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# SEXUAL CONFLICT: A NEW PARADIGM?

Author: SZÉKELY, TAMÁS

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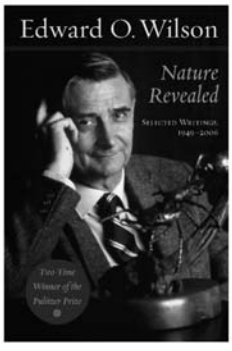
**Evolution of the Insects.** David Grimaldi and Michael Engel. Cambridge University Press, New York, 2005. 755 pp., illus. $80.00 (ISBN 9780521821490 cloth).

The field of entomology and the study of insects in general are fortunate to have a history of notable authors who have produced numerous excellent and readable books on a wide range of topics. However, there is room for many more, because (not surprisingly) the book-to-taxon ratio for invertebrates in general, and insects in particular, is extremely low compared with that for animals of larger size and those more closely related to us. This disparity is nowhere clearer than in texts on fossil organisms. In *Evolution of the Insects,* David Grimaldi and Michael Engel take on the demanding task of producing a high-quality work that covers the breadth of insect systematics, including a much-needed treatment of insect fossils, thus filling an important need in modern biological reference works.

I have often heard it said with a dismissive wave of the hand that the insect fossil record is too incomplete to be of much use. To be sure, it has some extremely inconvenient lacunae, right where we think the unknown forms would be that could provide the character data needed to answer important questions about the origins of insect wings and powered flight, or about the relationships among the main branches of the pterygote (winged) insect lineages. Relative to the vast species diversity of insects presumed in the past, we definitely could wish for more fossils. However, what Grimaldi and Engel make abundantly clear in their book is that throughout insects there is a significant and important array of fossils, which provide data that many, and probably most, biologists have not incorporated in their understanding of insect diversity and evolution. The taxonomic distribution and quality of fossil insect specimens are more than sufficient to greatly enhance our understanding of insect evolution and expand the known diversity and importance of insects in terms of the evolution of biodiversity on Earth. Once the information from insect fossils becomes a normal part of our discussion of insects in class lectures, in the same way that dinosaurs are a usual part of any discussion on vertebrate evolution, we will wonder how we ever did without it. Grimaldi and Engel have made a saltatory move for the field toward this state by writing a book that smoothly integrates fossil with extant insects. They also clear up or avoid some of the rampant speculation and questionable fossil interpretations posited by some individuals who have worked on fossil insects in the past. Grimaldi and Engel maintain a critical and sober view of the data throughout.

This reference work is filled with a great deal of accurate and important summary data about insects and their evolution. Grimaldi and Engel are careful and clear about the sources of their information and the limits of the interpretation of existing data. There are also many important insights of a more synthetic nature scattered through the book. One example is found in the section on the evolution of insect sociality. The fossil record shows that the highly sophisticated eusocial insects (insects with a form of social behavior beyond what we humans have, which includes anatomically different castes, reproduction only by certain castes, and overlapping generations) were present by the Cretaceous, 140 million to 115 million years ago, but made up probably only 1 percent of the fossil specimens from the period. The significant dominance of eusocial groups like termites and ants that we see now is not found in the fossil record until the

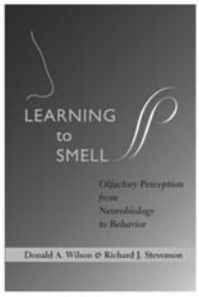
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Eocene, some 90 million years later. The implication is that the highly sophisticated social system of present-day insect species was not enough in itself to result in the success we see in these groups. Without the fossil evidence, we could easily and erroneously assume social complexity was the single causal factor.

One of the great benefits of the way that this book is written is that it follows a path like that of a good class in insect systematics. First it leads the reader through sections on basic and broad concepts that underlie scientists' understanding of insect evolution. Grimaldi and Engel briefly lay out their ideas on important issues such as homology, species, and phylogeny reconstruction. These areas of systematics remain steeped in debate, so the authors' particular take on such topics will not please everyone, but this is not the intent of the book.

