

health risk from inhaling tobacco smoke than from eating British beef. Infrequent but spectacularly damaging earthquakes and volcanoes make headlines; swelling clays do not.

Mitigating risk from natural hazards involves effective communication and mutual understanding of methods and priorities by technical advisers (scientists, economists, land-use planners) and civil authorities legally responsible for making decisions. These authorities must also take into account the urgent demands of existing land use, local economics and election politics. An economic factor of considerable importance today in the United States is the influence of the

availability and cost of insurance on decisions about land use and investment; reduced availability of property and liability protection in some high-risk areas has had profound effects on land value, economic activity and patterns of urbanization. Improved communication among scientists, economic managers, civil authorities and the public may well offer the largest cost-benefit ratio for society in the near-term mitigation of natural hazards. □

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Selfishness in a cooperative world

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Evolution of Social Insect Colonies: Sex Allocation and Kin Selection. By Ross H. Crozier and Pekka Pamilo. *Oxford University Press: 1996. Pp. 306. £39.50, \$62 (hbk); £19.95, \$32 (pbk).*

THERE is something distinctly odd about social insects. They provide some of the most fascinating examples of altruistic behaviour, with a worker caste whose individuals forgo their own reproduction to aid in the reproduction of the queen, as well as many other examples of self-sacrifice, including the evolution of 'kamikaze' weapons such as detachable stings and exploding abdomens used in defence of the colony. Yet life within the colony is not always as harmonious as it may at first appear. Individuals may use Machiavellian strategies to favour their own interest, and lethal fights are not uncommon. It is this complex dynamic between conflict and cooperation that Ross Crozier and Pekka Pamilo consider in this excellent book.

The authors convincingly demonstrate that kin selection is the main selective force responsible for the evolution and maintenance of sterile castes and altruistic behaviour in ants, bees, wasps and termites (the major groups of social insects). The general principle of kin-selection theory is that individuals can pass on copies of their genes not only by producing offspring but also by helping kin such as siblings to reproduce. To maximize their fitness, colony members should therefore favour individuals that are more closely related, and this provides the raw material for many potential conflicts within the colony. For example, the haplodiploid sex-determination system means that workers are more closely related to their sisters than to their brothers in ants and other Hymenoptera. So workers should favour a female-biased sex-ratio

investment by their colony. By contrast, because queens are equally related to their sons and daughters, they should favour an equal investment in both sexes. Queen-worker conflict over sex ratio is therefore predicted, and evidence indeed indicates that workers cannibalize males — their brothers — to manipulate colony sex ratio in their favour.

Two other important types of conflict between colony members concern the



The solitary masarine wasp *Ceramius clypeatus*. From *The Pollen Wasps: Ecology and Natural History of the Masarinae* by Sarah K. Gess. Harvard University Press, £31.50, \$49.95.

identity of individuals reproducing in the colony and the way in which resources should be allocated between reproductive and non-reproductive functions: that is, between the production of reproductive versus worker individuals. Crozier and Pamilo use formal kin-selection models to investigate how these conflicts are affected by variation in the genetic structure of the colony. Their analyses yield interesting predictions about how varia-

tion in the number of queens per colony and the mating frequency of queens — the main factors affecting colony genetic structure — should affect the nature of within-colony conflicts.

My only reservation about this book stems from its long gestation, which has resulted in several recent theoretical concepts and empirical findings being omitted or mentioned only briefly. For instance, several empirical studies of colony-level variation in sex ratios are only briefly treated and there is no mention at all of skew models, although these models provide powerful tools to investigate reproductive conflicts among colony members, by considering simultaneously the effects of relatedness, ecological factors and intrinsic benefits of cooperation.

I was expecting much overlap between this book and Andrew F. G. Bourke and Nigel R. Franks's recent *Social Evolution in Ants* (Princeton University Press, 1995). To my surprise, that is not the case. For one, Bourke and Franks's book deals only with ants, whereas Crozier and Pamilo's covers all social insects. The approach of the two books is also quite different. Crozier and Pamilo develop a new theoretical framework for analysing kin conflicts within insect societies. A lot of this work has been published in recent and already influential papers. Bourke and Franks use a less mathematical approach and provide a more general overview of empirical studies on social behaviour and sex ratio. The two books are therefore complementary. Bourke and Franks's book will be preferred for those looking for broad synthesis of the fascinating world of insect sociality, whereas Crozier and Pamilo's book is an excellent resource for those interested in a mathematical approach to kin conflicts and sex-ratio theory. The use of elegant kin-selection models also makes Crozier and Pamilo's book highly suitable for a course on theoretical modelling.

It took millions of years for social insects to attain their complex social organization. The rapid empirical and theoretical progress reported in this book provides some hope that it might take less time to attain a good understanding of how insects have evolved their sophisticated sociality. □

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