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Evolutionary Ecology and the Social Sciences

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1.1. INTRODUCTION

1.1.1. Problem and Rationale

Put as briefly as possible, evolutionary ecology is the study of evolution and adaptive design in ecological context. The contributors to this volume believe that evolutionary ecology is poised to make significant contributions to our understanding of human behavior. But we realize that acceptance of this approach within the human sciences is hampered by a history of controversy surrounding the use of evolutionary biology to analyze human behavior. Our hope is that careful integration of this approach with more standard social science, and a presentation of contemporary evolutionary ecology that makes clear its complexity and sophistication, will blunt much of the criticism that might otherwise arise.

The first two chapters of this volume are directed principally to social scientists for whom evolutionary terminology or ideas may be relatively unfamiliar. Evolutionary ecology depends on a coherent, well-defined investigative apparatus—premises, concepts, conventions, and terms that define a disciplined framework of study. We set out this framework and locate it with respect to other approaches to analyzing human evolution and behavior. This first chapter provides a broad overview of the questions addressed by evolutionary ecology with respect to human behavior. It relates evolutionary ecology to the approaches and concerns of social science generally. Chapter 2 provides a summary of the basic theoretical principles used throughout the volume, and compares these in some detail to selected social science frameworks.

Perhaps the first question that might occur to a social scientist is, Why *should* an evolutionary approach be applied to human behavior, especially

social behavior? After all, the skeptic might argue, this can only confuse levels of analysis and is likely to resurrect thoroughly discredited notions of biological determinism and innate differences between races and sexes. We will deal with the matter of biological determinism below (1.3). The more fundamental question—Why bother with evolution at all?—deserves an immediate response.

Put simply, our answer is that any comprehensive explanation of human behavior *requires* evolutionary forces. At the most basic level, humans, like other species, are products of biological evolution. Human societies are products of cultural evolution (which in turn is conditioned by biologically evolved propensities). Thus, evolutionary forces acting on both genetic and cultural variation are directly involved in making us, and our societies, what they are. A more detailed discussion of the necessary causal role of evolutionary forces in shaping human behavior is provided in section 1.3, as well as in Chapters 2 and 3. The fundamental point made here is that there is simply no alternative to evolutionary analysis with respect to origins and maintenance of certain primary beliefs and preferences shaping human action.

The qualities of behavior impose special demands on its analysis. Individual behavior and social life are complex and diverse, ephemeral in their observable manifestations, and subject to rapid change over time. They are shaped by several different kinds of causes ranging from genes to symbols. The evolutionary analysis of behavior provides an abundance of difficult materials. One can despair of finding regularities or explanations for them. Evolutionary ecologists seek to order investigation through clear theoretical, methodological, and topical commitments, as spelled out below.

1.1.2. Chapter Overview

In section 1.2.1 we describe the origins and basic premises of evolutionary ecology, discuss various ways to include environmental context in evolutionary analyses, and examine the different kinds of explanation that can be classified as evolutionary. From this theoretical beginning we shift to questions of methodology, starting with a brief description of the hypothetico-deductive method and the role of simple models in analyses of biological and social phenomena. We then appraise the difficulties of evaluating behavioral ecology hypotheses (1.2.2).

Section 1.3 examines some of the issues raised by the claim that an evolutionary and ecological framework is a necessary component of any comprehensive view of the causes of human behavior. We discuss problems associated with a biocultural framework (1.3.1) and then posit that a synthesis of biological and cultural views can be justified on both ontological (1.3.2) and methodological (1.3.3) grounds. The chapter concludes with a summary (1.4).

1.2. WHAT IS EVOLUTIONARY ECOLOGY?

1.2.1. Substantive Features

Evolutionary ecology is the application of natural selection theory to the study of adaptation and biological design in an ecological setting. When the features under examination involve behavior, as is the case in this volume, then the subset of evolutionary ecology is often termed *behavioral ecology* (e.g., Krebs and Davies 1991). If the behavior involves social interactions, then the term *socioecology* may be employed (e.g., Crook 1970). In any case, evolutionary ecology is simultaneously concerned with natural selection (or its effects) and ecological context.

Historical Origins. As a well-defined and integrated body of theory and research, evolutionary ecology is no more than about 30 years old. To be sure, styles of thought that are both evolutionary (in the Darwinian sense of giving explanatory precedence to natural selection) and ecological (i.e., focusing on organism–environment relations) predate the term itself. In fact, we might identify Darwin himself as the first evolutionary ecologist. But for reasons too varied to discuss here, ecological and evolutionary biology developed more or less independently.

Some groundwork for modern evolutionary ecology was laid in the 1930s through 1950s when mathematical biologists such as Lotka, Volterra, Gause, and Hutchinson developed the seminal mathematical models of ecological processes such as population dynamics, competition, and predation. These models were comparable in logical rigor and predictive power to those of population genetics (see Kingsland 1985; Hutchinson 1978). Building on this work, the two most prominent figures to forge an evolutionary ecology approach were David Lack (e.g., 1954, 1968) in England and Robert MacArthur (e.g., 1958, 1960, 1961) in the United States. MacArthur in particular brought all the elements of evolutionary ecology together in a creative synthesis: definition of central topics (e.g., community diversity, population regulation, sex ratios, feeding strategies, competitive equilibria), explicit Darwinian premises, hypothetico-deductive methods, and a reliance on simple mathematical models. When assessed against the highly descriptive tradition of 1950s ecology and the functionalism that then pervaded attempts to understand evolution in ecological terms, MacArthur's approach was radical. He inspired a generation of students and colleagues (Fretwell 1975) to pursue open-minded creation of abstract models and hypotheses, followed by their skeptical, empirical appraisal. Although Lack placed less emphasis on mathematical modeling, he played a similar role in the history of British biology.

