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Human Behavioral Ecology

Human behavioral ecology (sometimes referred to as evolutionary ecology) is the application of evolutionary biological models to the study of behavioral variation in humans. Evolutionary approaches to the study of human behavior fall under a variety of names such as sociobiology, biosociology, biocultural or biosocial science, human ethology, socioecology, and

evolutionary psychology (Cronk 1991, p. 25). While some of these names are synonyms others represent different emphases that will be described below. Human behavioral ecology attempts to explain behavioral diversity as a consequence of environmentally contingent responses made by individuals in their attempts to maximize their inclusive fitness. Critical to this goal is the specification of environmental factors that constrain an individual’s attempt to maximize fitness. As a consequence, individuals develop behavioral strategies designed to solve a variety of adaptive problems set by nature such as producing food, mating, investing in offspring, and managing social interactions between offspring, mates, kin, and unrelated individuals.

1. Origins and Early History of the Field

Behavioral ecology is a relatively new discipline and, for the most part, it is practiced by anthropologists. The publication of E. O. Wilson’s *Sociobiology* (1975) along with the earlier work of biosocial anthropologists such as Robin Fox and Lionel Tiger (Cronk 1991) and evolutionary biologist Richard Alexander (1974) were critical in stimulating interest in applying Darwinian approaches to the study of human behavioral diversity. Very quickly Wilson’s sociobiological approach was found to be limiting because it was largely based on older ethological approaches which posited relatively simple, general, and rigid models of the relationship between genes and human behavior (Winterhalder and Smith 1992, p. 9). This was especially apparent in his final chapter of *Sociobiology* (1975, pp. 547–75) where he considered humans. Here he suggested that certain behavioral traits such as territoriality among foraging peoples were universal (1975, pp. 564–5). This claim and the approach that generated it was shown to be limited in a paper by Dyson-Hudson and Smith (1978), a paper which represented perhaps one of the earliest applications of behavioral ecology to the study of human behavioral variation. Using a cost-benefit model developed by the avian behavioral ecologist J. Brown, they showed that territoriality was variable among tribal populations and was determined by specific environmental factors consistent with evolutionary theory.

As will be more fully described below, environmental cost-benefit approaches in the context optimization models is at the core of much of behavioral ecology. It is vital to understand that behavioral ecology is a branch of evolutionary biology and the core of evolutionary biology is about changes in the frequencies of genes through time. However, behavioral ecology is agnostic about the causative role of genes in the study of human behavioral variation. This position was clarified by Alan Grafen (1984) with his notion of the phenotypic gambit. Phenotypic variation

is shaped by an individual's genotype interacting with a variety of cultural, developmental, environmental, and other non-genetic factors. The degree to which variation in any trait is a consequence of genetic variation is not directly relevant to the formulation or evaluation of behavioral ecological models. This approach is consistent with analyses in non-human behavioral ecology (Alcock 1989).

1.1 Relationship to Other Fields Using Evolutionary Approaches to the Study of Human Behavioral Variation

The new field of evolutionary psychology (Barkow et al. 1992), and, to some extent, its congener human ethology, is often inappropriately confused with behavioral ecology and sociobiology, and it is useful to distinguish between these complementary Darwinian approaches to the study of human behavioral variation. Behavioral ecology attempts to develop hypotheses regarding variation in behavioral strategies that individuals employ to maximize their inclusive fitness. In many studies the central focus is on the reproductive consequences of behavior. In contrast, evolutionary psychologists are interested in elucidating the cognitive mechanisms (or mental modules) that evolved in humans in the 'environment of evolutionary adaptedness.' This concept stresses the fact that all adaptations are to historic environments and whether traits developed in the past are adaptive in current environments is problematical. As a consequence, evolutionary psychologists seek to uncover those mental modules that were designed by natural selection to solve problems such as: What criteria do people use to select mates? How does mate selection criteria differ between the sexes? What factors induce individuals to continue or abandon mating relationships? From this perspective, the reproductive consequences of behavior are not of concern. Other differences distinguishing these fields include behavioral ecology's reliance on naturalistic fieldwork in contrast to questionnaire survey and laboratory experiment, and the relationship between behavior and fertility. Winterhalder and Smith (2000) should be consulted for a more detailed examination of the assumptions, methods, and goals of these fields.

