Sociobiology

New scientific theories, especially when they touch on the mysteries of human behavior, seldom go unchallenged. Such has been the case since Harvard biologist Edward O. Wilson's *Sociobiology: The New Synthesis* was published in late 1975. Wilson sought a biological explanation for animal (and human) social behavior through a fresh application of Darwin's theories of evolution and natural selection. His book was "news" in both specialized journals and major newspapers. This "synthesis" brought heated reactions from other academics—in part, over what some critics perceived as its ethical, racial, and cultural implications. Last November, the American Anthropological Association devoted several sessions at its annual meeting to sociobiology, and the discussion shows no signs of abating. Here, zoologist David P. Barash discusses sociobiology's significance; sociologist Pierre L. van den Berghe explores its ethical aspects; and anthropologist Anthony Leeds offers a sharp but detailed critique of both Wilson and his more extreme detractors.

THE NEW SYNTHESIS

by David P. Barash

More than 100 years after *The Origin of the Species* was first published, students of behavior are finally coming to grips with Darwin's message. It's about time. The behavioral sciences in general—and social science in particular—have long suffered from an inferiority complex relative to the "harder" sciences, notably chemistry and physics. Even a cursory reading of the classic texts in these areas, such as Linus Pauling's *General Chemistry* and Richard Feynman's *Lectures on Physics,* explains why. The physical sciences unfold with an almost irresistible intellectual mo-

mentum as basic assumptions are checked against the data, hypotheses are generated, and these in turn are checked against more data, thereby generating more hypotheses. The result is a coherent explanation of how the world is put together, one that not only interprets our findings but also provides further insights.

In contrast to the masterful structures of these disciplines, behavioral science is a ramshackle affair indeed, a rickety Tower of Babel with as many viewpoints as there are practitioners and virtually no unifying intellectual underpinnings. But all this is changing with the recognition that biology—and behavior as a branch of biology—possesses an underlying unity. This unifying principle is evolution by natural selection, and it lies at the very core of the synthesis that is sociobiology. In fact, sociobiology is nothing more or less than the application of evolutionary biology to animal social behavior, a notion as old as Darwin but with implications that are only now being explored.

Experience Versus Evolution

Most scientific revolutions generate controversy and resistance as well as enthusiasm. Until the rise of sociobiology as a discipline, experience was considered to be pre-eminent in influencing behavior. Social scientists in particular have been wedded to the notion that behavior derives from learning and early experience—or from social traditions and cultural norms in the case of human social behavior as studied by anthropologists and sociologists. To some extent, therefore, the suggestion that evolution influences behavior is bound to be controversial. But the issue lies deeper. The infusion of evolutionary concepts into the study of behavior implies that behavior is subject to the same laws as anatomy and physiology. Despite the furor occasioned by evolution in the 19th century, we never fully appreciated Darwin's message. Granting that humans and all other living things share a common ancestry, we were still content to ignore the implications of evolution for behavior. In so doing, we may have gratified our need for being "special," but at the cost of forgoing an objective, critical examination of ourselves and our fellow creatures.

Although Darwin is its intellectual grandfather, sociobiology is very new, the product of a flurry of activity during the past 15 years. And although the controversy surrounding it derives largely from its application to human behavior, sociobiology itself derives almost entirely from studies of nonhuman animals.

In 1962, the Scottish ecologist V. C. Wynne-Edwards shook

the world of biology with his book *Animal Dispersion in Relation to Social Behaviour,* in which he suggested that virtually all social behavior—including dominance hierarchies, securing of territories, flocking in birds, herding in mammals, even the nocturnal dances of fireflies—is a means of regulating animal numbers and preventing populations from eating themselves into oblivion. It had long been recognized that socially subordinate individuals often fail to breed and that overpopulation is rare in nature. Wynne-Edwards suggested that social congregations serve to inform individuals of the local population density, so that individuals could avoid overpopulation by regulating their own breeding accordingly.

It was an appealing notion, but Wynne-Edwards recognized that it required altruistic reproductive restraint by the participating individuals counter to the expectations of Darwinian theory, which assumes that individuals will always behave so as to maximize their reproduction. He attempted to justify his suggestion by postulating "group selection"—in which individuals might evolve who reduced their personal reproductive success, providing such "altruistic" behavior contributed to the reproductive success of the groups to which they belonged. Biologists were quick to respond, pointing out that in virtually all such cases, selection operating upon individuals within their own groups would over-ride selection acting among groups.

