

# 1

## Two Decades of a New Paradigm

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This book is a collection of state-of-the-art empirical studies in a paradigm that has become known as human behavioral ecology. The emergence of this approach in anthropology was marked by the publication in 1979 of another collection of studies entitled *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (Chagnon and Irons 1979). During the two decades that have passed since then, the approach has matured and expanded into new areas. This chapter describes the origins of the approach, its early reception, and its subsequent development.

We use the phrase “human behavioral ecology” chiefly because it is the label used most often by those doing similar work on nonhumans, thereby accentuating the fact that this approach has its roots in animal behavior studies or ethology. It also has the advantage of avoiding notions of genetic determinism that are commonly (though mistakenly) associated with the term “sociobiology.” In addition, it serves to differentiate this approach from other, complementary approaches such as evolutionary psychology and cultural transmission theory (see Smith, chapter 2, this volume). However, it should be kept in mind that not everyone working within this approach uses this same label and that other labels, including human evolutionary ecology, human ethology, human socioecology, and human sociobiology, are also commonly used.

### THE ORIGINS OF HUMAN BEHAVIORAL ECOLOGY

The 1960s and the 1970s witnessed some very significant advances in evolutionary theory, especially theory relevant to the evolution of individual behavior. William D. Hamilton’s theory of kin selection and inclusive fitness was published in 1964, followed by his important work on senescence (1966), sex ratios (1967), and herding behavior (1971). In 1966, George C. Williams’s watershed book *Adaptation and Natural Selection* clarified a number of issues, especially the question of the level in the hierarchy of life (gene, individual, population, species, ecosystem) at which adaptations are most likely to evolve. That same year, Robert H.

MacArthur and Eric Pianka (1966) laid the foundations for the development of optimal foraging theory and the now widespread use of economic models in animal behavior studies. Robert L. Trivers presented the theory of reciprocal altruism in his classic 1971 paper, which was followed soon afterward by his theoretical papers on parental investment and sexual selection (1972; see also Trivers and Willard 1973) and parent-offspring conflict (1974; see also Trivers and Hare 1976).

These theoretical ideas formed a coherent perspective that viewed organisms as products of natural selection favoring phenotypes that enhanced the representation in future generations of the genes that coded for them. This approach is sometimes labeled “adaptationism” and “selectionist thinking” (Gray, chapter 21, this volume; see also Daly and Wilson 1988:2–5), but of course an understanding of natural selection and its role in designing adaptations had been around for a long time. What was new was the focus on behavior as something that, like physiology, may be subject to the forces of natural selection. With these theoretical developments in hand, animal behaviorists soon conducted a flurry of new field studies on a wide variety of taxa, including, to name just a few, arthropods, fish, birds, rodents, carnivores, and primates. Because primatology has long been an accepted branch of anthropology, it formed a bridge between anthropology and animal behavior studies in general, and primatologists such as Jeanne Altmann, Irvén DeVore, Sarah Blaffer Hrdy, Joan Silk, Barbara Smuts, and Richard Wrangham played an important role in introducing the insights of Hamilton, Trivers, and Williams to anthropology. Their long-term, detailed observational studies of animal behavior also drew on the ethological tradition of researchers such as Niko Tinbergen and Konrad Lorenz. At about the same time, a variety of anthropologists and others, including Earl Count, Robin Fox, Derek Freeman, Robert Hinde, Nicholas Humphrey, Desmond Morris, and Lionel Tiger, were beginning to use evolutionary theory to study human behavior, while human ethologists like Irenäus Eibl-Eibesfeldt and Nicholas Blurton Jones began to give the field an empirical base, and economists like Gary Becker pioneered the application of optimization models to noneconomic behavior.

The stage was set for the extension of the new refinements of evolutionary theory to the study of the human species. In 1974, University of Michigan zoologist Richard Alexander published a classic paper summarizing the evolutionary theory of sociality and making numerous specific suggestions about how this theory might enhance our understanding of human social behavior. In 1975, Harvard biologist E. O. Wilson published a large volume entitled *Sociobiology: The New Synthesis*, which summarized the evolutionary theory of social behavior and reviewed much of the evidence supporting this perspective from studies of social behavior of a wide range of animal taxa. In the final chapter of *Sociobiology*, Wilson suggested that this perspective could shed light on human social behavior and outlined some of what he thought this new insight might be. In 1976, Richard Dawkins published his classic popularization of the new approach entitled *The Selfish Gene*, which explained with unusual clarity the theoretical perspective

underlying the work of Hamilton, Williams, and Trivers. Like Alexander and Wilson, Dawkins also suggested that evolutionary theory might shed light on human behavior, though he advocated an emphasis on the role of culturally rather than genetically inherited information in shaping behavior.

## EARLY ATTEMPTS AT ANTHROPOLOGICAL APPLICATION

In 1974 and 1975, Napoleon Chagnon and William Irons were involved in an ongoing discussion about the use of these new refinements of evolutionary theory in anthropology, especially cultural anthropology. At that time they were both in the Anthropology Department at Pennsylvania State University; both had extensive fieldwork experience; and both were convinced that selectionist thinking would enrich their ethnographic research. After absorbing the works of Alexander, Hamilton, Trivers, Williams, and Wilson, they decided to organize two symposia on the use of evolutionary theory in anthropology for the 1976 annual meeting of the American Anthropological Association to present to the discipline their attempts to incorporate selectionist thinking into their ethnographic research. Eventually their symposia were coordinated with two symposia on the same topic organized by Irven DeVore of Harvard University. These symposia formed the basis for the edited volume *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (Chagnon and Irons 1979).

