The Situation of Sociobiology

Current Problems in Sociobiology. Papers from a conference, Cambridge, England, July 1980. King's College Sociobiology Group, Eds. Cambridge University Press, New York, 1982. xiv, 394 pp., illus. Cloth, $49.50; paper, $16.95.

Evolution of Social Behavior. Hypotheses and Empirical Tests. Papers from a workshop, Berlin, Feb. 1980. HUBERT MARKL, Ed. Verlag Chemie, Deerfield Beach, Fla., 1980. vi, 254 pp., illus. Paper, $22.50. Dahlem Konferenzen Life Sciences Research Report 18.

Natural Selection and Social Behavior. Recent Research and New Theory. Papers from a symposium, Ann Arbor, Mich., Oct. 1978. RICHARD D. ALEXANDER and DONALD W. TINKLE, Eds. Chiron, New York, 1981. xii, 532 pp., illus. $49.95.

Perhaps the most important conceptual breakthrough in evolutionary biology since Darwin's *Origin of Species* is William D. Hamilton's model of inclusive fitness. This model and the thesis championed with great vigor by Richard Dawkins and George C. Williams, that the gene may be the fundamental unit upon which selection acts, have given new focus to behavioral studies and have stimulated an increasing number of theoretical and empirical sociobiological investigations. Are these studies increasing our understanding of the evolution of behavior, or are sociobiologists becoming overwhelmed with new theory and the large quantities of new data that are appearing from numerous subdisciplines? Are empiricists and theoreticians understanding and communicating with one another? Are there sufficient data to justify the extraordinary amount of theoretical work that is going on?

Three volumes have recently appeared that will help to answer these questions. The most recently published volume, *Current Problems in Sociobiology* (edited by the King's College Sociobiology Group), incorporates papers from a conference held in 1980 at King's College, Cambridge. *Evolution of Social Behavior: Hypotheses and Empirical Tests* is a report based on a Dahlem workshop held in 1980 in Germany. *Natural Selection and Social Behavior* is a collection of papers based on a symposium held in 1978 at the University of Michigan. The first two volumes are similar in that they examine concepts in sociobiology and attempt to show how hypotheses can be constructed and tested.

The King's College Sociobiology Group is very successful in its attempt to confront current conceptual problems in sociobiology. For example, Maynard Smith's excellent paper epitomizes what has happened to the conceptual framework of sociobiology. He suggests that we must reclassify and redefine certain concepts such as altruism and levels of selection because new concepts (for example reciprocal altruism) have been put forward and because differences in usage have arisen. In great detail, Bertram dissects the concept of altruism, showing the inconsistencies in how the term is used and bringing new insight into how sociobiologists may study the phenomenon. Bateson is critical of "the untidy linguistic habits that continue to give sociobiology a bad name" (p. 147). For example, are genes selected upon directly or through their phenotypic effects? Bateson believes that this important distinction is muddled by excessive use of metaphors and sociobiological jargon in attempts to explain natural selection. Dawkins directly confronts this particular question in his chapter and states that "genetic replicators are selected not directly but by proxy, via their phenotypic effects" (p. 61). Dunbar addresses problems in defining terms and in using metaphors to describe processes and considers their implications with regard to the accusation that many evolutionary explanations are tautologies. Rubenstein, writing on risk and uncertainty in evolutionary strategies, notes that most models of evolutionary processes leave out the role of environmental variation by assuming that strategies always achieve their predicted fitness. This is obviously unrealistic, and Rubenstein's model and discussions suggesting that the fitness of an animal may be greatly influenced by a variable environment are a refreshing step in the direction of more realism in evolutionary models.

Of particular interest to field biologists and ultimately to all who venture into sociobiological studies are the chapters by Jarman, Harvey and Mace, and Davies under the heading Problems of Comparison. Jarman discusses the utility of interspecific comparisons in the formulation of explanations of social behavior. Although such comparisons have yielded important insights into how behaviors may have arisen and their adaptive values, Jarman points out limitations to this approach. Harvey and Mace believe that comparisons across taxa can be useful in testing general hypotheses. Their chapter is important because of the discussions of methodological problems that are encountered frequently in sociobiological studies. Davies suggests that little attention has been given to differences between individuals within species until recently. Such differences are generally ignored in models in which individuals or species interact, and Davies stresses the importance of studying them for a fuller understanding of the evolution of particular behaviors.

The Dahlem conference was broken up into four working groups that, according to Markl's introduction, were assigned the tasks of (i) clarifying and classifying theoretical concepts for explaining social behavior, (ii) assessing the current state of empirical knowledge about animal social systems, and (iii) defining the most important questions and the best methods for answering them. The group reports are preceded by a series of individual papers that bear on these problems.

Much of our basic understanding of sociobiology is based on good observational and, more recently, experimental studies of social insects and birds. This is most evident in reading the excellent review of discrimination mechanisms in social Hymenoptera by Hölldobler and Michener and papers by Crozier ("Genetical structure of social insect populations"), Baker and Marler ("Behavioral adaptations that constrain the gene pool in vertebrates"), and Brown ("Fitness in complex avian social systems"). The chapter by Sade on primate fitness parameters is not at the same level. Sade justifies working with primates on the grounds that they are organized by social interactions and are thus ideal subjects for testing kinship theories. Sade believes that "lower" organisms such as *Drosophila* lack the necessary social dimensions for such studies. These opinions and statements that "evolution should produce optimal behaviors" (p. 97) and the suggestion that one can prove that a social characteristic is optimal though correlational evidence that fitness is maximized are simplistic.

