Rethinking Human Adaptation: Biological and Cultural Models

Edited by
Rada Dyson-Hudson
Michael A. Little

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Most anthropologists agree that a comprehension of adaptation and adaptive processes is central to an understanding of human biological and behavioral systems. However, there is little agreement among archeologists, cultural anthropologists, and human biologists as to what adaptation means and how it should be analyzed. Because of this lack of a common underlying theory, method, and perspective, the subdisciplines have tended to move apart, and anthropology is no longer the integrated science envisaged at its inception in the nineteenth century.

In this book, the authors--both biological and cultural anthropologists--use a common theoretical framework based on recent evolutionary, ecological, and anthropological theory in their analyses of biological and social adaptive systems. Although a synthesis of the subdisciplines of anthropology lies somewhere in the future, the original essays in this volume are a first attempt at a unified perspective.

Dr. Rada Dyson-Hudson is associate professor in the Department of Anthropology, Cornell University. In the past, she was associate professor and research associate in the Department of Pathobiology at the School of Hygiene, Johns Hopkins University. Her attempt to reconcile the implications of natural selection theory with a commitment to social equality led to a rethinking of human adaptation and, among other things, the organization of the symposium at the American Anthropological Association of which this book is a result. *Dr. Michael A. Little* is professor of anthropology at the State University of New York at Binghamton. He has been scientific coordinator of the Human Adaptability Section of the International Biological Program and is coauthor of *Ecology, Energetics, and Human Variability* (1976).

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R. D-H.
M.A.L.

Introduction

The concept of adaptation is central to an understanding of human biology and behavior. Although biologists' studies of adaptation are firmly rooted in Darwin's theory of evolution through natural selection, anthropologists generally deal with morphological, physiological, and behavioral (cultural) adaptations as if they represent quite different phenomena. In this book, we suggest that Darwinian theory can provide a body of theory appropriate for the analysis of both biological and cultural adaptation. Only by focusing on interactive patterns in biological and behavioral systems can we understand human biological and cultural adaptive responses.

In their analysis of human biology and behavior, the authors in this volume approach adaptation from an interactive rather than a deterministic mode. Dyson-Hudson presents a model for the development of all human phenotypes which emphasizes that these must be based not only on evolved genetic programs but also on the environmental information encountered during the entire lifetime of the individual. Kellum and Haas demonstrate that deterministic models cannot deal adequately with biological phenomena such as the variations in human sex ratios at birth and variations in human reproductive success in high Andean populations. Interactive models are also clearly required for an understanding of human behavioral adaptations traditionally studied by cultural ecologists and ecological anthropologists. Moran, Dow, and Boone demonstrate the importance of considering environmental variables in assessing the adaptiveness of spatial mobility, "primitive" warfare, and warfare in complex and hierarchical societies. Smith shows that, by using interactive models based on a synthesis of neo-Darwinian theory with evolutionary ecology, human behavioral adaptations can be analyzed within the theoretical framework of recent advances in biology.

Anthropology has, since its inception, been identified as an integrated biological and social science. However, in recent years the sub-fields have tended to move apart in method, theory, and content. The contributions to this book, by sociocultural and biological anthropologists, treat adaptation within the framework of recent evolutionary theory. This is a positive trend and we firmly believe that only by these integrated approaches can adaptation in human populations be fully understood.

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An Interactive Model of Human Biological and Behavioral Adaptation

Rada Dyson-Hudson

Editors' Summary: In the first chapter, Rada Dyson-Hudson emphasizes an evolutionary perspective, based on Darwinian theory, on human biological and behavioral adaptation. Her approach differs from more deterministic scientists in its attempt to deal with the environmental lability of most human genetic systems and the tight interaction among behavioral, biological, and environmental features of human populations. Dyson-Hudson believes that if there is to be a unified theory of biological and cultural adaptation, it must be based on an explicit recognition that natural selection is the only force which can generate and maintain adaptation.

EVOLUTION AND ADAPTATION

The concepts of evolution and adaptation are widely used in both the biological and social sciences. However, there is often a great difference in the way the terms are used in these respective disciplines. This means that while biologists and social scientists may appear to be discussing the same thing, they are often, in fact, attempting to analyze and explain quite different phenomena.