The research presented in those contexts focused on traditional anthropological topics such as kinship, marriage, infanticide, and social stratification, and the methods and data were also largely of traditional anthropological varieties. The novel element was the use of such data to test hypotheses derived from the theoretical expectation that human social behavior would reflect strategies that would enhance inclusive fitness in environments similar to those of past human evolution. The questions asked were derived in straightforward ways mainly from the work of Alexander, Hamilton, and Trivers: Do human beings tend to be more helpful to genetic kin than non-kin, and more competitive in dealing with non-kin than kin? Can such a tendency influence family and village formation in traditional societies? Do parents manipulate sex ratios in ways that increase the number of their grandchildren? Can status striving be seen as means to reproductive success? Although not everyone working in this area was included either in the 1976 symposia or the 1979 volume, these fora did serve to mark the beginning of a new school of thought in anthropology by bringing together a large number of empirical studies that used ethnographic data to test hypotheses about human behavior derived from evolutionary theory.<sup>1</sup>

The year 1979 was a productive year for the new paradigm in other ways as well. Two journals that deal extensively with the use of evolutionary theory in the study of human social behavior, *Ethology and Sociobiology* (recently renamed *Evolution and Human Behavior*) and the *Journal of Social and Biological Structures* (now the

*Journal of Social and Evolutionary Systems*), began publication, and the journal *Behavioral Ecology and Sociobiology*, which focuses primarily on nonhumans but which has also included some work on humans, first appeared. In that same year, two important theoretical books were published, Alexander's *Darwinism and Human Affairs* and Donald Symons's *The Evolution of Human Sexuality*, while E. O. Wilson's *On Human Nature* had appeared the year before.

## THE RECEPTION BY CULTURAL ANTHROPOLOGY

At the same time that this new field was rapidly developing, a number of extraordinarily hostile attacks upon it soon appeared. The gist of these attacks was almost always twofold. First, it was argued that the theoretical perspective represented by Hamilton, Trivers, Williams, Alexander, and Wilson could easily be shown to be totally indefensible on both logical and empirical grounds. Second, it was argued that the perspective tends to justify an oppressive status quo by encouraging racism, sexism, elitism, and imperialism.

A general hostility to the new approach developed especially early and intensely among cultural anthropologists. At the 1976 meeting of the American Anthropological Association at which the symposia organized by Chagnon and Irons were held, a motion was introduced at the business meeting to condemn "sociobiology." The motion was hotly debated, but it was finally defeated by a narrow margin. Interestingly, several people who debated against the motion were also opposed to sociobiology itself. Marshall Sahlins, for example, argued that passage of the motion would tend to strengthen sociobiology by making its supporters look like martyrs, and Margaret Mead argued that the motion, if passed, could be misconstrued as condemning any use of Darwinian theory. It is interesting to speculate whether the motion would have passed had it not been for these arguments from leaders of the profession who were already on record as being sharply critical of "sociobiology." At about the same time, the journal of the American Anthropological Association, *American Anthropologist*, published very negative reviews of the first watershed books presenting the approach that was to become human behavioral ecology. For example, John Buettner-Janusch (1978) described Richard Dawkins's *The Selfish Gene* as "an example of the silliness that can result from an Oxbridge education" based on his misbelief that Dawkins attributed conscious intentions to "selfish genes." Elliot Chapple's (1976) review of E. O. Wilson's *Sociobiology* in the *American Anthropologist* said that it "clearly wins the prize as the worst book in biology for 1975."

At the time of the 1976 anthropology meetings, Marshall Sahlins's book *The Use and Abuse of Biology* was freshly in print. In this book, a recognized leader among cultural anthropologists unequivocally condemned sociobiology as logically and empirically indefensible and politically dangerous. At the time, the book sold well and convinced a great many anthropologists that the new approach was

both bad science and politically dangerous. When, as a freshman at Northwestern University, Cronk let it be known that he had read Wilson's and Dawkins's books while still a high school student and was interested in the new paradigm, he was instructed by an anthropology faculty member to read Sahlins's book as a purgative. Sahlins's book is still in print and is still cited favorably by anthropologists and other social scientists (e.g., Bodley 1994:66; Ohnuki-Tierney 1994; Rosenblatt 1997; Schubert 1991; Schultz and Lavenda 1995a:83, 1995b:224), suggesting that a significant number of people are still sympathetic to its arguments. Because of the continuing impact of Sahlins's arguments, we will use part of this chapter to explain why we and other behavioral ecologists do not find them persuasive.

Part of Sahlins's critique was the common theme that sociobiology justifies free markets and the oppression that many people believe such markets necessarily entail. He said that this was an example of culture doing what cultures always do, in other words, inventing an ideology that justifies the culture itself. In Western society, he argued, oppression is a manifestation of the capitalist system, and that system has somehow generated sociobiology as a projection of the capitalist ethic of competition onto the natural world to encourage the idea that capitalism is somehow natural and therefore inevitable. In his own words, "What is inscribed in the theory of sociobiology is the entrenched ideology of Western society: the assurance of its naturalness and the claim of its inevitability" (1976:101). This is a hard argument to take seriously. The fact that neither Sahlins nor anyone else has offered an alternative approach to the evolution of life that does not include the differential reproduction of competing genotypes as a central element suggests that any similarity between the logic of capitalism and the logic of natural selection is coincidental. Furthermore, the overwhelming evidence supporting the theory of evolution by natural selection would make it appear that it maintains its currency not because of its supposed usefulness as an ideological tool but rather because of its success in explaining why organisms are the way they are.

This ideological attack was especially surprising to the many early sociobiologists who were committed to political and economic change and enhanced social justice and who bridled at the accusation that they were unwitting propagandists for any particular political or economic system. Unlike Sahlins, they understood that a central tenet of modern evolutionary theory is that no argument about the naturalness of a behavior can be used as a moral justification of that behavior. To do otherwise is to commit what is well known in the field as "the naturalistic fallacy" (Moore 1903; see also Hume 1739/1740). They also understood that the ideas of Hamilton and Trivers have as much or more to do with cooperation than with competition among organisms. Evolutionary biologist David Queller (1995:488) notes that his own work on social insects "emphasizes altruistic behavior, focuses on females rather than the males, and suggests that collective worker interests are crucial determinants of advanced insect societies." He asks, "Does this make me a good guy, a nurturing feminist, and a stalwart of the working class?"

