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Reproductive Behavior of Insects: Individuals and Populations

W. J. Bailey & J. Ridsdill-Smith [eds.]

Chapman and Hall, London, 1991

339 pp., \$95.00

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A CONCEPTUAL SHIFT in thinking among evolutionary biologists—precipitated by reaction to Wynne-Edwards' (1962) *Animal Dispersion in Relation to Social Behaviour*—has become so well entrenched that recently-trained evolutionists might not know what the fuss was all about. Wynne-Edwards produced a masterly review of traits used in social competition for resources, yet argued that much individual behavior was geared to producing group-level benefits. The shift in thinking which followed involved the recognition that selection is more effective at lower levels of organization. Evolution of group-beneficial traits requires stringent conditions, and these seem rare in nature. A wide variety of studies now show that group-beneficial traits usually result from selective advantages to the individuals which perform them. If it costs them, then individuals are usually not concerned with the good of the species.

To what extent have ideas about levels of selection been tested in the world of economic biology? When faced with an outbreak of mosquitos, is it meaningful or practical to study behavioral variation among individuals, and behavioral flexibility within individuals? The answers to these respective questions are "very little," and "nobody knows." *Reproductive Behaviour of Insects* aims "to introduce selectionist thinking to a wider audience of entomologists" (p. 3), particularly those studying the population ecology of economically important pests. The editors are to be commended for building a bridge between two camps of biologists who probably have more in common than most individuals in either camp realize. Readers will find interesting reviews relating to sexual selection and reproductive competition, and some new ideas for applications of insect management. Except for the expensive price of the book, it can be recommended to an unusually broad audience of entomologists.

Reproductive Behaviour of Insects contains 10 review chapters, each with a separate bibliography; an introduction by the editors; and a subject index. Five chapters deal with host selection and oviposition by parasites and herbivores (animal parasites by P. W. Wellings, plant parasites by R. E. Jones, tephritid fruit flies by B. Fletcher and R. Prokopy, Heliiothinae by G. P. Fitt, and aphids by S. A. Ward); two chapters review mat-

ing behavior (evolution of mating systems by J. Alcock and D. T. Gwynne and acoustic sensory cues by W. J. Bailey); two chapters examine competitive interactions relating to oviposition (dung-breeding insects by J. Ridsdill-Smith and social wasps by J. P. Spradberry); and the final chapter examines larval contributions to fitness among folivore insects (D. Reavey and J. H. Lawton).

An excellent overview of selectionist thinking by Alcock and Gwynne describes how the tremendous diversity of insect mating behavior remained cryptic and out of sight to biologists who were looking in the wrong places (i.e., for benefits to the group). With the rediscovery of Darwinian ideas of sexual selection acting on individuals, an enormous number of alternative mating behaviors and morphologies exploded into view, and numerous patterns were expected and then discovered. One of these patterns involves the evolution of sensory cues for mate finding, the topic of Bailey's chapter. Bailey argues that receptors for acoustic social signals evolved from those primarily used for predator detection, which is elaborated upon for "coyness" during mating behavior. He also suggests some avenues for further research, and notes that a better understanding of insect acoustic signaling requires that ethologists design experiments testing specific proximate physiological mechanisms, while neurophysiologists address the individual variability that is so interesting to ethologists.

There is some repetition among the five chapters dealing with host location and oviposition, but it usefully serves to emphasize the tremendous variation among and within individuals, and re-enforces observations that these insects are vastly more complicated than previously believed. Insect parasites and plant parasitoids (1) search for and recognize hosts on the basis of some complex combination of chemical, auditory, visual, and textual cues, (2) they modify their behavior based on nutritional status, number of eggs available to lay, and numbers of competing parasites, (3) they sometimes prefer certain hosts, despite the fact that their offspring may develop normally on a non-preferred host, and (4) their behavior is often influenced by past experience. There are unknown interactions among genetic and environmental information, yet few studies of parasites have examined the reaction norm of traits for host location.

Ward's discussion of host specificity in aphids is particularly interesting. He shows that if there is a 1% success rate of searching for new hosts (a conservative estimate), then alleles for acceptance of a non-host will be selected if the fitness

of aphids on their non-host is greater than 1% of their fitness on the preferred host! He provides some preliminary comparative evidence for the hypothesis that selection favors host specificity *per se* as a rendezvous site for mating, but he argues that this would not result in sympatric speciation. He briefly develops the interesting idea that an important factor in the evolution of aphid host specificity might relate to phenological synchronization with the host plant. Synchronized emergence should increase the probability of successful dispersal to some new host and help contribute to a large enough fitness advantage for dispersers to evolutionarily capture the new host. Phenological synchronization also has significant implications for the fitness of caterpillars, as discussed by Reavey and Lawton. Fitt also raises the possibility that host shifts of *Heliothis* spp. onto cotton may relate to increased synchrony between emerging adults and this crop plant.

On the basis of the book's subtitle I anticipated learning much about how individual social competition relates to population ecology, and then wished that the topic was given more attention. Adam Lomnicki's (1988) *The Population Ecology of Individuals* (Princeton University Press) would nicely complement many of the chapters in this book. A focus on individuals has not yet produced any striking benefits to those concerned with the practical problems of regulating pest species, but as Alcock and Gwynne optimistically state, pest managers can tap the potential of social competition, "only if they are aware of its existence." In turn, as nicely demonstrated by this volume, economically important species also have wonderfully rich behavioral repertoires and deserve far more attention from evolutionary biologists.

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