MacArthur and Lack were key figures, but they did not define evolutionary ecology by themselves. By the 1960s, important work in this tradition

was being done by many researchers. On the theoretical front, prominent contributions include Levins's (1968) monograph on adaptation to changing environments, MacArthur and Wilson's (1967) on island biogeography, along with papers by MacArthur and Pianka (1966) and Emlen (1966) on foraging strategies, and Orians (1969) on the evolution of mating systems. Contributing to these advances were exemplary field studies, including those by Crook on weaverbirds (Crook 1965) and primates (Crook and Gartlan 1966). These showed clearly that variation in social organization between and within species could be analyzed as evolutionary responses to local social and ecological conditions. By the 1970s, the blossoming of evolutionary ecology as a distinct field of study was formalized with the publication of several textbooks and edited volumes (Emlen 1973; Ricklefs 1973; Pianka 1974; Cody and Diamond 1975; May 1976; Krebs and Davies 1978; Roughgarden 1979).

One early paper by Brown (1964) is particularly illustrative of the move from descriptive and functional studies to the kind of analysis developed in evolutionary ecology. Brown noted that the diversity observed in avian territorial systems had so far confounded specific, functional explanations. There seemed to be no consistent pattern, no means of generalizing about the different beneficial consequences that had been offered to explain territorial behavior. Brown sought to shift the reasoning used to examine this question in a manner suggested by his title, *The Evolution of Diversity in Avian Territorial Systems*.

Brown argued that for natural selection to favor territoriality—aggressive behavior with respect to a resource such as space—there must be some relative advantage to it. Since the argument was couched in neo-Darwinian terms, the advantage must be enhanced probability of survival and reproduction. That will depend on the balance of costs and benefits or, more specifically, on the cost of defending the resource and the competitive benefits gained by its exclusive use. Brown argued that resources are more defensible where they are concentrated and predictable in location and that the benefits of defense grow with the degree of competition for the resource (its effective scarcity).

Brown argued that these two factors, defendability and competition, are jointly necessary for aggressive defense of the resource to evolve. For instance, if the resource is not economically or physically defensible, even very intense competition for it could not lead to the evolution of territoriality. Neither would territoriality evolve if the resource were defensible but not the object of competition; for instance, if it were localized but so abundant that nothing was gained to offset the costs of safeguarding its exclusive use.

This model is explored in more detail below (8.4.3). Its general significance for the logic of evolutionary ecology models has several aspects:

1. As highlighted by his title, Brown's model begins with the evolutionary process, specifically with natural selection. His argument takes the form of a thought experiment: In what environmental circumstances will differential fertility and mortality select for defense of resources?

2. Brown's objective is to explain the acknowledged *diversity* of territorial systems, from complete defense to lack of it. Further, since the model does not specify a particular type of resource, it can be applied to food, space, mates, or any other factor that contributes to an organism's fitness. A population might express territoriality differently for each of these factors, and might switch its territorial behavior over time, as the relevant independent variables change (e.g., seasonal changes in the dispersion or predictability of resources, or in their scarcity).

3. Brown's thought experiment is an excellent example of a simple evolutionary ecology model. He has isolated a particular behavior and identified how it should vary as a consequence of a few independent variables. The verbal argument can be represented in the form of simple graphs or equations. Both the behavior and the variables are observable, making any particular application of the model a test of a hypothesis.

4. Finally, there is a more subtle point. Imagine Brown had given his essay this superficially similar title: *The Function of Territoriality in Avian Species*. Gone would be the explicit reference to an evolutionary approach and to the explanation of diversity. In their place would be a search for the function(s) of territory. These two titles might promise the same kind of analysis, but the differences are fundamental. Territoriality presumably has (or had) one or more functions. But the evolutionary ecologist seeks explanation causally in the process of natural selection in specified environmental conditions. A function or functions (e.g., ensuring adequate food supplies) may be identified by Brown's explanation, but the explanation does not begin or end with this.

Neo-Darwinism. Brown based his analysis solidly on the principle of natural selection. The observations that Darwin assembled in creating the concept of natural selection (Mayr 1977) are roughly the same that constitute its most parsimonious formulation today: More individuals are born than can live to reproduce, due to the constraints of environment; individuals show heritable differences that affect their relative ability to survive and reproduce; over time (multiple generations) their differential mortality and fertility will accumulate the more fit (or adaptive) of these variants in the population (see 2.2.1 for further discussion). The evolutionary ecologist typically studies the consequences of these principles at the phenotypic level (see 2.2.2). He or she focuses on the social and ecological processes and relationships—many of them behavioral—through which the implications of differential mortality and fertility are worked out.

Evolutionary ecology embraces a wide range of phenomena, from the behavioral strategies of individual organisms to the structure and evolution of ecological communities. Typically, the field embraces foraging strategies, spatial organization, group size and formation, sex allocation, mating systems, life history patterns, interspecific coevolution (of predators and prey, competitors, mutualists, and parasites and hosts), the evolution of niches, and the equilibrium structure and dynamic behaviors of ecological communities (see Krebs and Davies 1991; Roughgarden et al. 1989). Evolutionary ecology unites this diverse set of topics and foci by virtue of its base in neo-Darwinism, its focus on explaining phenotypic design, and its use of relatively simple mathematical models (often drawing on optimization or game theory) to understand complex systems.

