Feeding as Optimization

Foraging Behavior. Ecological, Ethological, and Psychological Approaches. Papers from a symposium, Seattle, June 1978. ALAN C. KAMIL and THEODORE D. SARGENT, Eds. Garland, New York, 1981. xviii, 534 pp., illus. $45. Garland Series in Ethology.

Why animals forage the way they do is a problem that has intrigued ecologists, ethologists, and psychologists for decades. Although workers in the three disciplines have approached the problem differently, all view foraging as a decision process, one in which animals choose where to search, what to hunt, when to search elsewhere, and so on. What unites the disciplines is the quest for the rules by which animals make these choices. During the last 15 years ecological theory has provided a series of optimal decision rules that early laboratory experiments showed to be realistic. Now, in this volume, the usefulness of the optimality approach and the accuracy of its predictions are evaluated. Kamil and Sargent have done a great service by including essays by ecologists, ethologists, and psychologists that examine the assumptions of the old models and present results from long-term field studies.

The volume is divided into four sections, the first of which critically examines optimal foraging theory (OFT). This section is particularly strong because it presents not only a short review of the assumptions and predictions of the first generation of models (Krebs, Houston, and Charnov) but also an alternative microeconomic theory that challenges the assumptions of the standard approach (Rapport). Since the behavior of many species described in this volume violates the OFT assumptions that (i) prey can be ranked according to energetic profitabilities and (ii) the relative abundance of a prey does not affect its value to the predator, the microeconomic model provides a new approach for deciphering decision rules.

One of the major criticisms of optimal foraging theory is that realistic versions of the models are difficult to construct, or test. This idea is echoed in an essay by Zach and Smith, who detail all the complexities of ovenbirds foraging in patchy environments or of song sparrows foraging for themselves and their young. They question the utility of the optimality approach if it can only delineate adaptive features in simple situations, such as those involving diet choice, where optimal solutions are easy to define. Though it may be true that some complex problems will remain outside the scope of optimality theory, their pessimism may be excessive since most of the field studies in this volume use some form of optimality to successfully make predictions concerning, or to interpret, how animals forage. Pyke, for example, actually delineates the steps by which complicated systems can be modeled and shows how predictions can be cleverly tested in the field.

The second section consists mainly of field studies that evaluate predictions of models of diet and habitat choice. Perhaps the finest test of diet choice predictions comes from Goss-Custard's studies of redshank foraging. In his essay he summarizes his previous work and elegantly shows that the two basic OFT predictions are supported: when feeding on worms, redshanks always consumed the high-value prey whenever it was encountered and only consumed the low-value prey depending on the abundance of the high-quality one. However, his finding that redshanks prefer an energetically poor amphipod to energetically rich worms calls in question the whole notion that energy is the sole concern, or "currency," of predators. This is a theme that reappears in many of the essays, but nowhere more forcefully than in Glander's study of howler monkeys. Howlers not only choose the energetically richest and most digestible plant parts, they also avoid certain chemicals and balance their diet with respect to protein or amino acid content. The importance of incorporating morphological, physiological, and information-processing features into optimality modes is also highlighted in other essays. Reichman shows that differences in the locomotory energetics of quadrupedal pocket mice and bipedal kangaroo rats force them to use different foods. Whereas kangaroo rats can travel economically over long distances in search of dispersed patches of high seed density, pocket mice cannot, and must utilize more abundant low-density patches.

Most of the decision rules examined in this volume assume that animals are able to learn and remember many features of their environment. In the third section, the essays explore this relationship between foraging and cognition. Some focus on general issues surrounding the evolution of learning. Orians points out that most optimality models fail to consider costs associated with acquiring information and fills this void with a simple model based on a trade-off between exploration and exploitation. Changing an animal's sensory capabilities and the magnitude of its memory errors has interesting consequences with respect to the evolution of memory capacity. In a similar vein, Pulliam demonstrates that behavior that maximizes reinforcement also maximizes the rate of energy intake and explores how this psychological process could be a proximate means of maximizing fitness. Both essays are exciting since they probe unexplored problems and temper speculation with fact. Other essays examine how types of learning match particular foraging patterns. Zahorik and Houpt suggest that the ability to learn depends as much upon ecological circumstances as it does on phylogenetic heritage. Large herbivores do not usually learn to avoid noxious foods that produce negative physiological consequences. The authors show that, like rats, large herbivores can learn the task as long as the noxious food is ingested in the absence of any other food. But since under natural conditions the likelihood of receiving any food by itself is vanishingly small, learning of this type is not usually used in selecting an optimal diet. Learning differences even occur among rodents. Olton, Handelman, and Walker show that rodents have a good memory of where they have been but that different species have different, and apparently adaptive, predispositions with regard to shifting locations after acquiring prey. For those species that tend to feed in dense food patches, the tendency to stay is much stronger than for those species that tend to feed in smaller, more continuously distributed patches.

