B

BEHAVIORAL ECOLOGY

Behavioral ecology is an evolutionary approach to explaining variation in behavior among all living things. Many of the problems of life that people try to solve are also problems for other animals. Because evolution has shaped us all, current understanding of the way it works gives researchers tools to explain the puzzles posed by the resulting dazzling variety of behavioral arrangements. The tools apply to variation within species and across species. Questions about particular ethnographic patterns can be informed not only by the wider context of cross-cultural variation but by the even wider context of behavioral variation among animals generally.

The approach depends on two fundamental assumptions: first, that natural selection is the process that has designed living organisms and, second, that time and energy are always limited and individuals must therefore make trade-offs in the face of constraints. The first assumption is the basis for expecting individuals to do things that are likely to maximize their reproductive success or, more generally, their inclusive fitness, that is, their relative contribution to descendant gene pools. Over evolutionary time, characteristics spread and persist when the individuals with those characteristics are better at contributing genes to descendant generations. The second assumption is the basis for the use of economic logic. Trade-offs are unavoidable, and everything has a cost. The more spent on one thing means less for something else.

With these working assumptions researchers use models, sometimes quite simple ones, to investigate such topics as why males and females behave differently, why the character and extent of those differences vary, why individuals do different things at different ages, why patterns of time allocation vary not only by sex and age but also by season or wealth or both, why individuals use different resources from one time and place to another, why family arrangements take different shapes, and why there is more sharing and help in some cases than in others, over some things more than others, and with some associates more than others. The theoretical foundation of behavioral ecology makes the answers to these questions in one research setting directly useful elsewhere—not because it explains away the variation, but because different cases show whether variables do actually covary in the ways expected. Work over the last few decades has revealed more variation than previously imagined (Krebs and Davies 1991, 1993), but it also reveals larger regularities within the variation, not only among other animals but among people as well (Betzig, Borgerhoff Mulder, and Turke 1988; Cronk 1991; Hill 1993; Smith and Winterhalder 1992).

ADAPTIVE FUNCTION VERSUS CAUSAL MECHANISM

Natural selection favors a characteristic when it increases the inclusive fitness of the individuals that carry it (Krebs and Davies 1991; Williams 1966). This process of differential success for alternative characteristics within populations does not maintain, maximize, or optimize any characteristic of groups or societies. It does not spread characteristics because they contribute to the survival of the species (Alexander 1979; Chagnon and Irons 1979; Williams 1966). The label "adaptation" is often used in behavioral ecology to mean something designed by natural selection, something that persists because of its fitness effects. In this narrow sense, adaptations are characteristics of individuals, not groups or social systems. Decision mechanisms designed by selection to direct an individual's allocation of time or energy are adaptations, according to this usage. The usual research task in behavioral ecology is to explain why subjects allocate their time or resources as they do by constructing and testing hypotheses about the adaptive (fitness-promoting) effects of the allocation. The questions posed are functional questions, representing a functional approach that is quite different from the traditional functionalisms of cultural anthropology.

The difference between the functional questions that behavioral ecologists usually ask and other kinds of questions is a large and important one. A full explanation for any empirical pattern requires answers to different kinds of questions. Useful distinctions among different kinds of questions have long been made in ethology (Krebs and Davies 1993), but the clarification has not been appreciated widely enough to prevent confusion and argument. The difference between a functional and a causal explanation is the most important. Sometimes it is described as the difference between why and how or between investigations of ultimate causes versus proximate mechanisms.

For example, a search for a functional explanation for the resource choice made by foraging men in a particular ethnographic setting might begin with a hypothesis about the (fitness-related) effects of their choice (their goal) and the alternatives available to them. A functional hypothesis might be that pursuing that chosen set of prey maximizes a man's mean rate of nutrient acquisition while he is foraging. Testing it requires data on encounter rates and profitabilities for each resource. Whatever the result of the test, that line of inquiry will not explain how those men make that choice. The proximate-mechanism question—how do they do it?—requires a different kind of investigation, different hypotheses, and different data. Partly because the functional explanation is silent about proximate causes, it can be extremely general. A similar functional explanation could account for the prey choice of men in another time and place, where people know different things about their environment and tell different stories about hunting. It could also account for prey choice among nonhuman foragers who tell no stories at all.

