ramifications of this conception of natural selection. Chapter 3 deals with questions concerning the level or levels at which selection occurs. I adopt David Hull's distinction of *interactors* and *replicators* (a generalization of the phenotype-genotype distinction). Selection (called *phenotypic selection* by quantitative geneticists) is an ecological process; as such it always occurs among interactors. For selection to result in evolution (i.e., transgenerational change), the variation on which selection acts must be heritable. This involves the process of replication. I argue that there is a hierarchy of plausible interactors, that is, a hierarchy of levels of selection, but that the replicators corresponding to each level of interaction do not form a neat hierarchy. This analysis differs significantly from those coming out of a population-genetics tradition, which conflate questions of levels of selection with questions of replication.

Chapter 4 is devoted to certain metatheoretical questions that concern the structure of the theory of evolution by natural selection. Although this is a philosophical exercise, the questions have been debated by reflective evolutionists for some time. For instance, what is the Principle of Natural Selection? Does it have empirical content? What is its role in the theory of evolution? Answers to these questions are directly relevant to how we distinguish selection from random drift, how we distinguish various levels of selection, and even how we distinguish the results of selection from those of random distribution of competing types across heterogeneous environments.

In chapter 5 I offer an account of what I call *ideally complete adaptation explanations*. According to this view, adaptation explanations are thoroughly mechanistic. This ideal is rarely, if ever, realized in practice because of the severe epistemological problems one encounters when trying to gather the requisite information.

But these problems do not detract from the overwhelming value of mechanistic explanations of how adaptations *could* evolve. Much recent criticism of the theory of natural selection, or of what Stephen Jay Gould and Richard Lewontin call the *adaptationist programme,* is based on the assumption that the *raison d'être* of the theory of adaptation is the explanation of particular traits. I argue that this is a mistaken assumption; that, although the explanation of particular adaptations is of interest in historical evolutionary biology, there is a purely process-oriented aspect of the theory to which such explanations are only tangentially relevant. Are adaptation explanations teleological? There is a sense in which they do explain teleological phenomena and in which they do answer a type of teleological question; but the explanations themselves are thoroughly mechanistic.

PHILOSOPHY of biology is an exciting field. And it surely is an interdisciplinary field. But dangers are inherent in such interdisciplinary work: one runs the risk of presenting baby philosophy for biologists and baby biology for philosophers. I hope I have been able to avoid that. I have tried to write this book not for two separate audiences—philosophers interested in biology and biologists interested in the conceptual foundations of their discipline—but for a single audience, one unified by a deep interest in evolutionary biology, especially in the theory of natural selection. The readers I have kept in mind are professional biologists or students of biology, and philosophers. I hope there will be some from other disciplines as well. I assume that the reader has a basic knowledge of genetics and statistics; those who lack it can consult one of the many textbooks that introduce this material far more effectively than I could. On the other hand, I have not assumed that the reader is thoroughly familiar with philosophical theories of causation and explanation. I am a philosopher, but I have studied evolutionary biology for the past fourteen years, and I do not try to classify problems as either philosophical or biological. Indeed, I doubt whether this could be done in a consistent and nonarbitrary manner and it is surely a fruitless exercise. Thus I have not tried to balance the "biological" and "philosophical" in order to satisfy a dual audience.

Although most biologists would readily admit to the importance of conceptual issues in evolutionary theory, many may doubt whether these issues have any direct impact on the practical concerns of evolutionary biologists. One of the purposes of this book is to show the tight relationship between conceptual issues and practical methodological issues. For example, the concept of selective environment that is introduced in chapter 2 has direct implications concerning both the importance and the design of "common garden experiments." In particular, when selection is frequency dependent, the proper design of a common garden experiment is different than when selection is not frequency dependent. This outcome runs contrary to some of our intuitions and expectations and has direct implications for the concept of evolutionary altruism (as discussed in chapter 3). Here, then, a conceptual analysis has ramifications for experimental design, and getting clear on proper experimental design helps resolve another conceptual question.

My goal is to answer the questions I pose and to convince the reader of the correctness of my solutions. I realize that I may fall short of that goal. But if I succeed in communicating the importance of some topics, if I succeed in showing the interrelations of topics that are not normally thought to be related, then my efforts will have been worthwhile.