For those of us less familiar with fossils, the book provides a good primer on fossil formation and different types of insect fossils. Fossils and fossilization of insects are extremely well treated, with a particularly fascinating overview of amber inclusions. One cannot help but be captivated by the remarkable quality of amber preservation, which makes it possible to view mitochondria in some fossils and recalls controversy over the amplification of ancient DNA.

The bulk of the book begins with a systematic treatment of arthropods that are near relatives of insects, and then details each of the major insect groups. The incorporation of fossils in the book is its most innovative aspect, but there is a very competent treatment of every insect order, providing a salient and mercifully brief historical overview of the taxonomic work in each group, tabular lists of significant characters in the included taxa, and overviews of both fossil and extant taxa. Clearly drawn phylogenetic trees are provided for all major groups. The trees that include fossil taxa, however, are by necessity composite compromise diagrams derived from several disparate sources, rather than actual cladograms based on an inclusive analysis of all data and taxa. But the authors are clear about the source of the trees, so the reader has



reasonable warning of their limitations. Current DNA evidence is discussed, and important morphological data are presented in many easily comprehensible figures.

Although the text is clearly geared to a relatively sophisticated readership, it is the most accessible treatment of fossil insects available. The organization of information follows historical and phylogenetic lines and so maximizes connectivity and information content. The book is beautifully illustrated with close to 1000 photographs and figures (most in full color), including adult, immature, fossil, and extant insects. Attention to detail and quality in the figures sets this work apart from other entomology texts. The book is up to date in its information and will be an invaluable resource for anyone teaching a course in insect systematics. I have already used it as background reading for class preparation.

This is a rich work and an excellent contribution to the study and teaching of insect and arthropod science. Anyone with an interest in insects—and just about any organismal biologist—will want to have access to this fine reference, either through an institutional library or on the bookshelf at home. Grimaldi and Engel have breathed life into old cuticle (or at least the traces of old cuticle) and have reinforced the idea that a broad and integrative view of any group is essential for understanding its evolution, and indeed for a full understanding of life on Earth.

KIPLING W. WILL
*Kipling W. Will (e-mail: kiplingw@nature.berkeley.edu) is an assistant professor of insect systematics and associate director of the Essig Museum of Entomology in the Department of Environmental Science, Policy, and Management, University of California–Berkeley.*

## SEXUAL CONFLICT: A NEW PARADIGM?

**Sexual Conflict.** Göran Arnqvist and Locke Rowe. Princeton University Press, Princeton, NJ, 2005. 360 pp., illus. $39.50 (ISBN 0691122180 paper).

I'm watching a breeding colony of southern elephant seals on a remote island in the Falklands. The harem master is an impressive behemoth, and as he makes his way through his courtiers to clash with rival males, some of his females and their pups are inevitably crushed. This does not seem to bother the master, since his main raison d'être is to sire the pups that will be born a year later. Females, which have only about a fifth of his mass, are powerless to fight him off to save themselves and the pups. A short distance away, southern giant petrels breed on the same beach. Giant petrels pair for life, and they raise their single offspring by sharing the incubation, brooding, and feeding of their young for a staggering 6 months.

So why and how did nature produce some species in which males and females have severe conflicts over reproduction, such as elephant seals, whereas in others, such as giant petrels, cooperation prevails? In *Sexual Conflict,* Göran Arnqvist and Locke Rowe offer some illumination, and in so doing they make a major contribution to the field of sexual selection. This is a wonderful book, packed with exciting natural history, distilled interpretation of recent experimental studies, and straightforward explanations of complicated mathematical models. If you want to learn how male bedbugs rape females (and fellow males), examine the tactics of penis fencing in marine flatworms, or discover the tricks a promiscuous penduline tit uses to cheat its mate, this is the source to turn to. These and other intricate examples illustrate that nature produces many bizarre examples of sexual conflict in which the interests of males and females are strikingly divergent.


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Reproduction is an uneasy alliance between the sexes, a game of tug of war. For a viable embryo, both a male and a female gamete are needed, though to achieve fertilization the sexes (and indeed hermaphrodites) use different means. For males, often the best strategy is to pursue matings persistently, whereas for females selective resistance may be the winning card. It is important, however, to realize that males and females are tied together in more than an allegorical way: If males harm females—for instance, by developing brutal intromittent organs—not only will the female's reproductive success in a population be reduced, but so will that of an average male.

