Book Reviews

The Evolution of Sociality

Sociobiology. The New Synthesis. EDWARD O. WILSON. Belknap Press of Harvard University Press, Cambridge, Mass., 1975. x, 698 pp., illus. $20.

The reductionistic triumphs of molecular biology having been thoroughly established, many of the great remaining challenges in biology lie in the evolution of the higher levels of organization, especially the social systems that integrate animal populations. The "new synthesis" of ecology, population genetics, and animal behavior brings an integrated theoretical system to confront this remaining biological frontier. At the conclusion of *The Insect Societies*, a synthesis of the population biology, physiology, and social behavior of the world's dominant terrestrial fauna, Wilson asks whether the same quantitative evolutionary theory he successfully used to interpret the social organization of insects could also be applied to societies within other phyla, and especially to those of vertebrates, leading to a unified theory of sociobiology. The present book is his attempt to answer the question by a comprehensive review and synthesis of the literature on social organization, ecology, and evolutionary genetics of all animal groups, from the myxobacteria to humans, whose members show forms of social behavior beyond mating. Occasional examples from the sociology of plant communities are given to illustrate a principle of wide applicability.

No book so ambitious has appeared since Wynne-Edwards's *Animal Dispersion in Relation to Social Behaviour* stirred a tempest of fruitful controversy over the role of group selection in the evolution of animal societies as mechanisms to limit population densities to optimal levels through conventional competition. Wilson differs from Wynne-Edwards in crucial matters of logic, selection and interpretation of facts, and style, not to mention access to the abundant new information obtained by the legions of fieldworkers, experimenters, and theoreticians who have swarmed about the subject during the dozen years since *Animal Dispersion* appeared. Both, however, seek the functional similarities or analogs between societies within diverse phyletic groups in order to reveal evolutionary rules of universal application. This approach is in contrast with, but not in contradiction to, a phylogenetical analysis of the features of a group of closely related animals, in which homologous traits and systems are identified and their transformations during evolution studied to reveal the constraints and potentialities inherent in the evolutionary choices made in the ancestry of a given lineage. (The studies of the anthropologist Earl Count on the vertebrate origins of human sociality—see his *Being and Becoming Human: Essays on the Biogram*, 1973—are the most recent major synthesis of the latter sort.) Wilson takes note of the role of phylogenetic constraints in evolution, particularly when contrasting the social insects and vertebrates, but his analysis is primarily functional rather than historical.

A page or two of review cannot begin to summarize even all the major points of this enormous, tightly written, beautifully detailed, abundantly illustrated, and carefully documented book. Not the least of its merits are the enticing tangential leads, such as the discussion of "tradition drift," that adumbrate theories and one hopes books to come. I will try to touch on the points that provide continuity to the book.

The first part of the book is an analysis of modern post-Darwinian evolutionary theory as it relates to social evolution. The attempt to define the boundaries of a group or society, and of the individual, leads immediately to the theory of the genetical structure of animal populations. On the one hand societal boundaries create more or less impermeable genetic barriers, and on the other hand a degree of genetic isolation and inbreeding heightens coefficients of relationship, enhancing the evolution of altruistic behavior through kin selection. The concept of "inclusive fitness," developed especially by W. D. Hamilton, is perhaps the central concept in the book. It states that an individual's genetic fitness is to be measured not only by the survival and reproduction of himself and his offspring but by the enhancement of the fitness of other relatives who share his genes. This allows the evolution of cooperative acts that may be detrimental to the individual's own survival or reproduction and are therefore by definition altruistic.

The local population, being, in contrast to casual aggregations, relatively stable in time and relatively closed to immigration, constitutes a "demographic society" in which birth and death rates play an important part in determining group structure. Events of evolutionary importance act to modify these parameters.

In relatively stable environments density-dependent controls, often operating through social mechanisms, result in stabilization of population size at an optimal species-specific equilibrium. Under these conditions rapid reproduction, more characteristic of species adapted to swiftly colonize transitory habitats, is less important than competitive ability in obtaining the more stable resources. These conditions favor the evolution of cooperative behaviors for antipredator defense, increased feeding efficiency, increased survival of offspring, improved population stability, and modifications of the environment.

