Introduction

This volume results from a symposium held at The University of Michigan, Ann Arbor, in October of 1978 and sponsored by the National Science Foundation. The papers included were, for the most part, presented at the symposium, though a few additional ones were requested for the publication.

The occasion for the symposium was the fiftieth anniversary of the University of Michigan Museum of Zoology in its present structure. It seemed to us that no better commemoration could be planned than a general discussion of the questions raised by the revolution in evolutionary biology that has occurred during the past two decades. The part of that revolution currently attracting the most attention concerns the evolutionary basis of social behavior in all parts of the animal kingdom—hence the title of the symposium and of this volume.

Museums have always played a special role in the nurture of evolutionary biology, and so it is not surprising that most of the participants in this symposium are now, or have been in the past, associated with such institutions. We are pleased that about half of the contributing authors have direct connections to the University of Michigan Museum of Zoology.

In planning the symposium we were particularly interested in including field studies designed to test significant predictions from recent new theory about the evolution of social behavior. As the list of authors demonstrates, such studies—as well as important theoretical contributions—are often the work of young investigators.

We believe that the papers included here represent most of the topics that have sparked the recent interest in behavioral evolution. Read in sequence, the papers provide an excellent overview of current research and theory. Differences of opinion and approach are obvious and are often provocative and stimulating. We have not tried to eliminate such differences, feeling instead that each paper should stand on its own merits. We also believe that this is the first major volume of original papers devoted almost wholly to research stimulated principally by George C. Williams and William D. Hamilton, who stressed two main ideas: first, it is valuable to identify the level (gene, individual, population, species) at which natural selection acts most consistently and powerfully and, second, natural selection can favor contributions to genetic reproduction not only through descendant but also through nondescendant relatives. The importance of these two ideas is apparent throughout the volume.

The organization of the volume is partly taxonomic and partly by subject. We thought it appropriate to begin with the social insects, for their sterile castes have, since Darwin, been a focal point in the understanding of natural selection. What, after all, could be more challenging to a theory of evolution based on differential reproduction than explaining the existence of individuals that normally produce no offspring of their own? The currently intensive study of cooperative breeding in birds, represented here by several investigations, involves obvious parallels, because helpers sometimes die without producing offspring; however, the conclusions reached in studies of social insects and cooperatively breeding birds often diverge intriguingly. Nevertheless, in both cases the emerging picture suggests that two crucial variables are genetic relatedness and fluctuations in the availability of breeding habitat.
Nearly all of the investigators in this symposium, including those interested in caste systems and cooperative breeding, have sought to measure the reproductive success of individuals in systems of sexual competition and parental care. Data on this long-neglected problem are presented for insects, fish, frogs, lizards, birds, and mammals, including humans.

Sexuality can be viewed as involving a kind of proto-social cooperative behavior. Among prominent questions in evolutionary biology at present, the evolutionary raison d'être of sexuality is fairly described as the most difficult. It is fitting, therefore, that this volume should include two papers with promising new ideas on this question.

Finally, we are particularly pleased with the section on human sociality, for it shows clearly that the theory of natural selection, which has for so long guided research at all levels of inquiry in biology, has significant implications for the study of human behavior and social systems as well.
NATURAL SELECTION AND
SOCIAL BEHAVIOR
Recent Research and New Theory

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This volume is dedicated to George C. Williams, whose pioneering efforts to return our attention to the crucial question of what are the units of selection and whose ideas regarding that crucial question, applied to such areas of research as senescence, sterile castes in the social insects, reproductive effort, sexuality, sex ratios, among many others, in large part fostered the revolution responsible for the research presented here.
In Memorium Donald W. Tinkle, 1930–1980

Donald W. Tinkle passed away on February 21, 1980. Without his efforts this volume would not have appeared. He was largely responsible for the symposium from which it derived, and he read and criticized carefully all of the chapters. As the authors themselves know, his unusual intelligence and perspicacity are reflected in the structure of many arguments throughout the book. His excellence in field research, teaching, and administration also affected in more direct ways, and sometimes profoundly, the lives of most of the authors represented here.

RDA

II

Our acquaintance with Donald Tinkle was unhappily brief and all too slight. We knew, of course, that he was a distinguished biologist, with a broad knowledge of evolution and an outstanding ability to devise experimental measurements of ecological theory. We also knew his reputation for being a gifted and imaginative administrator and a superb teacher. Our lasting impressions of him are his keen perception and intelligence and his open and generous spirit.

Since his death, we have talked about him with several of his students and friends. From knowledge of him far greater than ours, they bear multiple witness to these qualities. As a scientist, Donald Tinkle was highly productive, publishing some eighty papers and leaving more than a dozen manuscripts. He had a reverence for the classics and an understanding of what was important historically. In his thirties and forties, he displayed a willingness to go on learning new techniques and the capacity to master them. He was a well-rounded critic of both science and writing, and though unyielding, his criticism was inevitably friendly and constructive.

The quality of friendliness particularly impressed his students, to whom his door was always open. He seems to have given them the impression that he was learning from them, that he was their guide but they were his equals. He was absolutely lacking in pettiness and was absolutely fair. It all seems to have worked. One cannot fail to be struck by the excellence of his students. They may be his most remarkable legacy.

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