An Exuberance of Life

Plant-Animal Interactions. Evolutionary Ecology in Tropical and Temperate Regions. PETER W. PRICE, THOMAS M. LEWINSOHN, G. WILSON FERNANDES, and WOODRUFF W. BENSON, Eds. Wiley-Interscience, New York, 1991. xvi, 639 pp., illus. $125. From a symposium, Campinas, Brazil, 1988.

It was the sheer diversity of tropical species that fired the imaginations of Darwin and Wallace, and it was the diversity of interactions between those species that delighted and challenged the first evolutionary naturalists. Bates, Müller, Belt, and a few other 19th-century tropical naturalists observed carefully and thought deeply about the ways in which the lives of tropical species are linked through their interactions. Their studies gave us Batesian mimicry, Müllerian mimicry, and Beltian bodies. Those promising beginnings, however, fizzled in the early decades of the 20th century as animal and plant ecology developed in separate ways. With few exceptions, the new academic ecologists turned their attention to nonevolutionary description of temperate communities. Not until the 1960s did more than a handful of ecologists and naturalists give consideration to species interactions in the tropics.

In the introduction to this collection of 27 chapters by 49 authors, the editors credit this change in the 1960s to the development of the Smithsonian Tropical Research Institute in Panama and the Organization of Tropical Studies, which was developed by a group of North American universities to promote field courses in Costa Rica. To this list I would add the publication in the mid- to late 1960s of Daniel Janzen's landmark studies on coevolution of ants and acacias, which showed how the intricate relationships between species could be studied experimentally in the field. The 1960s and early 1970s were years in which evolutionary ecology, coevolution, and patterns in species diversity began to become major themes in ecological research. These subjects have turned out to be enduring concerns, making ecology now a very different science from what it was during the first two-thirds of this century.

These chapters build upon these unifying themes, probing them through studies of a wide range of plant-animal interactions. What is particularly satisfying is that most of the chapters have something new to say: new ideas, new data, or new compilations of results that point to ecological and evolutionary patterns. Most of the chapters concentrate on natural communities, but the book ends with a group of chapters discussing plant-insect interactions in agro-ecosystems. There is so much new natural history to absorb in these chapters that it is easy simply to revel in the marvelous diversity and complexity of it all, but in most chapters the major themes come through. In a few others, however, I had to work hard to separate the take-home message from the details.

A group of chapters grapples with the differences between tropical and temperate communities, suggesting patterns and hypotheses to explain the differences. Some of the suggested patterns are that tropical trees suffer higher rates of herbivory and more commonly produce alkaloids than temperate trees, tropical plant families more commonly have extrafloral nectaries than cosmopolitan or temperate families, and gall-making insects are more common in xeric than in mesic habitats in both tropical and temperate communities. The concern in most of these chapters on tropical-temperate differences is with understanding why different life-styles or defenses are favored in different environments.

A second major theme that weaves through many of the chapters is the evolution of specificity in plant-feeding species. This is a central theme in ecology because it links questions on the evolution of species diversity with questions on evolving interactions, coevolution, and community organization. Much of animal diversity appears to be a result of specialization on particular plant species. Some of the authors ask how patterns in the evolution of specialization are affected by plant chemistry, body size, mode of interaction, available genetic variation, and host abundance, size, and phenology. Moreover, some chapters provide a strong phylogenetic perspective to the evolution of host specificity, reflecting the increasing links between evolutionary ecology and systematics. Evident in most chapters on phytophagous insect and plant defenses is a move away from plant allelochemicals as the overriding determinant of patterns in host use. Plant chemistry becomes instead one of the constraints on the direction of host shifts within clades of insects, with other ecological pressures determining the degree of host specificity within local populations.

The level of specificity determines to some extent the kinds of coevolution that occur. Interactions between leaf-feeding insects and plants differ in specificity and in other fundamental ways from those between ants and plants, frugivores and fruits, and pollinators and flowers. As a result, the authors of these chapters differ in their views about the processes, outcomes, and scale of coevolution. These differences illustrate how important it is for us to study the ecological conditions that favor different forms of coevolution, rather than try to shoehorn our expectations simply into specific or diffuse coevolution.

The book is biased toward plant-insect interactions, but so is nature. Nonetheless, there are some obvious omissions of interactions that are equally important in the organization of communities. These include interactions between plants and pollinators (other than butterflies), plants and mammalian folivores (other than grazing ungulates) and frugivores, and plants and seed predators.

Altogether these chapters give a breathtaking view of the diversity of plant-animal interactions and some of the ecological and evolutionary patterns that have emerged in recent years. (Hence it is a shame that the publisher so horribly misjudged the potential audience for this book in pricing it beyond the budgets of most individuals.) I doubt that there is any evolutionary ecologist who would not learn something new and useful here. Read it and revel in the search for patterns within the "entangled bank."