The demographic profile of the genetically homogenous insect colony is said to be a directly adaptive feature, achieving an energetic (ergonomic) optimal proportion of individuals in each caste through group selection between colonies. Wilson suggests that among vertebrates the demographic profile is a secondary effect of the equilibration of contradictory forces: the inclusive fitness of altruistic acts balanced against the individual advantages of selfish behavior, and the advantage of increased parental investment competing with the advantages of producing more offspring.

The Euler-Lotka formula for the intrinsic rate of natural increase, "little r," is central to the mathematical treatment of these theoretical matters because it summarizes the combined effects of survivorship and natality for the group in competition with other populations, or for some genetical partition of the population compared with other competing genotypes. The use of "little r," calculated from the $l_x m_x$ schedules of a life table, has important implications for the conduct of research, because the action of social mechanisms must be translated into effects on the life-table schedules before their evolutionary results can become manifest. By and large this has not been done, except in modeling hypothetical cases, because most research on social behavior has been too short-term, lacking in sufficient time depth to produce the necessary information.

The first part of the book concludes with an analysis of the controversial concept of group selection. After a careful review of recent genetical and mathematical models, and some zoogeographical and genetical evidence, not confined to the celebrated t mutant of wild house mice, Wilson concludes that although interdemic selection cannot be ruled out as never occurring, it is likely to be generally unimportant because

of the high rate of extinction of populations required to counteract the forces of individual selection. Kin selection, the favoring of the genes of a group of closely related, cooperating individuals in competition with other groups, through the increased inclusive fitness of the genes favoring altruistic acts, is considered of major importance. Since the favored groups include more than parents and direct descendants, Wilson considers that kin selection is a form of group selection at the opposite extreme from interdemic selection.

The second and longest part of the book reviews the social mechanisms that have evolved as mediators between the ecological pressures to which the population must adapt and the demographic parameters that measure the success of the adjustment. The topics range from the allocation of time and energy to different activities that different species find profitable to a comparison of social symbiosis and parasitism among social insects and birds. Three chapters are devoted to communication, including its mathematical treatment by methods of information theory. These chapters are perhaps the clearest reviews of animal communication in the literature. The theory of causal networks operating in the evolution of social mechanisms is best developed in the chapter on parental care, because that topic has been so completely studied among numerous groups of social animals. Robert Trivers's models of parental investment play a prominent role in the arguments. They represent the effects of extending or shortening the duration of parental care on the differences between cost and benefit in terms of genetic fitness, and indicate that the competing interests of parent and offspring will produce a compromise optimal duration. The most detailed mathematical treatment of social mechanisms is in the discussion of the optimization of the proportion of social insects within each caste. Although the models gain support from the confirmation of some of their predictions, such as that the most specialized and numerous castes are found in the stable tropical environments, it is disappointing to learn that the models have not been applied to actual natural populations. Will the study of statuses and roles within vertebrate societies lead to a comparable ergonomics of the division of labor? This is one of the many questions raised in the advanced theory of sociality among insects that await detailed investigation among vertebrates.

In general, social mechanisms are discussed within the framework of the theory outlined in the first part of the book, but without detailed quantitative correspondence between theory and example. The models can be considered to be working hypotheses rather than confirmations of the theory.

The third and last major part of the book is a selective review of social behavior within the major groups of animals that include highly social species. Four groups receive special attention, having achieved degrees of sociality exceeding all others. The colonial invertebrates provide examples of the most perfect societies, in Wilson's view, because the genetic identity of members of the colony allows an extreme degree of altruism. Individual freedom can therefore be completely subordinated to the advantages of the colony, and the physiological plasticity of the individuals allows a degree of specialization one thinks of as more typical of the cells of more familiar animals. In insect colonies social imperfection arises from the independence of the individuals and the occasional competition between workers and queen to produce male offspring, counteracting the high degree of morphological differentiation and specialized division of labor between the castes and the elaborate altruistic behaviors that maintain the colony. The vertebrates have gone in another direction, emphasizing individual recognition, status based upon competition, and individual adaptability. Their societies consist of selfish subgroups of closely related kin, competing with other kin groups at the expense of the integrity of the society as a whole. These trends are carried the furthest among the mammals, which receive the bulk of Wilson's attention. He suggests that man has retained and accentuated these vertebrate characteristics but that greater intelligence has allowed a high degree of cooperative activity with little loss of individual fitness, resulting in man's unique position among the social species. The species accounts are supplemented with very valuable tables summarizing the taxonomy, sociobiology, and bibliography of each group.