Role and Characterization of Environment. Evolutionary ecology directs our attention to the role and characterization of the environment in which organisms live, reproduce, and die. In the drama of evolutionary ecology the "ecological theater" is as fundamental as the "evolutionary play" (Hutchinson 1965). In fact, we might say about evolution what Simon (1969) has said about human behavior: It is the product of simple rules played out in an exceptionally complex environment. For neo-Darwinism, the rules are given by natural selection, the structure of inheritance (haploid, diploid, cultural, etc.), population structure, and the like. Simon's observation challenges us to determine appropriate means of describing and evaluating the short- and long-term environmental influences on behavior.

In the studies that follow, environment is defined as everything external to an organism that impinges upon its probability of survival and reproduction. The effects can bear on development, physiology, or behavior, and their sources can be physical, biological, or social. Broadly, we distinguish between *strategic* and *parametric* environmental contexts (Elster 1986:7). Strategic contexts (or variables) are those in which the consequences of a behavior depend on the frequency of it and alternative behaviors in the population. There is an "interdependence of decisions," which means among other things that there are no truly independent variables in the analysis. Typically, an organism's social environment is one of strategic variables. For instance, a courting warbler changes behavior in concert with the response of potential mates and competitors. In evolutionary ecology, strategic processes are studied using the concept of evolutionarily stable strategies (ESS), with concepts and models that are based in game theory (2.2.3).

In contrast, decisions made in a parametric context do not yield different outcomes depending on their own frequency. The independent variable may be deterministic or probabilistic and uncertainty may be low or high, but it is nevertheless independent. Typically the physical environment con-

sists of parametric variables. A migrating warbler need not concern itself with the possibility that its decision to go south will provoke a change in the latitudinal distribution of seasonal climates. Decisions made in parametric situations can be analyzed with simple optimization models (2.4).

After deciding whether the environmental variables are strategic or parametric, it becomes important to decide how to reduce their complexity and to characterize them in a manner that best suits analysis of evolutionary questions. This is rarely easy or straightforward. At the simplest level a normative description of a few features of environment might suffice, for instance, to explain bird migration. But most behavior is a result of evolutionary mechanisms and processes operating on several scales of space and time. Behavioral responses, especially those involving learning, are most likely when the relevant environment has qualities of high variance, novelty, and unpredictability (Mayr 1974; Boyd and Richerson 1985). The spatial and temporal *pattern* of the relevant environmental features must be characterized with appropriate variables and in sufficient detail to capture these qualities (see Southwood 1977; Wiens 1984; Winterhalder 1980).

The attention of evolutionary ecology to the great complexity of the organism's environment helps to distinguish it from narrow versions of sociobiology. Key sociobiological models (kin selection, parent-offspring conflict, sexual selection, sex ratio manipulation) are derived from the basic features of Mendelian rules. They base predictions mainly on the properties of genetic inheritance systems, which are rather uniform. Because of this they achieve a high degree of generality. But sociobiological models without ecological variables can be *too* general if one is interested in the exceptional plasticity and diversity of behavior found *within* the human species.

In contrast, evolutionary ecology models give greater attention to the organism's environment. They predict diverse and flexible behavior, contingent on localized and often changing conditions. The great variety of states possible in the organism's immediate environment leads behavioral ecologists to expect a corresponding variety in the expression of behavior. While the chapters to follow sometimes draw upon sociobiological models, they attempt to complement these by being sensitive to the behavioral nuances arising from the socioecological setting.

Evolutionary Questions. Evolutionary biologists rarely dispute what questions are possible or even which kind of question is being asked in a particular instance. Compare programmatic statements by two evolutionary biologists, an ethologist (N. Tinbergen) and a systematist (E. Mayr). Tinbergen's (1968) commentary argues that it is the methods, not the results, of ethology that ought to be emulated by social scientists. Mayr's (1976 [1961]) views are stated in an essay titled, "Cause and Effect in Biology." Each sets

Table 1.1. A Comparison of Statements by Tinbergen (1968) and Mayr (1976) on the Forms of Explanation in Biology

Tinbergen	Mayr
I. Ultimate analysis in terms of Neo-Darwinian process	
1. In what ways does this phenomenon (behavior) influence the survival, the success of the animal?	1. An ecological cause. The warbler . . . must migrate, because it would starve to death if it should try to winter in New Hampshire.
II. Proximate analysis in terms of mechanism	
2. What makes behavior happen at any given moment? How does its "machinery" work?	3. An intrinsic physiological cause. The warbler flew south because its migration is tied in with photoperiodicity. It responds to decrease in day length.
	4. An extrinsic physiological cause . . . on the 25th . . . the sudden drop in temperature and the associated weather conditions affected the bird . . . so that it actually took off.
III. Proximate analysis in terms of ontogeny	
3. How does the behavior machinery develop as the individual grows up?	
IV. Ultimate analysis in terms of evolutionary history	
4. How have the behavior systems of each species evolved until they became what they are now?	2. A genetic cause. The warbler has acquired a genetic constitution in the course of the evolutionary history of its species which induces it to respond appropriately to the proper stimuli from the environment.

out four components to his scheme. Tinbergen poses his components as questions, whereas Mayr defines four "equally legitimate" types of causation, which he illustrates with answers to the general question: "Why did the warbler on my summer place in New Hampshire start his southward migration on the night of the 25th of August?"

