

## ANT COLONIES AS AN EVOLUTIONARY PARADIGM

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A review of  
SOCIAL EVOLUTION IN ANTS. *Monographs in Behavior  
and Ecology.*

*By Andrew F G Bourke and Nigel R Franks; Series Editors: John R Krebs and Tim Clutton-Brock. Princeton (New Jersey): Princeton University Press. \$75.00 (hardcover); \$29.95 (paper). xiii + 529 p; ill.; author, subject, and taxonomic indexes. ISBN: 0-691-04427-9 (hc); 0-691-04426-0 (pb). 1995.*

From the title of this book it might be supposed that it is a specialized volume, of interest only to myrmecologists and a few evolutionary biologists, but Bourke and Franks's aim is much broader than the title suggests. As they state in the preface, "Aided by the full panoply of modern adaptationist logic, we explore in depth the fundamental topics in evolutionary biology and behavioral ecology to which ant studies continue to make an important contribution" (p xi). They succeed in this aim admirably, and in so doing have produced a book that

reviews and synthesizes many of today's most important topics in evolutionary biology. As such, this book deserves a wide readership.

Bourke and Franks immediately nail their gene-selectionist, adaptationist colors to the mast, providing a framework for the arguments that they develop throughout the book. They use the first two chapters to justify their position and, more importantly, to show how it can accommodate various alternative, and at first sight contradictory, viewpoints.

Social insects are central to the debate over the level at which selection acts, because workers give up their own reproduction and help the queen to produce offspring. This reproductive altruism is a problem for individual-level selection, which Darwin saw as potentially fatal to his theory of evolution by natural selection. However, worker ants have not proved fatal to the Darwinian paradigm; rather, they have stimulated one of its most fascinating de-

velopments, Hamilton's kin selection theory. Kin selection theory explains worker sterility by demonstrating that genes can influence their own spread by acting on relatives, i.e., on individuals who are likely to bear copies of the same genes. The first chapter of the book is therefore dedicated to an in-depth introduction to kin selection theory. By using Dawkins's distinction between replicators and vehicles, the authors then proceed in Chapter 2 to provide a clear and comprehensive review of how different concepts of selection (gene, individual, kin, colony and group selection) can be unified by a population genetics approach that examines evolution in terms of changes in gene frequency. The evolution of altruism is treated in great detail, but other important areas, such as the evolution of individuality and conflicts within and between individuals and societies, are not neglected. Thus the introductory chapters provide a synthesis of immense value to evolutionary biologists, whether they are social insect biologists or not.

Eusociality is more highly developed in ants than in any other group of organisms, and may account for the enormous success of the ant life style. The next chapter examines the evolution of eusociality, a topic treated at length by many previous authors. Bourke and Franks make some valuable contributions to this field, particularly in providing a critique of previous work, and in stressing the importance of both ecology and genetics in determining the evolutionary route to eusociality.

The heart of the book is devoted to an examination of the various strategies and conflicts involved in the production of reproductives (queens and males) by ant colonies. While many of these are an outcome of the specialized haplodiploid sex-determining mechanism of the ants and most other social insects, Bourke and Franks discuss how they can arise from principles that are important for any sexually reproducing organism.

The first topic that Bourke and Franks tackle in this section is optimal sex-ratio theory, which is introduced by a clear explanation of Fisher's classic model, followed by the modifications introduced by Trivers and Hare to take into account the relatedness asymmetries that are a consequence of haplodiploid sex determination in ants. Ant workers can pass on more copies of their genes through their reproductive sisters than through brothers, while the queen is equally related to both her male and female offspring. Workers should therefore prefer a female-biased sex ratio, while queens should prefer an even one. Ant sex ratios are hence a textbook case of potential evolutionary conflict. However, the magnitude of the disagreement over preferred sex ratio depends on the genetic structure of the colony. For example, when the queen is multiply mated, the workers' interest in producing

females weakens, since females tend to be less related to them (owing to the occurrence of half-sisters) than in colonies headed by a singly-mated queen. Bourke and Franks provide a valuable review of how genetic structure is predicted to affect colony and population sex ratios. This section is comprehensive and up to date. For example, it has recently been predicted, and subsequently shown empirically, that colonies should often produce single-sex broods within ant populations (split-sex ratios). To our knowledge, *Social Evolution in Ants* is the first book to include these recent developments, and it does so in a very readable form. In chapter five, the reader is taken through several empirical tests of the population sex-ratio theories previously presented. This gives a valuable insight into how such theories can be tested among the diversity of reproductive strategies that are used by ants. The authors do not hesitate to point out cases where the theories do not fit with the empirical evidence, nor where there are unexplored possibilities.