Because very few studies on the social life of animals have provided the direct coordination of information on demography, social organization, and genetics necessary for a strict application of the sociobiological theory, the species accounts must stay close to the original reports, which represent theoretical diversity rather than synthesis. However, Wilson is at pains to evaluate and restate their findings as working hypotheses that could lead to a genuine testing of the theory.

More than a hundred pages of glossary, bibliography, and index follow the text, indicating the comprehensive coverage of the book.

The remainder of the review could be devoted to expressions of amazement at the mastery of diverse topics Wilson displays, the clarity of expression, the occasional ironies and twinkles of humor mostly restrained by objectivity, and the perfection of the panoramic drawings by Sarah Landry illustrating the major features of social organization of several species. Conversely, the peevish reviewer might point to the occasional printer's error that by changing a key word alters the author's meaning, or the inevitable although infrequent and unimportant error in fact, such as that the direction of grooming among macaques is a reliable indicator of dominance, that adult male baboons are organized as coalitions rather than in linear dominance hierarchies, or the illustration showing lemurs grooming with the tongue rather than the tooth comb.

More important, however, is to point out that this book is an excellent introduction to the broader field of evolutionary biology. If the problems raised in regard to the evolution of sociality could be solved, then any problem in evolutionary biology could be solved, because the social aspects of populations are the phenotypic characteristics furthest removed from the genotype and therefore the most difficult to account for in terms of current theory. This is a timely book because of the objective analysis it provides of ideas that are gaining popularity, particularly the concepts of inclusive fitness and kin selection. In the conference chambers of scientific meetings I have seen these ideas, like the sweet smoke of a forbidden weed, create a sense of euphoria among their advocates, who seem on the verge of some hidden truth, obscure until the inhalation of these heady notions. Wilson, by contrast, appears to intend his book to be a challenge.

The major value of the book will go beyond the specific models and observations it contains in such abundance and be found in the consistent display of scientific reasoning that insists that theory in all its aspects must be subjected to testing and potential falsification. The advocacy method of reasoning common in the writings of social scientists and popular writers dealing with animal behavior, and especially with notions of human origins, receives deserved flagellation in several barbed passages. But Wilson recognizes that the most insidious weakness of sociobiological theory is the ease with which particular models can gain advocates, for actual testing of these models requires studies of a duration and intensity beyond the current traditions of fieldwork. To conduct sociobiological research on the long-lived, slow-breeding mammals, including the primates, will require revision of the goals of fieldwork and a reallocation of resources for genuine long-term research, even if at the expense

of the currently popular 18-month field excursion. As an example, if the Euler-Lotka formula is actually to be applied to data, life tables must be provided, yet in spite of the large investment in research on primate societies there are essentially no life tables available for any primate species other than man.

Wilson acknowledges that sociobiological theory at present is dependent upon the current genetical models of competition between alleles at single loci and that these models may be revised and supplemented as work on polygenes, linkage disequilibria, and epistatic interactions proceeds. Classical selection theory is also currently confronted with evidence and increasingly accepted models emphasizing the role of random processes both in microevolution, as in the maintenance of high levels of genetic polymorphism, and in the broad patterns of emergence and extinction of phyletic groups on a geological time scale. Particularly among the vertebrates, individual adaptability and the flexibility of social systems suggest a degree of indeterminance between the gene and the environmental adaptation that is not fully accounted for in the simplistic single-locus models. Sociobiological studies may lead us into a period of profitable confusion and theoretical indigestion, and finally to a new level of understanding both in sociobiology and in evolutionary theory.

The greatest effort in empirical research should probably be directed to validating the postulated connections between the operation of social mechanisms and the values of the life-table parameters. The arguments about whether individual selection, kin selection, or higher levels of group selection are operating may really turn on how it is most convenient to classify the actual processes after the fact. Can they be distinguished in actual events in real populations? The problem becomes more difficult because random processes such as genetic drift also become important in the small, inbred groups in which kin selection is assumed to operate most effectively.

