ignore the most important concept of their new-found discipline—that anecdotes about animal behavior can be properly interpreted only in light of all the underlying ecological and demographic patterns of which they are a part.

We emphatically do not reject the practice of scientific speculation, even when seemingly wild and outlandish. We merely bear in mind that speculations, attractive models, and flashy concepts should be tested and examined in detail before being sold (and bought) as gospel. We fear that some such gospel is becoming entrenched at the core of sociobiology before being tested.

Ornithologists have unique opportunities to contribute significantly to sociobiology. (They also have the opportunity to be a part of the sloppy generalizing and uncritical popularizing of some of its concepts.) Many bird species are easy to watch, and most are easily marked for individual recognition without causing undue harm. The longevity of most species is optimum for study by humans: population turnover is neither so fast that its intricacies cannot be measured precisely, nor so slow that the observer is likely to die before the observable takes place. Finally, avian social systems even among related species show enough variation to afford illuminating comparisons, once adequate ecological data are gathered.

To summarize, we applaud careful experimentation and short-term observation for generating, or even testing, sociobiological hypotheses. But we suggest that the results cannot be interpreted correctly in the absence of long-term data showing how individual lives, interactions, and deaths fit together in unmolested populations.

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## ON EXPERIMENTAL TESTS OF SOCIOBIOLOGICAL THEORY

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One of the central problems facing sociobiology is that many of its propositions are difficult, if not impossible, to test. There are at least two reasons for this difficulty. First, much of sociobiological theory is based on the argument that evolution is an optimizing process. This has led many unwary investigators into attempts to discover how behavior optimizes fitness. As Maynard Smith (1978) has pointed out, the proposition that animals behave optimally is not a falsifiable hypothesis; nonetheless, judiciously applied, optimization techniques can be used to generate interesting hypotheses that are falsifiable.

A greater difficulty faced by sociobiology is that some of its propositions are extremely difficult to test because of the practical problem of manipulating the many factors affecting social behavior. How, for example, does one manipulate the food

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available to a pack of wolves or increase the size of a lion pride? Fortunately, some of the interesting hypotheses generated by sociobiologists are far easier to test on social birds than on other vertebrates. This is partially because many birds are small, diurnal, and easy to observe. Of course, some of these hypotheses could be tested yet more easily on social insects or even colonial microorganisms. Still, a theory of the social behavior of all animals, from slime molds to man, must be tested on many organisms, including some that exhibit complex social interactions that are extensively mediated by learning and social reinforcement.

Some of the finest nonmanipulative, field studies of vertebrate social behavior to date have been of mammals, for example the long-term studies of yellow baboons by Stuart and Jeanne Altmann and the extensive investigations of ground squirrel sociality by Paul Sherman and others. Nonetheless, it is difficult to think of any *experimental* field studies of the social behavior of mammals, and most of the extensive laboratory studies of mammalian social behavior are only indirectly relevant to sociobiological theory. Fortunately, this is not the case with studies of avian sociality.

Nectar-feeding birds and seed-eating birds are particularly good subjects for testing quantitative models of social behavior, because they are easy to keep in the lab and it is relatively easy to measure and manipulate their food resources in the field. The extensive field and laboratory studies of Larry Wolf and Frank Gill have quantified many of the energetic costs and benefits of the territorial behavior of nectar-feeding birds. Kodric-Brown and Brown (1978) were able to test the predictions of a cost-benefit model of territoriality by directly manipulating the availability of flowers and measuring subsequent changes in the behavior and territory size of Rufous Hummingbirds (*Selasphorus rufus*). The work on nectar-feeding birds to date shows that the critical factors thought to affect territoriality can be manipulated under field conditions, and this work should eventually lead to critical tests on the competing cost-benefit models of territoriality.

Pulliam et al. (1974) showed that, in the laboratory, energetic stress reduced the aggressiveness of Yellow-eyed Juncos (*Junco phaeonotus*) and that in the field fighting over food was less common on cold days. Caraco (1979) extended these results by showing that dominant juncos were less aggressive and flock sizes were larger on cold days. When Caraco decreased the energetic stress on dominants by adding food to their feeding areas, he found that they became more aggressive and average flock size decreased. In other field experiments on these juncos, Caraco et al. (1980a, b) showed that average flock size almost doubled when a trained hawk was in the vicinity and that average flock size increased when cover was added to baited feeding sites.

Given the preoccupation of sociobiology with the concept of kin selection, I find it surprising that there are so few experiments designed to vary the factors hypothesized to contribute to inclusive fitness. A notable exception is Brown and Brown's (1981) study of helpers at the nest in Grey-crowned Babblers (*Pomatostomus temporalis*). Having found a positive correlation between the presence of helpers and the number of offspring fledged, the Browns sought to establish a causal relationship by removing helpers. They found that the controls averaged roughly twice as many fledglings as did the breeding units from which helpers had been removed. It is clear that more experimental work along these lines needs to be done. The Browns' pioneering experiments at least indicate that sociobiological hypotheses about helping behavior are amenable to experimental tests in the field.

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

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