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ECOLOGY, HUMAN BEHAVIORAL (2,088 words)

Human behavioral ecology (HBE) applies principles of evolution by natural selection to explain behavioral and cultural diversity in human populations. It explores how features of social and physical environment constrain the suite of behaviors or 'strategies' of individuals, and applies the logic of optimization to make formal predictions about the conditions which favor or disfavor particular behaviors. The main focus of HBE is to explain behavioral variation within and among populations. Its intellectual roots stem from developments in biology (evolutionary biology, animal behavior, population and community ecology, life history theory), anthropology (cultural ecology, hunter-gatherer studies), and economics (micro-economics of consumer choice). Since HBE's formulation in the late 1970's, it has been referred to as human sociobiology, Darwinian anthropology, evolutionary or behavioral ecology, biocultural and biosocial anthropology. Currently HBE shares common goals and foundations with evolutionary psychology and cultural transmission theory, but differs in specific goals and methods. Initially focused on understanding foraging behavior among hunter-gatherers, HBE has expanded over the past 25 years to cover a wide scope of themes and problems, using a broad range of observational, ethnographic and experimental methods.

Natural Selection and Behavior

Natural selection will influence the frequency of traits when there is sufficient phenotypic variation in traits across individuals, when such variation is inheritable, and when it impacts biological "fitness" or reproductive success, via the ability to differentially survive or reproduce in a specific environment and population. Heritability of traits occurs through genetic transmission from parent to offspring, and through individual or social learning of information and behavior. HBE therefore focuses on behavioral and cultural "traits" which are likely to have fitness consequences. These include the suite of foraging, mating, parenting, and costly social behaviors found in all populations. People everywhere in all cultures develop ways to extract resources from their environment, find mates, defend access to resources, protect, feed, and care for offspring, form and maintain social partners and alliances, and must often trade-off time and energy among these tasks. While evolution can also occur due to founder effects in small populations, random mutation, and gene flow, only natural selection can produce directional change or complex, adaptive design.

HBE treats observed behaviors or traits of interest (phenotypes) as if they were controlled by a simple genetic system, even though most behaviors are multi-causal, involve networks of many genes and their interaction with stimuli from local environments. Biologist Alan Grafen has referred to this methodological tactic as the "phenotypic gambit". Behavioral ecologists usually assume that most fitness-related behaviors are sufficiently flexible, and so a safe working assumption is that behaviors can be examined without regards to the particulars of the form of inheritance.

Optimization

Most HBE research employs a hypothetico-deductive methodology, where explicit hypotheses are derived from theoretical models, and tested using information collected from fieldwork among living populations. Models are usually mathematical formulations of fundamental adaptive problems. Models balance tractability with realism, and specify key relationships among variables believed to best capture the theoretical dynamics of a problem. Two common approaches are optimality models and game-theoretic models. Optimality models examine conditions favoring an optimal behavioral "strategy" from a suite of available strategies, with the goal of maximizing some currency under a set of ecological constraints. The currency may be direct biological fitness, typically measured as the number of children surviving to some later age. The currency is often a proxy of direct fitness, such as foraging efficiency, growth rate, and fertility. While optimality models typically examine costs and benefits from the perspective of a single individual without any reference to what others in the population are doing, the success of strategies in game-theoretic models depends upon the frequency of other strategies in the reference population. For example, a lone cooperator may not fare well in a world populated by defectors.

Models are useful for generating qualitative, or specific quantitative predictions. One of the first models used in HBE was the prey choice model (see below). This examines the set of food resources which should or should not be observed in the optimal diet of a forager who attempts to maximize the currency of net energy gained per unit time, given the finding rate, and expected energetic returns from pursuing each specific resource type in the forager's environment. As with many optimality models, the currency used is not direct fitness, but rather a proxy, which is better suited for the specific problem at hand. More food per unit time, or the same amount of food in less time both result in a higher rate of energy gain, and in many circumstances should positively correlate with fitness.

HBE has been applied to an increasing number of broad topics such as foraging and subsistence practices, altruism and cooperation, resource conservation, mating and marriage systems, parental care of offspring, status and resource competition, and short-term and long-term life history patterns. Several themes highlighting the HBE approach are outlined below.

Foraging behavior

Studies of human foraging patterns focus primarily on the set of resources that comprise diets, and the choice of profitable resource patches and habitats. Group mobility and group size are also considered, as each has been modeled as flexible responses to ecological variables. The prey choice model predicts that upon an encounter with any kind of food resource, a forager should attempt to acquire it if the expected gain from doing so outweighs the expected gain from continued search (i.e. the long-term rate of caloric gain). This simple model has been used to predict the suite of resources people target in local environments in ethnographic and archaeological samples. Adjustments to the models have been made to fit characteristics of many human groups. Recent model specifications emphasize the importance of consuming macro- and micro-nutrients, cognitive limitations of the forager, information gathering, and the division of labor by sex and age. Changes in technology that increase the average caloric return rate, such as shotguns instead of bows and arrows, or trucks and snowmobiles instead of foot, have been shown to increase the number of resource types people acquire in their diet. Similarly, reduced processing or handling costs of certain resources such as seeds and grains raises the profitability of those resources, and so they enter the optimal diet. Declines in the abundance of very profitable resources, such as megafauna in North America, over historical time have been implicated as fundamental in the subsequent adoption of plant and animal domestication.

