COMMENTARY

ORNITHOLOGY AND SOCIOBIOLOGY: A FORUM

The "new synthesis" of sociobiology that E. O. Wilson advanced in 1975 has generated considerable heat and controversy. Much of the more dramatic argument has centered about the applicability of these ideas to human behavior and sociality, but more conventional biological applications of the ideas have also sparked spirited discussion. Sociobiology has indeed crystalized some previously existing concepts and developed new ideas, and these offer fresh and exciting ways of looking at sociality in biological systems. At the same time, however, some rather sloppy science has been disguised by adopting the catch-words of sociobiology. Ornithological studies have perhaps contributed in both ways.

Studies of birds comprise a substantial share of the empirical foundation of concepts of social behavior and organization (despite their rather slim treatment in Wilson's book), and contemporary investigations of avian sociality are in turn being strongly influenced by the ideas and approaches of sociobiology. Accordingly, in late 1980 I invited several individuals to contribute essays discussing the relationship between ornithology and sociobiology from their own personal perspective. I asked each to consider how fruitful the interplay between these disciplines has been, what each has contributed to the growth of the other, and what directions future studies might take. Each essayist participated independently, without knowledge of who else was contributing or what they said. Their comments reflect something of the diversity of approaches and views that characterize contemporary avian sociobiology. I hope that they will stimulate further thinking about the issues they raise, and perhaps some redirection of research to resolve these issues, while inevitably raising others.—John A. Wiens

THE ORNITHOLOGICAL ROOTS OF SOCIOBIOLOGY

STEPHEN T. EMLEN[1]

Sociobiology is nothing more than the study of the evolutionary adaptiveness of social behavior. One sometimes forgets this during the intellectual highs of research discussions with colleagues, or the emotional lows of debate with social scientist friends. At such times sociobiology somehow seems to be much more than just another branch of animal behavior, more than just the latest spin-off from evolutionary biology having its day in the sun. What is the real importance of sociobiology, why has it attracted such widespread attention, and what role is ornithology playing in its development?

Fields of science, like organisms, pass through developmental stages. The first occurs with the birth of one or more major discoveries that profoundly reshape our thinking about old problems. This is followed by a stage of rapid growth, analagous

[1] Division of Biological Sciences, Cornell University, Ithaca, New York 14853 USA.

to childhood, in which enthusiasm and excitement abound. Innumerable ideas are put forth—some of them brilliant, but many of them wrong. Later, during the third or adolescent stage, the harsh facts of reality come to temper the optimism of childhood. This is a difficult period for a maturing science. The hypotheses so excitedly developed in youth now face the rigors of empirical testing. Many fall by the wayside, for the extinction rate of ideas in a new field is always high; but others become more firmly established through repeated verification. The result is the emergence of a mature field, ready to take its place among the community of other sciences. Sociobiology is still a young science. It had its birth in the early 1960's, its childhood in the 1970's, and it now stands on the verge of its adolescence.

Sociobiology's origin occurred when a series of nearly simultaneous advances in behavioral ecology and genetics heralded a new synthesis of animal behavior with population ecology and genetics. On the behavioral-ecological side, the seminal contributors were J. H. Crook (1964, 1965), J. L. Brown (1964) D. Lack (1968) and G. H. Orians (1969)—all ornithologists. They argued that ecological constraints play a major role in shaping the form of an animal's society. The degree of gregariousness, the spatial dispersion pattern, the presence or absence of territorial defense, even the basic form of the mating system—all are profoundly influenced by the abundance and the spatial and temporal distribution of key resources, predators, and competitors. The structure of an animal's society can be viewed as an adaptive solution to the ecological problems faced by the individual members of that society. Animals faced with similar ecological problems should exhibit a predictable convergence in their solutions as shown in their social organizations. This premise is the cornerstone to the ecological side of sociobiology, the goal of which is to understand better the distribution pattern and functioning of different types of societies in nature.

Ornithology played the major role in the emergence of ecological sociobiology. The first attempt at a synthesis was J. H. Crook's (1964) monograph on weaverbird behavior. His ideas of the ecological shaping of social behavior gained unusually rapid and widespread acceptance. The reason, I believe, was due to the extraordinary wealth of pre-existing avian field data that had been accumulating in the literature since the turn of the century. Many ornithologists made immediate use of this library of data to verify Crook's correlational findings for other avian groups. Soon such analyses extended beyond ornithology, and parallel correlations between simple ecological predictors and social structure were uncovered in groups as diverse as coral reef fishes, tropical anurans, bats, and African ungulates, to mention but a few. The mere suggestion that concepts first formulated for weaverbird societies might have widespread applicability across phylogenetic lines, and thus might portend some very general and fundamental laws for the evolution of societal structure, created the initial surge of interest in the new field of sociobiology.