Dual inheritance theory (Boyd and Richerson 1985) is founded on the realization that cultural traits or memes are in some sense identical to genes because both are replicators that use vehicles (bodies) to transmit themselves across generations and are subject to selective forces. Cultural traits differ from genetic traits in their mode of transmission: they may be transmitted from mind to mind through natural selection of carriers of the trait (the trait has a positive effect on fitness), through emulation of high status people who exhibit the trait, by coercion, or by psychological

mechanisms that make the trait desirable or habit forming (e.g., various addictions). In addition, cultural traits may be transmitted laterally within generations instead of lineally through generations allowing them to spread more rapidly. Compared to behavioral ecology and evolutionary psychology little empirical work has been done employing dual inheritance models.

1.2 Relationship to Traditional Social and Behavioral Sciences

Behavioral ecology is distinguished from traditional anthropological and social science theory in its emphasis on the individual as the unit of selection and the idea that much of the content of culture is a consequence of decisions by individuals to enhance their inclusive fitness. Ever since its founding as a discipline, anthropologists have argued that individuals sacrifice themselves to enhance the integration or survival of the social systems in which they participate or are much like puppets or robots manipulated by culture (Cronk 1991). Furthermore, any attempt to reduce or link cultural behavior to lower levels of analysis was specifically condemned. Human behavior was believed to have emergent properties irreducible to the facts of psychology and biology. While it is clear that some dimension of human behavior are not usefully reduced to underlying psychological or biological processes simple observation tells us that humans are biological and psychological entities and some of the behavioral diversity can be usefully linked to underlying levels of analysis.

1.3 Theoretical Armamentarium

Behavioral ecology is strongly informed by a series of theoretical breakthroughs that developed in the early 1960s and 1970s in the evolutionary analysis of social and foraging behavior. These include inclusive fitness (or kin selection, Hamilton 1964), reciprocal altruism (Trivers 1971), sexual selection and parental investment (Trivers 1972), sex biasing in parental investment (Trivers and Willard 1973), optimal foraging theory (Winterhalder and Smith 2000), and, most recently, life history theory (Stearns 1992). These papers clearly demonstrated that behavioral variation was an apt subject for investigation from an evolutionary perspective consistent with the modern synthesis and a gene centered view of evolution. Early on in the development of behavioral ecology there was considerable expectation that kin selection would inspire considerable research especially in the areas of food exchange and other forms of cooperative behavior. As will be evident below, few studies have made kin selection a central focus of investigation.

2. Areas of Application

2.1 Foraging Theory

Human dietary selectivity has been a fundamental area of interest for anthropologists because of its strong implication for the structuring of social relations among hunter-gatherers, group size, mobility patterns, and our understanding of economic dimensions of human evolution. One of the earliest applications of behavioral ecological research came with the application of optimal foraging theory (OFT) in the study of hunting, fishing, and gathering (or foraging behavior) among modern hunter-gathers and foraging horticulturalists. OFT allows researchers to develop a large set of fundamental hypotheses that predict which food resources foragers will pursue when encountered during a search (diet breadth), or where foragers will travel to search for resources (patch choice models) and how long they will stay in these places before moving to other areas (marginal value theorem). These models assume that foragers have a goal, which is to maximize their net rate of return while foraging because by doing so they are ultimately able to maximize their fitness. The rate of return is indexed by a currency such as calories or another attribute of food value (e.g., Hill 1988). This assumption is reasonable because food resources are fundamental to survival and reproduction for one of two reasons. When the environment is poor, humans can be said to be 'resources limited.' Therefore, maximizing one's net rate of return allows foragers to acquire the greatest amount of food while foraging. On the other hand, when the environment is relatively rich, humans may be 'time limited' such that efficient acquisition of food resources leaves foragers with more time to engage in alternative fitness enhancing activities such as child care (Winterhalder and Smith 2000).

There have been a number of qualitative and quantitative tests of optimal foraging models applied to the problem of diet breadth (Hill and Kaplan 1992). Qualitative tests predict directional tendencies in prey choice by showing that diet breadth (the number of different species that will be pursued upon encounter), for example, will expand or contract depending on the encounter rates of highly profitable species (Winterhalder and Smith 2000). Quantitative tests predict the precise number of species a forager will pursue under a variety of environmental conditions (Hill and Kaplan 1992), which species will enter or drop out of the optimal diet breadth, and the exact rank-ordering of species in the diet breadth. Most studies of diet breadth show a division of labor between men and women, and children and adults (Hill and Kaplan 1992) which seem to be based on game versus vegetable products for the former and skill and strength levels for the latter.