Durham, N.C.
September 1989

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I know I could not have written this book without the help of many friends and colleagues. The following people read either part or all of my manuscript: John Beatty, Robert Boyd, Richard Burian, Henry Byerly, Kurt Fristrup, Michael Ghiselin, Marjorie Grene, Henry Horn, David Hull, Egbert Leigh, Marcia Lind, Rick Michod, Mark Rausher, Robert Richardson, and George Williams. Their comments have been invaluable. I owe a special debt to two of my colleagues at Duke, Janis Antonovics and Brent Mishler. Besides having carefully read each chapter, they were a constant source of encouragement and advice. In particular, chapter 2 is very much the product of my interaction with Antonovics. If the book has too much of a botanical ring to it, it is because I hung out too much with the damned botanists.

I owe a special debt of a different sort to my wife, Gloria Meares. She provided needed support during the difficult times I experienced in writing this book; she also carefully read the manuscript. On the other hand, my daughter Katherine was of no help whatsoever. She should have had the good sense not to have been born while I was trying to write a book.

At this point it is customary for an author to absolve those whose contributions have just been acknowledged from any blame for errors that remain. In the spirit of the Reagan '80s, I want to go one step further: I will frankly admit that mistakes were made; but these are free-floating mistakes for which no one should be blamed.

CONTENTS

ADAPTATION AND ENVIRONMENT

CHAPTER 1

Adaptation and Natural Selection

The existence of adaptations, the fit between organisms and their environments, is one of the most striking features of the biological world. Before Darwin (1859) numerous accounts were offered to explain adaptations, the most prominent among them being the creationist account. According to this account, organisms were designed by God to fit the demands of their environments. Darwin offered an alternative account: the theory of evolution by natural selection. There have been still other rival explanations of adaptations. Perhaps the most important of these is a "Lamarckian" theory whereby organisms somehow adapt to their environment during their lifetime and then pass on these acquired adaptive characteristics to their offspring. As is well known, Darwin put some credence in this account. Indeed, we should too, but only for those organisms capable of behaviorally transmitting information across generations. For example, in a well-studied colony of Japanese macaques, a single individual learned to separate wheat from its chaff by throwing it into water. This adaptive behavior was transmitted to other members of the colony and passed down to later generations so that this once absent behavior is now quite common. Although this is a mechanism by which organisms can adapt to their environments, it is probably quite limited and explains only a small fraction of the adaptations in nature.[1] As the creationist and "Lamarckian" theories illustrate, the theory of evolution by natural selection is not the only possible theory of adaptation, but for now it is by far the best theory we have to explain the bulk of adaptations in nature.

In this chapter we will explore three related concepts of adaptation: the concept of relative adaptedness, the concept of the process of adaptation, and the concept of adaptation as the product

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[1] See Bonner (1980), Boyd and Richerson (1985), and Brandon (1985b) for further discussion.

of that process. We will examine their interrelations and the roles they play in the theory of evolution by natural selection.

1.1. A SIMPLE CASE OF EVOLUTION BY NATURAL SELECTION

Let us start by describing a simple case of evolution by natural selection. Suppose that in a given population of organisms there is directional selection for increased height. To say that there is directional selection for increased height is to say that taller organisms have (or tend to have) greater reproductive success than shorter ones, that is, that reproductive success is an increasing function of height. The ecological reasons for this can be indefinitely varied. For instance, in one ecological setting taller plants may receive more sunlight and so have more energy available for seed production. In another setting, taller animals may be more resistant to predation. Also, differences in reproductive success can result from differences in fecundity (as in the first case) or from differences in survivorship (as in the second case) or from still other causes (e.g., differences in mating ability). To fix ideas, let us suppose that in our case taller organisms have a higher survivorship. Thus we can suppose that prior to selection the distribution of height in the population is as shown in figure 1.1. Selection occurs by differential survivorship. The postselection distribution

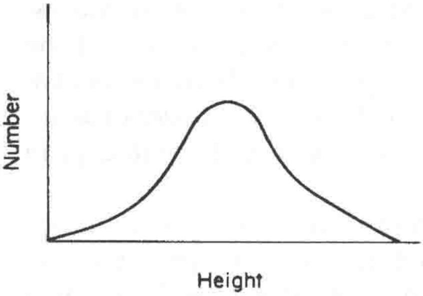

Figure 1.1. Schematic illustration of preselection distribution of height in a population.

