HOW NOT TO BE EATEN: THE BIOLOGY AND CHEMISTRY OF ARTHROPOD DEFENSES


Key words: arthropod defenses; chemical ecology; insects; prey-predator interactions.

The study of arthropod defenses has provided us with evidence for evolution and natural selection, been important in our understanding of prey-predator interactions, and given us wonderful examples of interactions among trophic levels. The world of arthropod defenses is delightfully introduced in this new book co-authored by one of the experts in the field, Tom Eisner, and two colleagues, his wife, Maria Eisner, and Melody Siegler. This volume is a series of fascinating vignettes (69 in all) about the multitudinous defenses used by arthropods, ranging from a variety of defensive sprays and secretions, to barbed hairs, to stings and venoms, to cryptic coloration. While the concentration is certainly on chemical defenses, there are others included as well, such as the “spittle” of spittle bugs, the trash heaps that lacewing larvae pile on their backs, and the click of the click beetle.

The authors write in an engaging and very readable style, making the sometimes complex anatomy and chemistry accessible to all those interested in behavior, ecology, chemistry, and evolution, whether from a professional or a personal perspective. The fascinating biology and chemistry of these animals provide examples that can be used to excite students about science at many levels.

As the authors acknowledge in the prologue, there had to be some limitations to the book. Therefore, they have drawn primarily, although certainly not exclusively, from their own research. Given the impressive volume of papers about arthropod defenses produced by Eisner and his co-workers, this seems appropriate. In addition, the examples are drawn mostly from North America. These limitations, however, do not in any way reduce the value or enjoyment of the book.

The chapters are organized taxonomically, with the first 12 about defenses of non-insect arthropods—spiders, centipedes, and millipedes, and the rest about the many kinds of insect defenses. Each chapter is devoted to a single species, and for each species, the classification, scientific name, and common name are provided. Where chemical compounds are involved, their structures are given and the chemistry explained. Each chapter is also illustrated with the superb photographs that always characterize Eisner’s work. They show the species being discussed and the anatomy of defensive glands or hairs, or other relevant anatomical structures. In some cases, there are photos of the defense in action. In general the photographs are excellent; my only quibble is that I would have liked many of them to be a good deal larger. At the end of each chapter is a list of very helpful references that serve to lead the reader deeper into the literature on a particular species and its defenses.

Some of the examples of arthropod defenses presented are the more familiar ones: the sting of the honeybee, the unpalatability of the monarch butterfly, and the spray of the bombardier beetle. Others are less familiar, such as the chemical defenses of millipedes, the recycling of the chemical defense of the prey by predators of cochineal insects, or the nuptial gift of the protective chemical cantharidin presented to females in a specialized cleft in the head of the male fire-colored beetle. Even for those who consider themselves knowledgeable in the fields of chemical ecology or arthropod defenses, there will be some new and fascinating stories. There have been articles published about all the examples presented here, but it is wonderful to have them in a single resource, complete with natural history, photographs, chemistry, and a set of references to allow the reader to delve deeper into a particular topic.

The book also includes a particularly beguiling epilogue, providing information about how to become a student of arthropod defenses and some of the fascinating questions that remain to be answered in this field. There is also an appendix about how to study arthropods, including the kinds of equipment that are required. These are both written in a way that truly encourages students to take up this fascinating field.

In sum, this was a thoroughly delightful introduction into the fascinating world of arthropod defenses. It was designed for a broad audience: for “…all those to whom nature has never ceased to be a source of wonder,” and it certainly fulfills that goal. “Secret weapons” brings together the fields of natural history, chemistry, behavior, ecology, and evolution and has appeal for professional scientists, students, and anyone fascinated with the natural world. This volume will be a wonderful resource for many years to come.

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**Key words:** community ecology; dispersal; metapopulation dynamics; spatial ecology; species interactions.