INTENTIONS VERSUS EFFECTS

The language of intention, often used as a shorthand by behavioral ecologists, is much more confusing when the subjects are human. The hypothesis that a bird chooses certain prey to maximize its mean rate of energy gain or lays a clutch of eggs of a certain size to maximize the number of surviving offspring per clutch will not lead readers to assume that anything is implied about the bird's cognitive plan. Similar hypotheses about human subjects invite a literal reading, yet the language is shorthand that displays the pattern because of its effects. The hypothesis is about function not intention. Functional explanations do not answer questions about how decision mechanisms work. Conversely, explanations of the workings of a mechanism—ontogenetic, physiological, or cognitive—do not explain its persistence in the face of evolution by natural selection. The focus on function is given priority in behavioral ecology because it provides a framework in which to describe and explain broad patterns.

OPTIMIZATION MODELS

The main tools behavioral ecologists use to guide their research are optimality models, both simple and frequency dependent. These models impose a tight discipline on the development of hypotheses, a particular strength of the approach and the source of what some see as its irritating inflexibility. Investigators make (biologically informed) guesses about the fitness-related problem faced by the subject, which requires hypotheses about the effects (or goal) of the behavior and about the costs and benefits of alternative means to achieve that goal. These are not hypotheses about the intention or cognized plan of the subject (human or otherwise). Formal models show what individuals would necessarily do to achieve a particular goal under the specified constraints. If subjects do not behave as modeled, they are not meeting that goal and face other constraints.

The models that have proven most useful focus on very simple trade-offs, use readily measured currencies to assess alternatives, and incorporate few constraints. For example, the prey model of foraging theory (Stephens and Krebs 1986) shows which resources a forager of any species will pursue to maximize its mean rate of energy capture if it can only spend time either searching for or handling resources (i.e., if this is the only trade-off) and if resources with known average profitabilities are encountered sequentially at a known rate (these are the only constraints). David Lack's model of optimal clutch size, constructed to explain why birds lay a predictable number of eggs at a time (and applied to offspring numbers for many nonavian species) is another example (Krebs and Davies 1993) in which the trade-off is between number of offspring and their survivorship, and the hypothesized goal is the maximum number of surviving offspring per clutch. The utility of the models is not just a matter of determining whether or how often subjects seek these goals under these constraints. The simplicity of the models and the relative ease with which key variables can be measured make patterns in falsification themselves informative. For example, the prey model predicts that foragers will either take or ignore all items of a given prey (resource) type, but partial preferences are often observed as well; clutch sizes are often smaller than Lack's model predicts. These patterned falsifications have stimulated the development of models that incorporate other trade-offs (Stephens and Krebs 1986; Krebs and Davies 1991).

INDIVIDUAL VERSUS COLLECTIVE INTERESTS

One of the biggest differences between behavioral ecology and other ecological approaches is the attention paid to conflicts of interest among individuals. When the net benefits that an actor is likely to gain for an action depend on what others do, frequency-dependent optimality models are the tools for constructing hypotheses about goals, constraints, and trade-offs. The models are frequency dependent because payoffs for a particular behavior change with how many others adopt the change. As with any optimization technique, the models impose discipline on the formation of hypotheses by showing what actors necessarily do to achieve the modeled goal under the modeled constraints. As with all formal models, this clarity can reveal previously unappreciated entailments of the goals and constraints that investigators guess to be important. The fundamental assumption that individuals are designed to serve their own fitness implies overlapping interests among those who are closely related, but it also implies conflicts of interest among even the very closest kin.

Evolutionary game theory, which is especially useful for modeling frequency-dependent costs and benefits, can be applied to a wide array of patterns. The most famous payoff structure in game theory is a very simple one called the "prisoner's dilemma." In showing how the benefits to a group may not be maximized when its members maximize their own benefits, it illustrates the essence of such famous collective action problems as Thomas Hobbes's state of "Warre" and Garrett Hardin's "tragedy of the commons." Another simple model, "chicken," applies to many collective-action problems and contributes hypotheses about the "free-rider" problem. Goods used by members of a group can be like public goods (e.g., community defense, public safety, clean air). When these goods are available to anyone, they can be consumed by all. As a consequence, self-interested actors do better to allocate their scarce resources to goods that they cannot get for free. Public goods are overconsumed or underprovided by voluntary actors. Externalities (the effects of an action that are beyond, that is, external to, the actor's own accounting but that alter the costs and benefits of others) shape social outcomes.

GENETIC DETERMINISM AND EVOLUTIONARY EQUILIBRIUM

People learn how to behave in different circumstances. If this framework did not apply to learned behavior, it would be of limited use to anthropologists. The theoretical foundation supports a general expectation that individuals have been designed by selection to be strategists with capacities and tendencies to pursue their own fitness. Learning, like anything else, has both costs and benefits. Elaborate learning and assessment mechanisms impose costs worth paying only if they result in adjustments that give large enough fitness benefits. Large differences in behavior among individuals with no correlated genetic differences can then result from adjustment to varying opportunities and constraints. Much of the work that has been done on other species explains why the same individual animals are likely to behave differently under different circumstances by showing that subjects adjust as different alternatives give higher payoffs. If the same individual does different things at different times because of the way it has been designed by selection to respond to its circumstances—for example, the potential prey flees only when it senses the predator or the forager widens its diet breadth only when encounter rates with more profitable items decline—then, in the same way, differences among individuals may result from the same response mechanism.

A working assumption in the chain of argument from selection to observable covariation between behavior and ecology is that subjects are in evolutionary equilibrium. This assumption is always a simplification for subjects of any species, so much so that its demonstrated utility is actually astonishing. The underlying theory about evolution by natural selection provides reason to expect organisms to be good at solving the problems of life only if these are problems that their ancestors encountered often enough over a long enough span of time. How good, as well as how often and how long, can be salient issues.

Optimality models identify solutions that are not just good, they are the best. This claim, however, and the expectation about individual allocations, are more modest than they may appear. "Best" for these purposes is never "the best of all possible solutions," only the best of a given feasible set. Local optima are the ones of interest, and therefore the best of the available alternatives can also mean "the best of a bad job." Models are more tractable; hypotheses are easier to test when they address adjustments in one thing at a time, taking the rest of the world as fixed.

There are thornier issues surrounding the assumption of evolutionary equilibrium. The problems that people now living confront are always specific to their current circumstances. Even to suggest that a set of problems for a particular ethnographic setting can be characterized in some average way—by sex, for example, or by sex but different for each season—overrides differences among days and individuals. Any particular moment or event is unique, but not just in human experience. Selection can design organisms to suit their circumstances and to learn from their own experience only if there are recurrent similarities in those circumstances and experiences. The working assumption that the specific problems that particular people confront may be problems with deep antiquity is a version of the general assumption about similarities that is required by the fundamental theoretical proposition about evolution by natural selection. The implicit working hypothesis about evolutionary equilibrium is that subjects are solving problems under constraints that are familiar in this evolutionary sense.

Where people live in small kin-based communities, especially when they depend on wild foods and use foot transport, many of their day-to-day problems and constraints seem to be very old ones, irrespective of whether the communities have a long history in which patterns of behavior have remained unchanged. Migration, war, and disease have had profound effects on the distribution of populations and resources on every continent, not only within the last few centuries but throughout the preceding millennia. Independent causes of climate change have inflated the ecological variation over that time period. Further back in the Pleistocene era, with its extreme climatic fluctuations, the colonization of new environments was a human, even a generally hominid, specialty. If extreme temporal ecological variation, migration, and displacement have been common, an ethnographic fit between people and their circumstances implies continual evaluation and adjustment to changing opportunities.

Where people make their livings by foraging, they confront problems faced by thousands of generations of ancestors, even if not by their own immediate forebears. Some problems differ for subsistence farmers or herders, but they may belong to general classes of problems of great antiquity. Industrial economies and large communities with complex structures present problems and constraints that seem obviously novel. Although some of the particularly novel problems may still fit into familiar categories, the tools of behavioral ecology will surely not suffice to explain many, perhaps most, patterns of behavioral response. There are some aspects of any pattern of behavior that use of those tools does not even address, but because they pose testable hypotheses about constraints and tradeoffs and link results among different studies, their limits are an empirical matter. Failures as well as successes in explaining human patterns help to show how we fit into the broader evolutionary story.

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SEE ALSO: Adaptation; Cultural Ecology; Historical Ecology; Optimal Foraging Theory

ALEXANDER, RICHARD D. *Darwinism and Human Affairs.* Seattle: University of Washington Press, 1979.

BETZIG, LAURA, MONIQUE BORGERHOFF MULDER, and PAUL TURKE, eds. *Human Reproductive Behavior: A Darwinian Perspective.* New York: Cambridge University Press, 1988.