A large part of Sahlins's attempt at a scientific argument against sociobiology focused on kinship: "The issue between sociobiology and social anthropology is decisively joined on the field of kinship" (1976:18). He claimed that the most elementary anthropological knowledge, "Anthropology 101," decisively refutes sociobiology's claim that human kinship is shaped by kin selection because in no society do kinship categories correspond with genealogical relatedness as measured by the proportion of genes individuals share by recent common descent, commonly represented as  $r$ . For instance, husbands of one's parents' sisters ( $r = 0$ ) may be lumped together with one's parents' brothers ( $r = .25$ ), or full brothers ( $r = 0.5$ ) may be lumped with male parallel cousins ( $r = 0.125$  for first cousins). Furthermore, he pointed out, households routinely contain people who are related in a wide variety of ways to a wide variety of degrees.

The problem is that Sahlins had derived a prediction from kin selection theory that no one who really understands evolutionary theory would ever make. No one expects that an individual will be more closely related to everyone in her household than to everyone outside of the household. The formation of a household represents a compromise between several competing goals. In an outbreeding sexual species, such as humans, individuals need to find mates who are not closely related. Inbreeding depression lowers fitness, and therefore close kin do not make good mates. Thus it is not surprising that people marry distant or non-kin and that one or both parties move after marriage so that typically one has a distantly related or unrelated spouse in one's household and full siblings who have taken up residence elsewhere. It is also the case that cooperating with an unrelated brother-in-law who is the father of one's nieces and nephews is not a violation of kin selection theory because affinal kin share a genetic interest in their common descendants (Alexander 1979:159–160; Dow 1984). Furthermore, human kinship systems are almost certainly based on a combination of kin altruism and reciprocal altruism (Trivers 1971).

Sahlins also argued that the whole project is flawed from the start by the fact that many other societies lack words for fractions and hence cannot calculate genealogical relatedness, adding as a side note that the obvious inability of animals to calculate fractions "introduces a considerable mysticism" to sociobiological theory (1976:45). Among animal behaviorists this has become known as "Sahlins's Fallacy," and it is considered a real howler. Dawkins (1979, 1989:291–292) points out that "A snail shell is an exquisite logarithmic spiral, but where does the snail keep its log tables?" and "How do 'green plants' figure out the formula for chlorophyll?" Similarly, although we may need differential equations in order to describe the trajectory of a baseball, that does not mean that an outfielder needs to solve any equations in order to catch one (Dawkins 1976:103–104, 1989:96). In short, although our understanding of many behaviors and biological processes is enhanced by mathematical models, this does not mean that organisms themselves need any understanding of mathematics in order to develop or behave.

A pioneering example of the use of inclusive fitness theory to shed light on human behavior was Chagnon and Bugos's (1979) analysis of a Yanomamö ax fight that was included in *Evolutionary Biology and Human Social Behavior*. The fight had been filmed and photographed (Asch and Chagnon 1975; Biella, Chagnon, and Seaman 1997; Chagnon 1997), and Chagnon had a complete set of genealogies for the participants. The data were used to test the prediction that the participants in the fight would tend to take sides with closer kin against more distant kin. Since almost everyone in the village was related to almost everyone else in the village, there was no question of taking sides with or against non-kin. The data indicated that those who chose to fight together were on average more highly related to one another than the village average. It also showed that those they chose to fight against were less related to them than the village average. Had the participants in the fight chosen sides without regard to genealogical distance, the expected result would be that average relatedness to their own faction and to their opposing faction would be the same as their average relatedness to the entire village. In this analysis, Chagnon and Bugos predicted that genealogical relatedness would be one factor, but not the only one, influencing individuals' choices of sides. Other factors considered include affinal ties and lineage affiliations. Judging from his discussion in *The Use and Abuse of Biology*, Sahlins's prediction regarding the ax fight would have been that the members of each faction would all be more closely related to all the members of their faction than to any members of the other faction. This would be reasonable only if kinship were the only factor influencing the choice of sides.

Another position taken by Sahlins (1976:84) was that if human behavior toward kin is thought of as being influenced by reciprocity as well as a tendency toward nepotism then the resulting model would be unfalsifiable: "If ego is good to his kinsmen, it benefits his own inclusive fitness; if on the other hand, he aids a stranger rather than a kinsman, it also comes back to his advantage in the form of reciprocal altruism." To behavioral ecologists, these are fighting words. Behavioral ecologists are committed to scientific methods and build their research around falsifiable theories and hypotheses. They find it especially annoying to be told their theories are unfalsifiable by a cultural anthropologist, a representative of a subdiscipline whose practitioners rarely concern themselves with the unfalsifiability of their own assertions. Fortunately, research on kin and reciprocal altruism has clearly shown that Sahlins has this wrong. Susan Essock-Vitale and Michael McGuire (1980), for example, did exactly what Sahlins said was impossible: they made falsifiable predictions based on Hamilton's theory of kin selection and on Trivers's theory of reciprocal altruism, analyzing fifteen studies from various societies in terms of a set of five predictions derived from the hypothesis that both genealogical relatedness and reciprocity would make various forms of altruism more probable. Because the data available did not allow each hypothesis to be tested in each of the fifteen societies, they were able to conduct a total of thirty tests of their predictions. Twenty-seven predictions were confirmed, one was