Although OFT was designed to account for foraging behavior in animals and then later extended to human foraging, recent applications have been made in the areas of the origins of agricultural and pastoral food production with considerable success (Winterhalder and Smith 2000). It has rekindled anthropological interest in the problem of conservation among native peoples. Thus far, research indicates that true conservation is rare among native peoples but even more importantly researchers are attempting to specify the conditions under which conservation is likely to emerge and an adaptive strategy.

2.2 Group and Resource Transfer

The movement of goods, and, to some extent, services, between families and individuals has received considerable attention by behavioral ecologists. Traditionally such research is subsumed under the terms of exchange or reciprocity. Behavioral ecologists term such activities transfers because it more neutrally characterizes resource movement between groups and/or individuals compared to traditional terms such as exchange or reciprocity (which assume that the transfer of good or services between individuals will be returned in some material form at some point in time). In the analysis of transfers, one assumes that giving or yielding a resource that one has acquired will be done such that acquirer of the resource gains something in return or avoids a cost in defending that resource. As a consequence, models of transfer assume that the benefits of giving are greater than the costs of monopolizing the resource. The models of transfer developed thus far include (a) scrounging (or tolerated theft); (b) risk minimization; (c) trade or exchange; and (d) the show-off hypothesis.

At one extreme, coercive models of scrounging or tolerated theft assume that the resource acquired cannot be easily or effectively defended against those who lack resources and that the benefit of giving or yielding a portion of the resource presents a higher payoff than the cost of defending it against another who are in greater need and thus more willing to contest the resource. At the other extreme are models of sharing, which assume that individuals give resources to others contingent upon an expectation that something of value will be returned to the giver in the future. For example, when resources cannot be predictably acquired (especially true in hunting) risk minimization or pooling strategies are employed through the mechanism of reciprocal altruism. Individuals who acquire resources share with those who have been unlucky in the hunt with the expectation that in the future should they return home without game others who have acquired game will share with them. Kin selection models have been used to explain why resource transfers tend to be biased toward close kin; sexual selection models (e.g., 'show off hypothesis') argue that actors attempt to acquire large but

high-variance resource packets (e.g., large game animals) to demonstrate their desirability as a mate; and trade models suggest that transfer occurs through specialization via the mechanism of reciprocal altruism.

2.3 Mating Strategies

Models of mating or marital strategies, in one form or another, are largely founded on the polygyny threshold model (Winterhalder and Smith 2000, p. 64). This model is relevant when males differentially control resources necessary for successful reproduction. The polygyny threshold model predicts that females will select mates according to the quantity of resources they control. In this situation, polygyny will emerge among those males who can offer more resources to females than unmarried or monogamous males. In short, wealthy males are much more likely to mate polygynously than poor males. In most cases, ownership of material resources (e.g., agricultural land) or high productive productivity (e.g., ownership of large herds) is what differentiates poor from wealthy men. However, in some societies where economic stratification is absent, some men are nevertheless exceptionally productive (e.g., excellent hunters) or have achieved political power or status (e.g., distinguished warriors, leaders, or shamans) and this may be the differentiator between polygynous and monogamous men.

The polygyny threshold model assumes female choice in marital affairs. In some cases this assumption is clearly suspect and male coercion may determine a woman's marital fate. At the same time, some researchers have identified counter strategies that females use to deal with coercive male mating tactics (Winterhalder and Smith 2000, pp. 60–1). Equally troubling is the fact that in some cases female fertility declines under polygyny (this is especially true for junior wives). At this point it is clear that polygyny will nearly always enhance a man's fertility but it frequently impairs a woman's. This latter issue is leading researchers to seek factors that could compensate for lowered fertility. For example, it may be the case that although a woman may bear fewer offspring under polygyny she may produce more grandchildren. This would be true if her sons were polygynous, married earlier than average, or married women with high reproductive value.