In Table 1.1 the statements of these two authors are listed in parallel columns. We have added headings but have retained the numbering and wording of the authors. There is a high degree of correspondence between these outlines despite their different forms and independent development. Mayr's warblers almost perfectly answer three of Tinbergen's behavioral questions. The modest deviations also are revealing (the following comments are keyed to the headings):

I. Both Tinbergen and Mayr draw attention to the mechanisms and processes of evolution, chiefly natural selection. Mayr calls this an "ultimate" source of causation; it refers to the evolutionary origins of the trait. It answers a *why* question: Why did the trait come about? We can generalize Mayr's reference to suit our present purposes by adding social causes to his ecological ones.

II. Mayr distinguishes two types of answers that match one of Tinbergen's inquiries: "What makes behavior happen at a given moment?" There is an intrinsic cause (characterizing the state of the organism) and an extrinsic cause (which characterizes its environment). For Mayr these are "proximate" causes located in the individual and its immediate circumstances. They answer *how* questions: How does the adaptation function?

III. Mayr's scheme of four parts omits reference to Tinbergen's question about ontogeny: How does the behavioral response develop? With our focus on complex phenotypes, we cannot afford to overlook this question. The study of learning during growth is vital to the analysis of behavior, especially human behavior. In fact, humans are so powerfully receptive to socialization that it constitutes the basis for a parallel system of inheritance (Chapter 3). Adapting Mayr's terminology, we might say that ontogeny falls closer to the proximate realm of functional inquiry. But for humans, or any creature heavily dependent on learning and social transmission of knowledge, ontogeny has engendered its own, partially independent mechanisms of evolutionary change.

IV. For both Tinbergen and Mayr the fourth realm of inquiry is a phylogenetic or historical one. It also is an ultimate or *why* type of inquiry. But phylogenetic analysis concerns evolutionary origins in the narrow historical sense and not the reasons why selection might continue to stabilize some phenotypic feature within a population.

1.2.2. Research Strategy

Evolutionary ecologists generally follow the research strategy known as the *hypothetico-deductive method*. This method involves a cyclical movement between the creation of abstract models and their testing against the empirical evidence. The logic and structure of this cycle is the concern of the present section.

Hypothetico-deductive Method. The hypothetico-deductive (HD) method consists of procedures that adhere to specific rules of logic and evidence, but also attempt to reflect the way scientists actually think and work. It is pragmatic science, somewhat wary of the more formal (and occasionally dogmatic or disputatious) philosophies of scientific method, which have contended for the attention of the physical, biological, and social sciences. Although anticipated by Kant and advocated at length by Popper, we prefer

Medawar's (1982:73–135) more accessible summary (see also Fretwell 1972:viii–ix).

The HD method distinguishes between the creative and evaluative components of scientific research; it acknowledges and draws our attention to differences between the processes of discovery and those of verification. HD advocates do not believe that the inventive stage of science can be formalized in a methodology. It depends rather on such scientifically elusive elements as the felicitous guess or inspired insight. These elements clearly are helped by experience with the relevant data and by knowledge of related theory, hypotheses, and concepts, but they cannot be reduced to a protocol of logical procedures.

The generation of theory or hypotheses is followed by processes of evaluation. Hypotheses are tested by experiment and observation and gain our respect by outliving the twin assaults of logic and evidence. In Medawar's (1982) words, "there is . . . reciprocity between an imaginative and a critical process, between imaginative conjecture and critical evaluation" (p. 100). The result is a "running adjustment" (p. 105) of ideas and data. The kind of confidence accruing to a veteran HD hypothesis falls short of notions such as proof, but it is consistent with contemporary views on logic and our normal experience with human intellectual fallibility. The HD method accepts the sharp distinction offered by logical positivism: Hypotheses cannot be strictly proven, only soundly disproved. But it insists that the practice of science is considerably less tidy. Some hypotheses are accepted with a high degree of confidence, while others are occasionally wrongly rejected. Evolutionary science in practice must work the more ambiguous middle ground between surely right and certainly wrong. It is rare, at least in the biological and social sciences, for an hypothesis to be rejected outright; an unequivocal disproof is hard to obtain. Rather, hypotheses are more commonly subject to tinkering, adjustment, and repair. They are assimilated into other ideas or, if unproductive or repeatedly unsubstantiated, they simply fade away.

Medawar describes the HD method as one that "potentiates common sense." It does not rest on claims that logical procedures (deductive or inductive) are infallible guides to truth; it does not grant unquestioned authenticity to facts but, rather, sees them as perceived and selected according to preexisting ideas. It thus allows for the influences of culture, context, and personality, while cautiously insisting that biases of each can be found out and corrected if the practice of science is disciplined.

Simple Models in a Complex World. Upon hearing Darwin's idea of natural selection, Huxley is supposed to have remarked, "How extremely stupid not to have thought of that" (Huxley 1920:94). Natural selection itself—differential survival and reproduction—is a simple notion (see 2.2.1).

But the consequences of the concept, its operation in the process of evolution, are anything but simple. Between the straightforward logic of the idea and the bewildering complexity and variety of the products of the evolutionary process lies the key to understanding the place of models in evolutionary ecology analyses. From a premise of a few sentences we must generate ideas adequate to explain the detail and complexity, say, of a primate troop or a tropical rain forest. Models are our best means of surmounting this detail while preserving at least some fidelity to its reality.

"We . . . build models to explore the consequences of what we believe to be true" (Starfield and Bleloch 1986:3). Models are especially useful when there is some understanding of the problem, but ideas about how to analyze the data are limited. They help to (1) define the problem, (2) organize thought about it, (3) understand data, (4) test the understanding, and (5) make further predictions. In effect, they are heuristic tools that discipline our attempts to work from general premises to concrete and testable illustrations of them.