The four group reports are critical and incisive. The group report on mechanisms of kin-correlated behavior is particularly interesting. It is important that kinship measures be reliable. An increasing number of studies on social insects and vertebrates suggest that multiple fertilization is common in many species, and uncertainty of paternity can greatly

complicate the interpretation of kin-oriented behaviors. One issue discussed in this group report that is now receiving a great deal of attention is kin recognition. Until recently, much of what was known about kin recognition was based on detailed studies of social insects. The group report reviews ideas concerning kin recognition based on the very few studies that existed at the time of the conference. Subsequently numerous experimental studies (conducted both in the laboratory and in the field) have appeared that shed light on some of the matters discussed in this section. For example, the study group suggests that "the absence of innate kin recognition systems on the hard-wired receptor side may be a consequence of one or more factors" (p. 194). Since the conference was held empirical evidence has been gathered that some organisms, such as certain amphibian larvae, mice, ground squirrels, and macaques, display kin recognition abilities that can be interpreted as incorporating an innate receptor.

Some basic conclusions reached by the group on methodology and modeling are especially noteworthy. It is their consensus that "imaginative and plausible sounding theories are not sufficient. Quantitative empirical tests must be carried out to sort out the theorists's lists of possibilities" (p. 175). They express the concern that theorists and empiricists are becoming separate subcultures whose studies are becoming incomprehensible to each other, and they encourage lucid reviews and interpretative syntheses for a remedy to this situation.

Natural Selection and Social Behavior offers a mixed bag of theoretical discussions, reviews, and original research papers that display the state of the art in sociobiology. Unfortunately, many of the pitfalls discussed at the other two conferences are evident in the volume.

Many of the papers do not explicitly define terms and assume that observed behaviors are adaptive. The assumption of adaptation is generally supported by correlation. Experimental analysis is rare. For example, Woolfenden suggests that helpers at the nest are beneficial. In Florida scrub jays a greater percentage of pairs with helpers succeed in fledging one young per season than pairs without helpers. The presence of helpers also "appears to lower the mortality of breeders" (p. 258). As Woolfenden admits, one must account for differences in breeding experience, territory quality, and other factors that may influence fledging success and mortality of breeders. The study by Brown and Brown is more convincing. These authors performed a field experiment, with controls, by selectively removing helpers from groups of gray crowned babblers and found that helpers indeed increase the fitness of the reproductive individuals. Their paper represents an ideal sociobiological study. They explicitly define terms, they know a good deal of the natural history of the species, they marked numerous individuals, and they performed the critical field experiment. Similarly, the paper by Downhower and Brown uses an experimental approach for analyzing reproductive success in sculpins. Howard's study of mating success in bullfrogs is based on many hours of careful observation. The next step in studies like Howard's is to incorporate field experiments to go along with the excellent observational information. Selective removal of some male bullfrogs from his field sites could yield important information on mate choice and reproductive success.

Although correlation does not necessarily mean causation, there are convincing studies based primarily on nonexperimental approaches. Sherman's study of ground squirrels is important because numerous marked animals have been observed for many hours over many years in the field. Although some findings Sherman presents may be interpreted in other ways, the overall assessment is that we probably know more about natural social behavior in Belding's ground squirrels than in most other rodents as a result of his careful observations.

Other noteworthy papers in the book are those on eusociality in insects (West-Eberhard; Noonan; Strassmann) and on the problems of sexuality (Hamilton, Henderson, and Moran; Hartung). There are some useful reviews and theoretical discussions on subjects ranging from parental behavior in frogs (Wells) to evolution of leks (Bradbury), as well as a good review on ecological factors and the role of kin selection in cooperatively breeding birds (Koenig and Pitelka). A good review of the major hypotheses concerning the origin and maintenance of vocal dialects in birds is presented by Payne. He points out some weaknesses in other attempts to differentiate among the hypotheses, but his paper is marred somewhat by the weaknesses of his own arguments when he tries to explain various dialect systems through his favored hypothesis of social adaptation. There is also a section on human sociobiology that is highly speculative and open to debate.

After reading these volumes one gets several distinct impressions about sociobiology: (i) Sociobiologists must define their terms explicitly, especially since there seems to be a coalescing of subdisciplines as far removed from one another as molecular genetics and anthropology. (ii) Theoretical work greatly outweighs empirical information. (iii) There is a great need for experimental studies, especially in the field. (iv) Empiricists and theorists must try to understand one another. (v) Some excellent studies are being conducted.

The volumes stemming from the King's College and Dahlem conferences are important for professionals to read and would be excellent choices for discussion in graduate courses. The volume edited by Alexander and Tinkle contains many useful chapters, but in overall impact it seems less important than the two other volumes.

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Cognitive Aspects of Aging

Aging and Cognitive Processes. Papers from a symposium, Toronto, 1980. F. I. M. CRAIK and SANDRA TREHUB, Eds. Plenum, New York, 1982. xviii, 396 pp., illus. $39.50. Advances in the Study of Communication and Affect, vol. 8.

Although research on how to stay young has always been popular, only lately have we begun to study how we grow old. The recent boom in gerontological research reflects an awareness by granting agencies of the increasing age of our population and the social and health problems this poses. Research into the psychological effects of aging has increased dramatically over the past 15 years, as has the number of books on the topic. The present volume is a report from a conference on the effects that normal and abnormal (dementia) aging have upon cognition and information processing in humans.

As in most books of this type, many chapters are merely recapitulations of their authors' long-published data. In several such chapters, however, (for example, that by Walsh) the summaries of experimental data have been combined with comprehensive reviews of the literature, producing a coherent picture of the current state of the field. This makes these chapters excellent starting places for a reader unfamiliar with the topics they cover.

However, what sets the book apart from similar books is that many of the authors attempt to compare the pattern