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*Book Review*

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**Why Bother with Behavior?**

**Host-Plant Selection by Phytophagous Insects.** By E. A. Bernays and R. F. Chapman. Chapman and Hall, New York, 1994, x + 312 pp., \$25.50 (paperback), \$67.50 (hardback).

A stroll through the woods, or better still a rain forest, presents our eyes with a bewildering array of green plants. If we stop and smell some flowers, and look more carefully, we meet an equally astonishing number of insects happily eating away at these plants. Why this great diversification of plants and of insects that eat them? *Host-Plant Selection by Phytophagous Insects* addresses this fundamental question and links studies of biochemistry with neurobiology, ecology, systematics, and evolution. These studies are of great practical importance because insects feeding on plants are our chief competitors for crops.

The literature in this area is so vast that an erudite book louse would suffer indigestion and surely ask, "Why another book reviewing host-plant selection?" Bernays and Chapman address this skeptical question at the outset of their excellent book. The inattention to how insects actually behave under natural conditions is striking. Behavior of free-living individuals is central to understanding host-plant selection but has been neglected in favor of more reductionist (e.g., plant biochemistry, insect sensory physiology) or more holistic (e.g., ecology) studies. Likewise, although this point is not explicitly discussed in this book, plants too behave (see Silvertown and Gordon, 1989), which is also neglected.

*Host-Plant Selection by Phytophagous Insects* contains a detailed table of contents, a glossary, taxonomic and subject indices, and over 500 references. Citations are not provided in the text, which improves its flow. Instead, each chapter is followed by a reference section which lists citations under subject headings and, also, provides citations for further general reading. As a literary device to facilitate an introduction to this vast literature, this approach works well. Specialists, however, may find the approach frustrating, since it is occasionally difficult to identify the source for a particularly intriguing (or suspect) statement.

The general pattern of host use among phytophagous insects is that many taxa contain individuals which are relatively restricted in the kinds of plants

they eat or on which they lay eggs, while far fewer are catholic in their choice of suitable resources. In addition to taxonomic specialization, there is often specialization on different plant tissues (leaves, stems, roots, etc.). As usual in volumes on phytophagous insects, bee lovers will once again feel neglected upon learning that pollen-feeding by the more than 20,000 species of bees is not even mentioned. Contrasts between bees and other phytophagous insects would help illuminate conflicts of interest between plants and insects: A plant's self-interests conflict with those of an insect feeding on its vegetative structures, while its selfish interests are somewhat congruent with those of a pollinator because of the latter's role in the plant's reproduction. Studies of bees also fill gaps in knowledge about mechanisms. For example, the authors state that there has been relatively little critical study of color discrimination by phytophagous insects (p. 89), even though studies by C. H. Turner, and later by K. von Frisch and others, have provided much information on such capabilities in bees.

A chapter on plant chemistry is an excellent introduction to nutritional aspects of plant quality and to the astonishing array of the many thousands of plant secondary compounds already identified. There are, for example, over 15,000 terpenoids characterized so far, with attraction, deterrent, and other functions. The potential complexity of the chemical environment in which phytophagous insects live and reproduce is staggering, as is the challenge that this presents to an insect's sensory system. An entire chapter is devoted to sensory systems, since an understanding of sensory physiology and neurobiology is essential to understanding host-choice behavior, given that the observed behaviors are manifestations of underlying physiological processes.

The bulk of the book addresses behavioral mechanisms and their development, integrating information from the chapters on plant chemistry and insect sensory systems. Host choice behavior can be influenced by plant odors, size, shape, color, and texture. Plant secondary compounds can deter or attract phytophagous insects, often with imperfect correlations with plants' nutritional quality; they can poison or protect insects. An individual's behavior can be modified by recent experience which might decrease (habituation) or enhance (sensitization) responses to particular stimuli; experience can also influence behavior over longer time spans (e.g., associative learning, induction). Host selection can be modified by ecological factors such as the diversity of other plants in the habitat, the relative abundance of competing con- or heterospecifics, and parasites and predators.

Ecologists sometimes take a typological view of behavior, so a chapter on genetic variation in host selection usefully emphasizes the extensive variability seen among individuals in nature. The mechanisms underlying this variability remain to be investigated and will be important in understanding host shifts and ecological specialization.

The concluding chapter presents an overview of hypotheses which might

account for widespread specialization in phytophagous insects. Factors relevant to specialization are divided into two categories, those which enable the origin of restricted diet breadth and those which maintain narrow diets. Evidence suggests that various factors are likely to be important for at least some taxa under some conditions, but none may be generally applicable. The authors repeatedly point out areas where it will be useful to have information on patterns of evolution, although presently phylogenetic studies are rare. In the end, Bernays and Chapman return to emphasize sensory physiology and information-processing, flagging such mechanisms as the most likely candidates associated with general explanations for restricted diets. Sensory and neural mechanisms which decrease the quantity of information to be processed may be a general advantage applicable to all individuals with centralized nervous systems.

One could pick nits, and argue about certain technical points in this book, but in looking at the forest instead of at particular trees, the book is admirable, especially as an introductory volume which uses behavior to break down barriers between traditional academic disciplines. I recommend it highly, particularly for students just getting interested in the topic, to agronomists desiring an overview of the field, and to biologists who want experienced guides into an area where they normally do not travel.

#### REFERENCE

- Silvertown, J., and Gordon, D. M. (1989). A framework for plant behavior. *Annu. Rev. Ecol. Syst.* **20**: 349-366.

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