ANTHROPOLOGY AND THE EVOLUTIONARY STUDY OF HUMAN BEHAVIOR

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INTRODUCTION

Anthropology is a discipline with an unusually broad subject matter, spanning virtually the entire human experience, from the origins of our species through human prehistory to modern cultural diversity. A diverse subject matter implies a diversity of approaches, and anthropologists run the gamut from the most technical genetic research to personal, poetic accounts of other cultures. This diversity makes for an interesting and lively discipline, but also one with a history of sharp divisions over issues as fundamental as the definition of the field and its subject matter. Traditionally, anthropologists have dealt with these internal divisions by following the old adage that good fences make good neighbors, i.e. by dividing the discipline into largely autonomous subdisciplines. These days American[1] anthropologists usually conceive of four such subdisciplines: social, cultural, or sociocultural anthropology; biological or physical anthropology, which includes human paleontology and primatology; archaeology; and linguistic anthropology. Sometimes applied anthropology is included as a fifth subdiscipline.

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EARLY DEVELOPMENT OF EVOLUTION AND BEHAVIOR STUDIES IN ANTHROPOLOGY

Evolution and culture have long been the two core concerns of anthropology. In the nineteenth century, major anthropological thinkers such as Lewis Henry Morgan, E. B. Tylor, and Herbert Spencer considered both of these issues at the same time, using archaeological and cross-cultural information to develop ambitiously broad accounts of human social and cultural evolution. This changed dramatically around the turn of the twentieth century when Franz Boas, the founder of anthropology as an academic discipline in the United States, pointed out that a great deal of theorizing was being done without very much information at hand (Boas, 1896). As a remedy, Boas eschewed theory and recommended long term immersion by ethnographers in different societies around the world. He also argued that the method used by the evolutionists, which relied heavily on analogies between contemporary societies and prehistoric ones, was on shaky logical ground. Contemporary societies, he argued, far from being living fossils of past societies, had their own particular histories that must be understood, and to do otherwise is to run the risk of being ethnocentric. Thanks to these sorts of arguments by Boas and his followers, not only the culture concept but also the closely related doctrines of cultural determinism and cultural relativism became central to the discipline of anthropology in general and to the subdiscipline of cultural anthropology in particular.

Outside the cultural subdiscipline, anthropologists retained evolution as a core concern. Archaeologists continued to ponder the long sequences of societal development they learned about through their excavations, and physical anthropologists continued to focus on hominid evolution and the causes of physical variations among contemporary humans.[2] An equilibrium of sorts developed between those anthropologists interested in evolution and those interested in culture. Evolutionary anthropologists were free to apply their principles to the study of hominids, prehistory, and even physical variation among contemporary humans, but for the most part they refrained from saying much about the behavior of modern humans. Behavior was considered to be within the realm of culture, and that subject was largely left to the cultural anthropologists.

This equilibrium began to be upset in the 1960s and early 1970s as a result of breakthroughs in the study of animal behavior. Some of these breakthroughs were empirical and methodological and are well represented by the work of people like Niko Tinbergen and Konrad Lorenz. Theoretical breakthroughs soon followed, with W. D. Hamilton's (1964) inclusive fitness theory leading the way. Hamilton pointed out that because related individuals share some of the same genes by virtue of the fact that they have common ancestors, selection

may sometimes favor genes that lead their bearers to do things that harm their own reproductive interests if in so doing they increase the reproductive success of relatives. This became the centerpiece of what is sometimes called "selfish gene theory" (Dawkins, 1976), the idea that we can gain great insight into behavior by focusing on the differential reproduction not of groups or individuals, but of genes. Williams (1966) contributed a key argument for why selection is likely in most circumstances to act most strongly through the differential survival and reproduction of individual organisms and the genes they carry rather than through groups of organisms. 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. In a series of seminal articles in the early 1970s, Trivers (Trivers, 1971, 1972, 1974; Trivers & Hare, 1976; Trivers & Willard, 1973) extended selfish gene thinking to topics such as reciprocity, parental behavior, and sexual selection.

This new, evolutionary approach to behavior was introduced to anthropology by the iconoclastic work of such scholars as Lionel Tiger and Robin Fox (e.g. Tiger, 1969; Tiger & Fox, 1971), who suggested that such an approach might be very revealing if applied to humans, as well. A number of other anthropologists also took an early interest in this approach, including Earl Count, Irven DeVore, Derek Freeman, and Robert Hinde. While most of the early work was rather speculative, that began to change in the mid-1970s following several key publications by biologists. First among these was University of Michigan biologist Richard Alexander's 1974 article on evolution and social behavior, in which he gave detailed suggestions for how hypotheses derived from evolutionary theory might be tested with data on behavior from different human societies. Soon thereafter, E. O. Wilson's *Sociobiology: The New Synthesis* (1975) and Richard Dawkins' *The Selfish Gene* (1976) attracted more attention, and more people became interested in testing the new models.

Armed with these new ideas, a small group of anthropologists began to reanalyze cross-cultural data and data from their own fieldwork. Some of this early work was showcased in two sets of sessions at the 1976 meetings of the American Anthropological Association, one organized by Napoleon Chagnon and William Irons and the other by Irven DeVore. These sessions formed the basis for the landmark 1979 edited volume *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (Chagnon & Irons, 1979). Other important early work included John Hartung's (1976) cross-cultural study of inheritance practices in light of the theory of natural selection and Bruce Winterhalder's (1977) study of hunting and gathering among the Cree of Canada, the first use of optimal foraging theory on data from humans. These

studies addressed many traditional concerns in anthropology, including kinship, marriage, and stratification. The methods and data were also largely of traditional anthropological varieties. Their key novel element was hypotheses derived from evolutionary biological theory: Are humans generally nepotistic? Does a tendency towards nepotism influence family organization and residential patterns? Do parents direct their investment in their offspring in ways that increase the number of their grandchildren? Do efforts to achieve high status enhance reproductive success? Are the choices people make about food acquisition, such as where to hunt, how long to hunt, and which species to hunt, efficient in terms of the amount of food acquired in the time available? Do patterns of food exchange among individuals and households reflect a concern with reciprocity?

