In summary, for a variety of reasons, including ease of observation and ease of manipulation, birds are particularly good subjects for experimental tests of sociobiological hypotheses. Still, I must end with a note of caution. Because one of the justifications for testing these hypotheses on birds rather than solely on lower forms (which are yet easier to study) is that learning plays a large role in bird behavior, more attention should be given to how birds learn characteristics of their environments and how they use this information to make decisions. For example, how do nectar-feeding birds assess the quality of their territories and how rapidly do flocking juncos respond to the presence or absence of a hawk? By answering such questions avian studies can make an important contribution to our understanding of animal social behavior.

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SOCIOBIOLOGY IS FOR THE BIRDS[1]

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The official birth of sociobiology was marked by the publication of E. O. Wilson's book "Sociobiology: The New Synthesis" (1975). Sociobiology is not primarily related to gathering new kinds of data; rather it is a way of looking at biological phenomena related to social behavior from a comprehensive and explicitly evolutionary perspective. As all birds exhibit social behavior, the studies of ecologically and behaviorally oriented ornithologists are by definition sociobiological in nature.

What does sociobiology offer to ornithology? First, the sociobiological approach can make us more aware of the extremely complex interactions between various selective pressures on phenotypes. Behavior is an especially relevant example of this. A second major influence of sociobiology on ornithology is the development of field studies based on testable (falsifiable) hypotheses—this does not necessarily imply experimental manipulations. Many ornithologists, myself certainly included, have invested large amounts of time and effort studying one or more species of bird simply because we enjoy discovering new facts about some aspect of bird biology. While this approach does contribute to the general catalog of knowledge, it usually does not in itself lead to increased understanding of more general phenomena, and the

[1] I thank Prof. J. A. Wiens for his insightful contribution of the title for this essay.

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studies thus are less useful than they might otherwise be. The value of the sociobiological outlook is that it provides the investigator with questions of broad interest to be addressed by his investigations. The field ornithologist who is aware of the theory dealing with mating systems can make major contributions to our understanding, for example, of the factors favoring polygyny. R. Trivers (certainly no ornithologist), in his theoretical papers on parental investment, mate choice, parent-young conflict, and reciprocal altruism (1971, 1972, 1974) has provided several basic questions that are specifically addressed in much recent bird research.

What does ornithology have to offer sociobiology? Factual information—real data, based on careful field studies (preferably with individually marked birds) can provide tests for sociobiological theory, thus modifying where necessary, refining, and in general increasing the accuracy of the theory.

As has been the case with so many aspects of ecological-evolutionary biology, ornithologists have made fundamental contributions to the framework of sociobiology, long before it was recognized as a titled discipline. Orians' work (1961, 1969) on blackbird social systems and on the evolution of mating systems in birds and mammals, Selander's (1965) paper on mating systems and sexual selection, and Crook's (1965) analyses of the relationship between social system and environmental variables in the Ploceidae come to mind as among the first to employ what is now recognized as the sociobiological approach.

Bird studies continue to contribute significantly to current questions of a sociobiological nature. For example, one critical and warmly debated aspect of sociobiology is the question of altruism and the theory referred to as kin selection. Kinship theory originated with the writings of Maynard Smith (1964) and especially Hamilton (1963, 1964). Hamilton, specifically considering the evolution of altruistic behavior (loss in personal fitness), reasoned that such behavior should evolve when the altruist obtains an evolutionary gain via the genes it shares with the recipient of its altruism. This theory, because of its logical intuitive appeal, has been widely and rather uncritically accepted by the biological community.

Kinship theory appears at first glance to be especially relevant to communally or cooperatively breeding birds, where nonbreeding nest helpers generally are related to the young birds they feed and protect, while apparently foregoing breeding on their own. It is of interest to review briefly the role of ornithological researchers in the ongoing "evolution" of thinking about kin selection and its importance in the evolution of avian communal systems, and thus to illustrate the kinds of contributions ornithologists can make to sociobiology. Brown (1970, 1972, 1974), in his studies of Mexican Jays (*Aphelocoma ultramarina*), was perhaps the first avian behaviorist to incorporate Hamilton's ideas on altruism and inclusive fitness into a theoretical framework designed to explain the adaptive significance of nest helpers. This interpretation has been widely accepted. The 1970's saw the initiation of several additional long-term studies of cooperative breeders, studies that focused on the lifetime behaviors and reproductive options of individually marked birds [e.g. Woolfenden and coworkers on Florida Scrub Jays, *Aphelocoma c. coerulescens* (Woolfenden 1975, Woolfenden and Fitzpatrick 1978), Zahavi (1974) on Arabian Babblers (*Turdiodes squamiceps*), Emlen (1978, 1981) on White-throated Bee-eaters (*Merops bullockoides*), Dow (1979a, b) on Noisy Miners (*Manorina melanocephala*), Ligon and Ligon (1978a, 1978b; Ligon 1981) on Green Woodhoopoes (*Phoeniculus purpureus*), Koenig and Pitelka (Koenig in press a, b; Koenig and Pitelka 1979, 1981), and Stacy (1979a, b) on Acorn Woodpeckers (*Melanerpes formicivorus*), Reyer (1980) on Pied

Kingfishers (*Ceryle rudis*)]. Although most of these stiudies are not completed, they already have been extremely important in refining and forcing redefinition of kinship theory as it is applied to avian communality. First, the concept of altruism (defined above) by helpers has been clearly supported by *none* of these studies, and its existence has been called into question by several authors (e.g. Ligon and Ligon 1978b, Reyer 1980), at least for their particular species. It is now recognized that the term "altruism" is inappropriate as an explanation for helper systems (e.g. Brown and Brown 1981). Second, kin selection theory, originally developed to explain altruistic behavior, has been redefined so that cooperative or mutually beneficial behavior between relatives is, by some writers' definition, kin selection.

In short, several ornithologists have conducted studies of systems that initially were thought to be based on kin-selected altruism and have independently determined that the originally crucial aspect of the theory, namely altruistic behavior (Hamilton 1963, 1964:13) was not supported by their findings. This has created the need to redefine kin selection. At present, many students of avian communal systems would agree that ecological rather then kinship factors are the primary molders of all social systems (e.g. Koenig and Pitelka 1981), communal or otherwise, and that it is questionable whether the kinship ties usually found within communal groups are essential to the evolution and maintenance of those systems.

To summarize, sociobiology can develop and mature only by the effort of the field researchers who gather data in the real world to test the abundant theory; on the other side of the coin, by providing a broad theoretical framework, the sociobiological approach can help the professional or amateur field biologist to view his efforts in a more comprehensive manner, and thus to increase greatly the significance of the data collected.

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SOME COMMENTS ON SOCIOBIOLOGY

AMOTZ ZAHAVI[1]

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 Smith1976) 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

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