CHAGNON, NAPOLEON A., and WILLIAM IRONS, eds. *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective.* North Scituate, Mass.: Duxbury Press, 1979.

CRONK, L. "Human Behavioral Ecology." *Annual Review of Anthropology* 20 (1991): 25–53.

HILL, KIM. "Lifehistory Theory and Evolutionary Anthropology." *Evolutionary Anthropology* 2 (1993): 78–88.

KREBS, JOHN R., and NICHOLAS B. DAVIES. *An Introduction to Behavioural Ecology,* 3rd ed. Oxford: Blackwell, 1993.

KREBS, JOHN R., and NICHOLAS B. DAVIES, eds. *Behavioural Ecology: An Evolutionary Approach,* 3rd ed. Oxford: Blackwell, 1991.

SMITH, ERIC A., and BRUCE WINTERHALDER, eds. *Evolutionary Ecology and Human Behavior.* New York: Aldine de Gruyter, 1992.

STEPHENS, DAVID W., and JOHN R. KREBS. *Foraging Theory.* Princeton, N.J.: Princeton University Press, 1986.

WILLIAMS, GEORGE C. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought.* Princeton, N.J.: Princeton University Press, 1966.

BELIEF SYSTEMS

Belief systems are those most deeply embedded creeds, ideas, understandings, and hopes that underlie and motivate one or more of the dominant operations of a culture. Such beliefs frequently are established at formative moments in the history of a culture, society, or nation. They often arise from a particular religion but also may originate in philosophical postulates, ethical proclamations, or in all three. Formative belief systems may have had an essential role in the historical beginnings of a settlement that later became a society; they may have entered an ongoing culture as an adaptational strategy at a moment of crisis; or they may have replaced forcibly other systems through military conquest and repression.

Once thoroughly embedded in a culture, belief systems tend for the most part to reside at the level of assumptions and presuppositions rather than at the level of constructed explanations. This is one of their most salient characteristics, and the importance of this feature can hardly be overstated for its relevance to the theory and practice of anthropology. Fundamental beliefs generate everyday practices, customs, expectations, and laws, yet they become so overladen with these later accretions that their contents become heavily veiled even to members of the group that embraces them. Churches often illustrate this pattern. While theological experts may know the specific dogmas and doctrines that justify and validate rites, ceremonies, moral requirements, and ascetical practices, the laity in general can participate fully and meaningfully in the religion without being able to produce satisfactory explanations for many of their religious actions.

Belief systems possess momentum. They continue their influence long after they have lost or shed their initial adaptive aptitude. These beliefs are not held unconsciously but are seldom subjected to examination or reflection. Persons who do not actually subscribe to the formal beliefs of the system or systems underlying their own culture, or even know what they are, nevertheless may organize and proceed through their lives influenced by these ancient understandings. These systems become such that no one member of a society embodies completely the beliefs they contain and yet vast numbers participate in them to some degree. Belief systems may allow a culture to remain vigorous and adaptive or cause it to degenerate into increasing stagnation and maladaptation, even though (or perhaps because) few of that culture's members understand the forces that are producing either of these outcomes.

When the dogmatic character of formative beliefs becomes diluted, creedal axioms gradually are transformed and infused into many more subtle genres of a society's representations. As they take hold, beliefs may take on a mythological quality, coming to be seen not as specific ideas or arguable hypotheses but as ultimate formulations of truth that express what things are and what things mean. They then shape the form and content of such diverse cultural elements as stories, songs, slogans, fables, poetry, economics, religion, politics, kinship, and socialization. They also generate ideal types, that is, distilled paradigmatic constructed personalities that embody and represent a culture's dominant values. These values then become attached to historical or fictional characters that are projected as exemplars for a society's self-understanding.

Belief systems are extraordinarily powerful. When they have reached the level of assumption they may be only vaguely discernible and inconsistently expressed, but this does not lessen their power. They affect the most objective of enterprises and indeed interfere with the proceedings of science itself. One of the most famous instances of the latter occurred in the work of the German astronomer Johannes Kepler during the late sixteenth and seventeenth century. He was so devoted to a particular doctrine of the nature and attributes of God that he spent years attempting to force his astronomical data into a model based on the five regular solids.

The assumptions and presuppositions arising from belief systems take on a prescriptive quality and operate

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