As is the case with many new fields, it took time for a consensus to develop on what to call this approach. In the 1970s, many followed E. O. Wilson's lead and called it sociobiology, while a few used anthropologist Lionel Tiger's older label "biosociology," instead. These neologisms reflected a felt need to distinguish the new approach based on the ideas of Hamilton, Williams, and Trivers from such earlier approaches as cultural ecology, human ecology, and ecological anthropology (see Orlove, 1980 for a review). When Wilson's application of evolutionary theory to human behavior attracted a great deal of criticism (e.g. Sahlins, 1976; Lewontin et al., 1984; Kitcher, 1985), sociobiology became less popular as a label, even though the approach itself was flourishing. Various other labels have been tried by both proponents and opponents of the new paradigm, including socioecology, evolutionary ecology, Darwinian ecological anthropology, evolution and behavior studies, and ethology. Most of the differences among these labels are cosmetic, but to some extent they do reflect slight differences between various groups of researchers in theoretical or substantive foci. In the 1980s and 1990s the label "behavioral ecology" came to be used more often than any other, and so that is the one chosen for use in the remainder of this article.

THE INITIAL RECEPTION BY ANTHROPOLOGISTS

The initial reaction to these ideas in anthropology was quite hostile. At the 1976 meeting of the American Anthropological Association, a motion was put before the business meeting to condemn sociobiology. The motion was defeated by a narrow margin following testimony against it by, paradoxically, some prominent anthropologists who were on record as opposing the new approach. 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 could be misconstrued as condemning any use of Darwinian theory. At about the same time, the journal of the American Anthropological Association, *American Anthropologist*, published negative reviews of some of the early books on the approach. For example, Elliot Chapple (1976) wrote that E. O. Wilson's *Sociobiology* "clearly wins the prize as the worst book in biology for 1975." John Buettner-Janusch (1976) described Richard Dawkins' *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." University of Chicago anthropologist Marshall Sahlins even went so far as to publish his own short book entitled *The Use and Abuse of Biology* (Sahlins, 1976) in an effort to nip the weed of sociobiology in the bud.

The hostility and suspiciousness that greeted the new paradigm had a number of causes, some justifiable but most the products of misunderstandings, ignorance, and flawed logic on the part of the critics. In the first place, it must be admitted that some of the most widely read early sociobiologists had a tendency to make pronouncements about the evolutionary origins of particular human behaviors without first subjecting them to rigorous hypothesis testing. But certainly the same could be said of much cultural anthropology, a sub-discipline without a good track record of adherence to the hypothetico-deductive method. Furthermore, since the mid-1970s human behavioral ecologists have gone to great lengths to emulate the rigor and precision of their colleagues in nonhuman behavioral ecology, and it is now not an idle boast to say that their studies include some of the more rigorously and thoroughly tested hypotheses in the history of anthropology.

Overall, the negative reaction of most anthropologists to human behavioral ecology seems to have had much less to do with the quality of the research than with the way it challenged existing and cherished ideas in the discipline. Most cultural anthropologists consider the discipline's main contribution to have been a demonstration of the overwhelming influence of culture on human affairs. Sometimes this emphasis on culture takes on the air of a religious conviction, as, for example, when two leading cultural anthropologists write that the purpose of ethnography is "to persuade the reader that culture matters more than he might have thought" (Marcus & Fischer, 1986: 43). Many cultural anthropologists are concerned that any study of possible biological influences on behavior will undermine this accomplishment. While it is true that the culture concept is absent from most human behavioral ecological writings, this is rapidly changing as more people in the field find ways to incorporate the culture concept into their research (see below and Cronk, 1995, 1999).

Cultural anthropologists also fear that human behavioral ecologists will commit a logical error known as the "naturalistic fallacy," the idea that what is natural is somehow good (Moore, 1903). In particular they worry that if behaviors (e.g. rape: Thornhill & Palmer, 2000) are described as products of natural selection and therefore "natural," this will be used to justify them morally. Fortunately, the naturalistic fallacy is something that human behavioral ecologists are well aware of, and most are scrupulous to avoid it and to encourage their students and readers to avoid it, as well. It is routine for articles by human behavioral ecologists to include disclaimers about the impossibility of deriving moral conclusions from arguments about the evolutionary origins or adaptiveness of particular behaviors in their publications. Perhaps cultural anthropologists are nervous about the naturalistic fallacy because they routinely commit virtually the same fallacy in another guise. Most cultural anthropologists believe in some form of cultural relativism. One implication of cultural relativism is that it is difficult, and perhaps impossible, to make valid value judgements across cultural boundaries because everyone's values are valid in their own particular societies, and there is no moral ground outside specific cultural traditions on which we can stand. So when we see people in other societies doing things we find objectionable, we are not allowed to criticize them because their behaviors are determined by their cultures. In other words, what is "cultural" is "good," or at least immune to criticism. Because this *reductio ad absurdum* of cultural relativism makes no more sense than the notion that what is "natural" is "good," it should be known as the "culturalistic fallacy" (Cronk, 1999: 114). Both the naturalistic and culturalistic fallacies are members of a much broader type of fallacy, first pointed out by David Hume ([1739/40] 1966), in which one derives a moral precept from a description of the way things are. It is no more acceptable to violate Hume's separation of "is" and "ought" statements when explaining behavior using the culture concept than when explaining it using evolutionary theory. Human behavioral ecologists are abundantly aware of the potential of their research to lead to the naturalistic fallacy; regrettably, most cultural anthropologists seem oblivious to the potential of their approach to lead to the culturalistic fallacy.[3]

Many of the arguments against human behavioral ecology have a clear political dimension. As Sahlins has argued, "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" (Sahlins, 1976: 101). In other words, the evolutionary approach to human behavior, far from being an objective account of the origins of human behavior, is merely a manifestation of the Western, capitalist, bourgeois worldview. As such, it is designed not to improve understanding but rather to further the interests of the capitalist ruling class.

Other critics have been equally clear about their political motivations: "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). The idea that they are little more than capitalist stooges comes as a bit of a shock and an affront to the many human behavioral ecologists who are committed to political and economic change and enhanced social justice. It also betrays the critics' ignorance of the fact that the basic theoretical ideas of people like Hamilton and Trivers have as much or more to do with co-operation as 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?"