disconfirmed, and in two cases the data were insufficiently clear to allow a decision of whether the data confirmed or disconfirmed a particular prediction. If we assume as a null hypothesis that nepotism and reciprocity have no effect on the occurrence of altruism, then we can estimate the chance of getting Essock-Vitale and McGuire's results simply by sampling error. We can do this by assuming that each prediction was as likely to be disconfirmed as confirmed. The conservative way to do this would be to count the questionable cases as disconfirmation. Thus the null hypothesis suggests a binomial distribution with a probability of .5 for both confirmation and disconfirmation in each test. The likelihood of getting this result, given the assumptions of this null hypothesis, would be roughly two in a thousand. The important point here is that the expectations of behavioral ecologists are statistical. They expect some cases will not fit their expectations, and the validity of their claim can be judged only from a large number of cases. Since the publication of Essock-Vitale and McGuire's study, many more studies testing inclusive fitness theory among humans have been published, and the result is to lend support both to the notion that a nepotistic tendency is at least widespread if not universal in our species and to the broader project of the evolutionary biological study of human social behavior (see Turke 1996).

In an ironic way, human behavioral ecology owes Marshall Sahlins an intellectual debt because his confusion over the theory and its application led to some important research. For example, Joan Silk's (1980) work on adoption in Polynesia was inspired by Sahlins's claim that the practice, which is widespread in that part of the world, falsified inclusive fitness theory. Similarly, Sahlins's concerns about the lack of fit between kin terminologies and genealogical relatedness led to Kristen Hawkes's (1983) research on relatedness, kin terms, and helping among the Binumarien of New Guinea. Finally, Sahlins's concerns about how individual organisms could know the identities of their relatives have been addressed by research on kin recognition among nonhumans (e.g., Fletcher and Michener 1987; Hepper 1991). Furthermore, the enthusiastic reception given Sahlins's book by cultural anthropologists makes it clear that, as Gray notes (this volume), "sociobiology" has long had a serious public relations problem.

## **DECONSTRUCTING CULTURAL ANTHROPOLOGY: SOME PERSONAL OBSERVATIONS**

Being cultural anthropologists gives us insights into why cultural anthropologists are suspicious of "sociobiology." In effect, we have done participant observation among cultural anthropologists. Numerous interactions with cultural anthropological colleagues over many years makes us aware of widespread beliefs among them. One such belief is that "sociobiology" encourages a long list of evil "isms": racism, sexism, elitism, imperialism, and essentialism. For some reason racism is the most frequently emphasized. Moral outrage is a salient component

of the typical cultural anthropologist's reaction to "sociobiology," and the morally outrageous quality of "sociobiology" makes it unnecessary to be careful with facts and logic when attacking it (cf. Sahlins's argument about animals not knowing fractions).

Heavy-handed criticisms of this sort were not at all rare in the first decade after the appearance of *Evolutionary Biology and Human Social Behavior*. They cropped up frequently in intellectual discussions of either a formal or an informal variety. Often they involved people who were not anthropologists. Psychologists, economists, and educated non-academics often expressed very negative views of "sociobiology," often based on strange misconceptions about the nature of "sociobiology." In the 1990s, however, conversations of this sort have become much rarer *except when talking to cultural anthropologists*. Evolutionary theory is now widely accepted among psychologists and psychiatrists, and we also encounter many economists, political scientists, and other academics who are informed and interested in evolutionary theory. Biological anthropologists have always been evolutionists, and the majority of them are now well-informed about behavioral ecology and sympathetic to its scientific objectives. However, for some reason cultural anthropologists are the last-ditch defenders of the view that human behavior and culture are *not* influenced by our evolutionary history and that serious social and political harm will flow from any attempt to argue that they are. Although some cultural anthropologists are informed and sympathetic, the majority of cultural anthropologists continue to accept the broad outlines of Sahlins's argument. They see selectionist thinking (which they usually insist on labeling "sociobiology") as scientifically unsound and politically dangerous. We do not think Sahlins's book caused cultural anthropologists to have these views. Rather, Sahlins's book expressed deeply held views that the majority of cultural anthropologists already had. Sahlins's book resonated with their views and provided a seemingly authoritative support for them.

These negative views of "sociobiology" are surprisingly persistent. In 1998, a prominent and influential cultural anthropologist presented a colloquium in Irons's department on the future of anthropology. This leader of the profession warned the audience that they should not get involved in "sociobiology" and emphasized the "fact" that sociobiology has "horrendous implications for social policy." Most of Irons's cultural colleagues expressed agreement with this view, but little was supplied in the way of specifics about these policy implications. Several days after the talk, Irons asked one of his cultural colleagues what some of these "horrendous implications" were. In response, his colleague offered as an example the fact that *The Bell Curve* (Herrnstein and Murray 1994) was being taken seriously as an argument against affirmative action. For this cultural anthropologist, the distinction between behavioral ecology and the psychometrics of *The Bell Curve* was too subtle to take into account. Anything that was somehow biological and somehow evil could be conveniently lumped under the label "sociobiology." It appears to be irrelevant to such moralistic reasoning that *The Bell Curve* and behavioral ecology have

next to nothing in common, as shown by the fact that the bibliographies of this volume and of *The Bell Curve* include almost none of the same sources.