Levins (1966) defined three desirable qualities of any model: realism, generality, and precision. Though each has clear virtues, one cannot pursue all three at once with equal vigor. One can get high precision, for example, but only at the cost of reduced generality or realism. Thus, an optimization model may specify a single currency to be maximized, which allows precise predictions about optima but overlooks the diversity of goals that may pertain in the real world. Similarly, maximal realism usually entails reduced generality or precision; a model that exactly fits a particular case will probably not fit other cases nearly so well (sacrifice generality) and may be so complex as to make precise prediction (and hence empirical test under changed conditions) impossible.

Evolutionary biologists typically emphasize particular qualities, depending on the question being asked or the answer sought. If fisheries management or economic policy, for example, is the objective, realism has high priority. If inferences that will contribute to the construction of theory with broad applicability are the objective, then generality will have a high priority. The attempt to establish recurrent relationships between types of food webs and community structure might be an example. If clearly distinguishing between competing hypotheses is desired, precision may be the most important quality. Whatever the balance of these qualities that the analyst seeks, models are devices to make complex problems tractable.

Models, however, may invite criticism because of their simplicity. Superficially there is an intuitive appeal to such critiques. The models of evolutionary ecologists are orders of magnitude short of the complexity and variety of the phenomena they purport to explain. They invite the accusations of simplemindedness and reductionism. But simple is not simpleminded. Simple models are a necessary, not a temporary or primitive stage

of scientific development. This is because "simple models are caricatures . . . capturing a few essential features of the problem in a recognizable but stylized manner, and with no attempt to represent features not of immediate interest" (Richerson and Boyd 1987:35). They often are implicit in our ability to understand the more complex models that may grow out of or supersede them. The Hardy–Weinberg formula and the logistic growth curve are examples of models that survive, enshrined in thought and textbooks, because they do enduring heuristic work.

In evolutionary ecology no single model exists or is used in isolation. Any subject is analyzed through a collection or family of models. Each model addresses a particular topic and has its own limitations. Their articulation into a more comprehensive account is a task that requires that we know their limitations, applicability, and representativeness. In particularly well-developed areas (e.g., optimal foraging theory—see Chapter 6), a set of complementary models can develop into a comprehensive analytical tool—a *theory*.

Reductionism. The use of simple models in the social sciences also invites charges of reductionism, especially if the models have a biological origin. To address this issue, we first define and distinguish among several different meanings of reductionism, following Mayr (1988:10–11). Mayr specifically examines the reduction of biology to physics, but his analysis is applicable one step up the scientific hierarchy, where the social sciences look back uneasily to their relationship with biology.

Constitutive reductionism applies to the "dissection of phenomena, events, and processes into the constituents of which they are composed" (Mayr 1988:10). It claims that higher-level phenomena are constituted of lower-level events and processes, which preserve their integrity whatever their context. A behaving human is constituted of organs, organs of cells, cells of molecules. Comprehending higher levels does not fundamentally change understanding of the lower ones, which have properties and processes that remain valid and applicable from whatever level they are studied. Thus, a molecule is not different by virtue of being in an organism; chemical reactions follow the same rules whether located in a puddle or the stomach of a tuna.

To the extent that higher levels are unique, their novel properties and processes emerge from differences linked to increased organizational complexity. Life is constituted of nonliving materials but has emergent properties all its own; the living brain is an organic structure, but mind is a different matter.

Novel emergent properties raise the issue of *explanatory reduction*, which "claims that all the phenomena and processes at higher hierarchical levels can be explained in terms of the actions and interactions of the components at the lowest hierarchical level" (Mayr 1988:11). In the extreme (signified by

reduction across several levels, or to the lowest level) explanatory reductionism is a failure. It is impossible to explain socialism in terms of molecular bonds. But a more modest claim to partial explanation at a lower level can be defended in many circumstances. Within this more limited scope, explanatory reductionism is a standard procedure of scientific analysis. The understanding to be gained from explaining a conditioned reflex in terms of neural circuitry illustrates its merits. However, in many circumstances it is difficult to evaluate the power and limitations or establish the appropriate degree of explanatory reductionism. This leaves room for controversy.

Finally, *theory reduction* implies that theories at one level are only special cases of theories formulated for lower levels and ultimately can be reduced to them. Theory reduction enjoys a limited success in physics but is almost universally rejected elsewhere (Mayr 1988:11). It confuses processes (for example, biochemical), which are common across levels (as recognized by general acceptance of constitutive reductionism), with concepts, which are not. The brain operates according to standard biochemical processes, but the workings of the mind cannot be explained in purely biochemical terms. The same can be said of natural selection and Mendelian inheritance relative to chemistry.

Evolutionary ecology presumes constitutive reductionism. It practices a limited degree of explanatory reductionism, as do most biological or social sciences. For example, a commitment to self-interest explanations permeates most of the models discussed in this book; many social science analyses also attempt to analyze social phenomena as the product of self-interested behavior (albeit for different theoretical reasons), although such reductionism sometimes is controversial in the social sciences (see 2.3.1). Finally, there is little if any theory reduction invoked in the studies summarized in this volume. Rather, evolutionary behavioral ecology involves a blending of complementary theoretical approaches: neo-Darwinism, cultural transmission models, decision theory, population ecology, and even models of bargaining and political dynamics. Thus, evolutionary ecology as exemplified by the studies summarized herein does not require or advocate greater amounts of reductionism than can be found in many realms of social science, nor does it invoke the most problematic form, theory reduction.