ACCOMPLISHMENTS

The project of early human behavioral ecology was conceived in very broad terms: To test the idea that human behavior across cultures tends to conform in broad outline with expectations derived from current evolutionary biological theory. The obvious alternative hypothesis was that because culture operates according to its own internal logic, human behavior should conform to predictions derived from evolutionary theory no more often than one would expect by chance (e.g. Sahlins, 1976). The conflict between these views of culture and its role in shaping human behavior was brought to the fore when William Irons proposed that, if evolutionary theory is relevant to the study of human behavior, there should be a correlation between individuals' achievement of the goals that are promoted by the cultures of the societies in which they live and their achievement of the goal hypothesized by evolutionary theory, enhanced inclusive fitness. In Irons' own terms, "in most human societies cultural success consists in accomplishing those things which make biological success (that is, high inclusive fitness) probable" (Irons, 1979: 258). It should be noted that this hypothesis is in no way contingent on anyone being aware of the connection between cultural and reproductive success. If culture is serving to guide people to behave in ways that in their particular local circumstances enhance reproduction, it should do so even if people are unaware not only of the goal of reproduction but even of how biological reproduction works.

One of the first tests of this hypothesis was Irons' own study of Yomut Turkmen pastoralists of northern Iran. He found that wealth correlated well with men's lifetime reproductive success (Irons, 1979). Similarly, Monique Borgerhoff Mulder (1987) found the same correlation among Kipsigis agro-pastoralists in western Kenya, as did I among Mukogodo pastoralists in north central Kenya (Cronk, 1991b). In all of these cases, the circumstances are somewhat similar: local definitions of male status and definitions of success are mainly determined by wealth, livestock are a large part of what constitutes wealth, substantial bridewealths must be paid by grooms to their in-laws in order to marry, and polygyny is allowed. Given these conditions, it may not seem surprising that men's wealth would correlate with both their numbers of wives and their reproductive success. But the situation is not as obvious as it might seem at first glance. If the local definitions of "success" were arbitrary cultural constructions and nothing more, then it would be surprising indeed to find so many societies in which success is defined largely in terms of wealth accumulation. The fact that wealth is a major determinant of status and prestige in so many societies in so many different parts of the world suggests that local definitions of success, far from being arbitrary, may be designed for a purpose.

But what about societies in which wealth is either not accumulated at all or not the sole or even a major correlate of status or prestige? In such cases, a variety of other locally valued characteristics have been found to correlate with reproductive success, including political status (Betzig, 1986; Chagnon, 1979), hunting skills (Kaplan & Hill, 1985), involvement in violence (Chagnon, 1988a), peace-keeping (Moore, 1990), and certain personality traits (Barkow, 1977). The pattern emerging seems to provide strong support for Irons' hypothesis in natural fertility societies (i.e. those without access to modern contraceptives): achievement of success as it is locally defined is a good predictor both of an individual's status and of his reproductive success, regardless of the details of the local environment, economy, or social system. This suggests that the highly variable definitions of high status across human societies may indeed be cultural constructions, but not randomly variable ones. Rather, local opinions about what constitutes success may be the outcomes of ongoing negotiations among fundamentally similar actors in highly variable environmental, political, social, and historical situations.

The widespread confirmation of Irons' prediction of a match between cultural and reproductive success helps justify a continuation of the human behavioral ecological project. Accordingly, over the past twenty-five years human behavioral ecologists have tested a wide variety of more specific hypotheses derived from evolutionary theory on a wide variety of topics. Because human behavioral ecologists are guided by the paradigm of non-human behavioral ecology, many

of the topics covered are the same as those one would find covered in animal behavior textbooks and journals: foraging behavior (e.g. Hawkes et al., 1982), conservation (e.g. Alvard, 1998), sex biased parental investment (e.g. Cronk, 2000; Irons, 2000), male parental behavior (e.g. Hewlett 1991; Lancaster & Kaplan 2000), menstruation (e.g. Strassmann, 1996), nepotism (e.g. Chagnon & Bugos, 1979), reciprocity (e.g. Hames, 2000; Patton, 2000; Sosis, 2000), conflict (e.g. Chagnon & Bugos, 1979; Chagnon, 1988a; Patton, 2000), termination of pair bonds (e.g. Betzig, 1989; Fisher, 1989; Blurton Jones et al., 2000), polygyny (e.g. Borgerhoff Mulder, 1990; Strassman, 2000), and polyandry (e.g. Haddix, in press).

The basic method of human behavioral ecology can be demonstrated by looking at a study of human behavior closely modelled on similar studies of animal behavior. Polygyny, a mating system in which one male mates with several females, is common among both humans and non-humans, and occurs for a variety of reasons. *Resource defense polygyny* occurs when males defend important resources such as nesting sites and food-bearing territories in order to mate with the females who need those resources (see Emlen & Oring, 1977). A question raised by resource defense polygyny is why a female would mate with an already mated male if an unmated male, who would provide the female with access to all of the resources he has monopolized, is also available. In order to explain such behavior, ornithologist Gordon Orians (1969) proposed that if the quantity or quality of the resources monopolized by the males varies a great deal from one male to another, then sometimes a female might gain access to more or better resources if she mates with a male who is already mated, forcing her to share the resources with at least one other breeding female, rather than by mating with a solitary male who has few or poor resources. This *polygyny threshold* model has been successfully applied to a variety of bird species (e.g. the indigo bunting: Carey & Nolan, 1975, 1979).

Resource defense polygyny is common in human societies, as well. Among the Kipsigis, an agropastoralist group in western Kenya, for example, men own land and livestock and can have more than one wife at a time. Women often marry men who are already married, and they usually move from their parents' households to their new husband's land. Monique Borgerhoff Mulder, an anthropologist and human behavioral ecologist at the University of California at Davis, wondered whether Kipsigis' decisions about marriage fit with the predictions of Orians' polygyny threshold model. Specifically, she wondered whether women and their families selected husbands with an eye toward their control of resources, taking into account the fact that if a woman marries an already-married man, she will have to share his land with his earlier wives. The data support this prediction: Kipsigis women have a statististically significant

tendency to choose men according to the amount of land they offered the woman to farm, regardless of the number of cowives they would have as a result (Borgerhoff Mulder, 1990).