Both ecological factors and the genetic structure of colonies will dictate whether there are potential kin conflicts, and if these will translate into actual conflicts. The genetic structure of colonies is highly variable, both within and across species, as seen in the variability in mating frequencies of queens and in their number per colony. This leads to a rich number of combinations of factors that can promote or prevent the outbreak of conflicts. Chapter 6 examines how genetic and ecological factors affect conflicts over sex ratio within colonies. Important areas that are discussed include which party—the queen or the workers—has control over sex allocation, and through what mechanisms.

Conflicts of interest among kin are likely to arise whenever group members vary in their degree of relatedness to each other. Chapter 7 examines more general kin conflicts over reproduction. The conflict examined in most detail is the one concerning who should reproduce—only the queen, or both the queen and workers. Another class of conflict is connected to varying queen number per colony: whether additional queens should be recruited, which queens should be recruited, and how reproduction should be divided among multiple queens. One issue that has been regarded as important in reproductive conflicts, but for which there is controversial support, is the ability of worker ants to discriminate among kin. Bourke and Franks review the available evidence, and discuss it in the light of whether such discrimination should be adaptive.

The archetypal ant colony has only a single queen, but the possession of multiple queens (polygyny) has arisen many times in ants, a feature that is examined in Chapter 8. As such queens are often unrelated, polygyny presents a potential challenge

for kin selection theory, since reproductive resources must be shared and the average relatedness among colony members is lowered. The evolution of multiple-queen colonies therefore requires that there be some benefit that outweighs these costs. Bourke and Franks present the different patterns of polygyny found in ants, along with their genetic consequences, and then provide various potential explanations for how queen associations could arise through mutualism or kin selection. Reproductive associations are not confined to ants, and the models presented in this chapter represent an up-to-date review useful to anyone interested in communal breeding; recent developments in the use of skew models to examine reproductive hierarchies are presented. However, it is also made clear that the empirical evidence supporting such explanations in ants is almost entirely lacking; Bourke and Franks provide some useful pointers for the direction in which research on this topic could proceed.

In Chapter 9, Bourke and Franks provide an introduction to an important field that has, somewhat surprisingly, received relatively little attention from social insect biologists: the evolution of life history strategies. In some ways ants provide ideal candidates for the examination of many allocation decisions, particularly those between reproduction and growth, which can be examined by the direct comparison of the production of reproductive and worker ants by colonies (although the authors stress that the physical structure of the nest is also part of ant colony growth). On the other hand, the genetic structure of colonies increases the conceptual complexity of such studies enormously, and colonies of often several hundreds of thousands of members that live inside elaborate structures are not easy to census. The authors therefore take the approach of identifying patterns of life history traits that are common in ants. Competition among ant colonies for space and resources appears to be a major determinant of ant life histories; as the Swiss entomologist Auguste Forel expressed it, "The greatest enemies of ants are other ants." Territoriality and high juvenile mortality of colonies are the consequence, with most ant species having perennial and iteroparous colonies. The indeterminate, modular growth and sedentary nature of ant colonies mean that they share features in common with plants. This parallel is explored further in a discussion of the application of gap dynamic models to ants, which provides a potential explanation of why colony reproduction seems to respond to high colony density and juvenile mortality with increased provisioning of propagules (which in ants are represented by colony-founding queens or colony buds). Seven case studies of life history patterns in ants are presented in Chapter 10. Since putting such cases in context requires the use of the comparative method, Bourke

and Franks make a plea for further work on ant phylogenies.

