Explaining an Evolutionary Success

Diversity of Insect Faunas. Papers from a symposium, London, Sept. 1977. L. A. MOUND and N. WALOFF, Eds. Published for the Royal Entomological Society by Blackwell, Oxford, 1979 (U.S. distributor, Halsted [Wiley], New York). x, 204 pp., illus. $37.50. Symposia of the Royal Entomological Society of London, No. 9.

Over 70 percent of the animal species on Earth are insects. Explaining why insects exist in such prodigious variety is an ideal theme for a symposium because it requires us to view things across established lines of investigation. This task is well accomplished in this volume; the 12 contributions sift and blend material from several disciplines, a process that leads them to highlight productive questions that have been generally overlooked.

T. R. E. Southwood provides the conceptual scheme that pulls together many of the themes developed by the other contributors. Briefly, he concludes that the diversity of insects is fostered by a combination of attributes (small size, metamorphosis, and flight) that permit them to subdivide the environment finely and to link small evolutionary opportunities, "fractional niches," into viable ways of life. This is a constructive way to frame the problem because it focuses attention on broad trends relating the most general characteristics of insects to basic features of the environment (for example the seasonality and architectural complexity of habitats).

The ability to undergo complete metamorphosis is one of the most obvious attributes associated with insect diversity. By passing through a pupal stage, holometabolous insects (which represent 88 percent of the species) are able to uncouple adaptations associated with growth from those employed in dispersal and reproduction. This permits them to "assemble" a niche by exploiting different resources which, taken alone, might be insufficient to support an entire generation. The significance of this route to diversification is reflected in the results of Evans and Murdoch (*J. Anim. Ecol.* **37**, 259 [1968]), who found that 75 percent of the insect species living in an old field switch food habits during development. The entomological literature is rich with examples that illustrate how different life stages enable insects to specialize on resources that are widely scattered or occur for brief periods. Considering the importance of metamorphosis to the central theme of this symposium, it is surprising that only Southwood treats the topic in any detail.

The role of size in promoting diversity receives more thorough attention. By virtue of their small size, insects generally have a high capacity for population increase. R. M. May reviews several hypotheses that link population growth potential with evolutionary rates and the ability to adopt fugitive life-styles. He concludes, however, that these are not significant factors for explaining the diversity of insects relative to other taxa. Instead he argues that small size simply permits insects to partition a given resource more finely than larger animals. This view is supported by Southwood's demonstration of a direct relationship between body size and the area over which insects move while feeding.

Small size and metamorphosis are not sufficient explanations for insect diversity because these attributes are shared with other taxa (for example many marine invertebrates, parasitic worms). This leads to the suspicion that vascular plants, which form the basis of complex food webs involving insects, might provide the missing ingredient. Much of the recent writing on this topic has stressed that diversity arises as a result of coevolution; insects specialize to override the herbivore defenses of their host plants. The simplest coevolutionary model predicts a direct correlation between the diversity of insects and plants. The reviews by R. I. Vane-Wright on butterflies, V. F. Eastop on Homoptera, and O. Halkka on spittlebugs illustrate that such a relationship is frequently obscured by historical, biogeographical, and local environmental factors. Furthermore, as a result of our preoccupation with plant defenses, we have tended to overlook other attributes that might promote diversity. One of the most obvious is the complex architecture of vascular plants, which creates many microhabitats that can be exploited by small animals. This neglected theme is nicely developed by Southwood and J. H. Lawton. Similarly, a novel hypothesis is advanced by W. D. Hamilton suggesting that the microenvironment under tree bark fostered the divergence of several major insect taxa.

The most thoughtful discussions of how insects partition resources naturally lead to a deeper, but unresolved, issue: to what extent does the diversity of insects reflect a superior ability to utilize the evolutionary opportunities available to them? Several lines of evidence bearing on this question are presented. G. R. Coope reviews recent research on Quaternary fossils to suggest that, contrary to common belief, glaciations did not cause widespread species formation and extinction among insects. The great geological longevity of many present-day species, taken together with fossil evidence demonstrating their capacity to shift their ranges great distances, implies that there has been a long association between most insects and their resources. Furthermore, Southwood notes that the combination of small size and flight frequently results in insects' blundering onto a new resource. This circumstance promotes faunal mixing and provides opportunity for frequent evolutionary testing.

Several papers are not concerned with explaining the species-rich status of insects but focus, instead, on the processes that determine local patterns of diversity. Generally, it appears that species diversity increases according to some measure of the resource "target" such as the size of the habitat patch (D. S. Simberloff, Lawton) or host density (L. E. Gilbert and J. T. Smiley). The number of insect species associated with particular plants is shown by Lawton to increase as a function of the host's geographical range; the interesting question of whether this circumstance leads to more complete saturation of a local resource, however, remains unresolved. Simberloff's cautious report of similarities in the trophic structure of the faunas associated with mangroves in different regions and Lawton's observation that the guild spectrum on bracken fern remains relatively constant despite changes in species composition suggest that insect communities are organized in some way. The role biotic factors play in producing such organization, however, remains as obscure as ever. For instance, traditional competition theory, with its focus on limiting similarities along ordered niche

axes, makes little sense when applied to phytophagous insects where the niche "units" appear to be plant tissues interconnected by the host's translocation system. The authors are unanimously aware of such difficulties and call for more critical data detailing species interactions.