Because most human behavioral ecologists are, for the most part, also anthropologists, their studies are guided not only by the concerns of animal behavior studies but also by the traditions of the field of anthropology. As a result, they also study a wide variety of topics that are unique to humans and for which appropriate models do not already exist in the literature on animal behavior. These include kinship terminologies (e.g. Chagnon, 1988b, 2000; Hawkes, 1983), inheritance practices (e.g. Hartung, 1976; Borgerhoff Mulder, 1989), menopause and long post-reproductive lifespans in women (e.g. Hawkes et al., 2000), systems of economic redistribution (e.g. Betzig, 1988), bridewealth and dowry (e.g. Borgerhoff Mulder, 1988; Gaulin & Boster, 1990), and morality (e.g. Alexander, 1987; Cronk, 1994; Irons, 1991). One way in which our species is unique is its extreme behavioral plasticity, which makes it possible for us to live in a wide variety of circumstances and swiftly to change basic elements of our lives, such as how we obtain food. My own behavioral ecological analysis of a quick transition in subsistence among the Mukogodo of Kenya explores this distinctively human phenomenon. Before 1900, the Mukogodo were foragers and beekeepers who lived in rockshelters in a rugged, forested range of hills in north central Kenya. They spoke their own distinct language, called Yaaku, and had their own religion and other customs, such as the payment of beehives as bridewealth. Within a few years early in the twentieth century, they dropped their old language, subsistence patterns, and religion in favor of those of the Maasai. This swift transition presents an opportunity to test an extension of Irons' hypothesis about cultural and reproductive success: when a society's environment changes, culture may help people track changing environments in a way that would enhance their fitness (Irons, 1979: 258). The reasons for the change lie in a combination of changes in the social environment of the Mukogodo brought on by the British colonial presence and the way the Mukogodo responded to those changes. Specifically, British policies led a variety of Maasai-speaking pastoralists groups into steady contact with the Mukogodo and also gave them strong incentives to marry the Mukogodo. Marrying daughters and sisters to pastoralists was attractive to Mukogodo because the bridewealths they received from the pastoralists in the form of livestock were worth many times the value of a traditional Mukogodo beehive bridewealth. Quickly, no Mukogodo fathers would accept mere beehives as bridewealth and remaining a hunter-gatherer was no longer a viable option: Mukogodo men had to obtain livestock and become pastoralists or never marry. In behavioral ecological terms, the environment had changed so drastically that

the cultural values and practices that previously had been good guides to enhanced inclusive fitness – hunting, gathering, beekeeping, Yaaku-speaking, and so on – no longer were, and the Mukogodo responded by shifting to the cultural values and practices of their new Maasai-speaking neighbors, such as pastoralism and the Maasai language (Cronk, 1989).

INSTITUTIONAL DEVELOPMENTS

Human behavioral ecology has sparked the development of several new professional associations, journals, and graduate programs. The most prominent of the new associations is the Human Behavior and Evolution Society (HBES). HBES has about a thousand members, mostly from anthropology and psychology but also from related fields such as biology, sociology, and even many humanities disciplines. HBES has held annual meetings since 1989, usually during the summer on a college campus, and it has adopted a previously existing journal, *Ethology and Sociobiology*, and renamed it *Evolution and Human Behavior*. Other groups to which many human behavioral ecologists belong include the International Society for Human Ethology, the International Society for Behavioral Ecology, and the European Sociobiological Society. In addition to *Evolution and Human Behavior*, human behavioral ecological research is routinely published in the journals *Human Nature: An Interdisciplinary Biosocial Perspective, Behavioral Ecology and Sociobiology*, and *Behavioral Ecology*, as well as in a variety of more general anthropology journals, particularly *Current Anthropology*.

Graduate study in human behavioral ecology is now possible in many of the world's top anthropology programs. The two most prominent programs in recent years have been at the Universities of Utah and New Mexico. Other institutions with human behavioral ecologists teaching in graduate anthropology programs include Emory, Harvard, Northwestern, Pennsylvania State, Rutgers, Texas A&M, and Washington State Universities; the Universities of Arkansas, Connecticut, Michigan, Missouri, Nebraska, North Carolina, Oregon, Pittsburgh, and Washington; and the University of California at Davis, Los Angeles, and Santa Barbara. Outside the United States, human behavioral ecology is taught at the graduate level at University College London and at Dalhousie University in Nova Scotia.

Anyone interested in learning more about this approach would do well to start with one of many good review articles available (e.g. Borgerhoff Mulder, 1991; Cronk, 1991a; Smith, 1992a, b; Voland, 1998; Winterhalder & Smith, 2000). The development of human behavioral ecology has also been marked by the publication of a series of excellent edited volumes: *Evolutionary Biology*

and Human Social Behavior (Chagnon & Irons, 1979), *Hunter-Gatherer Foraging Strategies* (Winterhalder & Smith, 1981), *Human Reproductive Behaviour* (Betzig, Borgerhoff Mulder & Turke, 1988), *Evolutionary Ecology and Human Behavior* (Smith & Winterhalder, 1992), and *Adaptation and Human Behavior* (Cronk, Chagnon & Irons, 2000). Some collections that consist primarily of research on nonhumans also contain important work in human behavioral ecology (e.g. Alexander & Tinkle, 1981; Rubenstein & Wrangham, 1986; Standen & Foley, 1989). Betzig's *Human Nature: A Critical Reader* (1997) is a useful collection of some landmarks in both human behavioral ecology and evolutionary psychology, together with review essays and retrospective comments by the original authors. Few textbooks have been produced that focus on human behavioral ecology, although Boyd and Silk's *How Humans Evolved* (1997), Daly and Wilson's *Sex, Evolution, and Behavior* (1983), Trivers' *Social Evolution* (1985), Badcock's *Evolution and Individual Behavior* (1991), Buss's *Evolutionary Psychology* (1998), and Alcock's *Animal Behavior* (1997) cover some of the same subject matter. Several good popular introductions to this and related approaches have also been published over the past decade, including Ridley's *The Red Queen* (1993) and *The Origins of Virtue* (1996), Low's *Why Sex Matters* (2000), Small's *What's Love Got To Do With It?* (1995) and *Our Babies, Ourselves* (1998), Hrdy's *Mother Nature* (1999), Allman's *The Stone Age Present* (1994), and Wright's *The Moral Animal* (1994).

