Book Reviews

Dynamics of Predation

The Dynamics of Arthropod Predator-Prey Systems. MICHAEL P. HASSELL. Princeton University Press, Princeton, N.J., 1978. viii, 238 pp., illus. Cloth, $16; paper, $6.95. Monographs in Population Biology, 13.

Over the last decade a seemingly uncountable number of papers on arthropod ecology have appeared in the *Journal of Animal Ecology*, written by various combinations and permutations of M. J. Hassell, R. M. May, J. H. Lawton, J. R. Beddington, C. A. Free, H. N. Comins, T. R. E. Southwood, and a few others. Those of us who have been suffering massive guilt from not assimilating this obviously important though rather lengthy and intricate body of literature at last will find relief: Hassell has coalesced it in this outstanding monograph. The book reads like a mystery novel, not only because of its lucid style but also because of the compelling, almost suspenseful way in which the subject is developed.

The plot begins with a venerable difference-equation model, that of Nicholson and Bailey, formulated particularly with hosts and parasitoids in mind. This model makes several simple assumptions: (i) that predator-host encounters are proportional to the product of the number of predators and hosts; (ii) that those encounters are distributed randomly among hosts; and (iii) that predators and hosts increase in direct proportion to the numbers of parasitized and unparasitized hosts, respectively. Unfortunately, the model proves too simple; no matter what the parameters (there are only two), the system is unstable, a result that must have been particularly irritating to Nicholson, a principal advocate of the density-dependence school of population regulation. If one admits the existence of stable predator-prey associations in nature, then a more complicated model is required. Allowing a predator's search rate to be host-dependent does not help; this is destabilizing. Fortunately, at least three major ways in which the assumptions of the model are brought closer to reality can result in stability. First, hosts or prey may show intraspecific density dependence. Second, predators may interfere with one another. Third, and perhaps foremost, predator-host encounters may not be random but may rather follow the rules that would be expected to prevail if hosts were aggregated and if predators concentrated on the aggregations. Having thoroughly convinced us that stability is often to be expected at least in theory, Hassell turns to more peripheral topics, such as polyphagy, hyperparasitism, and predator competition. The book concludes with a discussion of some implications for biological control, a section substantially more optimistic about the application of simple analytical models than would have been possible a few years ago.

The research reviewed in this book, which in addition to the list above includes work of Murdoch, Oaten, and others, has often shifted and sometimes overturned the conventional ecological wisdom. The model-results and facts that I found the most innovative are the following.

1) A variety of models that incorporate spatial heterogeneity in prey distributions give rise to more stable dynamics than models that do not. This is in accordance with Huffaker's classical data (though those can also be explained qualitatively simply by a reduction in the prey-predator contact rate). It is not, however, in agreement with the extensive treatment by Allen (*Am. Nat.* **109**, 319 [1975]), which is not cited.

2) Interference between predators is a very important laboratory phenomenon; its importance in nature is frequently, but not always, very small.

3) The S-shaped (type III) "functional response" (the relation between individual predator intake and prey density) not only is found in vertebrates but is common in invertebrates as well. In the latter, it can result from differences in the proportion of time spent feeding as a function of prey density.

4) Switching (the differential preference for the denser type of prey) most commonly results from predator concentration on local areas of high prey abundance, just as Royama (*J. Anim. Ecol.* **39**, 619 [1970]) initially proposed.

5) Constant-proportion prey refuges are commoner than constant-number refuges; both can impart stability, though the latter do so more readily.

6) A switching predator can maintain an otherwise unstable community of competitors, but so can a predator with a preference ranking that does not vary with relative abundances of prey types. The latter, in fact, is closer to the case in Paine's famous starfish system (Paine, personal communication).

Upon completing Hassell's book I had a feeling of satisfaction all too rarely obtained from documents in this area of science. Theory and data are combined in apparently ideal proportions to produce a major advance in our understanding of predator-prey systems. What could be the shortcomings of this book and the research contained therein? I mention several possibilities, in part acting as devil's advocate.

First, the way in which the book relates data to theory is usually very rough and qualitative. Statistics by which the assumptions could be justified or the predictions evaluated are virtually absent. Plausibility is generally accomplished by plots of data points or intervals, usually fitted by eye. Nonlinear regression is used only occasionally; confidence intervals for parameters so fitted must be interpreted with caution because of the assumptions involved, but such statistics are better than nothing.

Second, the only models presented are analytically tractable ones, which places some limit on their complexity. Repeatedly, Hassell pulls back from computer simulation—for example, "Building an ever more complicated model to which each new component is added to the last would soon lead to an unmanageable edifice." As I pointed out in an earlier review in *Science* (**178**, 389 [1972]), this modeling strategy necessitates the treatment of major effects one at a time, exactly as Hassell does. To resist replacing a natural system that is not understood with a model system that is not understood is, in my opinion, a great virtue. However, the approach assumes the nonexistence of qualitatively new outcomes resulting from interactions between major effects. Hassell recognizes the problem and claims that such interactions are unimportant, but this is supported in the book by only one example. The general proposition remains largely untested; indeed, because of what has been called the "curse of dimensionality," the matter could never completely be settled even with massive simulation.

Third, in common with nearly all population-dynamical approaches, this book makes little connection with "evolutionary ecology," particularly as regards feeding strategies. Hassell is aware of this, mentioning the shortcoming explicitly once and attempting a preliminary link in several places. The linkage is strongest in his discussion of disproportionate predator searching on aggregated prey; it is less strong in his discussion of how variation in the amount of time allocated to feeding causes a sigmoidal functional response. Improvement here should also result in improvement in the functions used in the population models, some of which seem to have been chosen for descriptive prowess rather than mechanistical derivation.