Understanding the dynamics of multispecies communities has traditionally been the purview of community ecology and food web theory. But in those fields the emphasis is largely on the processes that govern the stability, composition, and relative abundance of species within a single community with little consideration of interactions between communities. The developing field of metacommunity ecology attempts to fill the gaps in our understanding of the influence of intercommunity interactions. The view of metacommunity ecologists is that the organization and dynamics of species communities arise from the reciprocal influence of local and regional processes. According to this view, to understand the properties of a given community one must consider not only the environmental conditions and species interactions that occur locally but also the processes that connect the community to other communities near and far. This book attempts to articulate this multi-scale perspective by synthesizing the concepts and models developed within the fields of community ecology, metapopulation biology, island biogeography, and food web theory. Synthesis is a journey whose end is unification. What metacommunity theory seeks to unify is our understanding of the mechanisms and processes that determine species persistence, coexistence, and spatial distribution in communities.

This book reviews the theoretical heritage of metacommunity ecology, summarizes the current state of the field, and proposes a framework for tackling the difficult task of unification. It is a collaborative effort initiated during a symposium on metacommunities held at the 2001 annual meeting of the Ecological Society of America and later continued by the Metacommunity Working Group at the National Center for Ecological Analysis and Synthesis. In addition to the three editors, 30 people contributed to the volume. The topics range from modeling and theory to the results of empirical studies. The intended audience includes graduate students and researchers in theoretical and applied ecology.

The book is organized into 20 chapters arranged in four sections that address conventional themes. The introductory chapters are devoted to explaining key terms, describing essential concepts, and explicating the metacommunity viewpoint. The “Core concepts” chapters describe foundational issues such as the opposing influence of species sorting and mass effects. The book reviews spatially implicit and explicit two-species models, consumer-resource interactions in multi-species, multi-trophic food webs, and the relevant literature. Much of the information presented here is not new and can be found elsewhere. But students and researchers will be delighted to find material of such breadth organized and summarized in a single volume. Topics addressed in the “Empirical perspectives” section include an interesting discussion of the multitrrophic interactions of butterfly metacommunities, the influence of local and regional processes on pitcher plant communities, two experimental studies that focus on the effects of habitat fragmentation (one on invertebrate communities that inhabit bryophytes, the other on beetle metacommunities in a eucalyptus-pine mosaic), and two chapters that examine the effect of environmental heterogeneity on zooplankton species patterns (one using shallow ponds in Belgium, the other using small rock pools in Jamaica). While the chapters in this section are intended to highlight recent empirical results, they just as importantly contribute interesting hypotheses that both complement and broaden the concepts discussed in other sections of the book. The empirical chapters, while a bit of a hodge-podge, reveal that central themes are beginning to emerge that give shape to the metacommunity perspective. For example, it is a natural choice for examining the effects of habitat fragmentation on species diversity.

Early on, the book attempts to show that metacommunity ecology is a logical extension of the fields of community ecology, metapopulation biology, etc. This view is reinforced by the many tables, charts, and discussions presented throughout the book that draw connections across the literature and trace the theoretical development of each field. This deliberate attempt to find common ground imparts thematic cohesiveness and direction to the book, strengthening its message. It also enhances the book’s pedagogical value and usefulness as a reference. However, ecologists disagree on what constitutes the principal structuring forces of community organization, and any attempt at synthesis must address this dissent. The editors do recognize this disparity, which they describe as competing frameworks that emphasize different mechanisms for community patterns. These are identified as the patch-dynamic perspective, the species-sorting perspective, the mass effects perspective, and the neutral perspective. But while the editors explain the differences among the perspectives, they stop short of suggesting how they might be reconciled toward the goal of synthesis. The incoherence of the four competing hypotheses remains the biggest obstacle to building a comprehensive theory of metacommunity dynamics. Given the collaborative nature of the work here, I was surprised that it omits a plan for tackling this central problem. Some aspects of the problem are taken up later in the book (e.g., Chapter 10), but I was disappointed that the editors chose to blithely side-step the issue.