MORE RECENT REACTIONS AMONG ANTHROPOLOGISTS

Since the mid-1980s, the situation for human behavioral ecologists in anthropology has definitely improved. This improvement has a lot to do with changes within anthropology, such as how the subdisciplines are defined and how they divide up anthropology's traditional subject matter. In the 1970s, anthropologists who studied the behavior of living humans were classified as cultural anthropologists, and those who studied human biology in any way were classified as physical anthropologists. Since that time, both subdisciplines have changed significantly. Cultural anthropology, which used to have a place for a variety of scientifically-oriented, materialistic approaches, has moved strongly away from science and towards the humanities. Whereas cultural anthropologists at one time gained inspiration from such sciences as ecology and from the other social science disciplines, more often these days they draw upon ideas from such fields as literary criticism and semiotics. Cultural anthropology's movement towards the humanities is mainly a result of a long-term trend that goes at least as far back as Boas, but it may have been accelerated by the challenge presented

by the new, evolutionary approach to behavior. At the same time, physical anthropology has increasingly redefined itself as biological anthropology, a name change that reflects a broadening of focus beyond physiology and morphology to include the biological study of behavior. In the 1970s, most of the anthropologists who became interested in the new, evolutionary approach to behavior, including such notables as Lionel Tiger, Robin Fox, Napoleon Chagnon, William Irons, Derek Freeman, Jerome Barkow, and Raymond Hames, were members of the cultural subdiscipline. Now it is hard to find cultural anthropologists who identify themselves as human behavioral ecologists, but easy to find biological anthropologists who identify themselves as such.

The differences in how members of the cultural and biological subfields react to evolutionary analyses of behavior was made very clear by a survey conducted in 1984 by Leonard Lieberman (1989). Animal behaviorists, biological anthropologists, and cultural anthropologists were asked whether they considered a series of things identified as "sociobiological concepts" to be useful for future research on humans. The list included "kin selection," "reciprocal altruism," "genetic basis of altruism," "male-female reproduction strategy," "gene-culture coevolution," and "interaction of genes and environment." In every case, a majority of animal behaviorists agreed that the concept was likely to be useful in the study of humans, with agreement reaching as high as 82% in the cases of "kin selection" and "interaction of genes and environment." Biological anthropologists were only slightly more skeptical than animal behaviorists, with a majority seeing some usefulness in all of the concepts except "genetic basis of altruism." Cultural anthropologists were by far the most skeptical, with a majority seeing some usefulness only in the idea of an "interaction of genes and environment." Interestingly, the responses of all three groups were strongly affected by certain emotive words. The word "genetic" in the phrase "genetic basis of altruism" appears to have produced strong negative emotions in all three groups, despite the fact that the theoretically extremely similar phrases "kin selection" and "reciprocal altruism" received relatively high marks. Similarly, the word "culture" in the phrase "gene-culture coevolution" appears to have slightly warmed the hearts of the cultural anthropologists, who gave that phrase a relatively high rating.

Another recent development is a nascent reordering of anthropology's traditional subdisciplines. Whereas the divisions among the four old subdisciplines were ostensibly about subject matter, not ideology, the new division is about fundamental epistemological and ideological issues. In brief, those anthropologists who value a scientific, materialistic, and broadly evolutionary approach find themselves at odds with the majority of cultural anthropologists, many of whom

not only value a more humanistic and relativistic approach but who are openly hostile to science in general. What is emerging is a new, amalgam subdiscipline called "evolutionary anthropology," united by the use of scientific method and an interest in materialistic and evolutionary approaches, that includes archaeologists, biological anthropologists, and some former cultural anthropologists, along with human behavioral ecologists. This change is reflected in the internal organization of some departments (e.g. Rutgers), in the division of other formerly unified departments into two separate ones (e.g. Duke & Stanford), and in the success of the new journal *Evolutionary Anthropology*. This rearrangement of anthropology's intradisciplinary fences appears to be a good thing for human behavioral ecology in that it keeps them in the company of relatively sympathetic scholars. However there is a danger that it could impoverish human behavioral ecology by distancing it from cultural anthropology's traditional expertise in field methods and from the concept of culture itself (more about this below).

As the rift within anthropology has widened, cultural anthropologists' criticisms have expanded from a narrow focus on human behavioral ecology and related evolutionary approaches to behavior to a much broader critique of the possibility of a science of human behavior and culture in general. Relatively insightful and helpful critiques of human behavioral ecology itself have come from sources closer to home, i.e. from researchers who share with human behavioral ecology a scientific approach and an interest in the role of evolution in human affairs. For example, some evolutionary psychologists have argued that because any organism's current condition is a product of natural selection in ancestral environments, not current ones, the reproductive costs and benefits of particular behaviors are largely irrelevant to the identification of behavioral adaptations (e.g. Symons, 1989). This criticism reflects the fact that most evolutionary psychologists follow John Bowlby (1969) in locating the natural selection that led to our species in a long-past "Environment of Evolutionary Adaptedness," or EEA, often equated with Pleistocene hunting and gathering societies. To evolutionary psychologists who adhere closely to this view, contemporary societies, even those in which anthropologists usually work, are so radically different from the EEA that it is useless to measure the fitness consequences of particular behaviors in them. In response, human behavioral ecologists have argued that the evolutionary psychologists' understanding of the human EEA is simplistic, naive, and misleading, and that it should at least be made more sophisticated (e.g. Hrdy, 1999) or perhaps replaced with something else (e.g. Adaptively Relevant Environments: Irons, 1998). If humans are thought to have evolved not in a chronologically isolable EEA but rather over hundreds of millions of years in a series of quite different environments, then we ought to be composites of traits acquired in all of those environments. Some traits we will

share with a wide range of organisms (e.g. all vertebrates), others with a smaller range (e.g. all primates), and others might be distinctively human. To the extent to which current environments resemble past ones, current reproductive rates should indeed be useful indicators of specific adaptations. For example, one interpretation of the research on status striving and reproductive success discussed above is that, despite the tremendous changes that took place in human societies with the domestication of plants and animals, the reproductive rewards to those with high status continued as before.

Instead of examining behaviors' current fitness benefits, evolutionary psychologists usually examine the proximate psychological mechanisms behind particular behaviors and try to discern how they may have been produced by natural selection. For example, research into the psychological mechanisms involved in mate attraction suggest that there are similarities in the ways in which individuals evaluate members of the opposite sex that are consistent both within and among societies and that fit predictions derived from evolutionary theory (e.g. Buss, 1994). Human behavioral ecologists, in contrast, typically treat the specific psychological mechanisms involved in particular behaviors as unavailable for study, and they focus instead on the measurement of the costs and benefits of various behaviors. The failure of human behavioral ecologists to address proximate psychological mechanisms is one of the bases for another recent critique from a relatively sympathetic source, ecological anthropologist Andrew P. Vayda (1995). Vayda is well known in anthropology for his early work that applied evolutionary biological but group selectionist models to human behavior and cultural institutions, though he later broke with that approach in favor of one that focuses on more on individuals (Vayda & McKay, 1975). Vayda argues that true explanations of phenomena are accounts of causal chains, and because human behavioral ecologists usually fail to demonstrate all of the links in their causal chains, their explanations are inadequate. Human behavioral ecologists respond that: (a) it is normal procedure in many sciences to provide explanations without demonstrating all of the causal links involved, (b) they are most often ill-equipped by training to examine proximate psychological mechanisms, (c) their field situations and the cultural differences of the people they study often make such studies very difficult, and (d) further exploration of proximate mechanisms and other details of complete causal chains, which is a worthy if distant goal for all science, will come with time.