As we see it, the cultural anthropological condemnation of behavioral ecology as a justification for racism, sexism, or other forms of oppression is not based on solid knowledge of the paradigm.<sup>2</sup> Rather it is based on a simple assumption that any attempt to argue for an evolved human nature influencing human behavior can be rejected out of hand. Such arguments can be dismissed as “genetic determinism” and thinly veiled right-wing political plots. As the majority of cultural anthropologists see it, their discipline derives much of its value from its role in discouraging racism and sexism, and condemning “sociobiology” is an important part of that role.<sup>3</sup>

### **CHANGING TIDE: GROWING ACCEPTANCE IN MANY QUARTERS**

Sharply critical attacks on “sociobiology” continued in the late 1970s and early 1980s. Many of these critiques had provocative titles like *Not In Our Genes* (Lewontin et al. 1984), *Biology as a Social Weapon* (Ann Arbor Science for the People Editorial Collective 1977), and *Vaulting Ambition* (Kitcher 1985). The political motivation behind these books often was openly stated, as in the preface to *Not In Our Genes*: “We share a commitment to the prospect of the creation of a more socially just—a socialist—society. And we recognize that a critical science is an integral part of the struggle to create that society, just as we also believe that the social function of much of today’s science is to hinder the creation of that society by acting to preserve the interests of the dominant class, gender and race” (Lewontin et al. 1984:ix).

Since that time, the tide appears to have shifted. Kitcher (1985) was the last widely read book to attack sociobiology. Although Kitcher’s rhetoric was as negative as any of the preceding books, he conceded that nonhuman behavioral ecology was often quite sound, eventually (1990) taking the position that while “human sociobiology” was bad, “human behavioral ecology” was a promising approach. Another outsider to the approach, historian Carl Degler (1991), took a very different and much more positive view of it. Having examined the history of selectionist thinking in the social sciences since the nineteenth century, he regarded the return to this tradition in the 1970s as a corrective to an overemphasis on culture that had emerged in the early twentieth century. Furthermore, he argued that the “return of biology” did not justify racism or sexism and need not be feared on those grounds. Degler’s book was something new for behavioral ecologists who had become accustomed to a degree of “biophobia” on the part of outside reviewers. The wider acceptance of this approach in the 1990s is also evident in fields such as psychology and economics, where the testing of evolutionary biological hypotheses about behavior has become not only accepted but encouraged

and even institutionalized in some very progressive programs. At the same time, books like *Vaulting Ambition* have become rare, and instead we have a steady stream of popular books for the educated public that are positive about selectionist thinking by such authors as William F. Allman (1994), David Buss (1994), Helena Cronin (1991), Richard Dawkins (1976, 1982, 1986, 1989, 1995, 1996), Carl Degler (1991), Daniel C. Dennett (1995), Helen Fisher (1982, 1992), Sarah Hrdy (1999), Steven Pinker (1994, 1997), Matt Ridley (1993, 1996), Meredith Small (1995, 1998), and Robert Wright (1994).

Because most human behavioral ecologists are also anthropologists, special attention should be paid to the status of the approach within this discipline. Because they studied behavior and because behavior was traditionally dealt with by cultural anthropology, most anthropologists working in this approach in the 1970s identified themselves with that subdiscipline. At the time, most cultural anthropologists still felt themselves to be working within a scientific rather than a humanistic tradition. And at that time most biological anthropologists identified themselves as strictly *physical* anthropologists because they dealt with human physical evolution and modern human physical variation rather than with behavior. Since then things have changed considerably in both subdisciplines. Cultural anthropology has become increasingly humanistic and decreasingly scientific as it has embraced interpretive, hermeneutic, and postmodernist ideas from fields such as literary criticism. The study of behavior has largely been supplanted in cultural anthropology by the study of meaning. The continued biophobia of cultural anthropology is related, in a way, to the focus on meaning. It would be harder, we believe, to maintain biophobia while attempting to be scientific. Physical anthropologists, on the other hand, have increasingly identified themselves as *biological* anthropologists, reflecting that subdiscipline's expansion to include the study of behavior as well as physiology. The greater acceptance of behavioral ecological ideas among biological anthropologists than among cultural anthropologists was reflected in a survey conducted by Leonard Lieberman (1989). When asked, for example, whether the concept of kin selection was likely to be useful in the study of human behavior, 82% of animal behaviorists and 74% of biological anthropologists but only 35% of cultural anthropologists thought that it would. This difference between the subdisciplines is also reflected in an institutional shift that has occurred during the past twenty years. While most behavioral ecologists twenty years ago were identified by their departments as cultural anthropologists, these days it is more common to find behavioral ecologists being hired for positions in biological anthropology.

## DEVELOPMENTS IN HUMAN BEHAVIORAL ECOLOGY SINCE 1979

Since the heady times of the late 1970s several things have happened in human behavioral ecology. The first and most important is that, despite its public relations

problems, human behavioral ecology has become an established paradigm with a large empirical literature to its credit. While in 1976 there was one paper in print that explicitly tested a behavioral ecological hypothesis about traditional human societies (Hartung 1976), with a few more appearing in print by 1979, within a decade the number of such studies had grown dramatically. Monique Borgerhoff Mulder (1988b) did a count of all the studies she could find that met two criteria: (1) they presented a hypothesis about human social behavior derived from evolutionary theory; (2) they presented quantitative data from a traditional society to test the hypothesis. Her total count was 188. To make such a count today would be a momentous task given the enormous growth of the field during its second decade. Many of these studies have been published in the journals mentioned above, in the new journals *Human Nature* and *Evolutionary Anthropology*, and also in mainstream journals such as *Current Anthropology*, *Politics and the Life Sciences*, and *Behavioral and Brain Sciences*. A great many edited volumes on human behavioral ecology are also now available, including Winterhalder and Smith's collection of foraging studies (1981), Betzig, Borgerhoff Mulder, and Turke's collection of studies of reproduction (1988), Smith and Winterhalder's collection of critical reviews of major subfields within human behavioral ecology (1992), and Betzig's collection of classic articles along with critiques and updates (1997). The quality and rigor of the studies included in these various outlets is quite high, comparing extremely favorably with any of the other social and behavioral sciences and in particular with cultural anthropology. Reviews of this body of research have recently been published by Borgerhoff Mulder (1991), Cronk (1991), and Smith (1992), while Gray's 1985 book reviewing this research also remains very useful. At the same time, fields that currently lie outside behavioral ecology but that are essential to its continued development have also grown rapidly, including evolutionary psychology (see Buss 1995 for a recent review), cultural transmission or dual inheritance theory (see Smith, this volume), reproductive biology (e.g., Baker and Bellis 1995; Trevathan 1987), reproductive ecology (e.g., Ellison 1994; Wood 1994), evolutionary medicine (Nesse and Williams 1994), and behavior genetics (Plomin 1997).

