DEMOGRAPHY IS A CORNERSTONE OF SOCIOBIOLOGY

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The simple message we derived from Wilson's (1975) monumental synthesis is that animal social systems are as much a result of ecologically imposed selection pressures as are more readily measurable features of morphology and distribution. Social systems are evolutionary responses to innumerable environmental variables affecting an animal's habitat tolerance, age-specific survivorship and reproduction, dispersal, territorial economics, and a host of other life history features. It follows that an understanding of these evolutionary responses, however simple or complex, requires extensive *data* pertaining to all these demographic variables. In short, we cannot expect to understand a social system until we can view it in light of the species' overall demographic regime.

We believe that the necessary and appropriate demographic data for such an understanding can be obtained most accurately by knowing in detail the lifetime activities of individuals, their survival probabilities at various life stages, their dispersal behavior, their reproductive histories, and the exact genetic identities of the other individuals with whom they interact. Thus we conclude that the empirical side of sociobiology will make significant progress primarily through *long-term* field studies of considerable samples of individually recognizable animals.

We emphasize the concept of a "long-term" study. In birds, an adequate sample of lifetime histories cannot be obtained in the space of just a few years. Furthermore, for many of the pertinent questions asked about population-level phenomena, each year represents only a single data point. Thus, for instance, we recently found that even 11 years' data frequently offer only tantalizing patterns on graphs that will need many more points before critical hypotheses can be adequately tested. Indeed, only after a decade of preliminary work on Florida Scrub Jays (*Aphelocoma coerulescens*) are we even seeing the need to ask certain key questions.

Admirable precedents already have demonstrated that in sociobiology no substitute exists for long-term studies of avian life history. For example, it took 20 yr of study to find that a sea-faring gull shows differential sex- and age-specific mortality (Coulson and Wooller 1976); a sample of 234 dispersers over 11 yr was required to show a strong heritable component to dispersal distances in a woodland tit (*Parus major,* Greenwood et al. 1979). These and many other such demographic patterns have considerable impact on life history strategies relating to social behavior. We are only beginning to appreciate how many *more* data are required to answer more complicated questions about the genetics of social evolution in highly cooperative birds!

Sociobiologists have made popular a number of intriguing and alluring new concepts in the study of social evolution. Unfortunately, flashy words occasionally have been used to refer to patterns of animal behavior that are at best still incompletely understood. At their worst, we have seen buzz-words such as "altruism," "kin-group," "nepotism," "homosexual bonding," and "rape" become entirely inappropriate and oversimplified, but popular, descriptors of complex social interactions. In the rush to interpret early or incomplete results, many sociobiologists seem to

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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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