Sociobiology (I): Models of Social Behavior

Altruism, faithfulness to one's mate, parental sacrifices for the young, and other similar behavioral patterns occur in many species, ranging from social insects to mammals. Although numerous descriptions of such behavior have been published, only recently have models been proposed to explain why these patterns are so widespread. These models ascribe social behavior to a kind of genetic imperative—that is, behavior of individuals evolves so as to maximize their genetic contribution to the next generation. This far-reaching notion is the basis of an emerging field of inquiry known as sociobiology, which seems to be having an impact on the design of field studies of animal behavior and is also attracting the attention of social scientists as well as stirring up controversy among them.

Young birds often help their parents at the nest in the care of younger siblings. This type of altruistic behavior can be explained by proponents of sociobiology as follows: In order to maximize their genetic contribution to posterity, individuals would be expected to help their close relatives more often than they would help other members of their society. By helping close relatives, who are more likely to share their genes, individuals may increase the likelihood that their genes would be represented in future populations. This explanation of altruism as a form of selfishness, developed in part by W. D. Hamilton of the University of London, has been applied to explain behavior by individuals of many species, including social insects, birds, fish, and primates.

Ants, bees, and wasps, which are social insects that exhibit complex behavior, are often cited as a test case for theories of altruism because of the peculiar genetic relationship between brothers and sisters of these species. Males are haploid whereas females are diploid. (Fertilized eggs become females; unfertilized eggs become males.) Sisters, then, have in common an identical set of genes inherited from their haploid father. Thus sisters are more closely related to each other than to their brothers who have none of the father's genes and only half of their mother's genes. Hamilton predicted that females of these species should be more altruistic toward their sisters than toward either their brothers or their own offspring. According to Edward O. Wilson of Harvard University, there are many examples of behavior consistent with Hamilton's predictions and none that are inconsistent with them.

The manifestations of altruism toward close relatives have been carefully documented in birds. For example, Glen Woolfenden of the University of South Florida in Tampa finds that the offspring of the Florida scrub jay stay with their parents and do not breed for at least 1 to 3 years after they have matured and that they help their parents, primarily by guarding the nest against predators. A newly mated pair of these birds, who have not yet acquired offspring that could serve as helpers, suffer an increased chance that their offspring will not survive predation. Consistent with theory, Florida scrub jays—almost without exception—only guard nests of their parents, a parent and stepparent, or a sibling.

Sandra Vehrencamp of Cornell University in Ithaca, New York, has documented another type of altruistic behavior among birds. Groove-billed anis in Costa Rica build nests that are often densely distributed and close to the ground where they are easily preyed upon. These birds, Vehrencamp finds, appear to react to threats of predation by sharing nests. This results in a reduction in the number of nests in an area and decreases the likelihood that nests will be found by predators. Nests are sometimes shared by brothers. Vehrencamp notes that other birds, such as ostriches, rheas, magpie geese, and tinamous, also live at high densities and build nests on the ground where they are vulnerable to predation and have evolved so that females share a nest.

Sociobiological theories of altruism have been applied to primate behavior by Richard Alexander of the University of Michigan in Ann Arbor and by others. Among other examples, Alexander mentions that in primate societies older siblings often care for their younger brothers and sisters. More experienced, but unrelated, members of the group do not provide help.

An individual would be expected to help unrelated organisms only if that individual could expect its altruism to be reciprocated and if the risk associated with altruism is exceeded by the benefits expected by reciprocation. This behavior, called reciprocal altruism by Robert Trivers of Harvard University, can also occur between members of two species if each has more to gain than lose by such a relationship. Trivers cites cleaning symbioses in fish as an example of such behavior. One fish, the host, is cleaned of parasites by another fish or by a shrimp. The cleaner often enters the mouth and gill chambers of the host to do its job, but has never been observed to be eaten. Since cleaners are essential to the host's survival, sociobiologists would predict that the host's behavior, when it refrains from eating its cleaner, is inherited rather than learned. As evidence for this proposal, Trivers describes an experiment in which a grouper fish was raised from infancy alone in a tank, during which time it snapped up anything dropped in the tank. Since the grouper was apparently free from parasites, it did not need a cleaner. After the grouper had lived alone for 6 years, a small live cleaner was dropped into its tank. Rather than snapping up the cleaner, the grouper assumed a position it had never before been observed to assume and opened its mouth and spread its gills to allow the cleaner free access to its body.

Members of social groups may have different genetic groups that lead to conflicts of interest among related and unrelated individuals. Predictions about kinds and degrees of conflict are being tested by both observations and experiments involving a wide variety of species. By means of one such experiment, David Barash of the University of Washington in Seattle has been able to verify that a type of sexual conflict known among humans and predicted to occur among birds, does indeed occur in at least one species of mountain bluebird.