Another event that marks the maturation of behavioral ecology and related approaches is the formation of the Human Behavior and Evolution Society (HBES). In October 1988 at the University of Michigan a conference was held that focused on the work of psychologists and psychiatrists. At this conference a decision was made by a number of the participants to form a society, and the name of the society was settled in an open discussion among the participants. William Hamilton was chosen as the first president and Randolph Nesse, who initiated and led the discussion, was chosen as the president elect. HBES's first annual meeting was held at Northwestern University, and meetings have been held every year since then at various universities. The society now publishes a journal (*Evolution and Human Behavior*, formerly *Ethology and Sociobiology*), and has about seven hundred members from psychology, anthropology, and a wide variety of other fields.

In addition, many human behavioral ecologists are members of the European Sociobiology Society and the International Society for Human Ethology.

At the level of theory, human behavioral ecology has also made considerable strides. One major improvement since the late 1970s is the convergence of work on mating, parenting, and social behavior, on the one hand, with work on foraging strategies on the other. In the 1970s these areas were mostly explored by different groups of researchers, whereas in the 1980s and into the 1990s the distinction between them has become increasingly blurred and both lines of thought have become enriched. This has happened as people have considered the possibility that social and reproductive goals may influence economic strategies and, conversely, that the characteristics of resources and environments may affect mating, parenting, and social behavior. Examples include Smith's analysis of forager group size (1981, 1985, 1991); Hawkes's showoff model (1990, 1991, 1993); work by Winterhalder (1986, 1990), Kaplan and Hill (1985), Kaplan, Hill, Hawkes, and Hurtado (1984), Kaplan, Hill, and Hurtado (1990), and Blurton Jones (1987b) on food sharing (see also Bliege Bird and Bird 1997); Blurton Jones's (1987a) analysis of !Kung women's foraging work and birth spacing; Borgerhoff Mulder's application of the polygyny threshold model to the mate choices of Kipsigis women (1990); and Cronk's (1989) analysis of subsistence change among the Mukogodo as a result of reproductive rather than economic considerations. This approach is also well represented in the contents of this volume (e.g., the chapters by Hames, Hewlett and colleagues, Kaplan and Lancaster, Low, Sellen and colleagues, Sosis, and Sugiyama and Chacon).

Developments in nonhuman behavioral ecology and evolutionary biology also have had an impact on human behavioral ecology. For example, a persistent bugbear of this approach in its early years was the specter of "genetic determinism." Many people outside behavioral ecology thought that in order for the theory of natural selection to be relevant to the understanding of a particular behavior, that behavior must be under strict genetic control. The posture of behavioral ecology on this issue has been clarified by Alan Grafen (1984) under the label "the phenotypic gambit." This phrase refers to the fact that behavioral ecologists focus on phenotypes, which may be influenced by many nongenetic factors such as environment and culture, rather than genotypes, and set aside the details of the heritable basis of the traits in question as neither directly relevant to the behavioral ecological project nor feasible to demonstrate in most cases (see also Smith and Winterhalder 1992:33–34). Theoretical developments in other areas, such as sexual selection (e.g., Grafen 1990a, 1990b; Hamilton and Zuk 1982; Zahavi et al. 1997), sexual attractiveness (e.g., Gangestad and Thornhill 1996), life history theory (see Hill 1993), game theoretical models (see Weibull 1995), and animal communication (see Dawkins and Krebs 1978; Hauser 1996; Johnstone 1997; Krebs and Dawkins 1984; Zahavi et al. 1997) also have had an impact on human behavioral ecology and evolutionary psychology. At the same time, human behavioral ecologists and their allies have begun to tackle problems unique to the species they

study, including culture (e.g., Barkow 1989; Boyd and Richerson 1985; Cronk 1995; Durham 1991; and Irons 1979), morality (Alexander 1987; Cronk 1994a, 1994b; Frank 1988; Irons 1991, 1996; de Waal 1996), and the demographic transition (see chapters in this volume by Kaplan and Lancaster, Low, Luttbeg and colleagues, and Mace).

## BACKGROUND TO THIS VOLUME

This volume was conceived of as a way both to update and to commemorate *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. Accordingly, we thought an appropriate way to start would be with sessions at the 1996 annual meetings of the American Anthropological Association, and we eventually organized two long sessions involving a total of twenty-six papers and two discussants. As was the case with the 1976 session and the 1979 volume, the presentations at the 1996 meeting form the core of this volume.

For the most part, this volume is organized along fairly traditional lines in behavioral ecology. It begins with "Some Statements of Theory," a title borrowed from the 1979 volume. Whereas in the 1970s it was necessary to begin with chapters that introduced the general approach, its fundamental concepts, and some of its key hypotheses, twenty years later the basics of the paradigm are widely enough known and so generally agreed upon by most practitioners that restating the basics no longer seems necessary. Instead, we begin with this chapter that puts the volume in a historical context and the next chapter by Smith that compares the approach taken in most of this volume with other contemporary approaches to the evolutionary biological study of human behavior.