Natural selection is quintessentially selfish. Traits spread in a population when individuals possessing these traits produce more successful offspring than individuals with other traits. If some individuals within a group benefited the group by restricting their breeding, they would be at the mercy of selfish individuals within the same group who reproduced indiscriminately, even if this meant the extinction of the group. Observations of free-living animals strongly support this view. Reproductive restraint has repeatedly been shown to reflect each animal's attempts to maximize its own reproduction, including certain cases where this is accomplished by temporarily failing to breed. The

David P. Barash, 31, an associate professor in the Departments of Psychology and Zoology at the University of Washington, Seattle, was born in New York City. He graduated from Harpur College, Binghamton, N.Y. (1966) and received his master's degree and doctorate in zoology from the University of Wisconsin (1968, 1970). The author of numerous articles on ethology and animal behavior, his primary research interests entail field studies of vertebrates, especially the evolution of social behavior in birds and mammals, and the sociobiology of animals and humans.

current trend among evolutionary biologists is to regard group selection as theoretically feasible, but the requirements for its occurrence are so extreme that it is very improbable. Indeed, it has yet to be demonstrated in nature.

Why is the issue worth mentioning? Because, in responding to the challenge of group selection, biologists have been forced to examine natural selection as it operates upon individuals rather than groups or species. Out of this has come a new appreciation of the power of evolution. A cornerstone of this new thinking was unveiled in 1966 with the publication of George C. Williams' influential book *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought.*

Altruistic Workers

Another cornerstone of modern sociobiology had been in existence since 1964, when W. D. Hamilton's article "The Genetical Evolution of Social Behaviour" appeared. This British geneticist was particularly concerned with explaining a long-standing puzzle in the biology of the social insects—bees, wasps, and ants—but his findings had enormous significance for all social behavior, including our own. Hamilton addressed himself to the perplexing fact that among honeybees, for example, workers are sterile; they labor altruistically for the success of the queen while not breeding themselves. A case of group selection? Perhaps. But Hamilton pointed out that these insects exhibit a peculiar genetic system: Males are "haploid" (they develop from unfertilized eggs and therefore possess only half as many chromosomes as their "diploid" sisters). As a result, a female worker shares three-quarters of her genes with her sisters, whereas she would share only one-half with her offspring if she were to breed. Hence, a female worker does more to foster her own genotype by staying home and caring for sisters than if she were to leave the hive and attempt to rear a family of her own. Altruism? Again, perhaps, but an altruism that is ultimately selfish in that it promotes each individual's genes, albeit at the cost of producing offspring directly.

By focusing on genes, Hamilton emphasized that even parental behavior is only a special case of concern for others in proportion as those others share the parents' genes. Hence the term

"kin selection." For most vertebrates, parents share one-half of their genes with each offspring, one-quarter of their genes with nieces and nephews, and one-eight with cousins. Kin selection provides a coherent theory for the biology of nepotism, since the "closeness" of relatives depends on the proportion of the genes they share. At the same time, kin selection provides a more acceptable explanation of the evolution of altruistic behavior than group selection.

An animal can be said to behave altruistically if its actions increase the reproductive success (fitness) of another, while decreasing the personal fitness of the performer. In the cases presented thus far, altruism was evidenced by reproductive restraint, but in many cases the relevant behavior may be much more subtle, even though it ultimately results in reduced reproduction. Thus, individuals may share food, provision someone else's offspring, and defend others from predators or warn them when predators approach.

Take this example: Prairie dogs give a warning bark when a coyote appears in the prairie-dog town. In doing so, the alarm-giver is altruistic in that his action increases the chances of survival, and hence reproduction, of the prairie dogs warned by the alarm, but his own chances of reproducing successfully are reduced, since his bark draws the predator's attention to himself. However, if a sufficient number of the alarm-caller's relatives are saved as a result, genes for alarm-calling could spread in the population, even though individual alarm-callers are at a personal reproductive disadvantage.

Cost-Benefit Analysis

In discussions of the sociobiology of altruism, no assumptions need be made concerning consciousness or personal motivation. Altruism is defined solely by the consequences of a particular act for fitness, so it is acceptable to speak of altruistic turkeys, honeybees, or even viruses. Kin selection theory states that, in general, the occurrence of altruistic behavior increases with the "closeness" of the beneficiary (the more genes shared by common ancestry, the more likely is altruistic behavior). Similarly, altruism is more likely when the cost to the altruist, measured as a decline in its personal fitness, is low and the recipient's benefit is great. By manipulating these factors, we can derive various predictions for the occurrence of altruism as determined by kin selection.

Findings so far are consistent with this theory. Thus, in the

only vertebrate species known that practices "simultaneous polyandry" (several males sharing the same female), the males tend to be brothers so that each male, if not a father, is at least an uncle through his "altruistic" tolerance of his sib. In several bird species, young adults often help older pairs provision their offspring; significantly, this altruistic "helping at the nest" is invariably done by close relatives of the pair being aided. Most often, they are offspring from a previous brood. Their altruism promotes their own genotype, since it helps to rear siblings with whom the helpers share genes. Studies of Japanese macaque monkeys reveal that they are likely to share food with others in direct proportion to the closeness of the relationship. The list of such kin-selection cases is long and growing, providing sociobiologists with a valuable "handle" on social interactions between individuals—non-human animals for certain and quite possibly the human species as well.

Adaptive Social Behavior

A major insight of sociobiology is the recognition that behavior, even complex social behavior, has evolved just as teeth, feathers, and bone have evolved. If so, then social behavior should be adaptive. It should somehow be attuned to particular environments so as to maximize the reproductive success of individuals showing that behavior. By the 1960s, patterns began to emerge from the numerous long-term field studies of animal social behavior. These patterns differed for each animal group studied, but the underlying truth was clear: The complex social systems of free-living animals revealed the unmistakable imprint of natural selection.

An example from my own work on marmots should suffice. Woodchucks are marmots common in the eastern United States, where they occupy low-elevation fields. These animals are solitary and aggressive. The Olympic marmot, by contrast, lives above

GLOSSARY

Sociobiology The systematic study of the biological basis of all social behavior.

Adaptation In evolutionary biology, any structure, physiological process, or behavioral pattern that makes an organism more fit to survive and to reproduce in comparison with other members of the same species. Also, the evolutionary process leading to the formation of such a trait.

Altruism Self-destructive behavior performed for the benefit of others.

Chromosome A complex, often rodlike structure found in the nucleus of a cell, bearing part of the basic genetic units (genes) of the cell.

Darwinism The theory of evolution by natural selection, as originally propounded by Charles Darwin. The modern version of this theory still recognizes natural selection as the central process, and for this reason is often called Neo-Darwinism.

DNA (deoxyribonucleic acid) The basic hereditary material of all kinds of organisms. In higher organisms, including animals, the great bulk of DNA is located within the chromosomes.

Ethology The study of whole patterns of animal behavior in natural environments, stressing the analysis of adaptation and the evolution of the patterns.

Evolution Any gradual change. Organic evolution, often referred to as evolution for short, is any genetic change in organisms from generation to generation or, more strictly, a change in gene frequencies within populations from generation to generation.

the timberline in the Olympic Mountains of Washington. In this severe environment, Olympic marmots are socially tolerant, living in large colonies. Members of a third species, the yellow-bellied marmot, inhabit environments of intermediate severity in the Rockies and Sierras, and their social system is appropriately intermediate; they live in colonies, to be sure, but these are loosely organized, and the few interactions between residents tend to be rather aggressive. Furthermore, another high-mountain dweller, the hoary marmot of the northern Rockies and Cascades,

Genetic fitness The contribution to the next generation of one genotype in a population relative to the contributions of other genotypes. By definition, this process of natural selection leads to the prevalence of the genotypes with the highest fitness.

Genotype The genetic constitution of an individual organism, designated with reference either to a single trait or to a set of traits.

Kin selection The selection of genes due to one or more individuals favoring or disfavoring the survival and reproduction of relatives (other than offspring) who possess the same genes by common descent. One of the extreme forms of group selection.

Natural selection The differential contribution of offspring to the next generation by individuals of different genetic types but belonging to the same population. This is the basic mechanism proposed by Charles Darwin and is generally regarded today as the main guiding force in evolution.

Parental investment Any behavior toward offspring that increases the chances of the offspring's survival at the cost of the parent's ability to invest in other offspring.

Phenotype The observable properties of an organism as they have developed under the combined influences of the genetic constitution of the individual and the effects of environmental factors.

Reproductive success The number of surviving offspring of an individual.

Selfishness In the strict usage of sociobiology, behavior that benefits the individual in terms of genetic fitness at the expense of the genetic fitness of other members of the same species.

lives in a social system that closely resembles that of its high-elevation cousin, the Olympic marmot.

