Vignettes: Math

Those of us with little or no familiarity with formal mathematics are nevertheless used to thinking complex thoughts about complex subjects, namely other people. When we come to study mathematics, we find it hard, perhaps, because we cannot get used to thinking about such simple subjects.

—*A. K. Dewdney*, in *200% of Nothing: An Eye-Opening Tour Through the Twists and Turns of Math Abuse and Innumeracy* (Wiley)

Even among scientists, books dense with equations have always been unpopular, but the general phobia of simple mathematics is nowadays exaggerated. Also to be considered are those who find mathematics useful.

—*Philip Woodward*, in *My Own Right Time: An Exploration of Clockwork Design* (Oxford University Press)

whether she wanted to write a daughter's memoir or a detached, scholarly biography. She has tried to pursue the two projects simultaneously but, unfortunately, neither of them consistently. A thoroughly subjective daughter's portrait would perhaps have been preferable. Nevertheless, the present work is a good point of departure for a deeper and more contextualized portrait of this fascinating partnership in 20th-century biomedical science.

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Evolutionary Pinnacle

Social Evolution in Ants. ANDREW F. G. BOURKE and NIGEL R. FRANKS. Princeton University Press, Princeton, NJ, 1995. xiv, 529 pp., illus. $75 or £55; paper, $29.95 or £19.95. Monographs in Behavior and Ecology.

Ants represent a pinnacle of social evolution in that all species are highly eusocial, except for some that have secondarily lost this social system. Eusocial species have a reproductive division of labor, and highly eusocial species have overlap of generations and have reproductives and worker helpers that are morphologically distinct. Many ants, and many termites, go further and have elaborate caste systems, in which nonreproductives are further differentiated morphologically. Whence came this marvel of nature? What are the characteristics of ant evolution? This thorough and very readable book introduces readers to the evolution of ant eusociality, the evolutionary dynamics of ant society, and the evolution of caste.

The aim of the book is to help bring followers of ant sociobiology up to date following the monumental general treatise by Hölldobler and Wilson. Bourke and Franks use very little quantitative reasoning, basing their approach firmly on Dawkin's view of the gene as the unit of selection, which makes the book very accessible as an introduction to this important subject. This approach is likely seldom to err as to the outcome of selection, and it remains a task for the fairly near future to see how often the conditions necessary for its applicability are violated in nature.

The authors argue convincingly that kin selection is the single crucial factor involved in the evolution of eusociality and that the factors postulated by apparently rival theories of the past (enslavement by parents, mutualism) are but variants of kin selection. The combination of kin selection and sex allocation is vital to understanding ant social evolution, because the male-haploid genetic system of ants leads to drastic asymmetries in relatedness between colony members (a sister may be more closely related to her brother than he is to her!). The resulting conflict expected between queens and their worker progeny over the sex ratio of the colony has intrigued researchers for decades; studies of many species indicate that the workers generally win. This finding, for which this book will help to achieve general acceptance, further erodes the older idea of a truly regal queen dominating her myriad myrmidon offspring, as against the view of a colony as a sea of competing interests. Solomon (Proverbs 6:7) had it right.

Caste is the highest expression of eusociality, and Bourke and Franks give an authoritative and controversial account that deserves to be true even if eventually disproved. A central problem is age polyethism, the apparent dependence on a worker's age of the tasks she performs. The authors show, using simple models and elegant diagrams, how task need have little direct link to age: the relationship might arise simply from workers' switching to tasks for which there are too few attendants. A flow is set up as workers involved in outdoor tasks die off, drawing younger workers from well-tended tasks inside the nest.

This book clearly has a strong populational and behavioral basis, as works at this time must have because of the state of the field. How might the field develop? One way is by the expanding use of better molecular markers to unravel patterns in natural populations, but deeper questions of the molecular architecture of eusociality are becoming approachable. The sociality of the ants has been seen as disqualifying them from being a fit subject for the study of the evolution of sociality. This paradoxical conclusion stems from the fact that all ants are either highly eusocial or clearly descended from highly social ancestors: there are no species on the critical threshold of eusociality. Hence, bees and wasps with simpler social systems are supposedly where to look. But, compared to ants, eusocial bees and wasps remain minimally differentiated from their non-eusocial precursors; indeed, the sociality of such insects is labile, species switching back and forth. This minimal differentiation suggests that there are no significant genetic differences between bees and wasps with simple eusociality and their non-eusocial relatives. The basic genetic architecture is most likely to change only later, as complex morphological differentiation between colony members—caste—arises, better matching them to roles. This increase in complexity favors an increase in gene number, following the pattern by which *Drosophila* has more than twice as many genes as yeast though otherwise these organisms have similar constraints for developmental noise suppression. Termites and those aphids with sterile soldiers provide test comparisons for molecular sociobiologists of the future: do highly eusocial forms have more genes, and do they tend to be the same ones? Such questions would be unaskable without the groundwork laid by such as Bourke and Franks.

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