The patch choice model examines the suite of patches where individuals forage, and the length of time they spend in each of these patches before moving on to the next. The qualitative prediction is that optimizing foragers should leave a patch and proceed to the next patch before the former is depleted. Rather than reflecting a strategy of conservation, such behavior is consistent with the goal of caloric rate maximization. In a similar vein, foraging theory has recently been invoked to evaluate the validity of competing claims regarding the conservation ethic of indigenous populations. A conservationist might target fast-reproducing species, males, juvenile and older animals, such that future long-term gain is maximized, whereas according to foraging theory, an individual is more likely to target whichever resources maximize more immediate energy gain.

Altruism and cooperation

Altruism refers to the conferring of benefits upon others at personal cost. The prevalence of costly altruistic acts is a conundrum because exploiters, cheaters, or free-riders should out-compete selfless altruists in a Darwinian world. Consistent with evolutionary theory, altruism is expected when donor and recipient are close biological kin (kin selection), when recipients today send return benefits as donors in the future (reciprocal altruism), when giving acts honestly advertises phenotypic quality or the intent to cooperate (costly signaling), when forced to so by others (despotism), and when simultaneous mutual benefits can be gained (mutualism or trade). Altruism has been most studied in the context of collective production and distribution of food and services among small-scale hunter-gatherers and agriculturalists, group defense and warfare, wealth inheritance across generations, adoption of non-genetic offspring, and volunteerism and philanthropy in modern societies. Although evolutionary theory has shed much insight on the conditions that tend to favor more or less altruism in a particular context in small-scale societies, there is increasing evidence that some types of large-scale cooperation found in modern nation-states cannot be adequately explained by any of the above models. Alternatively, several forms of cultural group selection have been proposed where social norm compliance is enforced by punishment within cooperative groups.

Mating and marriage

The widespread variation in the ways that mating is publicly formalized as marriage across the globe has been examined as a function of the ecological interplay between the benefits men receive from investing their time and energy into parental care versus the gains of staying in the mating market, as well as the level of variation in mate "quality". Because women usually benefit more from increased access to resources than from increased access to mates, it is usually assumed that women's primary interests are coincident with child welfare. Pair bonds are expected when both parents have large positive effects on child welfare, and when extra-pair mating opportunities are few. These pair bonds should be monogamous when there wealth differences among men are few, and polygynous when some men monopolize valuable resources such as arable land and cattle. Women in polygynous societies thus become second or third wives to rich men who own more resources rather than first wives to single men with few resources. Polyandry is rare, and occurs only in extreme environments, where two or more men, usually brothers, share sexual access to one woman.

As described above, the payoffs to investments in parental care are an important feature of mating systems across and within societies. In environments where high parental investment can increase child fitness (via reduced mortality and increased likelihood of gaining necessary skills, education, and mating opportunities), and where paternity can be reasonably assured, higher paternal investment is likely. Higher investments by both parents in few children has been invoked as a crucial component in the fertility reductions so common in modern, industrialized countries, and among the wealthy in poorer countries. Such "demographic transitions" are seen as consequences of declining mortality, and a competitive skills-based labor market, where there are potentially few perceived diminishing returns to investments in a small number of children by educated and wealthy individuals.

Life history

The timing and development of important fitness-related events, such as birth, maturation, marriage, and death, constitute an individual's life history. At the species level, humans take a comparatively long time to become physical and functional adults, have large, costly brains, and have very long life-spans, much of which is spent in a post-reproductive state. Extended childhood has been explained as a time to develop the abilities and knowledge necessary to become an efficient adult food producer, or a socially shrewd adult. These explanations explore how the complex human foraging or social niche require a long time to master, and help to explain the buildup and maintenance of our large costly brain. Extended childhood has alternatively been described as a functionless artifact of humans having an extended lifespan. Long post-reproductive lifespan is explained as a form of indirect reproduction, in which older individuals positively impact descendant kin via food provisioning, direct care, education, and reconciliation, at a cost of reduced investments in reproduction earlier in the lifespan. There is strong evidence that the transfer of resources across and within generations may be a critical feature that shapes the life histories of humans and other social animals.

Life history variation has also been explored among individuals reared in different environments or exposed to different sets of circumstances and opportunities. These differences can impact the ways that people trade-off present benefits against future costs, or present costs against future benefits. Thus, a life history perspective has been used to investigate topics such as age at marriage and first birth, teenage pregnancy, infanticide and abortion, exercise and drug use, time preferences, and cooperation.

Future directions

Behavioral ecologists evaluate the adaptiveness of behavior given the set of constraints and options in the natural, social, and cultural environment. There has been a renewed appreciation for the ways in which cultural history can provide insight into the content and form of these constraints, and help to explain behavioral variation among peoples living in similar ecologies. Cognitive aspects of human decision-making have also received increased attention in helping to formulate the ways that people internalize, evaluate, and engage important parameters in typical models. Future directions will continue to integrate aspects of cultural anthropology and cognitive psychology with behavioral ecology.

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