In the first part of this paper, I review the different ways in which the concept of adaptation is used in the biological and social sciences, and then develop an interactive model that can help us to understand both biological and behavioral adaptation within a single theoretical framework. Then, I discuss what evolutionary theory leads us to predict about the relative importance of genes vs. environments in the genesis of specific phenotypes in particular species. Finally, I suggest that focusing on gene-environment interactions can help us to understand both adaptive and maladaptive human behaviors.

Biological Definitions

Charles Darwin's original definition of evolution was 'descent with modification.' He attributed changes

in phyletic lineages (changes in populations through time) to the process of natural selection--the accumulation in populations of favorable hereditary variations through differential survival and reproduction of individuals within those populations (Darwin 1859). Mendel recognized the particulate nature of hereditary variation and his 'laws' formed the basis for population genetics. The melding of Mendel's theory of particulate inheritance with Darwin's theory of evolution through natural selection (termed neo-Darwinian theory) underlies much of current evolutionary theory, and a definition of organic evolution now widely accepted by biologists is "a change in gene frequencies from generation to generation" (Wilson 1975:584). This definition differs from Darwin's original formulation, since the forces leading to changes in the gene pool (micro-evolution) include the random processes of mutation and genetic drift, as well as the non-random processes of gene flow (due to migration of individuals), selective mating, and natural selection. And random processes may also be implicated in macro-evolutionary trends within phyletic lineages, and patterns of divergence and extinction of species (Raup 1977). Although not all evolutionary biologists agree that natural selection plays the major role in organic evolution, there is general agreement that natural selection is the mechanism by which organisms adapt to their environment: that "Natural selection is the only acceptable explanation for the genesis and maintenance of adaptation" (Williams 1966: vii, italics mine).

Biological adaptation can be broadly defined as the fit between an organism and the external world in which it lives (Lewontin 1978:213). More specifically, adaptation is generally taken to refer to any feature of an organism which contributes to its survival and reproduction. Although adaptation is sometimes viewed as the process of evolutionary change by which the organism provides better and better 'solutions' to the 'problems set by the environment, it is important to recognize that, since environments are constantly changing, there is, in fact, no end to adaptation. Organisms do not become better and better adapted, but rather the adaptation process consists of a series of fine adjustments in the organism according to the environmental conditions at a given time, and the variability in the population. Hence there is no pinnacle of organic evolution. Some species in the face of constantly changing environments either have 'preadaptations' to the changed environments--that is characteristics evolved as adaptations to one environment which, fortuitously, enable an individual to survive in a different environment; and/or have sufficient heritable--genetically based--variation of the right kind to change adaptively, to track the environment. Other species become extinct.

Selective pressures depend on the nature of the environment, and the ways in which selective pressures in the environment can operate are constrained by the heritable variation present in the population. Thus organic evolution does not have a predictable direction. A species may, for example, adapt by evolving into larger or smaller forms; into more complex or simpler organisms; into social or solitary individuals.

Much of evolutionary biology has consisted of working out an adaptationist program, in which the evolutionary biologist assumes that each aspect of an organism's morphology, physiology, and behavior has been molded by natural selection as a solution to a problem posed by the environment. The biologist then constructs a plausible argument about how each part functions as an adaptive device. Developing adaptive explanations is fraught with difficulties (see Lewontin 1978: 216-228 for a discussion of some of these). For example, the assertion of universal adaptation is difficult to test, "because simplifying assumptions and ingenious explanations can almost always result in an ad hoc adaptive explanation" (Lewontin 1978: 230). However, as Lewontin stresses, an all-out adaptationist program must be adopted because if a weaker form of evolutionary explanation is accepted, and only some proportion of cases are explained by adaptation, it "would leave the biologist free to pursue the adaptationist program in the easy cases and leave the difficult ones to the scrap heap of chance" (1978: 230).

Some adaptive explanations can be tested. One method is testing how well predictions based on genetic and ecological theory fit the characteristics, behaviors, organizations found in real-life situations. (See Alexander and Tinkle 1981. Krebs and Davies 1981 and Wilson 1975 are reviews of the biological literature. Chagnon and Irons 1979, 1981; Dyson-Hudson and Smith 1978; McCay 1981; and Winterhalder and Smith 1981, apply these theories to humans. See also Smith Chapter 2.)