Although polygyny is permitted in nearly three-quarters of all anthropological populations, monogamy and the rare case of polyandry (a woman having more than one husband simultaneously) are being investigated through modified versions of the polygyny threshold model. In the case of monogamy it is becoming clear that extramarital mating (concubinage, affairs) and remarriage following divorce (serial monogamy) is more common among wealthy males. Although such systems are officially monogamous,

from a reproductive point of view they produce the high male reproductive variance characteristic of polygynous systems.

2.4 Reproduction: Mating, Parenting, and Life History Strategies

Given that the costs of reproduction vary greatly between males and females, they face fundamentally different trade-offs between the allocation of mating and parental effort in reproduction. The higher costs of reproduction for females limit the number of offspring they can produce and pursuit of additional males through mating effort will have little impact on the quantity or quality of offspring they can produce. As a consequence, they are concerned with the genetic quality of their mates (e.g., ability to deal with pathogens) since these qualities will be passed to offspring, and their ability and willingness to invest in offspring given the fact that humans require some degree of biparental care.

Studies of parental effort have focused on the issues of birth spacing, differential investment in offspring, and the interaction between mating and parenting. The ornithologist Lack was the first to recognize the trade-off between offspring number and offspring quality (or the ability of offspring to thrive and eventually reproduce). Since parental resources are limited, more offspring, through a shortening of the birth interval, will mean less investment per offspring and the potential for reducing each offspring's fitness. This trade-off suggests that there will be an optimal number of offspring that maximizes a parent's fitness and this number will vary with environmental circumstances. In general, one would predict that where parental resources are abundant birth intervals should be short and where parental resources are scarce birth intervals should increase. The crosscultural evidence from natural fertility traditional societies strongly supports the relationship between parental resources and reproductive success: wealthy parents or culturally successful parents have higher fertility than poor parents.

Paradoxically, the association between cultural success and fertility is absent in modern contracepting societies. The situation has led behavioral ecologists to reexamine the demographic transition that began in Western countries during the eighteenth and early nineteenth centuries, which has now spread to developing nations. During this transition fertility fell faster than mortality rates fell yielding smaller families while family wealth increased. One solution to this paradox has been to investigate whether parents are investing more in children (e.g., education) thereby creating 'higher quality' children who will be able to compete successfully in highly competitive labor markets. At the same time, these children are delaying reproduction as they pursue higher education and gain entry into high status occupations, which require

further delays in reproduction as they work hard to achieve secure occupational niches. This theoretical perspective derives from life history theory described in Sect. 2.4.3.

In a seminal article, Irons (1979) suggested that there ought to be a correlation between cultural and reproductive success. Cultural systems are structured so as to encourage individuals to achieve certain kinds of culturally valued statuses. These achievements vary culturally depending on local environmental constraints. Both in traditional and in a number of recent societies, which have not entered the most recent demographic transition, culturally valued statuses are achieved through hunting prowess, religious rank, herd ownership, political leadership, occupational status, or land holdings. At this point there are nearly 20 studies showing in nearly all cases a positive correlation between cultural achievement and fitness (either fertility or survivorship of offspring) or factors strongly associated with fitness (number of wives, frequency of extra-pair copulations). However, it is very important to note that this relationship is demonstrated for male but not female reproductive success. Significantly, attributes that lead to high male fitness such as polygyny decrease female fitness at least over the short-term but perhaps not the long term.

2.4.1 Parental investment. In general the amount of investment an offspring receives from parents depends on (a) the relatedness between parent and offspring; (b) the effect of investment on the offspring; and (c) the effect of investment on parents' future reproduction and survival. These hypotheses have been positively evaluated using crosscultural and ethnographic cases studies. For example, the probability of infanticide, abuse, and neglect has been shown to be strongly sensitive to these factors. Infants who are unrelated to a woman's current husband ((a) above), or who have congenital defects ((b) above), or who are born in times of economic privation ((c) above) receive little or no investment. The thinking explicit in this approach is that parents adjust their investment in children according to their perceptions of a child's quality, paternity, current environmental conditions, and the needs of other offspring. Further investigations into differential parental investment have been inspired by the Trivers and Willard (1973) model where sex of offspring may influence investment. This model predicts that wealthy parents will invest more in the sex that has greatest variance in reproductive success (usually males) while poor parents will invest more in offspring with least reproductive variance (usually females). Research on societies as diverse as hunter-gatherers, pastoralists, to eighteenth-century Germany and nineteenth-century India has demonstrated the predicted differential investment by sex and distortions in sex ratios.