Descriptive natural history has become somewhat passé of late. Yet the reach of the most interesting conclusions drawn in this symposium is limited by the lack of comparative data on such mundane matters as the size, food habits, and dispersal capacity of insects in particular habitats. One of the greatest achievements of this stimulating volume is its demonstration of how theory, experiment, and observation combine to form a context from which natural history can draw renewed vitality.

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Comparative Studies

Contrasts in Behavior. Adaptations in the Aquatic and Terrestrial Environments. ERNST S. REESE and FREDERICK J. LIGHTER, Eds. Wiley-Interscience, New York, 1979. xiv, 406 pp., illus. $27.50.

The diversity of coral-reef fishes and the complexity of the social, ecological, and physical environment they inhabit have stimulated widespread interest in their biology over the last decade. Behaviorists and ecologists, especially, are drawn to the reef, with the result that coral-reef fishes are beginning to rival songbirds as research subjects. *Contrasts in Behavior* testifies to this surge in interest. All but one of the 12 contributions deal wholly or largely with reef-dwelling fishes, each reviewing a different aspect of their biology and contrasting their behavior with that of terrestrial animals (mainly vertebrates). As reviews and in drawing contrasts, the papers vary widely in utility and depth. The best, Warner's treatment of hermaphroditism and unisexuality, discusses the occurrence of such modes of sexuality in animals and then speculates on the factors that permit their expression in some groups, such as reef fishes, but not in others, such as the "higher" vertebrates. Miller's review of agonism and Hobson's of aggregation are also well done and draw useful comparisons between various animal groups. A few of the papers in the book consist mainly of previously unpublished data and include only superficial comparisons with the behavior of terrestrial vertebrates; such papers are of interest and value but clearly belong in a refereed journal where their contents are subject to critical review before publication. Other contributions are dated, largely, one suspects, as a result of the long time lag (almost four years) between the symposium upon which the book is based and its publication. Keenleyside's discussion of parental care in birds and fishes, for example, was stimulating a few years ago but has been rendered superficial by theoretical treatments of such care by Maynard Smith, Williams, Dawkins, and others. Finally, the logic of a few papers is questionable. Loiselle and Barlow's "Do fishes lek like birds?" is an excellent review of lekking (the aggregation of territorial males at traditional courting grounds for the sole purpose of displaying to, and mating with, attracted females) but largely ignores the first half of the question—"do fishes lek?"—in favor of the last—"like birds." Although the term is widely used in the fish literature (two other authors in the book use it, for example), Loiselle and Barlow's paper would be stronger if it began with a more critical examination of whether an aggregation of males competing for the best position to launch pelagic gametes is truly comparable to an avian lek (a comparison seemingly analogous to that between individuals aggregating around a food source and those regularly spaced about one another in a school or flock). The proximate factors that result in such aggregations seem very different. One is therefore suspicious of any analysis that treats them as variations of a single phenomenon.

Though valuable as reviews, most of the papers in *Contrasts in Behavior* do not measure up to the editors' stated objective—the generation of useful insight into the universal "principles" of behavior. Although the expectation is raised that workers in one area will use secondary literature (reviews and the like) in others to generate such insight, the most successful contrasts are drawn by authors clearly familiar with the primary literature. Most of the other comparisons made between aquatic and terrestrial systems lack depth. Harmelin-Vivien's statement, for example, that herbivores forage both day and night in a terrestrial system (the African savannah) but only during the day on the reef could have been made only in ignorance of the numerous and well-studied invertebrates that forage over the reef at night and are an important component of the reef ecosystem. The editors should have been more demanding of such authors and, by eliminating such superficial comparisons, strengthened an otherwise stimulating and meritorious book.

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Brain Biochemistry

Cyclic Nucleotides, Phosphorylated Proteins, and Neuronal Function. PAUL GREENGARD. Raven, New York, 1978. x, 124 pp., illus. $12. Distinguished Lecture Series of the Society of General Physiologists, vol. 1.

One of the major themes of the rapidly expanding field of neuroscience is the role of cyclic nucleotides as mediators of neurotransmitter action. A most important current question has to do with the mechanism whereby the regulation of cyclic nucleotide formation by extracellular transmitter substances is translated into the diverse biological responses of target cells. This short volume outlines Greengard's approach to this question. While recognizing alternative hypotheses and the results of others, he describes the work from his own laboratory, which supports the hypothesis that cyclic nucleotides act primarily by activating protein kinases that specifically phosphorylate proteins. This suggests that the specificity of the effects of cyclic nucleotides is primarily dependent upon the substrate specificity of the activated protein kinases. Evidence is presented for a much wider role for phosphorylated proteins. Greengard proposes that the protein kinase mechanism provides the final common pathway for the expression of the specificity of a variety of agents in addition to the cyclic nucleotides, including steroid hormones and calcium.

The book has many carefully simplified outlines of the criteria for the evidence presented. For example, table 1 presents some criteria for evidence about one of the most current and important concerns in neuroscience—the mediation by a cyclic nucleotide of a postsynaptic permeability change. Selected examples are then described for neurotransmitter-sensitive adenylate cyclases in the nervous system for dopamine, serotonin, histamine, and norepinephrine. In each case the criteria mentioned