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Mary Jane West Eberhard

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NEW BIOLOGICAL BOOKS

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BORN: SOCIOBIOLOGY

BY MARY JANE WEST EBERHARD

Departamento de Biología, Universidad del Valle, Cali, Colombia and Smithsonian Tropical Research Institute, Balboa, Canal Zone



ONCE UPON a time there was a small community of modest scholars called natural historians, who devoted their lives to philosophy and the contemplation of humble plants and animals. With the passage of time and the invention of Science they began to take on new names. Some called themselves Systematists; others Ecologists; and still others Population Biologists and Ethologists. Only their enemies called them natural historians. All of the new sciences grew and became rich. However, there was one small group without a name. They went about dressed in the castoff clothing of the titled sciences, and often failed to recognize each other, even when they hurried along the same paths. So they suffered greatly. Sometimes they had to learn to collect birds or identify ants in order to get jobs. Then one day there rose up a man from among them. He had been called Entomologist, Ecologist, and even Biochemist. But that was not enough. All grew quiet as he raised his golden pen: "There shall be a new science," he said, "and it shall be called SOCIOBIOLOGY."

A Review of

SOCIOBIOLOGY. *The New Synthesis.*

By Edward O. Wilson. The Belknap Press of Harvard University Press, Cambridge, Massachusetts. \$20.00 x + 697 p.; ill.; index. 1975.

Edward Osborne Wilson, the kindly bespectacled father of sociobiology, has assumed god-like powers with this book. It is, in the author's words, "an attempt to codify sociobiology into a branch of evolutionary biology and particularly of modern population biology." The new science is named, defined ("the systematic study of the biological basis of all social behavior"), endowed with a set of goals (including the reformulation of the foundations of the social sciences "so as to draw them into the neo-Darwinist evolutionary theory") and given an encyclopedic theoretical and factual base—all in one broad sweep

of the golden pen. Ethology and comparative psychology are declared obsolete and behavioral biology is seen as restructured into neurophysiology and sensory physiology on the one hand, and sociobiology and behavioral ecology on the other. The book is monumental in size (697 pages, including glossary, index, and a bibliography of more than 2500 entries) and in scope, treating sociality in every conceivable form from slime molds to man. And it is unhesitating in tone (subtitle: "The New Synthesis"—emphasis mine). In short, it is enough to make any working animal behaviorist-ecologist tremble a bit with anticipation (what treasures of information will it hold?), with fear (will I be codified in? or out?), and with the athletic strain of holding its flopping five pounds at reading level.

The book does indeed contain treasures of information, and there is little need to worry about

being codified out. Virtually every area of biology which might contribute to an understanding of sociality is included, with tireless summaries of basic work in related fields, and in one after another of the taxa (bacteria, invertebrates, insects, fish, frogs, reptiles, birds, and mammals) containing species covered by Wilson's broad usage of the word "social" (which, oddly, is never specifically defined). There are few aspects of animal behavior not fitting under the rubric of sociobiology. Even courtship behavior, excluded by the definitions given in the chapter on "Elementary Concepts," ends up being repeatedly discussed because of its involvement in such important activities as territoriality and parental care.

One has to marvel at the intellectual marathon it was to write this book with sustained enthusiasm and authoritativeness even in fields (such as vertebrate endocrinology and primate ecology) only remotely related to Wilson's own sociobiological specialty (caste and communication in ants). To mention just a few of the numerous topical reviews that could be cited for their usefulness, there is a chapter on "Development and Modification of Social Behavior," showing how both laboratory studies of development and behavioral genetics and comparative studies among different taxa can be combined in an attempt to understand the evolution of social behavior; a critical review of the concept of aggressiveness, discussing its functions, ecological correlates, and physiological bases; and a summary of recent findings on the social behavior of elephants based on studies not heretofore widely available. Scattered throughout the text are many smaller original reviews of such phenomena as adoption of orphans, teat order in mammals, and lek behavior in a variety of taxa, which, while presented without flash or fanfare, demonstrate an impressive breadth of research and outlook. One of the few places where Wilson's interest seemed to flag was in the surprisingly brief chapter on birds. It deals primarily only with cooperative breeding, and treats in detail only two groups, the anis (*Crotophaginae*) and the jays, with the incomplete 1942 work of Davis on anis considered "still both modern and definitive" despite the availability of more recent studies using marked birds (e.g., F. Köster, 1971, *Bonn. zoll. Beitr.*, 22: 4-27). Although ornithological work is extensively cited in other sections, as the author points out, this does not really make up for the lack of a concise overview like those given insects, primates, bats, and even colonial microorganisms.