On the genetic side, population biologists were increasing our understanding of the processes of natural selection. G. C. Williams and others sounded the final death knell to the idea that selection could promote traits that existed "for the good of the species" (Williams, 1966). W. D. Hamilton (1964) and J. Maynard Smith (1964) elegantly demonstrated that in calculating the genetic fitness of an individual, one must incorporate the fitnesses of genetic relatives (each devalued by the appropriate coefficient or relatedness), because they have a measurable probability of sharing the same genes by virtue of common descent. In essence, biologists had been omitting a component of fitness in their previous thinking and modelling about behavior. The implications of these changes in our thinking about natural selection were

staggering, and they led to a second, parallel surge of interest in emerging sociobiology.

The basic premise of selfish genery (sensu Dawkins 1976) is that an organism will behave in a manner that benefits another individual, yet entails a cost to itself, only when (1) there is a high likelihood that the recipient shares the determining genes with the donor, or (2) there is a high likelihood of later reciprocation. Ecologically speaking, we can add a third: (3) when ecological constraints favor group living and the behavior is important in promoting continued cohesiveness of the group. Such thinking has led to the development of several models that spell out the necessary and sufficient conditions under which phenotypically altruistic behavior can evolve. Some models have examined the types of societal structure in which kin recognition and/or behavioral nepotism is expected. Others predict that when promiscuous matings are common in a population, males will show paternal behavior in accordance with their certainty of paternity. Similarly, when the ecological potential for polygyny is high, male and female members of a pair are expected to disagree over the amount of nestling care provided by the male. Conflict also is predicted between parents and their offspring over the amount of parental investment provided by the former. Analogously, in species with helpers at the nest, the breeder and helper are predicted to disagree over the point at which the helper will terminate its helping activities and initiate breeding on its own.

The take-home message from this genetic side of sociobiology is that different members of a population—even different members of a social group—often are selected to adopt behavioral strategies that are predictably different from one another. As a result of asymmetries in sex, reproductive value, experience, dominance, and kinship, the costs and benefits associated with particular behaviors differ for different individuals. Consequently, the patterns of social interaction that result in maximizing fitnesses for one category of individuals may differ from those that are optimal for another.

Taken together, ecological and genetic sociobiology have revolutionized our thinking about social biology. Natural history, once a largely descriptive field, is being transformed into a predictive science. Just how predictive it will become is still a matter of conjecture, for sociobiology is still in its childhood, growth phase. Bouyed by its early successes, it is now applying the evolutionary approach to virtually every aspect of animal and human behavior. We are witnessing a veritable flood of interpretative and theoretical papers in our journals. In just a few short years, theoretical ideas have proliferated to the point where they have outstripped the data bases so essential for their own evaluation. The result is an acute shortage of relevant empirical data. There is a desperate need for new, more sophisticated, field studies designed specifically to test the hypotheses that are emerging from sociobiology.

Ornithology is playing, and will continue to play, a major contributing role as sociobiology matures in the 1980's. Not only are ornithologists well trained to conduct such research (as adaptiveness has always been at the heart of avian field studies), but birds are ideal organisms for collecting the types of data that are so badly needed. Birds are visually-oriented, diurnal organisms, and thus relatively easy to observe. Many of their behaviors are stereotyped, easing the task of quantification and interpretation in the field. Genealogies often can be constructed without the immense problems of paternity determination that plague so many mammalian studies. And the short lifespan of most birds makes the collection of lifetime fitness data an achieveable goal (something rarely possible with long-lived groups,

such as primates). Birds display sufficient diversity and complexity in their social systems to make them valuable as models for understanding the social behavior of other, higher forms; yet they retain sufficient simplicity to make quantitative data collection relatively easy. For these reasons I expect that avian examples will provide many of the model systems used in the critical future testing of sociobiological theory.

In summary, the historical interactions between ornithology and sociobiology have always been mutualistic. Ornithological concepts provided one of the original impetuses for sociobiology, and the quantity of the avian literature helped speed the early growth of the new field. But, as genetic theory advanced, ornithology became a major beneficiary as well as contributor. Ornithologists are now better able to see and understand patterns in the diverse array of avian social organizations, and they are better able to ask more meaningful and testable questions about their subjects. As ornithologists make use of these newlyfound, interpretative skills, they will, in turn, be building the empirical data base that will lead to the refutation of some, and the modification and ultimate verification of other, sociobiological hypotheses. This feedback between empirical data and theoretical ideas is the very foundation of the scientific method. The fields of ornithology and sociobiology are deeply interwoven, and each has benefited tremendously from the activities of the other. Let us hope that the mutualistic cross-benefits continue into the decades ahead.

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SOCIOBIOLOGY IN RELATION TO ORNITHOLOGY

Brian C. R. Bertram[1]

I do not see sociobiology and ornithology as separate subjects that "relate" to one another, but as fields of interest with a wide area of overlap. Thus there are some areas of pure ornithology, such as communal nesting or alarm calls, that are at the heart of sociobiological interest, whereas there are other important areas, such as bird physiology or navigation, that are outside and uninfluenced by sociobiology.

In my view bird studies were one of the most important spawning grounds of sociobiology. In particular, and rather paradoxically, the fundamental disagreement between Wynne-Edwards (1962) and Lack (1966) over the mechanisms of population

[1] Curator of Mammals, Zoological Society of London, Regent's Park, London, England.