Present Issues in Behavioral Ecology

Behavioural Ecology. An Evolutionary Approach. J. R. KREBS and N. B. DAVIES, Eds. Second edition. Sinauer, Sunderland, Mass., 1984. xi, 493 pp., illus. $42; paper, $25.

Behavioral ecology is the study of "how behavior is influenced by natural selection in relation to ecological conditions" (p. ix). The first edition of this book (1978) defined the field; the second demonstrates its growth in momentum and maturity. Like its predecessor, the new edition is a collection of (15) review papers. These are state-of-the-art summaries, and the book reads more like an *Annual Reviews* volume than a basic textbook. Although the second edition covers many of the same topics as the first, it is not simply a rehash. Most of the chapters have been rewritten and updated, and the volume as a whole has been reorganized and expanded. In addition, the conceptual spotlight now focuses clearly on the use of game and optimality theory to model evolutionarily stable strategies (ESS's). The increased importance of these approaches is a frequently reiterated theme, and J. Maynard Smith's *Evolution and the Theory of Games* (1982) is the most widely cited book in this edition (as E. O. Wilson's *Sociobiology* was in the first).

The volume opens with four chapters that introduce concepts and research methodologies. In the first, T. H. Clutton-Brock and P. H. Harvey outline the use of multivariate techniques for making quantitative interspecific comparisons to study adaptation. They also discuss the formidable biological and statistical assumptions involved, dwelling on pitfalls that have trapped numerous predecessors. Then, G. A. Parker explains ESS's, including their assumptions and limitations, and provides a detailed taxonomy of game-theoretic models in behavioral ecology. His treatment emphasizes the mathematics behind ESS models and demonstrates the rapidity with which game theory has outstripped supporting data.

Next, A. Grafen discusses the uses and abuses of inclusive fitness. In his view, field workers measuring inclusive fitness should count only the offspring attributable to the efforts of a parent when unaided by relatives and only the extra young reared by relatives as a result of assistance. Grafen also dissects several recent "group selection" models (for example D. S. Wilson's) and shows that their similarities to kin selection make them less iconoclastic than their promoters claim. Finally, J. R. Krebs and R. H. McCleery review applications of optimization theory to foraging ecology and evaluate several laboratory tests of optimal foraging models. Although they conclude (p. 121) that "the fit to predictions has ranged from excellent to moderate," the artificiality of the experimental circumstances emphasizes the need for long-term naturalistic studies.

Having introduced its conceptual framework, the book proceeds to demonstrate the uses of the various modeling techniques. A diversity of topics is addressed, including optimal group size (H. R. Pulliam and T. Caraco), territory economics (N. B. Davies and A. I. Houston), life-history adaptations (H. S. Horn and D. I. Rubenstein), animal mating systems (S. L. Vehrencamp and J. W. Bradbury), and plant reproductive strategies (E. L. Charnov). These chapters highlight the issues involved in choosing among game and optimality theory models for analyzing specific problems. Additionally, they focus attention on identifying alternative behavioral "strategies" and quantifying the components of fitness within each through cost-benefit analyses. However, they also indicate the potential difficulties of gathering appropriate data in the field.

Indeed, the complexity of field testing the models sometimes overwhelms even the authors. For example, Vehrencamp and Bradbury argue that all published tests of G. H. Orians's "threshold" model for the evolution of resource-based polygyny are either misdirected or inconclusive. They recommend (p. 253) adopting "a third-generation approach [that] would measure, rank and examine correlations for all components of fitness concurrently, would adjust for the propagation of stochastic variation through nonlinear functions, and would use game theory where appropriate . . . the inclusion of genetic constraints may also be required." Later (p. 258) they admit that "no one has ever performed the kind of analysis proposed above. Perhaps, in fact, no one ever will and it is at best only a mental masturbation."

Although most of the book's authors think in terms of ESS's, several chapters do not explicitly involve modeling. Among these is L. Partridge and T. R. Halliday's synthesis of the causes and genetic consequences of nonrandom mating (for example, mate choice and assortative and frequency-dependent mating). Interestingly, they conclude that evidence of active female choice of mates is rare or nonexistent; whether this is because male-male competition is really the more important component of sexual selection or is just the more obvious awaits further investigation. Another intriguing chapter is S. J. Shettleworth's summary of the implications of behavioral ecology for learning psychology, and vice versa. After discussing the adaptive significance of various forms of learning (such as flavor aversion and imprinting), she suggests a number of as yet uninvestigated "how?" questions about learning and memory arising from optimal foraging theory (for example, how do animals assess the relative quality of food patches?) Finally, H. J. Brockmann recapitulates the phylogeny and ontogeny of social behavior in insects, and Maynard Smith outlines the advantages and disadvantages of sexual reproduction (his paper is virtually unchanged from the earlier version).

Two other chapters are interesting because of the evolution in the authors' thinking between the two editions of the book. First, S. T. Emlen discusses cooperative breeding in birds and mammals. He cites recently gathered data to bolster his prior conclusion that nonbreeding helpers-at-the-nest (or -den) augment breeders' reproduction but not their own. Why then do the auxiliaries remain? Emlen presents persuasive evidence, based on several long-term field studies, to show that in most cases helpers are offspring who have been forced to remain at home by severe ecological constraints, such as shortages of breeding habitats or prohibitive costs of leaving the group. Once possibilities for independent reproduction are restricted, Emlen argues, individuals have little choice but to salvage some phenotypic (for example, experience) or genotypic (for example, inclusive fitness) benefits by helping. In 1978, whether cooperative breeding results mainly from ecological factors or from kin selection was ardently debated; now the verdict seems clear.

