BOOK REVIEWS

THE GENETICS OF ALTRUISM. S. A. Boorman and P. R. Levitt. Academic Press, New York, 1980. Pp. xx+459. Price: \$29.50.

There has recently been considerable interest amongst evolutionists in the problem of altruistic behaviour, *i.e.*, behaviour that increases the fitness of other individuals, with no direct benefits or even a disadvantage to the individual who exhibits it. Three main evolutionary mechanisms have been proposed to account for such behaviour, associated with the work of Trivers, Hamilton and Wynne-Edwards respectively: reciprocal altruism (where pairs of interacting individuals derive a mutual benefit from their interaction), kin selection (where relatives are benefitted), and group selection (where the local population as a whole is benefitted). This book is an elaborate attempt to investigate each of these processes by means of population genetics models of single locus systems.

Chapters 2-5 deal with reciprocal altruism. It is shown that (not surprisingly) a gene causing reciprocal altruism is subject to positive frequency-dependent selection, such that there is a critical gene frequency which must be reached before it becomes favoured by selection. Reciprocal altruism is thus unlikely to evolve in a large randomly mating population. But, as is discussed at length in Chapters 2-5, it can evolve in a species divided into partially isolated, small, local populations, as a result of a chance increase in the frequency of a gene promoting reciprocal altruism in one population, followed by its transfer to adjoining populations by migration. This process is called a *cascade* by the authors, whose results make it clear that it requires quite restricted conditions on population structure and migration rates.

Chapters 6-9 are concerned with models of kin selection, mostly in terms of altruism between siblings. A rather general model of fitness effects with kin selection in sibships is first laid out and conditions for spread and fixation of an allele causing altruism are established in terms of these fitness effects. These conditions are then subjected to a somewhat opaque process of "axiomatisation", in an attempt to relate them to Hamilton's well-known inclusive fitness formulation. Subsequently, special cases involving explicit behavioural models generating particular patterns of fitness effects are analysed. These show that Hamilton's results are, in general, to be regarded as limiting approximations for weak selection. With arbitrary selection intensities, kin selection is often frequency-dependent, so that polymorphism for altruistic behaviour is established.

Chapters 10 and 11 deal with group selection. Despite the complexity of much of the mathematical analysis, nothing much in the way of novel insights about group selection seems to emerge. The models in Chapter 10 do not incorporate the effects of genetic drift in generating between-group diversity, on which group selection depends, and thus resemble Hamlet without the Prince, Chapter 11 goes to the opposite extreme, and assumes populations founded by only two individuals.

The Genetics of Altruism is clearly intended as a record of the authors' own research and does not attempt to give an overview of the theoretical

literature on the subject. It is not very clear why the authors wished to present such a mass of detailed results in book form rather than as separate journal papers. The utility of the book is impaired by its lack of coverage of the work of others. For example, several papers on kin selection were published in 1978 which yield conclusions paralleling those mentioned above, but they are not even referred to. The authors do not seem to be aware that their cascade effect with reciprocal altruism is a special case of Wright's famous shifting-balance theory of evolution. Indeed, the book seems to be aimed at an audience of applied mathematicians rather than biologists, and is written in a style that makes it inaccessible to all but the most dedicated student of evolutionary theory. Despite the authors' stated aim to develop models of social evolution based on the tradition of population genetics, they seem to wish to distance themselves from this tradition by their choice of notation (*e.g.*, β for gene frequency, Σ for mean fitness), their tortuous approach to model building, and their unwillingness to give intuitive interpretations of their formal results. Although the book deals with several interesting and important problems and has points of real substance to make, it thus seems to me to be more or less a failure as an attempt to communicate with the audience to which it should be addressed.

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INSECT CYTOGENETICS. SYMPOSIA OF THE ROYAL ENTOMOLOGICAL SOCIETY: NUMBER TEN. R. L. Blackman, G. M. Hewitt and M. Ashburner (Eds). Blackwell Scientific Publications, Oxford London Edinburgh Boston Melbourne, 1980. Pp viii + 278. Price: £22.50.

Insects have figured prominently in cytogenetic studies from the early years of chromosome studies to the present day. This is doubtless in part a reflection of the phenomenal evolutionary success of the class Insecta, accounting as they do for an estimated 75 per cent of all animal species. The cytogeneticist in search of a problem could hardly avoid this vast and diverse group. The fortuitous choice of an insect, *Drosophila melanogaster*, as an organism for genetical research, the exceptional quality in terms of number, size and clarity of chromosomes possessed by certain insect groups such as the Orthoptera, and the economic importance of many insect species as agricultural pests and vectors of human diseases must also be accounted important factors.

This volume reports the proceedings of the tenth symposium of the Royal Entomological Society held in September 1979, the aim of which was to summarise recent developments in insect cytogenetics and in particular to present a juxtaposition, and hopefully a synthesis, of developments at the molecular level with the applications of cytogenetics to problems of population and evolutionary biology. The molecular end of the subject is represented by three papers on DNA sequence organisation in insects (mostly *Drosophila*) by Peacock and Lohe, Dover, and Glover *et al.*, followed by useful reviews of structural and functional aspects of polytene chromosomes (Ashburner) and lampbrush chromosomes (Kunz and Glätzer). Forer presents a review of chromosome movement in insect spermatocytes. In further papers, the eccentricities of chromosomal mechanisms in scale insects are described by Nur while the cytogenetic systems of