Finally, the difference-equation models Hassell uses throughout have some nasty mathematical properties in the "unstable" region. Limit cycles having long periods and even "chaotic" population dynamics (random numbers within an interval) are possible with single-species models, once certain parameter bounds are exceeded. Such properties become more frequent and more varied in several-species models, such as those for predator and prey (Guckenheimer *et al., J. Math. Biol.* **4**, 101 [1977]). For a particular single-species model, Hassell shows that most real populations have parameters that imply stable dynamics. This optimistic result is tempered by the fact that another model results in substantially more unstable cases; moreover, this kind of analysis is not made for predator-prey models at all. An important current issue in ecology is the extent to which chaotic or infrequently repeating limit-cycle dynamics, which characterize difference-equation models, equivalently characterize nature. Certain models that assume less pulselike processes than do pure difference equations (E. Poulsen, cited in F. Christiansen and T. Fenchel, *Theories of Population in Biological Communities*, Springer-Verlag, 1977) and certain difference-equation models that restrict density dependence to particular portions of the life cycle (R. Deriso, Ph.D. thesis in biomathematics, University of Washington, 1978) are less unstable than the sort of model Hassell uses; the issue even in theory is still very much open. A major task will be to investigate the probable biological importance of the unstable region for those models that produce one.

In my opinion, none of these shortcomings, except possibly to a limited extent the first, could easily have been avoided in a book written now. Among other issues raised but not settled in Hassell's excellent book, they provide a wealth of departure points for future research in this galloping area of ecology.

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Marsupial Model

Opossum Neurobiology. (Neurobiologia do Gambá.) The Opossum as an Experimental Model for the Study of the Mammalian Nervous System. Proceedings of a symposium, Rio de Janeiro, May 1978. C. E. ROCHA-MIRANDA and ROBERTO LENT, Eds. Academia Brasileira de Ciências, Rio de Janeiro, 1978. vi, 292 pp., illus. Paper, $10.

Opossum Neurobiology is a collection of 15 research reports from experiments utilizing the opossum as an experimental animal. The volume is an outgrowth of a symposium held at the Brazilian Academy of Sciences that was organized to advertise the opossum as an experimental model for studies of the mammalian nervous system. In the foreword the editors describe the advantages offered by the opossum, which include its phylogenetic significance as well as its usefulness for developmental studies. The latter is particularly emphasized because of recent interest in mammalian neurogenesis. The opossum is born after a gestation period of only 13½ days and immediately climbs into an external pouch (marsupium), where it remains attached to a teat for two months or more. In this immature but externalized state, the opossum young are available for direct observation and experimental manipulation.

Except for a paper by Ford Ebner from the United States, the volume is limited to contributions from Brazilian investigators and heavily weighted toward the work of the group from the Universidade Federal do Rio de Janeiro. The Brazilian workers present several good papers on specifics of the opossum's eye, retina, optic nerve, visual cortex, and superior colliculus, as well as one that deals with the development of certain areas related to vision. The paper by Lent and Rocha-Miranda on aberrant projections after eye removal and tectal lesions is particularly interesting because it shows by example how the opossum's embryology can be used to advantage in an experimental situation. Although most of the papers deal with the opossum's visual system and cortex, there is one that reports the results of body mapping experiments within the dorsal column nuclei and another that describes the pattern of monoaminergic innervation of the opossum brainstem.

The quality of the papers is somewhat variable, but the data presented appear to be reliable. Much of the information contained in the volume will be interesting to investigators who might consider using the opossum as an experimental animal or who want to compare its visual system with that of more commonly used laboratory animals. In my view, the major contribution of the book is its attempt to emphasize the potential importance of marsupials for developmental studies.

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A Cephalopod

Octopus. Physiology and Behaviour of an Advanced Invertebrate. M. J. WELLS. Chapman and Hall, London, and Halsted (Wiley), New York, 1978. xiv, 418 pp., illus. + plates. $42.50.

Wells has long been known for his work on cephalopod behavior and physiology. The present book, which follows a previous one (*Brain and Behaviour in Cephalopods*, Stanford University Press, 1962) by Wells, is testimony to his steadfast interest in cephalopods. The goal of the new book is "to produce a comprehensive physiology of a single invertebrate species. Here it should be possible, for once, to get a feel for the workings of an animal as a whole, rather than as a series of isolated organ systems." This rather ambitious goal is tempered, however, by another statement: "A monograph is, inevitably, a rather personal thing and the account is bound to be skewed by too much print squandered on things that interest the author, and too little on the things that may interest others."

The author has collected in every chapter a wealth of information, through which he leads the reader with a sure hand. The literature is adequately reviewed, and the observations of the author do not overshadow other people's data.

The book begins with an anatomical overview of the octopus and continues with accounts of respiration, circulation, feeding, digestion, reproduction, and endocrinology. Each of these subjects is treated comprehensively and well, notwithstanding the author's claims that on matters not close to his interest he is reluctant to do the necessary homework. The last portion of the book, constituting more than half of it, deals with the nervous system and brings together work done mostly by J. Z. Young and by the author. As is customary, a major portion of the account is devoted to visual system physiology and behavior. Mechanoreception is also extensively treated,