Furthermore neo-Darwinism theory has reached the stage where authors of adaptive explanations do not have a free rein: they must conform to certain rules in framing their 'just-so-stories'. The requirements for an evolutionary argument about a particular attribute of a specific organism, include the following:[1] (see Dyson-Hudson 1979 for a more detailed discussion of these points).

1. A characteristic must be a meaningful trait, that is, it must have been a unit under natural selection.

2. A characteristic must be heritable, that is, some of the variation of that characteristic within the population must (in the evolutionary past) have been due to genetic differences among individuals.

3. A characteristic must have contributed to reproductive success. More accurately, a characteristic must have contributed to 'inclusive fitness', that is, the individual's contribution to the gene pool of future generations, as measured by personal reproductive success, plus the reproductive success of relatives, with relative's contribution devalued in proportion to their genetic distance.

4. Selection must have been strong enough to modify the character within the time span available.

5. Alternative explanations must be explored.

6. It must be recognized that a characteristic can change its function during the evolutionary history of a species.

7. If an adaptive argument is used, the reason why other organisms in similar niches (with similar roles in the environment) have not evolved the same characteristics must be considered.

8. Adaptiveness must be defined in an explicit environmental context.

9. Since natural selection generally operates through differential survival and reproduction of individuals rather than of groups, evolved traits should be adaptive primarily to individuals, and only secondarily to higher levels of organization. Thus, adaptation should be attributed to no higher level of organization than is demanded by the evidence.

Although no adaptive explanation can possibly meet these stringent criteria because we do not have sufficient knowledge and understanding of past environments and of the functioning of organisms within these, nonetheless they are extremely useful because they make it possible to identify inadequate adaptive explanations--those which clearly violate some or all of these requirements.

In summary, there is a general consensus among neo-Darwinian theorists that evolution does not occur according to a pre-ordained plan, that adaptation is the product of natural selection, and that natural selection generally operates at lower rather than higher levels of organization. It operates at the level of the individual (or possibly even gene complexes), rather than at the level of the group, the population, the species, the society or the 'culture'. Evolutionary theory has developed to a stage which makes it possible to make rules for formulating adaptive explanations and, at least in some cases, adaptive explanations can be tested.

Definitions Used by Anthropologists

Among anthropologists dealing with human adaptation, there is no consensus as to the meaning of the terms 'evolution' and 'adaptation'; nor is there any set of rules for writing evolutionary and adaptive explanations

which would be acceptable to the large body of scholars interested in human adaptation. It is not possible in this chapter to review the diversity of views, but some examples will be cited. Some biological anthropologists focus on adaptation as morphological and physiological adjustments which occur during growth and development (cf. Haas, chapter 3). Others study biological phenomena such as human genetics, mating systems, and fertility. In contrast, for many cultural ecologists evolution refers to the process of social change through which egalitarian societies develop into complex and hierarchical societies--through which 'primitive' societies inevitably 'progress' to become more and more like modern 'civilized' societies. According to these theorists, extant societies represent stages in a progression from egalitarian through tribal to ranked societies and states (cf. Fried 1967).

Inspired by the work of Leslie White (1943) and F. W. Cottrell (1951), some cultural ecologists have focused on energy use as the indicator of the level of adaptation. For example, according to Y. A. Cohen (1974:46) "Adaptation in man is the process by which he makes effective use for productive ends of the energy potential of his habitat. . . . He accomplishes this by harnessing increasingly effective sources of energy and by shaping his institutions to meet the demands of each energy system so he can make maximum use of it." Although Cohen does not define the terms 'efficient', or 'effective', he appears to use them to mean a greater dependence on non-food energy (e.g. hydroelectric power, fossil fuels, etc.). This leads him to equate the stages of adaptation with the trajectory of cultural change based on greater and greater energy consumption which led to present-day Western society. For example, he concludes that although "some hunter-gatherers . . . enjoy a greater abundance of food than their horticultural neighbors; we nevertheless speak of the latter as representing a higher level of development because horticulture is a strategy based on more efficient energy systems" (Cohen 1974:47).