Another impressive evolution is seen in Krebs and R. Dawkins's lively chapter on communication. In the first edition of the book they argued that because the reproductive interests of signalers and receivers usually differ, the entire concept of communication is antiquated since "if information is shared at all it is likely to be false information." In the new version the authors still believe that they are dealing with a "coevolutionary arms race" between "manipulators" (signalers) and "mind readers" (receivers), but now they clearly distinguish signals among genetic competitors from communication between cooperators. In the former case, Krebs and Dawkins hypothesize the evolution of exaggerated, conspicuous, repetitive (for example, ritualized) signals that are basically "dishonest." On the other hand, when individuals' reproductive interests coincide, so that manipulators benefit from having their minds read, more "honest" communication will occur. In this situation the signals will be muted and inconspicuous ("conspiratorial whispers," the authors call them), both to minimize signaling costs and to prevent eavesdropping.

Overall this volume is a clearly written, well-produced, and reasonably priced guide to the hot topics in behavioral ecology. It will make for informative reading and spirited discussion among practitioners, graduate students, and others hoping to keep up with this exciting, fast-moving field. On the other hand, the book's long-term value hinges largely on whether parameters of the various models can be measured in nature and, if so, on the correspondence between theoretical predictions and reality.

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The Invertebrate Integument

Biology of the Integument. Vol. 1, Invertebrates. J. BEREITER-HAHN, A. G. MATOLTSY, and K. SYLVIA RICHARDS, Eds. Springer-Verlag, New York, 1984. xvi, 841 pp., illus. $111.

This volume provides a comprehensive examination of the integumentary features of the major invertebrate phyla, with some review of the more limited information available on the minor phyla. For many invertebrate phyla (for example, Cnidaria, Turbellaria), the dominant feature of the integument is its transporting function. For other invertebrates, especially the Arthropoda, its salient feature is its barrier function. The integument of insects is skeleton as well as skin and serves very well in protecting the terrestrial insect from desiccation while limiting the respiratory surface (the tracheal system).

The great variety of integumental innovations among the various invertebrate phyla is covered by 45 chapters organized into 12 sections including Acoelomata (Turbellaria, Trematoda, Nemertea), Pseudocoelomata (Nematoda, Acanthocephala), Annelida, Mollusca, Arthropoda, Echinodermata, and Protochordata. The sections on the Annelida and the Mollusca are about 100 pages each; that on the Arthropoda is over 200 pages. A scientist with a special interest in one of these groups would find a detailed treatment in *Biology of the Integument*. (Porifera are omitted.)

The exclusive use of ciliated surfaces by certain invertebrate groups justifies an introductory chapter on cilia. Cilia are found at specialized sites on the external epithelium of the Ctenophora. On the other hand, the Turbellaria are characterized by an extensive ciliated epithelium. Similarly, the reader is prepared for later reference to epithelial cell interactions by an introductory chapter on intercellular junctions. Both sealing functions and gap junctions between epithelial cells appear in the Coelenterata and provide both the necessary restrictions on "leakage" and the basis for an integument that is both environmental barrier and selective transporter. These cellular interactive features are missing in the Porifera.

I found the discussions of cuticle in the various phyla to be of considerable interest. The primitive origin of cuticular coverings is emphasized by Rieger, who states that "cuticles are likely to be as old as flagellated epithelia in the Eumetazoa and are likely to be a primitive feature of the adult organization of Eumetazoa." The primitive cuticle was probably a simple surface coat of mucoproteins or mucopolysaccharides. The collagenous cuticle of the Annelida is considered in detail by Richards. There is also a careful treatment of Nematoda cuticle by Bird. The most extensive discussion of cuticle occurs in five chapters in the section on the Arthropoda. These cover the biochemistry (Hackman), structure (Neville), mechanical properties (Hillerton), molting (Gnatry and Romer), and ecological significance (Hadley) of cuticles. An additional chapter (Gilby) treats insect cuticle in relation to penetration by insecticides but does not consider the pesticides that are thought to inhibit chitin synthesis. All of this is introduced by an excellent overview of the cell biology of cuticle formation in a chapter by Locke.

Although the organization of the book is phylogenetic, the subchapter headings are detailed enough that a reader interested in such topics as sensory cells and structures on the integument or permeability and transport functions can quickly find the appropriate sections for review and comparison. Readers will be aided by a substantial list of references that covers the literature through at least 1982 as well as a detailed index of genera covered in the book.

Throughout the work there are numerous drawings, histological photos, and electron micrographs. There are few tables, and few data *per se* are provided. Nevertheless, scientists with an interest in a specific phylum or in physiological, biochemical, or structural features of invertebrate integument will find that the book is an excellent resource.

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Primordial Germ Cells

Current Problems in Germ Cell Differentiation. A. MCLAREN and C. C. WYLIE, Eds. Cambridge University Press, New York, 1983. x, 401 pp., illus. $79.50. From a symposium, London, Sept. 1982.

This book emerges from the seventh international symposium of the British Society for Developmental Biology. It contains 19 contributions that evaluate some of the major research involving primordial germ cells and animal eggs; the species covered include representatives of amphibians, insects, birds, and mammals.

The book is divided into six parts. In the first part, Mahowald and Boswell, Smith *et al.*, and Eddy and Hahnel analyze the nature of the evidence that primordial germ cells are determined through the action of cytoplasmic molecules. The authors go back and wrestle with dogma from the older literature. The papers are lucid and scholarly reviews of a fascinating subject that has not been critically assessed in recent years.