2.4.2 Parenting as mating effort. Providing care and giving food to children are conventionally seen as kinds of parental effort by males. However, recent research reveals that care and food provisioning are sometimes allocated to children who are unrelated to males. Consequently, such behavior may be fruitfully viewed as attempts to create or maintain a mating relationship. Essentially males are attempting to demonstrate their ability to invest in offspring and therefore convince a female that they would be a valuable partner.

2.4.3 Life history. Life history strategies deal with age specific schedules of mortality and fecundity and the traits that are directly a result of these schedules (Hill and Kaplan 1999, p. 397). It deals with important developmental events such as age at first and last reproduction, growth rates, birth intervals, and senescence. The theory is based on the assumption that effort allocated to somatic effort (growth, development, and maintaining the body) cannot be allocated to reproductive effort (e.g., mating and parenting). Formal research in this area is relatively new and has focused on the peculiar human trait of menopause, inter-birth intervals among foragers, and demographic transition theory.

The grandmother hypothesis attempts to explain the evolution of menopause, a life history trait that is exceptionally rare among mammals and well documented in humans. The model predicts that women will cease reproduction prior to death in order to insure required investment in current dependent offspring and to assist their children in the rearing of grand offspring. Although attractive, the model does not, as yet, show that continued reproduction until death is not a superior alternative.

Throughout history, humans have passed through a number of demographic transitions beginning with a high mortality and high fertility regime to today's worldwide transition to a low mortality and low fertility regime. A central issue behavioral ecologists are confronting is the apparent paradox between fertility and wealth. In tribal and in many state-level historical populations there is a consistent positive correlation between fertility and wealth. This means that the traditional human pattern was to convert wealth into reproduction. However, at the end of the twentieth century there is a global tendency for parents to reduce reproduction where wealth increases. Several explanations are offered for this trend. An initial set of explanations suggested that parents are now concerned with maximizing the number of offspring over more than one generation by reducing risk through an increase in heritable wealth. The 'human capital' perspective notes that in the current environment there is an increased requirement of parental investment needed to make children competitive in a modern

labor market where earning capacity is determined by parental investment in such things as education. Finally, more recent resolutions of the paradox focus on risk sensitive strategies that seek to lower the variance in expected completed family size. An important point evolutionary psychologists make in this problem is that, for the first time in human history, we possess safe and effective means of contraception, an alternative that humans did not previously have as they made their reproductive decisions. This has led to research demonstrating that there is a kind of correlation between wealth and reproductive success, at least for men. This research shows that wealthy men have greater numbers of premarital and extramarital unions than poor men. This lends some credence to the perspective that some of the adaptations we currently possess cannot be easily understood by looking at the reproductive consequences of behavior.

3. Summary

Human behavioral ecology is a young and explicitly Darwinian approach to the study of human behavioral variation. It redresses an absence of evolutionary considerations in the analysis of human behavior and social organization in the social and behavioral sciences. Since its inception in the late 1970s it has spawned the development of new journals and academic specialties explicitly devoted to training students to query the evolutionary bases of behavior. Its penetration into academic life has been uneven. It is most prominent in those disciplines such as anthropology and psychology where human evolution is considered relevant for a holistic understanding of human behavior or in economics where self-interest, methodological individualism, and maximization are key elements in modeling behavior. It has been resisted in departments such as sociology and political science where the findings on human evolution are either ignored or regarded as irrelevant.

See also: Adaptation, Fitness, and Evolution; Cultural Evolution: Overview; Cultural Evolution: Theory and Models; Ecology, Cultural; Environmental Psychology: Overview; Evolution, History of; Evolution, Natural and Social: Philosophical Aspects; Evolution: Optimization; Evolutionary Social Psychology; Evolutionism, Including Social Darwinism; Human Ecology; Lifespan Development: Evolutionary Perspectives; Natural Environmental Psychology; Psychological Development: Ethological and Evolutionary Approaches

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R. Hames

Human Capital: Educational Aspects

The notion of ‘human capital’ is an economic concept, based on the distinction between two types of economic activity: investment and consumption. Economists use the term ‘investment’ to refer to an activity or use of resources which will generate income in the future, in contrast with ‘consumption,’ which produces immediate satisfaction or benefits, but does not create capacity to earn future monetary

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