Sexual conflict is becoming a major concept in evolutionary biology for two main reasons. First, teasing apart the male and female perspectives is genuinely fascinating. Unlike some other relationships involving conflict, such as predator–prey and host–parasite interactions, sexual conflict has fighting teams (labeled "males" and "females") that share the vast majority of their genes. Second, sexual conflict can be studied at several levels using a variety of research tools and model organisms, from genes through individuals to macroevolution. Thus researchers use advanced techniques borrowed from molecular genetics, population genetics, behavioral ecology, and comparative phylogenetics. Indeed, as Arnqvist and Rowe argue, a single type of methodology is unlikely to be successful for revealing the details, directions, and intensity of sexual conflict.

The concept of sexual conflict goes back to seminal papers by Robert Trivers and Geoffrey Parker in the early 1970s, but present-day students can draw on recent rapid advances in genetics, behavioral biology, and phylogenetics. For instance, clever genetic techniques allow researchers to speed up sperm competition in fruit flies and pit the resulting supercompetitive males against unaltered populations of females. The unlucky females are likely to die, an unfortunate side effect of the enhanced seminal fluids produced by supercompetitive males. These achievements warrant a full-fledged new paradigm that cuts through the boundaries of traditional biological disciplines, although only time will tell how far we can push the Trivers–Parker paradigm. It seems certain, however, that Arnqvist and Rowe's well-balanced and carefully worded book is a landmark, and it is likely to recruit new fans to the sexual conflict camp.

Two major challenges, in my view, remain to be tackled. First, we need a full understanding of the costs and benefits of mating, for both sexes. There are convincing demonstrations that mating is costly for females. However, gaining access to the females and achieving copulation may be exceedingly costly for males as well; for example, bull elephant seals can rarely sustain their bloody fights with rivals beyond a single breeding season. Second, we need to find out why life histories, physiology, and ecology appear to make some species more prone to conflicting interests than others, so that many exhibit overt sexual conflicts, like the elephant seals, whereas others, like petrels, become cooperative. Are the effects of ecology and life history unidirectional, leading to the presence or absence of sexual conflict? Or does strife between the sexes feed back to ecology and life history, amplifying or dampening their effects? The balance between conflict and cooperation may lie at the heart of success (or failure) of alleles, individuals, and populations.

Although I enjoyed this book from cover to cover, some explanatory notes or boxes on the details of the major research techniques would have been a welcome addition. Researchers on sexual conflict use vastly different techniques, so brief descriptions of the principal ones would be especially valuable for postgraduates and for those whose research background is in just one field.

Nevertheless, I expect that *Sexual Conflict* will be popular among postgraduates, evolutionary biologists, and behavioral ecologists. I have already found it excellent material for my final-year undergraduate course on sexual conflict. And though the book is aimed primarily at professional biologists, I hope and expect the fascinating examples on the behavior and natural history of various beasts will appeal also to the general public.

TAMÁS SZÉKELY
*Tamás Székely (e-mail: bssts@bath.ac.uk) is a reader in the Department of Biology and Biochemistry, University of Bath, Bath, BA2 7AY, United Kingdom.*

## AN INSTRUCTION MANUAL FOR THE ENDANGERED SPECIES ACT

**Species at Risk: Using Economic Incentives to Shelter Endangered Species on Private Lands.** Jason F. Shogren, ed. University of Texas Press, Austin, 2005. 283 pp. $21.95 (ISBN 0292705972 paper).

Many biodiversity conservation efforts can be described by the proverb, "If all you have is a hammer, every problem looks like a nail." While we conservationists have developed a vast array of different tools, we have not been very good about developing the instruction manuals that help our practitioners figure out the conditions under which to use or not use any specific one. *Species at Risk: Using Economic Incentives to Shelter Endangered Species on Private Lands* attempts to meet this need by providing a guide to using one family of conservation tools—the various incentives for conservation of endangered species on private lands, particularly in relation to the US Endangered Species Act (ESA).