Rappaport (1971b) defines adaptation as:

> . . . the process by which organisms or groups of organisms, through responsive changes in their states, structures, or compositions, maintain homeostatis in and among themselves in the face of both short-term environmental fluctuations and long-term changes in the composition or structure of their environments. (p. 60)

While for Sahlins (1964):

> . . . adaptation implies maximizing the social life chances. But maximization is almost always a com-

> promise, a vector in the internal structure of culture and the external pressure of environment. (p. 136)

Bennett (1976) recognizes the importance of the concept of behavioral adaptation, which he defines as:

> . . . the coping mechanisms that humans display in obtaining their wants or adjusting their lives to the surrounding milieu, or the milieu of their lives and purposes. (p. 246)

He views the concept of adaptation as providing a framework which focuses "on the active mode of human engagement with natural phenomena" and allows for "the inclusion of society as a part of the environment with which men cope." (See Alland 1975, Alland and McCay 1974, and Hardesty 1977 for other views on human adaptation.)

Marvin Harris, another major figure in cultural-ecological theory, also views adaptation as central to an understanding of human behavior. He strongly rejects the notion that 'progress' is adaptive; and seeks to explain such 'riddles of culture' as India's sacred cow, Jewish and Muslim prohibitions on eating pork, and Aztec cannibalism, as adaptive cultural phenomena (Harris 1974, 1977).

However, it is not possible to discern any rules underlying his ingenious adaptive explanations of human culture, except for the assumption that many, but not all, cultural phenomena can best be understood as adaptive responses to the material world, with adaptation meaning survival of the group, not the individual.

Cultural ecologists usually view the population, the species, the group, or the culture, as the unit of adaptation and adjustment. For example Cohen states that "at each successive stage of cultural evolution man is better adapted for the survival of his group--that is, the survival of his adaptive unit--and in turn, of the species as a whole" (1974:47). Harris also regularly uses group benefit as the criterion of adaptive behavior. For example, he suggests that: "Reciprocity is a form of economic exchange that is primarily adapted to the conditions in which the stimulation of intensive extra productive efforts would have an adverse effect upon group survival" (1974:126). Organic evolution through natural selection operating at the level of the individual is virtually never invoked by cultural ecologists as the underlying reason for human adaptive behavior.

Anthropologists are becoming increasingly aware of the ethnocentric bias of the idea that cultural evolution represents progress toward becoming more and more like us (see Greenwood and Stini 1977:409-426). Also, there is a growing recognition that the group level of analysis which characterizes cultural evolutionary theory

in the social sciences has not yielded the kind of theoretical strides that biologists have made by focusing on individual selection through natural selection (Van den Berghe 1978:36). Some anthropologists are turning to neo-Darwinian theory in their attempts to understand human behavior (see articles and references in Chagnon and Irons 1979, 1981, Winterhalder and Smith 1981). However, despite these recent advances in the application of evolutionary theory to human behavior, biological and behavioral adaptation are still very generally dealt with as if they represent totally different processes. It is very widely assumed that nature--as represented by the genes--is the prime force in human morphological and physiological adaptation. In contrast, although some biologists and anthropologists have suggested that certain human behaviors are strongly genetically programmed, nurture--the environment in the broadest sense--is generally assumed to be the prime force in human behavioral (cultural) adaptation.

GENE-ENVIRONMENT INTERACTIONS

An emphasis on the dichotomies genes/environment, nature/nurture has hindered our understanding of adaptive processes. As Lewontin (1974) observed, one of the difficulties in the full understanding of genetic/environmental effects in the past arose from a confusion between the concepts of analysis of alternative causes (genes or environments) and the analysis of interacting causes (genes and environments). However, the interactions between genes and environments is now being documented in anthropological research. On the one hand, recent work in biological anthropology (e.g. Haas 1980b) documents that some human responses to high altitude which have often been attributed to biological adaptations cannot be understood without taking into consideration environmental variables (see Haas, Chapter 3). On the other hand, the extent to which sociobiological and ecological theory is successful in predicting and/or explaining certain human behaviors (Chagnon and Irons 1979, 1981; Winterhalder and Smith 1981) suggests that, despite the strong influence of environment on how humans behave, there is an evolved genetic program underlying some aspects of human behavior.

The growing understanding of gene action also makes it clear that both genetic and environmental information must be involved in the genesis of any phenotype, be it morphological, physiological, or behavioral. The unique information encoded in the DNA of the fertilized egg is always necessary for the development of each and every individual and all phenotypic attributes--how each individual looks, functions, and behaves--must be based to some degree on genetic information. Also there is a continuous exposure of each and every individual to the en-