Behavioral ecologists think in terms of the allocation of effort, and traditionally the starting point is somatic effort, in other words, what an organism does to develop and maintain itself. Although a few years ago a book like this probably would have begun with a section on somatic behavior featuring a series of optimal foraging studies, in the 1990s most research on human foraging is being conducted not solely with an eye toward understanding diet and patch choices but rather as integral parts of examinations of reproductive and social behavior. In this volume, for example, data on food acquisition play a role in but are not the central focus of chapters by Blurton Jones and colleagues on divorce in hunting and gathering societies, by Hawkes and her coauthors on grandmothers and the origins of human females' long postmenopausal lifespans, by Sugiyama and Chacon on injury risk and foraging strategies, and by Sosis on cooperative fishing. Accordingly, although this volume contains a great deal of information about foraging, the data are distributed throughout the volume rather than collected in a single section.

Two sections of the book concern reproductive behavior, divided into the traditional categories of mating and parenting. Beverly Strassmann's chapter on the Dogon of Mali examines the costs of polygyny to women in terms of child sur-

vivorship. The chapter by Nicholas Blurton Jones, Frank W. Marlowe, Kristen Hawkes, and James F. O'Connell examines divorce rates in several hunter-gatherer societies and finds little support for the traditional paternal investment theory of human pair bonding. The chapter by Daniel W. Sellen, Monique Borgerhoff Mulder, and Daniela Sieff examines the costs and benefits of polygyny among the Eyasi Datoga of Tanzania, finding, among other things, that having a single co-wife can be costly, especially to women married to poor men, and suggesting that we need to look at the constraints on women's choices if we are to understand the maintenance of polygyny in this group. Napoleon Chagnon updates his earlier work (1988) on Yanomamö kin term manipulation as a form of reproductive competition, showing that adult males are more accurate than adult females in classifying their kin. Doug Jones combines an anthropological interest in the cultural construction of race with an evolutionary psychological interest in physical attractiveness in a study of racial categorization and attractiveness ratings by Brazilian men and women.

The next group of chapters examines why people take care of children in the ways that they do: Why do some parents invest more in their offspring than do other parents? Why do some men invest in children that are not their own? Why do some parents invest more heavily in sons while others invest more in daughters? Why do women's life histories make it possible for them to invest in their grandoffspring rather than having more offspring of their own? Barry S. Hewlett, Michael E. Lamb, Birgit Leyendecker, and Axel Schölmerich use data from foraging, farming, and industrialized societies to evaluate three adaptationist models of parental investment. Jane B. Lancaster and Hillard S. Kaplan use data from their large survey of men in Albuquerque, New Mexico, to examine the question of why men sometimes behave parentally toward children they know not to be their own offspring, finding that the child in question is usually either a relative of the investor, making the investment a form of kin altruism, or the investor's mate's child, making the investment a form of mating effort. The chapters by Lee Cronk and William Irons present tests of the Trivers-Willard hypothesis of sex-biased parental investment both in a society known for female-biased parental behavior and in one with a reputation for male favoritism. In their chapter, Kristen Hawkes, James F. O'Connell, Nicholas Blurton Jones, H. Alvarez, and E. L. Charnov propose that human females' long postmenopausal lifespans may have evolved because of the ability of older women to help their younger kin reproduce.

The next section breaks from tradition in human behavioral ecology by looking not at why or how people have so many children but rather at why in some societies they have so few. With encouragement from critics like Vining (1986), in recent years a number of behavioral ecologists have examined the problem of the demographic transition: Why have people in the wealthiest, most economically developed societies increasingly chosen to have so few offspring? Does this fact undermine and even falsify the entire behavioral ecological project, as some would argue, or is there instead an evolutionary logic behind the limitation of

family size? Ruth Mace's chapter examines this question with a dynamic model of decisions about the timing of reproduction and the inheritance of wealth and finds that increases in the costs of children may be a key to the fertility reduction associated with the demographic transition. Hillard S. Kaplan and Jane B. Lancaster use data from their large survey of Albuquerque men to test their hypothesis that fertility reductions in modern societies reflect a response on the part of parents to an environment in which the wages workers receive, and hence their wealth, is directly linked to the costs of obtaining the skills necessary to be competitive in today's skills-based labor markets. Bobbi Low takes a critical look at the problem of the demographic transition, arguing that in order to solve it we need better data as well as a better understanding of the relationship between resource consumption and fertility. Finally in this section, Barney Luttbeg, Monique Borgerhoff Mulder, and Marc Mangel present the results of a dynamic model of men's decisions to take additional wives, recommending that similar modeling methods would be useful in the study of the reproductive decisions of people during the demographic transition.<sup>4</sup>

The chapters on sociality demonstrate the extent to which human behavioral ecologists have gone beyond simple demonstrations of nepotism to the examination of a range of other factors influencing reciprocal aid and cooperation. Lawrence Sugiyama and Richard Chacon examine the effects of pathology on the productivity of foraging among the Yora and Shiwiari of the Ecuadorian Amazon, suggesting that the need to receive aid when disabled may help explain a variety of social phenomena including group sizes and food sharing. Raymond Hames looks at food sharing among the Yanomamö, finding that it is mostly restricted to groups of households who preferentially share with each other. John Q. Patton examines the role of altruism in warfare in the Ecuadorian Amazon. Richard Sosis tests theoretical models of the emergence and stability of cooperative foraging with data on cooperative fishing and fish catch distribution from the Micronesian atoll of Ifaluk. Finally, J. Patrick Gray provides a critical and constructive commentary on the state of this approach more than two decades after it began to take off, suggesting, among other things, that in the future selectionist social science needs to do more to incorporate the concept of culture.