CURRENT FRONTIERS AND FUTURE DIRECTIONS

Two broad trends will shape the immediate future of human behavioral ecology. First, human behavioral ecologists will continue to adopt and adapt new theories,

models, and methods developed by nonhuman behavioral ecologists. Second, human behavioral ecology will benefit from contacts with two rapidly developing and closely related approaches, evolutionary psychology and memetics. The first trend is already a well established habit. Human behavioral ecology exists not in isolation but rather as a part not only of anthropology but also of behavioral ecology in general. Unique as humans may be, one of the basic ideas of human behavioral ecology is that because, like all other living things, we are products of a history of natural selection, it would make little more sense to have a separate sort of behavioral ecology for humans than it would for any other individual species. Fortunately for human behavioral ecology, nonhuman behavioral ecology is a lively field percolating with new ideas. Here I will briefly discuss three recent development in nonhuman behavioral ecology that are already beginning to influence work in human behavioral ecology: life history theory, dynamic modeling methods, and the study of animal communication.

Life history theory developed in biology as a way to understand the evolution of the timing of events during an organism's lifetime, including the age at which the organism matures sexually, the age of its first reproduction, and its overall life span (Hill & Kaplan, 1999). Because organisms vary so widely in terms of life history traits, the body of theory involved is enormous and is still undergoing rapid development. What unifies this complex body of theory is the idea that, throughout their lifetimes, organisms must allocate a limited supply of energy. Life history theory predicts that natural selection will shape the way organisms allocate the energy they have available over the course of a lifetime in a way that will, on average, optimize the benefits to their inclusive fitness, taking into consideration all relevant constraints on their allocation patterns. For example, an organism may have a choice between investment in its own maintenance and development (referred to as "somatic effort"), investing in its own reproductive success either by trying to obtain a mate ("mating effort") or by helping its offspring ("parental effort"), or investing in relatives in order to enhance their reproductive success ("indirect reproduction," "nepotism," or "kin selection"). The costs and benefits to different patterns of allocation among these options might change considerably through an organism's lifetime. For example, when an organism is young an emphasis is often placed on somatic effort, with the emphasis shifting to reproductive effort when it reaches sexual maturity. Kristen Hawkes and her colleagues (Hawkes et al., 2000) have suggested that might help explain the evolution of menopause and long post-reproductive lifespans in human females. In brief, the idea is that women may reach a point where they can enhance their own inclusive fitness more effectively by avoiding the risks of pregnancy and childbirth and helping their daughters

instead. Such aid may be particularly beneficial if it comes at a time in the daughters' lives when there is a conflict between the demands of subsistence and the desire to reproduce, e.g. if their ability to nurse an infant were diminished by a need to forage. If the costs of continued direct reproduction are high enough and the benefits of shifting to a nepotistic strategy are great enough, then natural selection may have favored the evolution of menopause and a long postreproductive lifespan for human females. Data from some contemporary hunter-gatherers supports this. Older women among the Hadza of Tanzania, for example, are more productive foragers than younger women (Hawkes et al., 1989).

Life history theory bears many similarities to demography because both fields examine the scheduling of major life events, particularly fertility and mortality. Accordingly, some human behavioral ecologists have begun to use life history theory to organize and analyze demographic data from traditional societies (e.g. Hill & Hurtado, 1996). Life history theory may also help shed light on current demographic patterns in industrial and post-industrial societies, which are seen by some as presenting a major challenge to human behavioral ecology (e.g. Vining, 1986). Such societies have undergone a drastic shift, known as the demographic transition, from high rates of fertility and mortality to low rates of fertility and mortality. The choice made by the wealthiest people on earth to reduce their fertility rather than to use their tremendous resources to have more offspring appears to run counter to the expectations of evolutionary theory. Kaplan and his colleagues (e.g. Kaplan & Lancaster, 2000) have examined this issue in light of life history theory, suggesting 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 competitive labor markets. In such an economic environment, having fewer but better endowed children may be a better long-run strategy than having many children (for other behavioral ecological work on the demographic transition, see Barkow & Burley, 1980; Bereczkei, 1998; Borgerhoff Mulder, 1998; Low, 2000a, b; Luttbeg et al., 2000; Rogers, 1992; Turke, 1989).

Dynamic modeling (Mangel & Clark, 1988) is one aspect of an increasing methodological sophistication in behavioral ecology. Traditional optimization models in behavioral ecology posit a decision maker faced with a set of possible choices, each one of which is associated with certain costs and benefits, and a set of constraints. Dynamic models extend the decision-making process over time and give it a capacity for self-adjustment. They do this by including variables that describe the state of the decision maker and his "state dynamics," i.e. some rules that specify how the decision maker's state will change over

time as he makes various choices (Mace, 1993: 364). Human behavioral ecologists have applied dynamic modeling methods to such phenomena as subsistence change (Mace, 1993), family size (Anderies, 1996; Beauchamp, 1994; Mace, 1996, 2000), and marriage (Luttbeg et al., 2000), and the potential exists for this technique to be applied to a great many other phenomena. Like life history theory, dynamic modeling may even be helpful in cracking that tough old nut, the demographic transition. Toward that end, Mace (1996, 2000) developed a dynamic model of reproductive decisions among the Gabbra, a pastoralist group in northern Kenya. Wealth among the Gabbra, as among many peoples, is inherited, and inherited wealth contributes greatly to both future wealth and reproductive success. Mace modeled two decisions made by parents: when to have another baby and how to distribute the family's resources among the children when a parent dies. She defines the state variables as the parent's wealth and number of living sons, and an optimal decision rule is defined as one that produces the most grandchildren. Her main finding is that increased costs of children is the main thing likely to lead to a decision to limit fertility, which supports conclusions reached independently by demographers (e.g. Caldwell, 1982) and other human behavioral ecologists (e.g. Kaplan & Lancaster, 2000).