The quantitative theory of sociobiology has been most successfully applied to the social insects, and the societies of vertebrates remain incompletely explained. The trend in vertebrate evolution toward greater individuality, culminating in the mammals and particularly in man, seems difficult to reconcile with the fact that the most elaborate vertebrate societies are also found within this group. There is no reason to think that all the classes of models have yet been devised, or that all the ways of classifying the processes that result in natural selection have yet been exhausted. It is not proved that the ultimate analogy to the evolution of complex systems is found in the current models based upon capitalistic economic theory, where profits and losses in units of the hypothetical currency of genetic fitness are computed for each compromise in the life history of individuals.

To be complete, sociobiological theory must account for the emergence of man and absorb both anthropology and sociology, providing these disciplines with a truly scientific basis for their practice. The greatest and perhaps final challenge to sociobiology will come when it invades the province of the humanities and attempts to incorporate them, as it must or be proved false, into the strictly materialistic theory of evolutionary biology. In the humanities we see the trend in vertebrate evolution toward individuality carried to its extreme, and artistic expression, being channeled into unique cultural patterns and idiosyncratically enriched, surely is the aspect of the phenotype furthest removed from the determinism of the gene. The highly elaborate, multimodal communication systems among vertebrates may have evolved as devices of social integration in which large amounts of energy are invested to counteract the socially disintegrating trend toward individualization. Here again the humanities may present us with the maximum elaboration of a vertebrate trend. It may be that in order to achieve its final success sociobiology will have to turn somewhat away from the functional models of very general applicability emphasized in the current theory to examine the unique phylogenetic constraints and potentials operating within the specific phyletic line leading to man.

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Loxodonta

Elephants and Their Habitats. The Ecology of Elephants in North Bunyoro, Uganda. R. M. LAWS, I. S. C. PARKER, and R. C. B. JOHNSTONE. Clarendon (Oxford University Press), New York, 1975. xii, 376 pp., illus. $42.

The elephant epitomizes the conservation problems faced by all wildlife in Africa. With much of their range usurped by man, animals are increasingly confined to reserves whose boundaries are not ecological but political. Protected from hunting and unable to emigrate, ungulate populations tend to increase up to and beyond the limits of their food supply. As the carrying capacity of a habitat is reached, animals respond to crowded conditions by deferring maturity and reducing fecundity, but these adaptive responses may not prevent a population crash and damage to the habitat. Elephants are second only to man in their propensity to modify their environment. By breaking and pushing over trees elephants convert woodlands into grasslands, destroying their habitat as well as reducing the complexity of the ecosystem. Should elephants be allowed to find their own destiny no matter what the consequences, or should they be brought into balance with the habitat? This problem has generated an amazing amount of political indecision and emotional turbulence in East Africa. Laws and his co-workers build a solid case for the latter alternative, using the elephant population centered in Murchison Falls (Kabalega) National Park as an example.

The Bunyoro elephants' range has declined in 25 years from 6300 to 3200 square kilometers and the population from 22,000 to 7,900 animals. Some of this decrease was due to a haphazard control program by the Game Department aimed at reducing conflict between human and elephant interests. Laws *et al.* cropped 2000 elephants between 1965 and 1967, and the data from these animals form the basis for thorough chapters on nutrition and growth, reproduction, and population dynamics in this book. By shooting whole family units—the matriarch with her grown daughters, the subadults, and any attending bulls—not only was disturbance to the elephants' society as a whole reduced but fascinating information on the age and reproductive status of each family member was obtained. Over half of the population decrease has been due to a decline in recruitment, the result of the animals' living on a poor diet. Yet elephant biomass has remained almost constant since 1946, the animals now crowded into the small remaining range. The authors reason that the habitat can recover only if some 3500 elephants are shot immediately and the remainder cropped on a sustained yield basis of 5 percent of the population annually.

By censusing animals, autopsying carcases, and analyzing vegetation, the authors have produced an excellent ecological study of an elephant population, a study which concisely presents the facts and proposes sensible solutions to a management problem. Being wholly ecological in outlook, the authors made no special attempt to observe elephants and their society, but this important gap has been partially filled by other workers. In the scientific rigor of its field techniques and the depth of analysis of the data this study is