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SOME COMMENTS ON SOCIOBIOLOGY

AMOTZ ZAHAVI¹

The main contribution of sociobiology to the study of social behavior has been its readiness to derive its principles from the theory of evolution through logical deduction. Fisher (1930) pioneered in this field with his discussions of sexual selection, sex ratio, etc. The increase in field studies of animal behavior after World War II has triggered a growing interest in the principles of social interactions. Individual selection (as distinct from group selection; Lack 1966), kin selection (Hamilton 1964), reciprocal altruism and parental investment (Trivers 1971, 1974), parental manipulation (Alexander 1978), and the use of game theory (Parker and Maynard Smith 1976) have become the accepted dogmas of sociobiology (Wilson 1975, Dawkins 1976). Although I accept the basic tenets of sociobiology, I disagree with many of the theories that are generally accepted by sociobiologists today, primarily kin

¹ Institute for Nature Conservation Research, Faculty of Life Sciences, The George S. Wise Center for Life Sciences, Tel-Aviv University, Tel-Aviv, Israel.

selection, reciprocal altruism, and the growing use of models of Evolutionary Stable Strategies.

Before criticizing accepted theories I should summarize my own version of socio-biology. As a student of David Lack, I have developed my arguments following strict individual selection. Years of close acquaintance with populations of individually marked birds, particularly the group-living Arabian Babbler (*Turdoides squamiceps*), have convinced me that they base their social behavior on detailed information that they gather continuously. A substantial part of this information is relayed to them by means of signals such as vocalizations, postures, and tactile signals. The receiver of a signal can never know for sure whether its interests at any one time conflict with those of the signaller or conform with them; hence the receivers of signals should always make sure whether the signals are reliable. This reasoning has led me to suggest that signals evolve through a special evolutionary mechanism that I termed signal selection (Zahavi 1977, 1981). Signals are selected to have a cost that is responsible for the reliability of the signal. The cost bears a logical relation to the message encoded in the signal; for example, the signal "I am strong" should involve weak individuals trying to perform it in serious difficulties. This is the essence of the "Handicap principle" in communication (Zahavi 1975). I consider Darwin's sexual selection to be a subset of signal selection.

If indeed signals have a necessary relationship with their messages, they cannot be arbitrary. There should be certain optimally reliable signals for each message and set of circumstances. I have consequently suggested (Zahavi 1978, 1980) that "conventions," "rituals," and "set specific signals" have evolved owing to their adaptations to carry precise information about small quantitative differences between individuals.

The theory that signals, to be reliable, must have a cost, suggested an interpretation of altruism. Observations of altruistic activities of babblers have shown that the higher the social status of the individual, the more altruistic it is. It seems reasonable that their altruism may be the cost of advertising their social status (Zahavi 1977). Long-term detailed study of their behavior supports the theory that altruism is a selfish advertisement of the quality of the individual, which consequently gains in its social status (Zahavi in prep.). This may be a general model to interpret altruism among nonrelatives by simple individual selection.

I shall now criticize four conventions that are generally held by sociobiologists today.

Kin selection.—The theory of kin selection has been formulated in order to explain altruism. Actually, in many species even the most complex types of altruism occur among nonrelatives. In the case of babblers it is clear that they recognize their relatives because they avoid incest, yet they are altruistic even towards nonrelatives. Altruists also compete in altruistic activities. Often they avoid being helped and suppress altruism in others (Zahavi in prep.). It is now also known that what look like altruistic activities do not necessarily increase the fitness of the individuals they help. It is obvious that kin selection cannot by itself explain the evolution of altruism in any of the above cases. Yet any selection mechanism that would fit these cases could fit the evolution of altruism among relatives as well. Thus, kin selection theory may come to be superfluous.