To complete the correlation between environments and social systems for this group, I found that some yellow-bellied marmots (the intermediate-elevation, intermediately aggressive species) also live in high-elevation situations and display the social system shown by Olympic and hoary marmots. Of course, it is one thing to document a correlation and quite another to determine its cause. In this case, there are other correlations: Animals at

higher elevations grow more slowly than at low elevations, become sexually mature later, and reproduce less often. It appears that such animals have evolved social systems whose tolerance varies with the necessity for young animals to remain within the colony and thus enhance their own chances of survival and, eventually, reproduction.

With their attention newly focused upon natural selection, behavioral biologists developed a whole new range of theory relating evolution to social behavior. For example, a model was developed showing how female choice is largely responsible for the evolution of mating systems in birds and mammals, the choice in each case attuned to the maximizing of evolutionary fitness. Thus, some red-winged blackbird males typically mate with several females, leaving some males with no females at all. Given that females profit from male assistance in rearing offspring, it seems that females would prefer to mate with a bachelor and thus receive his undivided attention, rather than share their mate with other females. It was shown, however, that females prefer harem membership to cozy monogamy, so long as the haremmaster offers enough benefits to compensate for the loss of his undivided attention. This occurs especially when territories offered by males differ in such matters as food supply and protection from predators, which maximize their reproduction and that of their relatives. The niceties of domesticity take second place to the selfish realities of evolution.

Reciprocal Altruism

Males, or any individuals that defend a territory, have also been shown to be sensitive to economic considerations of cost and benefit. Territories are maintained when they are objects of competition and contain resources that can be economically defended. A model has been proposed for the evolution of "reciprocal altruism," a system in which altruistic tendencies can be selected, even in the absence of genetic relatedness. The point here is that the beneficiaries have an opportunity to reciprocate, thereby repaying the original altruist; again, as with all sociobiologic considerations, "payment" is measured ultimately in units of evolutionary fitness.

The evolution of reciprocity is sensitive to the appearance of "cheaters," individuals who receive help from others but refuse to reciprocate when the opportunity arises. Cheating tendencies would spread in such a population, since cheaters would gain fitness at the expense of the altruists. On the other hand, this

should result in selection on the basis of ability to discriminate cheaters from non-cheaters—especially important for our own species, given our extraordinary concern with character and past behavior.

Sociobiologic theory has also dealt with the ubiquitous phenomenon of male-female differences in behavior, especially reproductive behavior. Among animals, males are nearly always the sexual aggressors, playing relatively fast and loose, whereas females tend to be coy and discriminating. Harvard biologist Robert Trivers (responsible for the concept of reciprocal altruism, discussed above) has made an enormous contribution with his elaboration of the idea of "parental investment," defined as any investment directed toward offspring that enhances their chances of survival and reproduction and is made at the cost of the parent's ability to invest in subsequent offspring and other kin. Females generally invest more than males: Eggs "cost" more than sperm. Furthermore, reproducing females among mammals must undergo pregnancy and lactation. Small wonder males are the aggressive adversaries and females the careful comparison shoppers.

Game Theory

The implications of parental investment theory go even further. Thus, individuals of the sex investing less—usually the males—can be expected to compete among themselves for access to individuals of the sex investing more. This explains the occurrence of large, brightly colored, aggressive males in most birds and mammals. The exact opposite is found in those rare species in which the males invest more than do females. In such cases, the females are appropriately large, brightly colored, and aggressive. Moreover, male-female differences in parenting behavior are related to differences in confidence of the genetic relatedness to the offspring. Females are always related to the young they produce; males have no such assurance. Significantly, male involvement in care of the young in most animals is greatest when male confidence in paternity is most assured.

Sociobiologists have applied the mathematics of game theory to aggressive encounters between animals, arguing that stable strategies of behavior should evolve when fixed costs and benefits are associated with different behaviors. For example, there is a cost associated with fighting (risk of injury and time expended) but also a possible benefit (access to food, female, nest site, or whatever). When appropriate values are given to these

considerations, the results help explain why animals often stop short of killing, or even injuring, defeated opponents. Such animals adopt the behavioral strategy that maximizes their evolutionary fitness, consistent with the other findings described above.

With all these exciting theories and supporting data in the air, it remained for Harvard zoologist E. O. Wilson to bring it all together in a masterful, encyclopedic synthesis in 1975.* Sociobiology existed before Wilson's book, but it has not been the same since. He gave it a name, gathered the materials in one convenient place, and received a great deal of acclaim—and no small amount of criticism and abuse.

