

Parasitoids: attractive model systems

Parasitoids: Behavioral and Evolutionary Ecology

by H.C.J. Godfray

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Work on insect parasitoids has enjoyed two traditions. The elder tradition has focused on natural history, descriptive biology and mechanistic explanations of behavior. Many species were chosen for study because of their importance as regulators of host-insect populations, frequently pests of crops. A prodigious amount of information was gathered in this tradition, as analysed by Clausen¹ and Askew², who highlighted the tremendous diversity of parasitoid life histories and behavior. A newer tradition has emerged among modern behavioral and evolutionary ecologists, who have been drawn to parasitoids because of their advantages as model systems. Much of parasitoid behavior has an unusually intimate connection with fitness. Parasitoids are also easily manipulated in the laboratory, and their diversity provides avenues for addressing a wide array of questions. In particular, the facultative control over sex allocation afforded by haplodiploidy made them prime subjects for the development of sex-ratio theory by Hamilton³ and Charnov⁴.

Godfray's book represents the first single-author synthesis of these two traditions, and the result is an effective and exciting synergism. Godfray builds on the volume edited by Waage and Greathead⁵ in 1986, and documents a remarkable amount of intervening progress. The book's stated goals are to review recent advances, demonstrate the utility of parasitoids as models for ecologists, and underline the contributions that fundamental studies can make to applications in insect management. The book integrates empirical results with theory, although theoretical results are not derived (apparently to save the reader from the rigors of mathematics).

The focus is on parasitoids, defined by a larval stage that feeds upon a single arthropod host, thereby killing it. As implied by the title, the coverage mostly excludes issues of strict population dynamics; this is almost a pity, as the few forays into the dynamics literature (e.g. a discussion of the influence of spatially density-dependent parasitism on the stability of host-parasitoid interactions) are gems. Godfray uses the modern behavioral ecology approach to address a series of topics, organized around

a cycle of host search, oviposition, sex allocation, immature stages, the adult parasitoid, and finally life history evolution and community ecology. Although few previously unpublished research results are presented, the book is far from a mere digest of prior work. Each chapter has important new perspectives and syntheses. Key empirical and theoretical works are critically assessed; in many cases cogent arguments are presented calling into question conclusions drawn by original authors and highlighting the need for additional work. I found these critiques to be uniformly well-balanced and very valuable.

Perhaps most importantly, this volume clearly frames key research needs and approaches most likely to be fruitful in advancing our understanding of parasitoids and behavioral ecology. These are many. For example, parasitoids can make valuable contributions to the study of how proximate behavioral rules, experimentally decipherable using statistical modeling, can implement near-optimal search behavior. The increasing availability of molecular phylogenies should also allow us to employ the taxonomic and behavioral diversity of parasitoids in formal comparative analyses of evolutionary innovations, such as major shifts in life histories. Other fascinating questions are identified in the areas of superparasitism, the molecular basis for interactions between hosts and internally-developing parasitoids, selfish genetic elements, mating systems and the influence of variance in host availability on the evolution of parasitoid fecundity.

Godfray argues convincingly that the single greatest obstacle to progress in the behavioral ecology of parasitoids is our failure to measure the relationship between parasitoid size and fitness under natural field conditions. This unresolved relationship is pivotal to our understanding of host acceptance, superparasitism, clutch size, sex allocation, sibling interactions and parent-offspring conflict. In this regard, the growing number of successful field studies of parasitoid behavior described in this book puts the lie to the tired assertion that parasitoids are too small and mobile to study in nature.

Throughout the text, Godfray provides a didactic analysis of the tools of the trade, including critical evaluations of optimality theory, comparisons of static and dynamic optimization models, statistical modeling techniques and the multitude of statistical and interpretational pitfalls that surround comparative analyses (in this case of host range and parasitoid species load). This is important reading.

Godfray writes with a lucid and relaxed style. The work is remarkably concise for the level of comprehensiveness obtained, and the reader will find an exhaustive sup-

ply of references to the primary literature. The quality of Godfray's effort is such that I think it reasonable to expect that it will both reinvigorate current researchers in this area as well as spur new workers to adopt parasitoids as models for work in behavioral and evolutionary ecology.

Jay A. Rosenheim

Dept of Entomology, University of California,
Davis, CA 95616, USA

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A literary radiation of antarctic fishes

Antarctic Fish Biology: Evolution in a Unique Environment

by Joseph T. Eastman

Academic Press, 1993.
\$74.95 hbk (xiii + 322 pages)
ISBN 0 12 228140 3

A History and Atlas of the Fishes of the Antarctic Ocean

by Richard G. Miller

Foresta Institute for Ocean and Mountain Studies, 1993.
\$95.00 hbk, \$78.00 pbk (xx + 792 pages)
ISBN 0 9634436 0 7

The sesquicentenary of the first scientific descriptions of fishes from the icy Southern Ocean, collected aboard *Erebus* and *Terror* under James Clark Ross, has been heralded by a school of Antarctic fish books. Five have surfaced since 1990, and this latest cohort of two substantially increases the accessibility of information on these fascinating fishes. The two books are quite different in their intent and scope; Eastman concentrates on phylogenetics, form and function, while Miller is concerned primarily with species identification.

Both books commence with brief discussions of the Antarctic Ocean, zoogeography, continental drift and dispersal routes. In the absence of any recognizable fossil record, Eastman presents a systematic analysis of relationships within the Notothenioidei based on computerized parsimony analysis of published characters.