## THE FUTURE

Explanation in biology is usually conceived of as occurring on four complementary levels: evolutionary or phylogenetic explanations that focus on the origins and evolutionary history of a trait; ultimate or distal explanations that focus on how the trait is spread and maintained through its positive effects on the inclusive fitness of its bearers; developmental or ontogenetic explanations that focus on how the trait develops during the lifetime of the individual organisms; and proximate explanations that focus on the immediate details of the trait's expression in individual organisms (based on Mayr 1961 and Tinbergen 1963). Behavioral ecol-

ogy has focused primarily on ultimate or distal explanations, but we agree with Barkow (1989), Cronk (1991), and others who have called for increased vertical integration in the evolutionary study of human behavior. Major steps in this direction have already been taken, particularly in the areas of hominid evolutionary ecology (Alexander 1990; Foley 1987, 1992), evolutionary developmental psychology (e.g., Belsky, Steinberg, and Draper 1991), and the study of the proximate psychological and physiological factors influencing human behavior (e.g., Flinn and England 1995). Along with increased vertical integration, there is a need for increased horizontal integration among a variety of complementary and closely related approaches, including behavioral ecology, cultural transmission theory, evolutionary psychology, behavior genetics, and reproductive ecology. In addition, we need to improve our field methods, our models, and our methods of analysis, and we need to tackle tougher subjects that either may challenge our approach or lie outside our traditional areas of inquiry.

These tendencies are already evident in current research, and many of them are well demonstrated in this volume. A move toward a blending of behavioral ecology and evolutionary psychology is indicated by Jones's chapter on sexual attractiveness in Brazil. Improved research design and field methods are evident in many chapters, including the prospective design of Strassmann's study of Dogon polygyny and child mortality, Cronk's and Sellen and his coauthors' use of anthropometry to assess child growth performance, the systematic behavioral observations used in Strassmann's, Cronk's, and Hewlett and colleagues' chapters to assess childcare patterns, Chagnon's creative interview techniques, and the large-scale survey of Kaplan and Lancaster and Lancaster and Kaplan. More sophisticated modeling techniques are demonstrated in the chapters by Luttbeg and colleagues, Mace, and Sosis. Innovations in data analysis are exemplified by Jones's and Patton's use of multidimensional scaling techniques. Theoretical progress is evident in many chapters, including Blurton Jones and colleagues' rethinking of the nature of human pair bonding, Hawkes and colleagues' use of new developments in life history theory, Sugiyama and Chacon's insights into the influence of pathology risk on human social behavior, the distinction Hames draws between food-sharing patterns among the horticultural Yanomamö and that seen in foraging groups, and Kaplan and Lancaster's skills-based competitive labor markets theory of the demographic transition. And, finally, a willingness—indeed, an eagerness—to tackle subjects that are daunting in their complexity and that have been promoted as challenges to the entire approach (e.g., Vining 1986) is well demonstrated by the four chapters on demographic transition theory by Kaplan and Lancaster, Low, Luttbeg and colleagues, and Mace.

## CONCLUSION

A legitimate question to ask of any research program is whether it has produced any new knowledge. Human behavioral ecology and closely related approaches

can give a confident affirmative answer to this question. Thanks to the research that has gone on over the past twenty years, we know that human nature is not the blank slate it once was thought to be. Rather, to continue the metaphor, the slate has much written on it, and some things are much easier to write on it than others. We know for example that human beings tend to learn with ease who their relatives are and to be more cooperative and less competitive in dealing with them than with nonrelatives. We know that they tend to adjust their parenting strategies so as to be more nurturing of children of the sex with the greater reproductive potential if there is a predictable difference in reproductive opportunities. We know that although men's and women's mate preferences have considerable overlap, they also differ, on average, in a way predicted by evolutionary theory. We know that in a variety of contexts, ranging from foraging to cooperative arrangements, people tend to respond to costs and benefits as measured in terms of inclusive fitness or a good proxy currency. We know that in societies that resemble those in which humans evolved, the goals people consciously strive to achieve generally correlate with reproductive success. This accumulated knowledge represents considerable progress since the time of *Evolutionary Biology and Human Social Behavior*, when we hypothesized these tendencies but could offer only a few empirical tests of them. We now have a large body of data from many different societies, giving the field a solid foundation and setting the stage for further refinements of the approach. We hope that the readers of this volume find that the studies included here take us even further toward our goals.

## SUMMARY

1. Human behavioral ecology has its theoretical roots primarily in the 1960s and early 1970s in work by W. D. Hamilton and Robert Trivers on sociality and parental investment, George C. Williams on the issues of adaptation and levels of selection, and Robert MacArthur and Eric Pianka on foraging strategies.

2. Research into the evolutionary biology of human behavior began in earnest in the 1970s and was showcased in a session organized by Napoleon A. Chagnon and William Irons at the 1976 annual meetings of the American Anthropological Association and in a subsequent edited volume, *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (Chagnon and Irons 1979). The present volume is in part in commemoration of the twentieth anniversary of that early work.

3. Although initial reaction to this new approach was sharply critical, especially among cultural anthropologists, over the past two decades the approach has gained new adherents and has developed in terms of its empirical findings, its methods, and its theories. Its development has been aided in this by the establishment of a number of new journals and organizations dedicated to research on the evolution of human behavior.

4. Human behavioral ecology can claim to have produced a great deal of new knowledge on many fundamental issues in the evolution of human behavior. The state of the art of this new and still rapidly developing approach is exemplified by the chapters in this volume on such issues as mating, parenting, the demographic transition, and sociality.

## NOTES

1. For example, Jerome Barkow, Rada Dyson-Hudson, and Eric Alden Smith presented papers at the AAA symposia that, for various reasons, were not included in the 1979 volume, Nicholas Blurton Jones and John Hartung began to publish such work at about this time, and Bruce Winterhalder (1977) had recently completed the first application of optimal foraging theory to humans.

2. Justifying oppression and describing it are not the same thing. One needs to keep the naturalistic fallacy in mind. We challenge anyone to make a good argument to the effect that any of the chapters in this volume justify, as opposed to describe, oppression.

3. For a recent example, see Dagg 1998 and the response by Silk and Stanford 1999.

4. For other evolutionary approaches to the demographic transition not included in this volume, see Bereczkei 1998; Rogers 1992; and Turke 1989.

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