Chapters 10–19 wrestle with other theoretical and conceptual issues that remain tough challenges for unification. Topics include an excellent review and assessment of source-sink dynamics and competition-colonization trade-offs, and a graph-based model of assembly dynamics that addresses the multi-scale nature of metacommunities. Two chapters (12 and 13) are devoted to scale transition theory which attempts to formalize the relationship between local nonlinear dynamics and spatial averaging which becomes important at regional scales. Here, species coexistence at the metacommunity scale is governed by the interaction between spatial variance and covariance in species densities across communities with local scale interactions and population dynamics within communities. The upshot is that spatial variation can disrupt the mean-field community patterns that would arise by simple averaging in the absence of spatial heterogeneity. The chapter on scale transition theory is one of the highlights of the book. I found it to be an exceptionally well-written and accessible presentation of this important topic.

At 513 pages, the book is heftier than similar review-and-synthesize books. I found the construction of the paperback volume to be solid. The pages are off-white, smooth but not glossy. I noted a few errors (e.g., it is clear from the caption that Figure 2.1 is turned 90 degrees from its correct orientation). The material is clearly presented and the quality
of writing is generally high. In its liberal use of tables and diagrams, the book serves as an excellent introduction to the foundational concepts and theoretical lineage of metacommunity theory. It certainly is an excellent choice for a graduate seminar, although it would be difficult to cover in its entirety, given the duration of a single semester.

This work is not the first attempt to unify ecology under the banner of spatial scale and process. But five years ago Stephen Hubbell created quite a stir with his ambitiously titled monograph The unified neutral theory of biodiversity and biogeography (2001, Princeton University Press, Princeton, New Jersey). Hubbell’s singular focus on the explanatory power of neutral dynamics made his theory the target of much criticism. It’s a good bet that the present volume will also have its critics. The difference here is that the contributors do not introduce a new theory so much as co-opt several different research areas into a single topic. Metapopulation biology, community ecology, food web theory, and island biogeography often reach different conclusions about which processes impart structure to species communities. The overarching view expressed in this book is that understanding multi-scale, multi-species spatial dynamics is the key to reconciling these different perspectives. Without a recognizable plan, this sanguine outlook seems to overlook the enormity of the undertaking. Some ecologists may therefore be skeptical of the notion that such disparate models and theories can be neatly subsumed under the banner of metacommunity ecology. Controversy may ensue, but controversy is generally good for progress in science. This book is certain to stimulate discussion about whether and how ecologists ought to go about searching for a unified theory.

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**WEE GUPPIES PACK AN EVOLUTIONARY PUNCH**

The monograph begins with a lay of the land (Chapters 1 and 2), describing in detail the scene (the Trinidad river system) and the players (guppies, their predators, other community members, and the physical environment) that constitute a veritable natural research laboratory. Magurran’s enthusiasm for Trinidad’s yet untapped empirical cache is evident throughout the book but tempered with realistic perspectives on the limitations of field research and the potential impacts of ever-expanding exploratory traffic into the area (Chapters 7 and 8). The balance of the monograph relies heavily on the groundwork laid down in Chapter 3, which provides an overview of the guppy’s arsenal of anti-predator and shoaling behavior, recapitulates variation in predation risk among Trinidadian streams, and reveals some of the phenotypic consequences of variable predation pressure. Chapter 4 tackles some of the less mainstream, and poorly understood aspects of reproduction and mating systems in *P. reticulata*, including empirically driven, insightful commentaries on male mate choice, the ramifications of multiple mating (for males and females), and cryptic female choice. In the next chapter (Chapter 5), it becomes abundantly clear that predation pressure has left an indelible, genetically encoded mark on guppy life history traits. From the reader’s perspective, it is difficult at this point not to earmark the consequences of variable predation risk as the dominant knitting of guppy evolutionary ecology research. “Crenicichla site” and “Rivulus site” should be engraved in long-term memory. But should all roads lead to predation? On the one hand, I enjoyed being immersed in Magurran’s comprehensive yet concise accounts of this fascinating area of guppy research. On the other hand, it was a bit frustrating to find that I couldn’t escape reference to predators, even when there was promise for understanding how primary productivity, invertebrate biomass, canopy cover, or the social milieu might influence the evolution of divergent phenotypes existing among streams and/or the expression of labile phenotypic characters. As an outsider looking in, this predation-centric view is, indeed, productive and quite exciting. But, in the same breath, I applaud Magurran’s underscoring, despite the paucity of replicated data, the potential for other
factors to operate alongside voracious pike cichlids, rivulids, and prawns.