Animal communication has always been a central concern of behavioral ecologists. While communication might at first glance appear to be a simple matter of information transfer, in some circumstances signallers may be trying not so much to inform receivers as to manipulate them. A key variable is whether there is a conflict or a confluence of interests between signallers and receivers. When there is a clear conflict of interests between the two parties, i.e. where the signaller would benefit if the receiver were to do something that is not in the receiver's best interests, behavioral ecologists predict that an evolutionary arms race will develop. The signaller should send increasingly elaborate and conspicuous signals in order to influence the behavior of a receiver that is increasingly resistant to manipulation (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984). This might explain such very refined signalling systems as an anglerfish's lure, which has evolved to attract smaller fish towards the anglerfish's waiting mouth, which is clearly not in the best interests of the prey. This line of thought has inspired a great deal of research on deception in animal communication systems (e.g. Mitchell & Thompson, Eds, 1986).

When there is a confluence of interests between signallers and receivers, in contrast, natural selection should favor the evolution of signals that are only as elaborate, conspicuous, and costly as they need to be in order to get the information across. When both parties are aware of such a confluence of interests, for example in a mated pair of organisms cooperatively rearing offspring, then

signals should be muted and economical (Dawkins & Krebs, 1978). However, this apparently simple situation becomes quite complicated by the fact that sometimes only the signaller is aware of the existence of a confluence of interests. In such circumstances, the signaller may need to send a very elaborate, conspicuous and costly signal in order to convince the receiver that they do indeed share some interests (Zahavi et al., 1997). Such confluences of interest may arise even in situations we normally think of as being essentially conflictual, such as an encounter between a predator and its prey. A Thompson's gazelle, for instance, actually has a confluence of interests with a lion trying to kill and eat it: the gazelle wants to avoid being eaten, and the lion wants to avoid wasting time and energy on a failed hunt. This helps explain why such gazelles "stot," a peculiar sort of theatrical hopping display, when pursued by lions: Stotting sends a signal to the lion that alerts her to their underlying confluence of interests (FitzGibbon & Fanshawe, 1988). By stotting, a gazelle tells a lion that it is aware of her presence and that it is clearly too fit to be easily caught. The implication is that both parties would benefit if the lion were to look elsewhere for a meal. Similarly, a high quality male and a female he is pursuing as a mate have a confluence of interests: he wants a mate, and she wants a high quality male. Their confluence of interests rests on the fact that he is indeed a high quality male, but, at the outset of the interaction, only the male can be aware of his own high quality and hence of their confluence of interests, and he must put on an elaborate and costly display to convince the female of it. In both of these cases, there is a broad conflict of interest between two classes of individuals (prey and predators; males and females) but a confluence of interests between the receivers (predators and females) and *certain members* of the signalling class (*fit, alert* prey and *high quality* males), allowing for a cooperative type of signal to evolve despite the wider conflict. Thus, surprisingly, some very elaborate and expensive signals may actually fit the predictions of cooperative signalling theory in that they are as economical as they can be and still get their message across.[4]

These ideas about animal communication have begun to have an impact on human behavioral ecology. Harpending, Draper and Rogers (1987) have suggested that the idea that situations of conflict will lead to loud, conspicuous, and manipulative signals might help make sense of propaganda and other public pronouncements typically seen in situations in which there is a marked difference in power between two groups, such as elites and nonelites or, in some societies, between males and females. Boone (1998) has used animal signalling theory to shed light on conspicuous consumption and magnanimity. Thus, the lavish displays of generosity, sometimes even including the destruction of wealth, at potlatches among Northwest Coast Indians (Drucker & Heizer, 1967)

or in the *moka* gift-giving ceremonies in highland New Guinea (Strathern, 1971) may be analogous to the way that a small bird called the Arabian babbler competes for status by magnanimously feeding others (Carlisle & Zahavi, 1986; Zahavi, 1990). Even big game hunting may be a way for men to show off, i.e. to send a signal to others about their value as a provider of food to the group and as a potential mate (Hawkes, 1991).

Evolutionary psychology and *memetics* have developed alongside human behavioral ecology as ways of applying selectionist thinking to human affairs. While there has been some competition between these three approaches in the past, a consensus is emerging that they are actually quite complementary (e.g. Smith, 2000), and there is sure to be more interaction between them in the future. Evolutionary psychology is the more developed of the two fields and has lately received widespread attention both among scholars and in the popular press. Some of the most impressive work in evolutionary psychology has been Leda Cosmides and John Tooby's (1992) studies of social cognition, which suggests that humans are especially good at dealing with logical problems when there is a social rule involved. They have shown that success rates on the Wason selection task, which involves questions with a logical structure of the "If p then q" variety, vary tremendously depending on how the test questions are phrased. If the question is simply descriptive ("If a card has a D on one side, then it must have a 3 on the other side") then success rates in all groups tested are much lower than if the question involves the application of a social rule ("If a person is drinking alcohol, then he or she must be at least 21 years of age"). This result is not contingent on the subject being familiar with the social rule in question. Even when the question is posed in terms of an exotic rule in an exotic setting ("If a person is eating taro, then he or she must have a tattoo"), success rates are still much higher than when the rule is phrased in a more abstract way. These results support the idea that the human mind is not a general purpose problem solver but rather a bundle of special purpose modules, one of which has been designed by natural selection to be especially adept at monitoring others' adherence to social rules.

Although these results on the Wason selection task are consistent across samples taken from American society, the case for a special mental module for monitoring adherence to social rules would be strengthened if the study were replicated in other societies, as well, particularly ones isolated from Western society and its particular forms of logic. This was recently done by Larry Sugiyama, an anthropologist and human behavioral ecologist trained by Cosmides and Tooby, among the Shiwiar of the Ecuadorian Amazon (Sugiyama, 1996). The Wason selection task is usually administered in written form, but, because few Shiwiar are literate, Sugiyama had to redesign the test in order to administer

it using only pictures and oral instructions. On the descriptive question, Shiwiar subjects performed much like American subjects: badly. That is, the descriptive question elicited a logically correct response about as often as would be expected by chance. The social contract questions, in contrast, elicited correct responses significantly more often than would be expected by chance. Furthermore, the errors committed by Shiwiar subjects were mostly errors of commission (turning over too many cards) not omission (turning over too few cards). Hence, most of those giving incorrect responses to the social contract questions would still have succeeded in enforcing the social rule. Their only error was in collecting more information than they needed in order to accomplish this task.