In the last section, two essays examine the genetic and environmental control of feeding behavior. Using western garter snakes Arnold shows that populations vary genetically in their tendency to attack particular prey species and estimates the time necessary for evolutionary divergence. In a similar fashion Gray demonstrates that different populations of deer mice show differences in foraging stereotypy. Some support for his suggestion that environmental stability leads to more specialized foraging behavior de-

rives from his ontogenetic studies showing that individuals of one population when raised under fluctuating feeding conditions forage in a more variable manner than those raised under stable conditions. Both essays highlight the importance of understanding the genetics that underlies and possibly constrains the evolution of feeding behavior.

As these examples show, great strides have been made toward understanding the rules by which animals make foraging decisions. Nevertheless, there is still a long way to go. Maximizing the rate of energy acquisition, or any other "basket of currencies," is not the same as maximizing fitness. Only the most rudimentary beginnings have been made toward integrating physiological, morphological, and information-processing constraints into foraging theory. And more work is needed at integrating foraging behavior with social behavior. In this volume a start is made, and the melding of the different perspectives and techniques of workers in three disciplines highlights many important issues for the future. Since the results of so many field studies are summarized and used to assess the significance of theoretical predictions the book will be required reading for anyone working on feeding behavior. In general, the essays are short, are well written, and contain just enough figures to convey clearly the results of the experiments. These features place the volume within the grasp of anyone with a basic understanding of behavior, ecology, or psychology.

DANIEL I. RUBENSTEIN
Department of Biology,
Princeton University,
Princeton, New Jersey 08544

The Shift from DDT

Insects, Experts, and the Insecticide Crisis. The Quest for New Pest Management Strategies. JOHN H. PERKINS. Plenum, New York, 1982. xx, 304 pp. $29.50.

This book is an account of economic entomologists' response to the "insecticide crisis" of the late 1960's, when public concern about the environment, coupled with the problems caused by continued use of persistent chemicals, forced economic entomologists to develop and test, in short order, other ways of dealing with insect damage. Perkins discusses the major alternatives tried in the 1970's, not in a narrowly technical fashion (though economic entomologists will find much of interest) but stressing the social, political, intellectual, and economic context of the work. He shows how the organization and professional goals of economic entomologists, the bureaucratic and political structure that supported them, and their own beliefs about humanity's place in nature affected their search for control methods. Perkins's own training in history and biology, his experience as a staff member evaluating some of this work, and his thorough research (including interviews with many of the people involved) make this an unusually detailed and sophisticated study.

"Sterile screwworm flies ready for aerial release." [From *Insects, Experts, and the Insecticide Crisis*; source, USDA/APHIS]

The book begins by presenting the background to the insecticide crisis in two chapters that discuss, respectively, the discovery and application of the discovery of the problems raised by its use. Perkins is less concerned with the environmental problems and the hazards to human health than with insect resistance and the destruction of natural enemies, and he passes over the entomologists' reactions to the relevations of *Silent Spring* and to the public attack on DDT in the late 1960's by the Environmental Defense Fund.

The second section has three chapters on the development and testing of alternatives to chemical control. There were two main methods, integrated pest management and—a name Perkins coined—total population management. The first, developed from classical biological control, used a combination of techniques to reduce pest populations to a level below that at which they would cause economic damage. It stressed the need to establish a system that would allow the farmer to live with the insect. The second, which grew out of the combination of techniques and a sophisticated understanding of insect population dynamics and behavior, had a more ambitious end—to eradicate major imported crop pests. Integrated pest management was tested against pests of several major crop systems in a study (the Huffaker project) funded by the Department of Agriculture, the Environmental Protection Agency, and the National Science Foundation—a strange assortment of bedfellows. Total population management was tested in controversial boll weevil eradication projects in the Deep South and North Carolina.

The third section, almost half the book, considers the framework in which the insecticide crisis arose and solutions were proposed—the conceptual and philosophical foundations of economic entomology and the 20-century revolution in agricultural technology and production. Two chapters deal with the dual character of economic entomology as science and technology, the generation and use of knowledge in the field, and the ideas about nature and humanity's relationship to it that affected entomologists. All this is placed in the framework of Thomas Kuhn's concept of paradigms, a word I find more confusing than enlightening. Two chapters on the changes in agriculture in the 20th century and how they affected economic entomology and entomologists bring us to a final chapter in which Perkins reviews the ways in which he has linked the research strategies of insect control specialists to the demands and ideas of the