Genetic Influence, Not Determinism

Sociobiologists do not claim that behavior is somehow "controlled" by genes, ignoring the roles of experience and culture. Genes are merely blueprints, patterns for eventual products that may be susceptible to a great deal of modification along the way. Genes influence behavior only to the extent that they code for a range of possible behaviors. In a case like the blink reflex, the range may be narrow and not particularly subject to learning. In other cases, such as the development of personality, the range may be extremely broad. Critics who accuse sociobiology of genetic determinism unfairly oversimplify the issue, since the claim for evolution's relevance to behavior rests on genetic influence, not determinism.

The question of the place of free will in sociobiology is an especially fascinating one. Merely proposing that human behavior is "determined," or even influenced, by previous experience does not leave us with any more control over our destiny than we had before. I suggest that one is possessed of maximum free will when behaving in accord with one's inclinations; specifying the source of these inclinations does not help to answer the question of free will, although it may help us to understand ourselves. Sociobiology may not explain why we voted for one presidential candidate over another, but it may have a lot to say about why we choose leaders at all. It offers potential insight into the deep structure of human behavior, although this is not to deny the role of experience and culture in producing the final product.

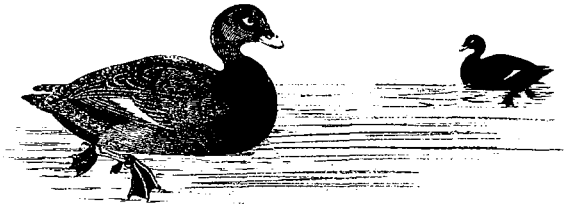
We cannot doubt that the behavior of *Homo sapiens* is the farthest removed from genetic influence of all animals. However,

* *Sociobiology: The New Synthesis.* See Background Books, page 143.

this does not mean that we are not susceptible to such influence, and our particular self-interest demands that we use whatever tools we possess to better understand our own nature. Indeed, if biology seems arrogant in claiming insight into human behavior, what of the greater arrogance of a social science that claims no help is needed?

Imagine you have been seriously nearsighted all your life but haven't been aware of it until you are fitted for eyeglasses. Things seen only dimly, if at all, are suddenly clear. Blurry images make sense, and vague relationships have a sharp, new meaning. Sociobiologists have undergone the same kind of an exciting experience in recent years, thanks to the conceptual clarity provided by the application of evolutionary biology to animal social behavior. Since fitness—the key to sociobiology—is so dependent on reproductive success, we might expect reproductive behaviors to be especially sensitive to natural selection, and, indeed, sociobiologic studies of reproductive behavior have been particularly rewarding.

Courtship serves the important function of permitting an individual to assess the characteristics of a prospective mate and to reject those less suitable. Accordingly, predatory birds practice acrobatic, aerial courtships, and most monogamous species insist on prolonged pre-copulatory engagement periods. Among gulls, mated pairs that fail to rear offspring one year are significantly more likely to seek a new mate the following year than are pairs that were reproductively successful. (Isn't this equivalent to divorce?) Male hummingbirds permit females to feed on their territories only when the females permit the males to copulate with them. (Equivalent to prostitution?) A male mountain bluebird who discovers a strange male near his mate will aggressively attack the stranger and will attack his own female as well, provided this occurs at the time copulation normally occurs in nature. (Male response to adultery?)



Rape is common among many ducks: Unmated males are especially likely to be rapists, and males whose females are being raped often try to intervene; if too late, they often rape the female themselves. Apparently, the males' best (fittest) strategy in such cases is to introduce their sperm as quickly as possible, to compete with the sperm of the rapists. Male lions and langur monkeys who take over a harem of females are apt to kill the infants, thereby eliminating individuals with whom they share no genes and inducing the females to become sexually receptive again, so they can produce their own offspring as quickly as possible—an unpleasant procedure, but, if it results in an increase in gene frequency, animals can be counted on to do it.

A real difficulty in studying human sociobiology is that we are so complex and the ethical restraints on genetic experimentation are so real that it may be virtually impossible to disentangle biological from cultural elements. A productive approach to overcoming this difficulty might be to combine anthropology with evolutionary biology in order to search out the cross-cultural universals in human behavior—the pan-human cake that underlies the diverse cultural icing. With adroit use of the Central Theorem of fitness maximization, it might then be possible to make real and valid predictions in regard to human behavior.