There is another property of human behavior that elicits the charge of simplicity and sometimes that of reductionism: It is multicausal. Multicausality arises because any and all behavior results from the interacting effects of genes, environment, and learning. The classical example in biology is bird song (Lehrman 1970), but the issues are the same for human musicians. The primary question to be asked (but what a question!) is how and to what degree each of these causes leads to the behavioral variation seen in musicianship (or any other trait), avian or human. Whatever their relative importance, separate study of each of these factors is necessary to

understand their consequences taken all together. Once their separate effects can be predicted, it is an empirical matter to determine if any factor predominates.

This point bears emphasis. To study the causes of phenotypically complex traits like behavior one must analyze the causes of behavioral variance (Lewontin 1974). For individuals of a species formed through complicated and prolonged processes of growth and development, this entails analyses in which genotype, experience, and learning are the minimum set of independent variables. One can wrongly assess the relative importance of those variables, but there is no logical basis for claiming that analysis of one or another of them is in itself reductionism.

When charges of biological reductionism are evaluated by the distinctions Mayr outlines:

1. Many collapse, usually because they confuse or fail to distinguish among the various types of reductionism, or because they treat as reductionism legitimate analytical choices (see 1.2.1).
2. Some raise important and thought-provoking issues, although often they must be shorn of rhetorical baggage and exaggerated claims of critical impact.
3. Those which constitute valid critiques thereby assume an important role in the self-correcting processes of the HD method.

The analysis of human behavior from an evolutionary ecology perspective will benefit from more careful and tolerant understanding of the role of simplifying models. Specialized analyses that take up a limited set of problems or causal factors do not for that reason alone represent inappropriate instances of reductionism.

Evaluation. Evolutionary theory is multifaceted and the determinants of behavior are diverse. The questions we might ask are various, and they must be asked by means of families of models that represent a sometimes uneasy compromise between the complexity of the situation being investigated and analytical feasibility. As argued above, the HD method alerts one to the potential for errors in the process of theory evaluation. What sense then can we make of the claim that an idea has survived empirical test?

First, hypothesis testing allows us to correct our view of the world as it is expressed in choices about the variables, constraints, currencies, and other concrete elements that we use to construct an evolutionary ecology model. It helps to articulate theory. For instance, in the prey choice model (6.2.3) we make certain assumptions about the environment (random distribution of prey), about the organism (that it can sense and assess the costs and benefits associated with different prey species), about selection (that it has acted to enhance the prey capture abilities of the predator), about the value of the

prey to the predator (calories are more important than nutrients), and so on. Based on these assumptions, the model provides explicit predictions. If empirical observations do not conform to those hypotheses, at least they may provide clues concerning which of the model assumptions were wrong. The formal structure of the model becomes the template upon which we use data to track down and correct errors in our initial understanding.

Second, most evolutionary ecology models produce hypotheses concerning the form, direction, and degree of the relationship between variables. Precision often has a low priority to the kind of knowledge being sought. Hypotheses like the following are common: As resource density and predictability increase, territoriality is more likely. If prey density increases, the diet breadth of the organism (the number of prey types it pursues) will diminish. Females in better than average health and resource circumstances should, if they can expect their offspring to experience the same, produce more of the sex that most benefits from the maternal condition. Note that these hypotheses are stated in the form of inequalities, correlations, and functions without constants. They distinguish among qualitative possibilities and often are tested through comparative research designs. When evolutionary ecology models *do* seek quantitative precision, it is usually in order to maximize the power of the empirical test, rather than to obtain precision for its own sake or for the reasons that policymakers might wish to have precise predictive accuracy.

Third, evolutionary ecology models are quite explicit about the kinds of information required to evaluate them. Unfortunately, their data requirements often are extensive and difficult to meet. They also may be novel relative to information already collected on the topic. For instance, before optimal foraging theory was applied to hunter-gatherers, most anthropologists studying hunter-gatherers assumed that prey selection was a function mainly of prey abundance. In contrast, the prey choice model suggested that other variables, such as the food value of prey types and their pursuit and handling costs, likely were equally or more important. Making such measurements became a new task for fieldwork. Because they make broad and sometimes unexpected demands on our empirical resources, evolutionary ecology models can appear to be far ahead of their empirical validation. This also is a strength, as they direct us to new data and novel ways of the seeing the old.

Fourth, neither these observations on data nor the HD method itself suggest that we should expect definitive results from single tests. Evolutionary ecologists have learned to be patient with somewhat fuzzy data, suggestive results, and tests of hypotheses that result in partial acceptance or modification of the prediction rather than its outright rejection. A sound empirical investigation can weigh for or against a hypothesis but also may be inconclusive. The analyst must tolerate some ambiguity and partial resolution.

1.3. EVOLUTIONARY ECOLOGY AND THE SOCIAL SCIENCES

Social scientists often ignore or actively discourage linkages between their studies and evolutionary theory. In contrast, the authors of this volume believe that the relationships are direct and compelling. Underlying this claim are the biological origins and continuing biocultural character of human capacities and behavior. These alone are sufficient to motivate a comprehensive search for an integrated, evolutionary science of human behavior. However, any synthesis must come to terms with the troubled history of biocultural analyses of human behavior. And it must identify clear ontological and methodological grounds for such synthesis.

1.3.1. Skirmishes Along the Biocultural Frontier

The long history of battles over the causation of human behavior has left many biological and social scientists wary of the whole enterprise. Unpleasant scientific and ideological skirmishes have tended to alternate with periods of uneasy standoff. The more prominent battles—over Darwinism, social Darwinism, and sociobiology, in turn—have been episodic and inconclusive. The reasons for this procession of relatively unproductive disputes are various. Here we briefly consider three of the more important ones.