Wilson must certainly go on record as one of biology's most able writers and phrase-makers. In the past he has authored, co-authored, or effectively publicized such apt and well known terms as "character displacement," "K-" and "r-selection," and "pheromone." In this book a number of attractive Wilsonisms make their appearance. It sometimes takes a moment's thought to realize that they are not always

matched in brilliance and newness by the concepts underlying them, and to translate them into old-fashioned neo-Darwinese. "Phylogenetic inertia," "evolutionary pacemaker," and "behavioral scaling" refer, respectively, to pre-adaptation (plus pre-unadaptation); the familiar idea that behavior is more labile than morphology and therefore often takes the lead in evolutionary change; and the fact that behavior is often adaptively different in different situations. The catchy term "social drift," denoting a so-far undemonstrated and theoretically vague process by which social behavior or organization undergoes "random" divergence having a "tradition drift" and a "genetic drift" component, is introduced in the commendable hope that "a formal theory of tradition can be created." But it is given only a shaky beginning. The suggestion that "the amount of variance within a population of societies is the sum of the variances due to genetic drift, tradition drift, and their interaction" (p. 14) disregards the possibilities of variance due to natural selection in populations undergoing evolutionary change, balanced polymorphism among groups, and non-random phenotypic lability. Indeed, when "tradition drift" is discussed regarding the spread of ideas among humans, it is said to involve change in frequency due to advantageousness, which identifies it more with natural selection than with "drift." However, what such occasional hit-and-run theorizing lacks in scientific substance it makes up for in poetic appeal. To combine Wilsonisms (mixed metaphors excused), you can reach the pinnacle of the cutting edge through optimization phraseology in the sociobiological adaptive landscape. That is, clever words pay.

Readers interested in the implications of sociobiology for the study of human behavior will find plenty to think about in this book. In terms of human intellectual history, sociobiology marks one more step in the progressive disillusionment of man. As science has gradually encroached on the old domains of religion and philosophy, thinking man has had to admit that he does not inhabit the center of the universe, that he is an animal not too different from other apes, that his own free will is constantly undermined by a powerful and elusive subconscious, and that his dearest values and standards of behavior are just cultural artifacts—no better or worse than any others. Sociobiology, which applies modern evolutionary theory to the behavior of group-living animals, including man, has some disillusioning things to say about the nature of society. Social cooperation is seen as biologically advantageous, and hence basically "selfish." Altruistic aid is expected to occur only in carefully regulated amounts among relatives; and cooperation among non-relatives should involve strict guarantees of reciprocity. These and other ethically significant generalizations—including the ecological nature of the social contract—are discussed in a

thoughtful and provocative chapter on man, which makes some interesting tentative efforts to cross the borders between evolutionary biology and philosophy, psychology, anthropology, sociology, and economics. Elsewhere in the book, Wilson comments that the failure of psychology (one could say the social sciences) to arrive at a general, comprehensive theory is rooted in a preoccupation with "nebulous independent variables" which "can seldom be linked either to neurophysiology of evolutionary biology and hence to the remainder of science" (p. 23). The trial-by-fire for sociobiology will be to see if it can do any better with the formidable complexity of human society. *Homo sapiens* could well serve as the prototypal unsuitable organism for sociobiological research. It is a secretive, self-conscious, and untruthful species whose closest relatives are extinct, as is the natural environment to which it is best adapted. These are just the characteristics that produce a need for the broad comparative approach offered by evolutionary sociobiology. It is to be hoped that it will yield generalizations applicable to man and suggesting answers to questions not amenable to direct examination. The social sciences, on the other hand, provide sociobiology with its best-studied species. They have already gathered masses of detailed data on the behavior of man as a social animal. It will be the task of sociobiology to dissect out carefully those aspects which pertain to man's evolved nature, and to interpret them in terms of generally valid concepts.

Much of the success of this venture will depend on care and sophistication in applying principles of modern evolutionary biology. Wilson has a great deal to say on this topic. Appropriately, it is the unifying theme of the book, and the subject of the first of three major subdivisions ("Social Evolution," "Social Mechanisms," and "The Social Species"). His discussion once again raises, and unfortunately confounds, the important question of levels of selection in the evolution of social behavior. There seem to be two emotional subspecies among evolutionary biologists: straight-laced individual selectionists, who do not want to admit any role for selection above that level, even when traditional concepts are overstretched; and diehard group selectionists, who want to apply higher level explanations whenever they possibly can in a world where history and the better part of reason are usually (though not entirely) on the side of the individualists. Wilson is a well-informed hybrid tending toward the latter type. He repeatedly asserts that in the social insects the unit of selection is the colony (group), tacitly contradicting the careful (cited) arguments of Hamilton and of Trivers that selection can operate independently on the workers, and of Alexander that it can operate on individual queens (of which there can be several per colony). And his discussion of levels of selection gives the erroneous impression that individual, kin, and interdemic selec-