Reciprocal altruism.—According to Trivers (1971), the evolution of altruism is dependent on gains by reciprocation. His model does not explain why the benefited should reciprocate. If punishment of nonreciprocators is the solution, one should be

able to show how the punishment provides gains to its performer. The problem of enforcing reciprocation is no less difficult than that of altruism; in fact it is the same problem in another disguise. Describing a reciprocal interaction, even when it can be proved that all collaborators benefit, does not explain why one of the collaborators should not exploit the others.

The application of game theory.—Following Parker and Maynard Smith (1976), game theory has been applied to interpret social interactions using simple probabilistic genetic models (e.g. whether it is a better strategy to attack or to flee). Actually, animals I have known in the field react in a highly variable way. The same individual will attack, threaten, flee, or avoid interaction altogether, according to differing circumstances. Reaction seems to be determined by information gathered rather than by a pre-set program activated by simple arbitrary signals.

Cheating, psychological manipulation, and nonadaptive responses.—These have found their place in sociobiological models as a consequence of the belief that signals are rituals that all individuals may use with equal ease. But if signals are selected to have a cost that ensures their reliability, as I claim, there is little room in social interactions for models based on the assumption that one party manipulates the other, which has not yet evolved to cope with the manipulation. If one party is cheated it is because it cannot evolve the ability to cope with the cheater—the interesting question is why it cannot. Unless that is clarified the chances are that the assumption of cheating is wrong. In my experience, a growing acquaintance with the observed species would show that they are not in fact cheated or psychologically manipulated (Zahavi 1979). They seem to act according to their best interests, however small their options are. They look for any advantage their environments might give them, collect detailed information, test their rivals and collaborators, and find out the best options open to them; in short, they act according to a very wise and complex genetic program to make the best use of the uncertainty produced by their necessarily variable environment.

I have reached this evolutionary approach as a consequence of observing social interactions of birds in the field, but the principles involved are logical derivatives of one single assumption: that evolution is a competitive process. Like other sociobiologists, I believe that these principles, if indeed true, must hold for all organisms.

Birds are excellent subjects for any study of social interactions. Populations can be individually marked and followed in the field. Most species are diurnal and use visual and acoustic signals, like humans. The comparatively short lifespan of many species allows for easy studies of their overall life strategy. Some species are easily tamed, and one may thus study them easily in their natural environment. Such studies may involve many years of field work, which fortunately contributes to the joy of ornithologists.

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SOCIOBIOLOGY AS LEARNED FROM A DRAB, BLUE BIRD

RUSSELL P. BALDA¹

As with all subspecies of biology, the tenets and principles of sociobiology are formulated from evolutionary theory based on fitness, adaptation, and natural selection. Individuals within a group (be it with mate, family, or nonrelative) perform in such a manner as to enhance their opportunities for present and/or future reproduction (individual fitness) and/or that of their relatives (inclusive fitness). Sociobiology simply adds emphasis to the latter without diminishing the more usual, historical emphasis placed on the former. Social organizations of birds, according to evolutionary theory, are a means of improving fitness.

Fitness is the conversion of ecological constraints such as food supply, nesting sites, and escape cover into viable offspring. Fitness improves when an organism becomes more efficient in the conversion process or expands the resource base available for conversion. Different social organizations should then reflect different ecological constraints (different kinds of efficiencies), expansion of the resource base (efficiencies that convert more of the resource base), or simply alternative methods to achieve some given level of efficiency in the conversion process. Although these three alternatives are not mutually exclusive, there should be enough differences between them to allow for the construction of competing hypotheses. This has seldom been done, as evolutionary biologists have concentrated on the former two options, the ecological ones. Social systems are said to reflect ecological conditions. These conditions can all be lumped into what are called *ultimate factors*. Current theories about avian social systems deal extensively with these ultimate factors. This is what one would expect from a new, fledgling science. In some cases theories about social behavior have come into direct conflict with one another. Helper systems in some species are said to occur where the climate is harsh and unpredictable and the breeding birds must marshal all available reserves in the form of time and energy to breed successfully before inhospitable conditions reoccur. Yet most social birds are found in areas of temperate climate, where migration is not so extensive and

¹ Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA.