comparisons based on dead museum specimens are not important for the purpose of learning about the structure and function of organisms. It merely means that data of more critical importance to the systematist working at all three levels of taxonomic analysis is available through the use of newer techniques. Therefore the museum or other taxonomically oriented institution that fails to furnish its staff with a

biochemical laboratory is not providing an essential component of modern taxonomic work. The costs of using these new methods are generally not exorbitant in comparison with those for other essentials of up-to-date taxonomic research (field expeditions, computer time for numerical taxonomy, electron microscopy for working with microorganisms, etc.).

SOCIOBIOLOGY EVOLVING[1]

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A Dahlem conference on the evolution of social behavior catches the field of sociobiology at a critical stage in its evolution. As Oster remarked during the conference, "The Romantic Age of sociobiology is over." Although we can look forward to additional illuminating entries in the catalog of social phenomenology, the field is moving towards a new analytical phase with a focus on evolutionary process. Both theory and empiricism are strained as new results pour in. This conference successfully captures the new excitement in sociobiology, chronicles its growing maturity and pluralism and charts its future directions. The discipline is moving rapidly and not surprisingly several promising outlooks were not represented at the conference. Nevertheless, this book is essential reading for sociobiologists, interested evolutionists and for a generation planning doctoral research.

Dahlem conferences are sponsored by the West German government with the aims of crystallizing outlooks in expanding fields and promoting communication between German scientists and their colleagues. This conference brought together nearly 50 scientists from three continents in February 1980 to "assess the validity of evolutionary theories of social behavior" and to identify future directions. The resulting volume consists of ten single or coauthored background papers and four group reports with Oster, Harvey, J. Krebs and Feldman acting as rapporteurs for groups of eight to twelve discussants.

Markl introduces the conference with a crisp review of sociobiology and a list of issues, like learning, that will occupy the discussions. Brian Charlesworth gives a historical perspective on kin selection, a review of theory and some new results. He incorporates inclusive fitness into his model and shows that

Hamiltonian expectations are modified by the penetrance of a gene for altruism. Some new age-structured models by Charnov and Craig are summarized, and they also fail to support Hamiltonian predictions when genes for altruism are common. Charlesworth concludes by stressing the heuristic value and domain of the inclusive fitness approach. His argument that one-locus models of social evolution can be extrapolated to polygenic inheritance fails if social behavior consists of more than one character and there is pleiotropy. Maynard Smith discusses the "power and limits of optimization." He emphasizes the point that optimization (fitness maximization) is an inappropriate modeling approach to social evolution since selection will almost invariably be frequency dependent. He promotes the ESS approach and describes its many limitations relative to dynamic models of change in gene frequency or mean phenotype.

Hölldobler and Michener review the fascinating studies of kin recognition in social insects. In one well studied example (bees of the genus *Lasioglossum*) there is learned recognition of heritable family odors, although the genetics of odor production have not been worked out. Baker and Marler call for a new research focus on population structure. This is a timely plea since sociobiologists have tended to drift away from the relevant issues in population genetics (population size, spatial array and migration) and to ignore both the classical and recent literature. They also plea for more realistic models of evolution in structured populations. The prospects for measuring fitness in natural populations are discussed by Metcalf (social insects) and Sade (primates). Sade is candid about the technical difficulties presented by primates and stresses the need for long-term longitudinal studies.

Jerram Brown discusses the unexpected complexities that arise when theory is taken into the field. The discussion centers around "helpers" in bird society. The tension between theory and empiricism is apparent and instructive. Theoreticians will proba-

bly not be pleased with the unwieldy concept of the "fitness network," a child of field study, and Brown goes on to ask for models that incorporate age structure and learning phenotypes. The need for more work at the interface of theory and empiricism is clear. Likewise, Crozier's report on the genetical structure of social insect populations underscores the need for models with three or more levels of selection (corresponding, say, to families, colonies and demes) and complex mating structure (inbreeding and multiple paternity). Ayala reviews the recent literature on the genetic and evolutionary relationships of apes and humans. There are, however, only a few timid ventures into human sociobiology elsewhere in the volume (p. 216, p. 240). As Markl points out, "This was not planned to be a conference on human sociobiology. Social animals give us enough to chew on."

Oster et al. report on "methodology and sociobiology modeling." Theoretical work is reviewed, but important, recent contributions by Lande, Michod, Slatkin, Templeton, Wade and D. S. Wilson (to name a few) are not represented. Nevertheless, the rationale for the modeling approach is beautifully presented: models are "guides to the possible, not deductions about the actual." The authors raise the question, "What is the relevance of single locus models to the study of behavioral evolution?" Haldane handled the issues better in his defense of "bean bag genetics." Their opening argument that there are no serviceable alternatives overlooks Wright's four volume treatise (they mangle his shifting balance theory), quantitative genetic theory and Lande's recent success with models of multivariate evolution. Their arguments neglect constraints imposed by pleiotropy, for example. There is, however, a useful summary of some future directions for research.

Harvey et al. discuss mechanisms of kin-correlated behavior. Recent empirical results are thoroughly reviewed. The discussion ranges far beyond altruism and covers alliances between brothers for mating success and other topics. The empirical results will force theoreticians to deal with some new issues, like multiple paternity and plastic phenotypes. Krebs et al. discuss the prospects for measuring fitness in social systems. Unfortunately the review misses a landslide of new results in studies of sexual selection. The discussion is limited to helping birds and social insects. Field techniques for estimating coefficients of relationship (interested readers should also consult Michod and Anderson's recent paper) and fitness changes due to helping are discussed. As Brown points out, altruism is a very slippery behavioral category. A levels-of-selection approach, advocated elsewhere by Wade and D. S. Wilson, might have emphasized the importance of measuring the between family variance in fitness.

Feldman et al. discuss the genetical aspects of social behavior. Quantitative genetics is presented as the appropriate tool for analysis since behaviors are likely to be polygenic and continuously distributed.

The classic limitations of this approach are reiterated, but the shocking lack of a data base does not receive the emphasis it deserves. We don't have *any* estimates of heritability and genetic correlation for social behaviors in natural populations. There is not a single complete genetical analysis of a sender-receiver system. Some relevant topics in population genetics (e.g., population structure) are reviewed.

In the concluding chapter Williams attempts a defense of panselectionism. He employs the "selfish bean bag" model of evolution popularized by Dawkins and criticized by Sewall Wright. Pleiotropy, for example, is noticeably lacking from William's list of confounding genetic factors. "It seems to be generally true that whatever variability is needed for response to a certain kind of selection, it will be available." Now, if this were true, selection could make a silk purse out of a sow's ear. This "genetic variability for everything" optimism is contradicted by the results of plant and animal breeding. As is well known, a kind of "sow's ear lag" is created by genetic constraints imposed by genetic variance and covariance (e.g., from pleiotropy) and undesirable correlated responses to selection impede evolution. We still don't have a chicken that lays more than one egg a day after decades of intense selection. Williams goes on to present maximization of inclusive fitness as the "Rosetta Stone" (his phrase) of social evolution. This optimism may also be without foundation. Although Michod and Abugov have recently shown that mean inclusive fitness is maximized under a one-locus model of altruism with additive fitness effects, it is not at all clear that maximization will be preserved as an operating principle under more general models. The general results from frequency dependent models (with suboptimal mean fitness at equilibrium) suggest that inclusive fitness maximization will not be a winning horse. Indeed, this is the theme of Charlesworth's paper.

This is an important volume that will reward the careful reader. Because of the current flux in theory, researchers are advised to concentrate on basic issues that bear on a variety of theoretical postures. Are population structures conducive to social evolution by kin and interdemic selection? What are the most prevalent modes of inheritance for social behaviors? We still don't have a unified theory of social evolution that is known to subsume existing models as special cases. That day may not be far off and this volume makes some headway. In this light it is surprising that the continuum between kin and group selection was not stressed at the conference. Wade has recently shown that the total change in gene frequency under kin selection can be decomposed into separate components due to individual selection and to group (between family) selection. This view casts Hamiltonian evolution into the classic levels-of-selection models of Crow, Falconer, Wright and many others and makes the applied literature on family selection relevant to sociobiology.