Memetics is the newest and least tested of the three selectionist approaches to human affairs. It also goes by such names as cultural transmission theory, dual inheritance theory, and evolutionary culture theory. Prominent figures in the field include Boyd and Richerson (1985), Cavalli-Sforza and Feldman (1981), Durham (1991), and Lumsden and Wilson (1981; for recent popular accounts, see Brodie, 1995; Dennett, 1995; Lynch, 1996). The name "memetics" is based on the word "meme," which was coined by Richard Dawkins (1976) to describe a culture trait. Just as the name implies, the central metaphor is between the meme and the gene. Both memes and genes are replicators and, as such, both may undergo an evolutionary process, with memes that are successful in being copied from mind to mind spreading just as successful genes spread in a gene pool. Because genes are passed from parents to offspring, in general they are beneficial for their bearers, and a broad expectation in memetics is that most memes will also be helpful to their bearers in solving life's problems and guiding behavior toward adaptive ends. The finding described above that there is a widespread correlation between culturally defined success and enhanced inclusive fitness fits this expectation neatly, but it also means that this prediction of memetics is neither unique nor very interesting. However, memes can also be spread between nonrelatives and even strangers, much like viruses, and just as viruses can be successful at spreading at the expense of those who become infected by them, so, in theory, might memes spread from mind to mind even if they have detrimental consequences for their bearers. Because the prediction of conflict between cultural traits and genes is unique and serves to distinguish memetics from human behavioral ecology, much of the research in memetics has focused on just such traits. So far the quest for maladaptive memes has been interesting but not very fruitful. Durham (1991) offers one possible example from New Guinea: cannibalism among a group called the Fore. The Fore adopted cannibalism because they found that human flesh was a surprisingly tasty type of food. Unfortunately, cannibalism also provided an avenue for the spread of an infectious agent that produced a lethal

form of spongiform encephalopathy called *kuru*, which is very similar to mad cow disease, scrapie, and Creutzfeld-Jakob disease. But the link between cannibalism and the spread of *kuru* was so difficult to discern, not only for the Fore themselves but also for Western medical researchers, that the practice of cannibalism continued for some time even though it was spreading a devastating disease. It is not just food consumed that can cause health problems: food not consumed due to taboos can also deprive people of needed nutrients. Robert Aunger examined the potential conflict between memes for food taboos and peoples' fitness interests among four different ethnic groups in the Ituri forest in eastern Zaire (now Congo), where individuals typically maintain a variety of complex food taboos. He found a discernable reduction in nutritional status attributable to food taboos among only pregnant women in one of the four groups (Aunger, 1992).

Whether maladaptive memes turn out to be common or rare, memetics has provided a service to human behavioral ecology by redirecting attention to the issue of culture. Most behavioral ecological theory is devoid of culture simply because most nonhuman species have little or no discernable culture. One way other than memetics to make greater use of the culture concept in human behavioral ecology would be through more studies of communication because, among humans, culture is the raw materials out of which signals are fashioned (Cronk, 1995, 1999). A nice example is Napoleon Chagnon's work on how Yanomamö men manipulate their kin terminology (Chagnon, 1988b, 2000). The Yanomamö kin terminology system includes terms that specify which women a man can marry and which he cannot. Chagnon has shown that men systematically fudge the rules of the system by reclassifying young women as marriageable kin. In other words, they use the raw material of a cultural system for defining marriageable kin to construct manipulative, fitness-enhancing signals. Work of this kind also dovetails nicely with a rapidly growing body of research on animal cognition (e.g. Ristau, Ed., 1991) and animal culture (e.g. Bonner, 1980), particularly among nonhuman primates (e.g. McGrew, 1992; Wrangham et al., Eds, 1994).

CONCLUSION

Because evolution has always been a central theme in anthropology, human behavioral ecology represents a sort of return to the discipline's roots. Over the past twenty five or thirty years, human behavioral ecology has developed from a largely speculative field to a theoretically and methodologically rigorous one with a good foundation in empirical research. In addition to confirming the validity and usefulness of an evolutionary approach to human behavior, human

behavioral ecology's findings also necessitate a rethinking of many of anthropology's central theoretical concepts and traditional topics. Although it has accomplished much, human behavioral ecology's work has barely begun. It is a field in which new and exciting possibilities are always opening up thanks to a rapidly developing body of theory and endless opportunities for new field research.

NOTES

1. The idea that anthropology is a discipline consisting of these four subdisciplines is distinctively American. In other countries with strong traditions of anthropological research, such as Britain and France, these are often treated as entirely separate disciplines. Nevertheless, because of the much larger number of anthropologists at work in the United States compared to any other country, theoretical concerns that arise out of the American four-field conception of the field tend to influence theoretical developments even in countries where that conception is not widely shared.

2. It is important not to put too fine a point on this. Even in the heyday of Boasian cultural relativism, some cultural anthropologists maintained an interest in evolution. Some, such as Julian Steward (1955) and his followers in cultural ecology and ecological anthropology, were influenced by the new science of ecology. Others, including Leslie White (1959) and Marvin Harris (1979), were inspired by Marxist theory, which was itself a form of nineteenth century evolutionism.

3. There are exceptions, including Scheper-Hughes (1995), a cultural anthropologist who rejects relativism for fear that it will place objectionable behaviors such as oppression and exploitation beyond the reach of moral judgement, and Bagish (1982).

4. I have presented models of animal communication developed by Dawkins and Krebs and by Zahavi as complementary, with Zahavi's account of how costly, honest signals can evolve in apparently conflictual situations as a special case of Dawkins and Krebs' more general model. This is not how these two models are usually presented in the literature on animal signalling. Rather, they are usually seen as being in conflict because they appear to make different predictions about the reasons for costly signals and about their honesty. In this section I have attempted to show that the conflict between them is more apparent than real. Dawkins and Krebs' prediction that conspicuous, perhaps costly, and even deceptive signals will evolve in situations of clear conflict between signallers and receivers still holds despite Zahavi's evidence that conspicuous, costly, but honest signals can also evolve in circumstances where, even within a situation that may be rife with conflict, there is a confluence of interests between signaller and receiver of which only the signaller is initially aware.

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