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New Immigrants

The "African" Honey Bee. MARLA SPIVAK, DAVID J. C. FLETCHER, and MICHAEL D. BREED, Eds. Westview, Boulder, CO, 1991. viii, 435 pp., illus. $55. Westview Studies in Insect Biology.

The publication of *The "African" Honey Bee* comes at an opportune time. These feisty bees, which have been spreading across South and Central America since their introduction to Brazil in 1956, are now entering the United States. The book is

described by its editors as the first review of the scientific literature on the Africanized honey bee; contributors summarize current research on "African" bee identification, ecology, defensive behavior, and population expansion. Although a major book on "African" bees—*Africanized Honey Bees and Bee Mites*, edited by G. R. Needham *et al.* (Horwood)—was published in 1988, enough progress has been made to warrant a new book on this controversial subject.

The first "African" bee controversy, summarized neatly by Fletcher, pitted the view that "African" bees are hybrids of European and African subspecies of *Apis mellifera* against the view that feral "African" bees retain behavioral and morphological characters of their African ancestors, largely unaffected by hybridization. Partisans of the former view preferred the term "Africanized" for both the feral population and the hybridized apiary populations, whereas partisans of the latter preferred to call the feral population "African" or "neotropical African" to distinguish it from the clearly hybrid or "Africanized" populations found in apiaries. The editors' use of "African" in the title of this book is an attempt to take an impartial stand on this point.

Many papers in the 1988 volume were devoted to the development of morphological, genetic, and other markers for "African" bee identification and detection of gene flow between "African" and European bees (elegantly summarized by Daly). Subsequent genetic studies using allozymes and nuclear and mitochondrial DNA markers (reviewed by Hall) have shown that the feral population, at least in tropical regions, retains a high frequency of African genetic markers. Thus in the new volume many of the papers on the spread of "African" bees start from the premise that the feral "African" population is to some degree genetically distinct from European apiary populations, although enough difference of opinion is still present to give some of the flavor of the original controversy. Much more emphasis is placed on studies of the natural history, ecology, and behavior of the feral "African" population. Chapters by Winston and Otis on population dynamics and by Roubik on ecology and interaction with native bee species are particularly good, as they are based on careful, long-term field studies.

How is a high frequency of African markers maintained in the feral "African" population? One hypothesis is that mating takes place freely between European and "African" bees, and in both directions ("African" drones to European queens, European drones to "African" queens), followed by selection reducing the European genetic input to the feral "African" population. Another hypothesis is that there are mating barriers reducing effective gene flow from the European to the "African" population. These hypotheses are not mutually exclusive, and they are examined, along with other aspects of the spread of "African" bees, in chapters by Fletcher, Rinderer and Hellmich, Ratnieks, and Spivak.

What effect will "African" bees have on the general public and on beekeeping in North America? Several chapters discuss defensive behavior (stinging) and present practical information on queen-rearing and methods of selection for desirable traits. In general, these chapters reflect a shift in emphasis away from keeping "African" bees out of North America and toward learning how to manage them. Several chapters that present the varied experiences of researchers and beekeepers in South America are a particularly valuable feature. Many South and Central American studies of "African" bees have not been published in English and have largely been ignored by North American biologists.

One minor shortcoming lies in what is missing from the South American literature. The editors mention that there is still uncertainty concerning the events that took place within the first few years of the introduction of *A. m. scutellata* to Brazil. These questions, involving the origins and effective size of the founding population and the extent to which early spread of the "African" bees was human-assisted, are important in understanding how invading populations became established and evolved. For example, Fletcher's provocative suggestion that undesirable traits of the neotropical "African" bees could be ameliorated by importation of additional *A. m. scutellata* with more docile temperaments would gain support if it were demonstrated that the neotropical population was derived from a very small sample of southern African genetic diversity.

In general, *The "African" Honey Bee* is an excellent book for those actively involved in honey bee research and for others who want a current and balanced picture of progress in a field that, as the editors say, "has often been clouded by emotions." In fact, one fascinating chapter in this story is yet to be written—a study of the personalities and social interactions of biologists studying the "African" bees.

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Venezuelan beekeepers removing honey-laden superhives. Many Venezuelan beekeepers remove "Africanized" bees from the supers by smoking and then shaking or brushing the supers, but as many bees may enter the supers as leave, especially when the bees become agitated; hence a preferred method, shown here, is the use of bee blowers. Because Africanized bees have a tendency to scatter honey stores and often swarm before enough honey is capped for harvesting, beekeepers restrict comb space by providing only one super at a time and visit apiaries two to three times as often as is necessary with European bees. [From Hellmich and Rinderer's chapter in *The "African" Honey Bee*]