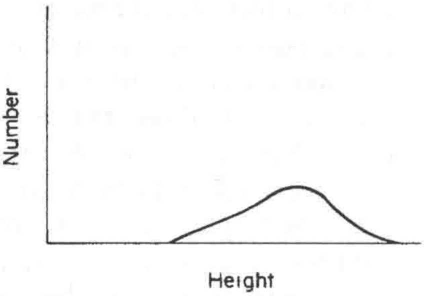

Figure 1.2. Schematic illustration of postselection distribution of height in a population.

of height is given in figure 1.2. This is the first step in the process of evolution by natural selection.[2]

From the point of view of population biology, evolution is any change in the distribution of "types" over *generational* time. Population geneticists define evolution as any change in the relative frequency of alleles over generational time. If a more organismic approach is preferred, evolution could be defined as any change in phenotypic distributions over generational time. The important point is that evolution involves change over generational time. Thus in our example, although selection has produced change, evolution has yet to occur.

The next step in this process involves reproduction. We can assume that all organisms surviving to this stage will have equal reproductive success. But because of viability selection a disproportionate number of taller organisms is left to reproduce. Through reproduction the next generation is formed. If selection is to result in evolutionary change in this case, height must be heritable. Phenomenologically, that means that taller than average organisms must tend to have taller than average offspring, and shorter than average organisms must tend to have shorter than average offspring. Of course, in standard cases genes, not height, are directly transmitted from parent to offspring. Thus taller parents tend to have genotypes different from those of shorter parents, and these genes are transmitted to the respective offspring. The offspring of taller parents tend to have genotypes that are different from those of offspring of shorter parents. According to the population-genetic definition of evolution, evolution has occurred.

But in order to go full circle, in order to get to the stage where selection occurs in the offspring generation, a final step is required. These differing offspring genotypes must develop. During the process of epigenesis (i.e., the process of the development of the fertilized egg into a mature organism), these genotypic differences are translated into phenotypic differences. Thus, in our case, the offspring distribution of height is shifted to the right of that of the preselection distribution of the parental generation (as shown in figure 1.1). How far it is shifted depends on the degree of heri-

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[2] Mayr (1978) has described evolution by natural selection as a two-step process. My description essentially follows his and will be discussed in greater detail in chapter 3.

tability (and the strength of selection, which is represented by the difference between figures 1.1 and 1.2). In any case, evolution has occurred; the frequency distribution of height has changed over generational time.[3]

1.2. DARWIN'S THREE PRINCIPLES

The case described above is a simple example of evolution by natural selection.[4] By examination we can abstract from it the conditions necessary for the evolutionary process to work.

The first condition is that there be variation in height. To say that there is directional selection for increased height, to say that taller organisms have greater reproductive success than shorter organisms, implies that there is variation in height. The selection process we described worked by means of differential survival; but whatever the means of selection, there can be no selection for increased height if there is no variation in height. Height is a morphological trait. We can also imagine selection on physiological or behavioral traits, or more generally on any sort of *phenotypic* trait. Thus the first condition is that there must be some variation in some phenotypic traits.[5]

For selection to occur there must be variation, but a second condition is necessary for selection to have an evolutionary effect. Recall that in the above example selection changed the population distribution of height from that of figure 1.1 to that of figure 1.2. But this is not evolutionary (i.e., cross-generational) change; for

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[3] I have distinguished three steps in the process of evolution by natural selection: selection, the differential replication of genes, and development. A discussion of why this process is described as a three-step rather than a two-step process can be found in chapter 3.

[4] Of course, no one example is fully representative of all cases. My example is special in two regards. First, it is a case of directional selection, which favors one extreme in a phenotypic distribution. Other types of selection are stabilizing, which favors the mean phenotype, and disruptive, which favors both ends of the distribution (see Endler 1986, pp. 16ff.). Second, in my example selection occurs by means of differential survivorship rather than by means of differential fecundity, differential mating ability, or other possible means. The special features of the example do not affect the conclusions we will draw from it.

[5] I am assuming here that, to use Mayr's words, "natural selection favors (or discriminates) phenotypes, not genes or genotypes" (1963, p. 184). I will argue for this position in chapter 3.