Ant sex has its own rules, starting with haplodiploid sex determination. An overview of the mating biology of ants is presented in Chapter 11. Most ants mate and disperse in mating flights occurring over vast areas during short time windows. There will not be more than one mating flight in an ant's life, since mating is followed by the shedding of the wings. In the mating cloud, males often aggregate in a way that resembles a lek. However, whether direct female choice occurs is unknown. Males have neither antlers nor peacock's tails: obvious adaptations for male-male competition or intersexual selection are apparently absent from most species. The authors argue that this might be owing to the constraints imposed on males by the necessity of undergoing single, short duration flights, and then potentially copulating with a female in mid-air. Nevertheless, students of sexual selection might find new, fruitful inspiration here. While ant males usually mate singly, female mating frequencies are on average higher than one in half of the investigated species. Hence there is potential for sperm competition, with a special twist: Each male should prefer to have his sperm used for fertilizing sexual female offspring and not workers. Where mating occurs without dispersal on a mating flight, the issue of inbreeding avoidance becomes crucial, not least because in some species homozygosity at the sex-determination locus causes fertilized eggs to develop not into workers but into sterile, diploid males, which are a heavy burden to the colony. In some ant species one of the sexes can enter a nest seeking a partner that remains resident. The workers, by deciding whether to let the intruder in, might exercise a type of partner choice that may be the closest to direct democracy in the animal kingdom.

The book closes with a chapter on the division of labor, one of the most striking features of social insect societies, and one that has inspired biologists since the time of Aristotle. It might be thought that there is little left to say on this subject, but Bourke and Franks take a novel approach to this subject by examining the ways in which division of labor could result from self-organizing rules within the colony. The model they use is that of "foraging for work." If ants carry out discrete tasks, but can switch between tasks according to simple rules based on the supply and demand of workers for each task, all tasks can be accomplished by the optimum proportion of the worker force. Since each worker specializes on only one task at any one time, this system should be more efficient than one in which every worker does every task. Similarly, the ability of workers to switch tasks according to the amount of work that is to be done means that it should be more flexible than one in which workers specialize exclusively on particular

tasks, or switch between tasks according to some predestined schedule. It has often been observed that as they age, worker ants change task, from the care of the queen and eggs, to the care of larvae and pupae, and finally to more risky tasks outside the nest, such as foraging for food. Bourke and Franks argue that the usual explanation of this temporal polyethism as a predetermined consequence of age does not fit the known facts (such as reversals in the direction and variation in the timing of task switching) for ants, while the self-organization approach provides a more consistent explanation. They also show that the division of labor within and between physical worker castes can be consistent with the foraging for work approach, and that some features of nest architecture in social insects could arise from such self-organizing mechanisms. This field is still in its infancy, so this chapter provides a very useful introduction to the ideas involved, although some are still rather vague. The concept of self-organization is a potentially powerful method of investigating patterns of social structure, but one that has yielded few testable hypotheses thus far, perhaps owing to lack of knowledge of the processes involved.

In summary, *Social Evolution in Ants* is a very well-presented book that will appeal to many biologists for many reasons. It not only provides a good review of our present knowledge of ant biology, but it also

presents fields that are promising new frontiers in ant research, such as life history theory, sexual selection and colony self-organization. We believe that it will be valuable reading for all those wishing to understand the biology of sociality from an evolutionary perspective, as well as for those who wish to experience some of the exciting debates that have been central to evolutionary thought, such as the controversy over levels of selection. The authors have succeeded in producing authoritative and up-to-date reviews on many interesting areas of evolutionary biology, but are also refreshingly honest about inexplicable patterns and gaps in our knowledge. Every chapter provides explicit or implicit suggestions for future research projects for ant specialists and evolutionary biologists alike.

Although much of the book deals with quite complex theoretical concepts, they are always presented in a way that is easy to read and to understand. The solution to a particular problem is often approached in several complementary ways, which gives the reader a more profound grasp of the ideas involved. The text is heavily referenced throughout, and the collection of so many valuable references in an accessible form is a praiseworthy undertaking in its own right. Author, subject and taxonomic indexes, summaries of each chapter, and boxes that clearly and simply develop and derive the concepts discussed make this book a valuable reference work as well as a good read.