Mountain bluebirds, like most bird species, are monogamous. Males invest time and effort in raising and protecting their offspring. Thus a male mountain bluebird might be expected to react violently if it appeared as though his mate might have been fertilized by another male. Barash verified that such violent behavior occurred when a model of a male mountain bluebird was placed near a female while her mate was out foraging for food. When Barash performed this

The helper phenomenon in the Florida scrub jay *Aphelocoma coerulescens*. At the nest the two parents and a yearling feed the nestlings, which are the siblings of the helpers. To the right two other helpers have spotted an indigo snake (*Drymarchon corais*), one of the dangerous predators of jay nestlings. One crouches on the ground in a threat posture. The other perches nearby in the "hiccup stance," an alarm signal that will soon alert the birds at the nest. [Drawing by Sarah Landry for E. O. Wilson, *Sociobiology: The New Synthesis*, copyright © 1975 by the President and Fellows of Harvard College]

experiment during the breeding season, the returning male attacked both his mate and the model of a male. In one case, the returning male drove his female from the nest and took another mate—a virtually unheard of occurrence among these birds. When Barash performed his experiment after the female had laid her eggs, he never saw a returning male attack its mate, although it did try to drive away the model of a male.

Trivers suggests that the evolution of territorial aggression, during the breeding season, by males of monogamous species may be explained in part by the need to protect the male from investing in offspring sired by another male. He notes that a male pigeon without a mate is attacked by other males when it arrives alone at the group's nocturnal roosting place. When such a male acquires a mate, it is accepted by the other males of the group.

Courtship, too, Trivers believes, may have evolved so as to assure a monogamous male that he alone fertilized his mate. Thus a male would avoid copulating with a female upon first encountering her, and would court her until sufficient time had passed for the possibility to be ruled out that she had been inseminated by another male. Trivers supports this hypothesis with evidence that monogamous birds have long courtship periods, whereas promiscuous birds do not.

Trivers has recently proposed a model of another kind of conflict —that between parents and offspring —in terms of the premises of sociobiology. Parents and offspring, he reasons, have different interests. Parents want to maximize their genetic contributions to posterity and so want to raise to maturity as many offspring as possible. Offspring want to monopolize their parents' care. Subjects of conflict, then, might include the amount of parental investment in offspring, how long the period of parental investment should last, and how altruistic and egotistic the offspring should be toward other relatives. Several investigators have observed conflicts between parents and offspring that are consistent with predictions of this theory.

Weaning conflict is a particularly well documented example between parent and offspring that can be explained in terms of Trivers's hypothesis. When an infant is first born, nursing would be in the interest of both the mother and the infant. Later, the infant would want to continue nursing, whereas the mother would want to devote her attention and give her milk to new infants. Weaning conflicts are known to occur among dogs, cats, rhesus macaques, and sheep.

Conflicts between parents and offspring, altruism toward relatives or those unrelated individuals who might reciprocate, and sexual conflicts have obvious analogs in human behavior. Several sociobiologists are anxious to extend their theories to explain phenomena described by anthropologists, psychologists, and sociologists. Many social scientists, however, are uneasy about this extension of sociobiology. They worry that theories in sociobiology seem too facile. "They can explain everything," complains one anthropologist, "and, in effect, explain nothing." Others bring up the old nature-nurture quandary: How does one distinguish between inherited and acquired traits in humans? Alexander suggests that this distinction may be irrelevant and that even learned behavior might be analyzed in terms of sociobiology since, for example, some things are learned more easily than others.

Barash, who is a psychologist as well as a sociobiologist, cautions that investigators must differentiate between analogy and homology. The finding that similar behavior is exhibited among insects, primates, and humans does not necessarily indicate that such behavior has a similar cause. The analogy between behavior among humans and other animals is still intriguing, however. Even the most cautious of sociobiologists are convinced that their approach to the study of animal behavior will have to influence those who study only humans. Stuart Altmann of the University of Chicago believes that the most important influence of sociobiology on the social sciences will be the "delicate, nondisruptive" methods sociobiologists use and the types of questions they ask. In this way, at least, sociobiology is being predicted to change the direction of research in the social sciences.—GINA BARI KOLATA

Additional Reading

1. R. D. Alexander, in *Annual Review of Ecology and Systematics*, R. F. Johnson, P. W. Frank, C. D. Michener, Eds. (Annual Reviews, Palo Alto, Calif., 1974), vol. 5, pp. 325–383.
2. R. L. Trivers, *Amer. Zool.* **14**, 249 (1974).
3. E. O. Wilson, *Sociobiology: The New Synthesis* (Belknap, Cambridge, Mass., in press).