tion comes successively into play as group or sample size increases, with interdemic selection likely to be most important once the group under consideration numbers over 100 (when aggregations are "genetically fragmented"). The gratuitous introduction of a fourth category called "migrant selection" further confuses the issue, since migration need not imply another level of selection but can be explained in terms of the other three. Wilson is fully aware of all the complications involved in applying group-selection models. In a careful and lucid summary of the subject (p. 107-117) he concludes that "evolution of an altruist gene by means of pure interdemic selection, based on differential population extinction, is an improbable event"; that only in "special conditions" can interdemic selection proceed without differential deme extinction; and that "the evidence for interdemic selection is fragmentary and somewhat peculiar in nature" with actual cases only "rarely reported." This would seem to place severe limits on the justifiable use of the words "group selection" in discussions of sociobiology. But the battered old phrase is quickly revived with a kind of artificial respiration: "kin selection," a hypothetical mechanism for the evolution of self-sacrificing behavior now widely considered a plausible explanation for certain cases of "altruism" among relatives, is renamed "group selection," and the two terms are used interchangeably throughout the book! This is confusing and misleading almost to the point of being irresponsible, since the kin-selection hypothesis actually shows how "altruism" can be considered advantageous from the point of view of the individual altruist—in terms of individual inclusive fitness, not group fitness—and has therefore been effectively used as an *alternative* to group-selection hypotheses. In the same trivial sense that kin selection is group selection, all of natural selection is group selection, since even "individual" selection really concerns the summed genetic contribution of a group—the individual's offspring. It seems much less confusing to follow conventional usage and consider "kin selection" an extension of classical individual-level selection, reserving the term "group selection" for selection among what are conventionally called demes (allopatric populations) (see J. L. Brown, 1966, *Nature*, 211: 870).

Clarity in thinking about levels of selection is so indispensable in evolutionary sociobiology, and so fundamental to many large and small conclusions throughout this book, that confusion in this regard has to be cited as cause for attaching a reservation to the wholehearted recommendation of this generally excellent book. In spite of the revolutionary appeal of group-selection and kin-selection models, most explanations in modern work-a-day sociobiology still depend on an adequate understanding of old-fashioned Darwinian natural selection—reproductive competition among individuals. This topic may seem

hum-drum and even a bit passé (Wilson in one place refers to modern evolutionary biology as "Post-Darwinism"). But it seems of primary importance for a book of this type, which seems designed at least partly as an introduction to evolutionary sociobiology for people (like social scientists) not practiced in evolutionary thinking. A short section on troublesome evolutionary concepts headed "The Dualities of Evolutionary Biology" is helpful. But the chapter called "The Prime Movers of Social Evolution"—really a discussion of why group living is advantageous, and in what circumstances it evolves—treats adaptation in terms of the "phylogenetic inertia" of populations and species, and their evolutionary responses to "ecological pressures" and does not focus on the underlying process of reproductive competition among individuals. Much of the long chapter on "The Relevant Principles of Population Biology" will probably prove too technical for most readers.

It is difficult for a single book to be all things to all people. The ambitious attempt to include everything that might prove useful and illuminating to sociobiologists of all kinds is both a strength and a weakness. It has the great virtue of encouraging a broad multi-factorial approach to the study of societies. Indeed, Wilson specifically argues against mere "advocacy" of particular ideas, eschews the tendency to make sweeping generalizations based on enthusiastic insights into a few species, and maintains an open-door policy regarding the kinds of information which might prove significant. This is perhaps wise and is certainly politic. It leaves the new science totipotent; on the other hand it makes for a certain conceptual diffuseness, and a disappointing hesitance about making the kind of strident new generalizations that might be expected to emerge from such an unprecedented review of the literature. In this book sociobiology is a patchwork neatly stitched from

relevant pieces of other fields, without a bold new theoretical pattern of its own. In that sense the book is more an interrelated collection of thoughtful reviews than a definitive theoretical synthesis—which Wilson sees as "one of the great manageable problems of biology for the next 20 or 30 years."

I believe that more in the way of "unified theorizing" could have been done now, beginning, for example, with a more precise handling of the idea of inclusive fitness, and a clear separation of factors promoting group life and those coming into play after groups are established. But how much can one ask of one book, and one man, at one time? As a compendium of ideas and information this volume is brilliant and timely, and some of its conceptual awkwardness is a reflection of the adolescent state of the science itself. Whatever shortcomings the reader may find, given his own specialized sensitivities (this review, of course, reflects mine), this book will stand as a landmark in the comparative study of social behavior. For the first time and in once-and-for-all fashion it marks out the territory of an important subarea of biology, at the same time providing it with the impetus that comes from a clear identity and eloquent publicity. Biologists interested in the study of sociality per se will no longer have to start conversations and courses from scratch with a rationalization for what seemed only a personal *raison d'être*. There is enough raw material here to keep adventuresome theorists busy for years, with entrées into the literature on virtually every important social group. The whole thing is beautifully written and well illustrated. Perhaps its most important accomplishment is to have argued broadly and convincingly in favor of one central, transforming idea: that it is possible and desirable to generalize about animal societies, from colonial sponges to toks of capercaillies and bands of Yanomamö Indians.