“Evolution of reproductive isolation” (Chapter 6) was invigorating, as a forward-looking analysis pitting evidence for putative reproductive isolation mechanisms against pre-ventative measures (e.g., sexual coercion) inherent in the behavior or biogeography of Trinidadian guppies. Will speciation occur among genetically divergent guppy populations? Stay tuned. In Chapter 7, Magurran reflects on some of the perils facing the Trinidadian ecosystem, the natural experiment in which guppies have assumed a starring role, and provides some solutions particularly with respect to coordinating scientific efforts towards the end of minimal impact.

Without reservation, the first seven chapters supply an authoritative view of the guppy’s prominent place in evolutionary ecology research. The organization of text within chapters and the descriptions of lavish phenotypic variation within the guppy system, however, sometimes made it difficult to discern the focal level of variation. There are phenotypic differences among individuals of different populations, among individuals within a population, and within a single individual in space and time. Unfortunately, these disparate levels of variation are not delineated with as much care as the forces underlying phenotypic diversity (e.g., predation). Magurran cites a fair number of convincing examples of relatively rapid divergence in genetically encoded traits (e.g., color pattern). But with some early examples of behavioral or life history trait variation (e.g., courtship, brood size), the reader is left to ruminate (until page 97) about whether consensus has been established regarding the extent to which selection has favored phenotypic flexibility or the particular trait (or suite of traits) in question.

The closing chapter identifies fruitful areas for future investigation, which complement the innovative perspectives and challenging questions that Magurran provides throughout the text. Indeed, I found this to be one of the strengths of Evolutionary ecology: the Trinidadian guppy. That is, there are an abundance of heretofore untouched, or understudied topics revealed by Magurran on at least fifteen pages of text (in addition to Chapter 8) that are ripe for the picking. Headlining Magurran’s “Future directions” section is some excitement about emerging genomic resources, which are of great import for discovering possible genetic underpinnings of phenotypic variation. An area that has been neglected by guppy researchers, save a handful of studies on endocrine disruptors, is the quest to understand the neuroendocrine basis for phenotypic variation. Implementation of non-invasive techniques for steroid hormone sampling in small fishes, and continued improvement of neurobiological assays could facilitate the identification of important neuroendocrine targets. Expression or synthesis of these target molecules (e.g., hormones or neuropeptides) might covary with or be causally linked to population differences in behavior, reproduction, or immunological competence. Incorporating these intermediate molecular assays—downstream of genes and upstream of the trait—is compatible with a more global and integrative understanding of guppy evolutionary ecology. With that said, Magurran’s monograph is an excellent resource, and should find a not-so-sedentary home on the bookshelves of any student interested in pursuing the guppy, or poeciliids generally, as a model system.

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PLANT–POLLINATOR INTERACTIONS: WHAT ARE THEY TELLING US ABOUT COMMUNITY ASSEMBLY, CONSERVATION, AND ECOSYSTEM MANAGEMENT?


Key words: community structure; generalist; neutral; niche; specialist.

The concept of pollination and the diversity of strategies plants employ to attract pollinators are among the most fascinating facets of nature that can capture the imagination, even of a child. This sense of wonder is especially well conveyed in the historical perspective of this book (Chapter 1). From this chapter one feels that the studies on plant–pollinator interactions bridge the gap between natural history and synthetic studies that use large datasets. This marriage of approaches can test old ideas rigorously: are flowers with specialized structures visited exclusively by specialists? Current large data sets tell us that plants offering poor, nonfood floral resources are rather specialized, but their visitors are usually generalist pollinators. At the same time, the majority of floral visitors are rare and tend to be specialized on abundant, generalized plant species offering copious rewards.

I read the book with the aim of detecting a unifying framework, not only in the plant–pollinator interactions, but also in any kind of ecological interactions. After reading the book, I think that this framework is starting to be developed, and niche-neutral community assembly models linking ecology and evolution could capture the background of most chapters of the book. Of course, we still lack a framework where we could test the available data on specialization and generalization with the output from niche-neutral models. However, this book helps us explore new questions such as the following. How are highly specialized organisms embedded in large networks of interacting species and communities? Are there specific pollination syndromes in morphological structures? Are floral structures independent of specific pollinators? Are general structures adapted to the broadest niche? Are pollinator
structures independent of floral morphology? Are communities neutral or niche assembled?

Paul Aigner’s Chapter 2 helps illuminate the previous questions. He explores fine-grained environment models, which imply multiple pollination types interacting with each plant’s floral morphology. Aigner discusses Lem’s Paradox, a situation in which the phenotype of a species seems specialized but the behavior of the species is generalized. So species that appear highly specialized on the basis of their phenotype also sometimes act as ecological generalists. One message from Aigner’s chapter is that there are intriguing similarities between pollinators and the cichlid fish fauna. He suggests a new way to look at trade-offs, which form the basis for understanding the niche or neutral selection and evolution of species in large and complex communities. In other words, do equivalent mutualist and competitive abilities at the individual level predict community patterns?

Paul Wilson and colleagues (Chapter 3), and James H. Cane and Sedonia Sipes (Chapter 5) focus on flower specialization by bees (both chapters) and bees and hummingbirds (Chapter 3). These chapters contrast with the previous one in one important aspect: Aigner remarked on the possibility of finding adaptations to relatively uncommon or ineffective pollinators when there is no sacrifice in the ability to use more common and effective ones. New questions arose to me as a consequence of the previous chapters: Does floral specialization appear to respond more to common or uncommon pollinator groups? Does floral specialization imply trade-offs? Does floral specialization limit the number of visitors?

Robert L. Minkley and T’ai H. Roulston (Chapter 4) suggest that in order to understand the evolutionary dynamics of pollination systems, a better understanding of the animal side of pollination in the context of communities is required. They make two interesting arguments: (1) resource abundance is closely associated with evolution of pollinator specificity in bees and the kinds of pollination interactions among bees and plants, and (2) many floral traits often interpreted in the context of pollination have little or no effect on the species composition of the floral visitors. Two important conclusions from this chapter are that (1) even the most extreme relationship is highly asymmetric, and (2) even specific morphological traits do not preclude pollinators from using flowers with very different shapes and sizes. These conclusions suggest that selection on bee morphology apparently occurs in the absence of exclusive host-plant relationships.

Once I started to understand the context of floral specialization, Susanne S. Renner (Chapter 6), and José M. Gómez and Regino Zamora (Chapter 7) brought me new perspectives on plant-pollinator interactions. Renner focuses on flowers that do not provide a reward to their pollinators and she asks why exploitative systems persist. Gómez and Zamora address the following dilemma: how is it possible for generalization to be so common in nature despite the frequently demonstrated ability of pollinators to act as selective agents on plant phenotype? These chapters set up the following general question which is partially answered in the third part of the book: how can we connect the facts of plant specialization, flowers that do not provide reward, and selection of resources in plant-pollinator interactions?

Part three of the book focuses on community and biogeographic perspectives. Four out of six chapters focus on network properties of mutualistic networks (Chapters 8, 9, 10, and 11). Pedro Jordano and colleagues (Chapter 8) attempt to review recent findings of network structure: from the number of links per node to the amount of nestedness. They review almost all of the results in network topology of the past few years. One suggestion from this chapter that would lead to a more complete synthesis is that we should test phenotypic and phylogenetic correlates with the number of links for each species, the phylogenetic diversity of core species, and whether there are repeated patterns among networks.

This last suggestion ties in strongly with the chapter by Scott Armbruster (Chapter 12). Armbruster’s main conclusion is that specialized features of plants are the result of adaptation to exploit generalist pollinators, in other research, through a process of developmental specialization or the process of evolving toward greater specialization in response to selection generated by pollinators. One intriguing result from Armbruster’s work is that specialized pollination has mostly evolved from more generalized pollination. This opens the door to test the neutral and niche predictions of community structure and evolution. For example, Hubbell’s neutral theory predicts that most rare and endemic species are relatively recent in origin, whereas widespread and abundant species are expected to be older. Can we expect that older species are more abundant and have a greater number of pollinators than recent and rare species?

A first step to test if individuals and not species interact randomly is introduced by Diego P. Vázquez and Marcelo Aizen (Chapter 9). Their main result supports the strong effect of species with more individuals on network structure. But, does this pattern mean neutral ecology and evolution of communities? As Vázquez and Aizen comment, future efforts to develop neutral models may help elucidate the different factors in shaping the structure of plant-pollinator interaction webs.

Can we use any of the previous results in agriculture and conservation? As Nickolas M. Waser and Margaret M. Mayfield comment, the benefits of insect pollination are not fully appreciated by many farmers. However, it should be noted that specialist parasitic flowers have been used to test ideas about race formation on several commercial fruits and vegetables. These ideas have improved the understanding of some underlying mechanisms of speciation and biological control. The opposite seems to have happened to mutualistic interactions. The ancient domestication of the European and generalist honey bee, *Apis mellifera*, to virtually all agricultural ends, confirms the human inability to observe the subtle effects of mutualistic interactions.

The final part of this book attempts to overcome this lack of appreciation. This situation is mainly accomplished in the conservation part, but the ecosystem management part is still poor. One specific detail on ecosystem management is partially covered by the brief summary given by Ingolf Steffan-Dewenter and his colleagues (Chapter 17) on coffee pollination. They show the effect of pollen limitation on yields increases with a decrease in species diversity of native tropical bees, uncovering the potential link between conservation and agriculture in human transformed landscapes.

Suzanne Koptur (Chapter 15) points out that specialist and generalist plants do not seem to differ with respect to extinction risk. Waser and Mayfield suggest that a possible explanation is one convergent result from different chapters (4, 8, 9, and 15): the observation that a general feature of plant-pollinator interactions is a tendency of generalist plants to associate with specialist pollinators and vice versa. Does the structure of only one interaction type promote such an equal extinction probability? We must keep in mind that most approaches to detecting patterns in community structure assume: (1) spatial homogeneity (Chapters 13 and 17 are the only ones to explicitly consider spatial scale), and (2) independence between different types of interactions (see Renner, Chapter 6). However, we must recognize that we still don’t know very much about the structure and the dynamics of multiple interaction types in existing landscapes. Further network and synthetic studies are needed here to extract and apply some useful probabilistic intuition to the effects of mutualistic interactions in natural and human transformed landscapes.

Finally, I have three minor criticisms. First, I think that the final consideration by Jeff Ollerton (Chapter 18) should be in...
the first part of the book. Ollerton does a great job in introducing and explaining the whole idea of mutualism. Second, there are no models that link the evolution of specialization and generalization to predictions of community structure in time and space. Third, there are no studies of biological control using mutualistic interactions in human transformed landscapes.

Overall, this book contributes to a better understanding of the role of specialists and generalists, not only in the plant-pollinator research, but in the evolution and ecology of trophic interactions. Specifically, we know better the subtle effects of mutualistic interactions and their roles in generating new morphological traits in a broader community context.

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Spotlight

Recent Publications of Particular Interest


Books and Monographs Received Through May 2006