First, analysts of all persuasions frequently conflate scientific issues with ideological ones. By historical precedent, Western academics associate biology with politically conservative views and culture with liberal ones. Once established, these associations are reinforced by academic traditions and polarization. Conservatives frequently advance the cause of biology, and radicals that of culture.

But there are good reasons to reject these associations, on both logical and empirical grounds. Empirically, there are many historical and contemporary examples where biology is the basis for radical views and culture the redoubt of conservative ones. The later work of A. R. Wallace (e.g., 1913) is an excellent example of the former. Contrary to the conservative, *laissez-faire* social Darwinism of the day, Wallace argued that Darwinism substantiates the case for political socialism. Similarly, the radical environmentalism of B. F. Skinner (e.g., 1972), although not linked by Skinner himself to conservative views, certainly was attacked by progressives as robbing humans of dignity and self-determination. In the contemporary scene, we have to look no farther than the debate over evolutionism and creationism to see that the denial of biology in human affairs is not necessarily a progressive view. The feminist sociobiology of Hrdy (1981) is another striking disconfirmation of the conventional wisdom. More generally, there is no necessary

or logically invariant relationship between biology or culture as a causal influence on behavior and the ethical or political content or implications of that behavior. In sum, although biological determinism *can* be used to bolster conservative views, to think it *must* be so used is a prejudice, albeit a widespread and sometimes self-fulfilling one.

Second, among the many unnecessary and unfortunate associations that inhere to the nature–nurture dichotomy of Western thought is the belief that nature constrains and culture facilitates the expression of variety in human behavior. When someone refers to “human nature” versus culture, it is predictable that nature and not culture is seen as setting the boundaries (cf. Young 1974). While it is true that species-specific behaviors exist, much vertebrate social behavior varies dramatically depending on ecological circumstances, stage of life cycle, and other factors, which we can attempt to understand by means of evolutionary ecology models. The models are deterministic in that they attempt to analyze diverse manifestations of behavior using a common causality; but they do not predict a uniform outcome.

Conversely, anthropologists repeatedly emphasize (even while avoiding the word) the determining character of cultural life. When Geertz says that “man is an animal suspended in [cultural] webs of significance” (1973:5) the captive, constraining (and naturalistic) imagery evokes no cries of reductionism, determinism, or conservatism. Conversely, if a biologist says that humans are “entangled in the message of DNA” an uproar is likely to follow. A priori there is no justification for the automatic association between biological causation and determinism or limitations, nor between cultural causation and flexibility or variety.

Evolutionary ecology is more heterogeneous as a theory, more probabilistic as a process, and in outcome more productive of diversity and flexibility than is commonly believed by social scientists. The role of culture currently advanced by several approaches in the social sciences may be more causally restrictive or deterministic than is the case for the evolved propensities assumed in human behavioral ecology.

Third, disagreement has been exacerbated by the ambitious tone of some recent biological analyses of human social behavior (Kitcher 1985) and the disputatious replies of some social scientists. The contributors to this volume offer a cautious assessment of what evolutionary ecology has to offer to social science. We are acutely aware of limitations, some due to the youthful state of evolutionary ecology and others to the very nature of evolutionary explanations. The authors of this volume do not claim that natural selection and ecological adaptation *by themselves* explain all of human action, only that they are important causes of its variation. And even when selection and adaptation are the prime causal forces, they do not necessarily produce uniformity; instead, they often produce patterns of

(adaptive) phenotypic variation keyed to varying environmental states, historically unique evolutionary trajectories, or indeterminate outcomes with multiple possible equilibria. Each of these possibilities is discussed in models and empirical analyses throughout this volume.

Environmental Determinism. Because evolutionary ecology gives the environment a central explanatory role (see 1.2.1), it may appear vulnerable to the charge of environmental determinism. The debate over environmental determinism has a long history in social science (reviewed in Vayda and Rappaport 1968; Ellen 1981:Chapters 1 and 2); it remains a loaded issue, subject to frequent misapprehensions.

Taken literally, environmental determinism is indefensible: No aspect of the environment *in itself* directly and solely determines features of human behavior or society. There is always an interaction between environmental problems or opportunities, and the beliefs, goals, and capabilities of the human actors who confront them. The environmental determinism that found favor in scholarly circles early in this century erred in overlooking the great differences in beliefs, goals, and capabilities found in different human societies. It thus ignored important intervening variables (technology, social structure, economic organization, etc.).

But simply refuting environmental determinism (as Franz Boas and his associates were so fond of doing) yields the equally problematic environmental possibilism. Possibilism holds that the environment sets *limits* (usually broad ones) on the forms of behavior that can occur but plays no determining role within those limits. Possibilism is not wrong; it is just incomplete—hopelessly so. To say that the environment only limits, and therefore does not play any determining role, is to ignore more subtle forms and degrees of causation. For example, Kroeber is often quoted for his statements that climate cannot explain why agriculture spread where it did, only why it failed to spread to some areas (i.e., those too dry or cold). But more recent analyses suggest that some areas that are not physically too extreme for agriculture nevertheless are marginal enough that other forms of subsistence are *more profitable*, and hence preferred by inhabitants of these regions.

To a large degree, it was this last type of argument that Julian Steward (1955) introduced in his pathbreaking theory of “cultural ecology.” Steward wished to go beyond the sterility of the possibilist/determinist debate and “the fruitless assumption that culture comes from culture” (p. 36) offered by Boasian possibilism. In Steward’s formulation, heavily influenced by his training in evolutionary biology, environment determined the payoffs to various behavior patterns and thus exercised influence even within the limits of what was possible:

Over the millennia, cultures in different environments have changed tremendously, and these changes are basically traceable to new adaptations required by changing technology and productive arrangements. . . . Whether or not new technologies are valuable is, however, a function of the society’s cultural level as well as of environmental potential. (pp. 37–38)

Thus, Steward took full account of intervening variables and of degrees of adaptive advantage.

In sum we might say that cultural ecology replaced the possibilism of the Boasians with a rather primitive notion of adaptive optimization, foreshadowing the approach of contemporary evolutionary ecology. However, Steward—and cultural ecology in general—never came up with an explanation or mechanism for adaptive optimization. Only two plausible mechanisms have yet been proposed: rational choice and natural selection. The former is a powerful element of human adaptation (and seems to operate in other species with complex nervous systems as well); but it implies preexisting preferences for options with high-payoffs and hence ultimately depends on a history of natural selection (see 2.3.2). Natural selection can shape preferences and resulting behavioral patterns not only via genetic evolution, but also via cultural evolution (see Chapter 3). By bringing both these explanatory mechanisms to bear, and by utilizing a methodology based on model-building and HD processes, evolutionary ecology promises to put Steward’s seminal insights on a more solid and productive footing.

1.3.2. Ontological Syntheses

One encouraging basis for synthesis between evolutionary biology and social science is ontological. Humans are evolved creatures that through their history have been subject to the same evolutionary processes as other organisms (see Chapters 3 and 5). Our cultural capabilities, to whatever degree they constitute emergent properties, are a product of that process. Further, in evolutionary terms, they are a fairly recent phenomenon. They had their beginnings in creatures that anatomically and physiologically were quite like us. These observations do not necessarily provide grounds for a thoroughgoing reductionism, however. We cannot simply replace culture theory with evolutionary biology. The problem is that while culture may have begun simply enough as an aspect of phenotype, it has properties that made it into a parallel, partially independent, and very powerful evolutionary mechanism (see Chapter 3). The result is a creature heavily dependent on learning and experience. Whatever the relative balance of causation in human behavior, its analysis requires theory that can deal synthetically with our biocultural heritage.

It is no surprise that solid understanding of the relationship of culture to biology is yet modest and that consensus remains elusive. Indeed, the contributors to the present volume occasionally do not have complete agreement on these issues. Nevertheless, we all believe that evolutionary ecology can contribute substantially to the resolution of many of these disagreements. We also agree that the conventional terms of debate—biology versus culture, determinism versus intentionality, reductionism versus holism, biological versus social science—are now unproductive and need to be left behind for more sophisticated ways of framing the issues.

1.3.3. Methodological Syntheses

Methodology is another area of potential synthesis. The models employed in evolutionary ecology often transcend the conventional division between the biological and social sciences. They do so in at least two ways.

First, they create a more general arena for the use of concepts that span the biology/culture dichotomy. Those familiar with the history of the social sciences (especially economics) immediately will recognize many of the premises and concepts used in this volume. Optimization, rational choice, game theory, and methodological individualism are tools familiar to many social scientists. Evolutionary ecologists use this terminology with some caution. The precise meaning of terms can shift or become ambiguous in a new context, and simple borrowing of terms rarely is analytically rewarding. But here we believe that the rationales for common usage are sound (see 2.3 and 2.4).

Second, there are methodological issues common to the biological and social sciences. To what degree is microlevel theory sufficient to explain macrolevel phenomena? In the biological sciences, to what extent are macroevolutionary phenomena susceptible to microevolutionary explanation? In the social sciences, to what degree are the broad phenomena of human history (e.g., the origin of the state) explicable through principles of methodological individualism, what Elster (1983) calls "microfoundations"? Within a comprehensive, evolutionary framework these become versions of the same question: To what extent are the properties of complex systems (ecosystems or societies), including their historical development, the product of microlevel processes channeled through the actions of individuals? Similarly, what are the proper form and limits of functionalism or (as it is often termed in evolutionary biology) adaptationism? We defer discussion of these issues to Chapter 2, but their listing here should give ample evidence of the common methodological issues linking evolutionary ecology and conventional social science.

1.4. SUMMARY

The main arguments presented in this chapter can be summarized as follows:

1. Synthetic studies combining evolutionary and ecological elements in the study of behavior are fairly recent. Evolutionary behavioral ecology is characterized by a reliance on natural selection theory, a hypothetico-deductive methodology based in models, and a focus on the levels of individual phenotypes and social systems.
2. Simple models are a necessary tool for the analysis of complex systems. The competing characteristics of generality, precision, and realism cannot be simultaneously maximized in any model or analysis. The analyst must make choices about which to emphasize in a given inquiry.
3. Evolutionary ecology analyses typically take the form of the following question: In what environmental circumstances are the costs and benefits of behavior X such that selection would favor its evolution? Framing the analysis this way encourages the search for general (widely applicable) answers, without ignoring the importance of individual and populational diversity.
4. Behavioral diversity is largely the result of diversity in the socio-ecological environment of the organism. Strong attention to this environmental setting distinguishes evolutionary ecology from narrow forms of sociobiology.
5. Most evolutionary ecology analyses take up ultimate or *why* questions, while giving less attention to (though not denying the importance of) questions of proximate mechanisms.
6. The charges of determinism and reductionism leveled by critics of evolutionary analyses of human behavior often are misdirected complaints about legitimate analytical choices and procedures. Analyses based on natural selection and environmental variables are not inherently more deterministic or reductionistic than those based on cultural or social variables.
7. The need for synthetic, evolutionary analyses of human behavior rests on both ontological grounds (humans have evolved as biocultural creatures) and methodological ones (the biological and social sciences share important issues and can profitably share certain methods).

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