The introduction to the book, by editor Jason Shogren, quotes Jim Berger, the former president of the Wyoming Stock Growers Association, as saying that "the best wildlife management we can have is a local game warden, a rancher, and a cup of coffee." Shogren goes on to point out, however, that "many others might add that a fat checkbook would be helpful too. This book addresses whether this ESA checkbook makes sense from several vantage points" (pp. 18–19). In effect, the problem is how to keep the owners of habitat that could be used by an endangered species from destroying that


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habitat to avoid the legal and economic consequences of having the species on their property. One egregious example cited in the book is that "ten days before the Fish and Wildlife Service listed the golden-cheeked warbler, a firm owned by Ross Perot hired migrant workers with chain saws to destroy hundreds of acres of oak and juniper warbler habitat."

The book is an edited volume with two introductory chapters, several chapters exploring specific topics in more detail, and then a summary chapter. There is an old joke that says, "There are three kinds of economists in the world — those who can count and those who can't." As a member of the latter group, I am pleased to report that *Species at Risk* describes some challenging economic concepts in simple and accessible language.

After Shogren's general introduction to the topic, the second introductory chapter, by Debra Donahue, provides a succinct overview of the ESA and the major tools providing incentives for conservation on private property: the habitat conservation planning process, the no-surprises policy, and the safe harbor and candidate conservation agreement programs. One of the greatest challenges in writing this type of overview is what I think of as the "cat" problem in the dictionary: Most people reading a dictionary probably know what the word means and how to spell it, and yet to be comprehensive, the editor needs to include it alongside the more difficult entries. Overall, Donahue does a good job both of introducing the basics of the ESA and its key tools and of providing a detailed critique of them.

Gregory Parkhurst and Shogren then provide a detailed review of eight different incentive mechanisms for promoting conservation of endangered species on private lands. The tools that they review are zoning, impact fees, subsidies, tradable development rights, conservation banking, fee simple acquisition, and conservation easements in the form of purchased development rights or donations for tax relief. For each mechanism, the authors provide a basic description and then discuss its pros and cons. Overall, they provide a helpful summary of each tool and some simple examples. As a novice in this field, I did not always understand the relationship between the incentive tools introduced in Donahue's chapter and those outlined in this one.



It's also not immediately clear under which conditions one might employ each tool, although the authors do return to this topic in the final chapter. Finally, it may be an obvious point, but it also would be helpful if the authors were to emphasize that none of these tools are necessarily sufficient to ensure conservation by themselves—for example, if you purchase a tract of land, you still need to manage it to ensure that it is not overrun by invasive species or illegal hunting efforts.

Subsequent chapters go deeper into different topics related to the ESA. I found these to be something of a mixed bag. They include a historical–philosophical exploration of the ethics of different approaches to land conservation; a very





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nuts-and-bolts description of how to write a report to appraise the conservation value of a piece of land; a theoretical assessment of the markets for habitat conservation, complete with an appendix full of equations accessible only to economists who can count; and a more qualitative discussion of how inequalities in information held by different parties potentially distort the market for species conservation. I suspect that some of these chapters will appeal to readers with specific interests, but most readers will skip over them.

The last chapter gets back to the main subject at hand, looking critically at the different incentive tools presented earlier by Parkhurst and Shogren. I particularly liked the table that provides, in a concise format, the author's assessment of the utility of each tool against a range of different evaluation criteria. This table is the key to helping practitioners determine the right tool for their particular needs.

Two groups of readers might benefit from this book include (1) students and other individuals who are interested in learning more about the ESA and (2) conservation practitioners in the United States who want to find out about potential tools for promoting conservation of species on private lands. Since the subject matter, discussion, and examples in this book are tied very closely to US laws and policies, *Species at Risk* will be useful mostly in the United States; it is not really applicable to other countries, except perhaps to help policy-oriented conservationists consider what lessons they might apply to the policy debates in their homelands.

This book should also be provided as a model to all aspiring editors of academic volumes that emerge from a conference or workshop. The editors here have dodged many of the pitfalls that plague this genre; they have selected a narrow and useful topic, included introductory chapters that provide historical background and a survey of the current state of the field, made use of brief examples interspersed with the text (instead of long and dreary case studies), and provided a good summary chapter that brings the various chapters together and makes recommendations that practitioners will find useful. The one trap they fall into is to include a few chapters on topics that are only marginally related to the topic at hand, presumably so as to give all the original conference speakers a platform in the final product.

In sum, this is a useful instruction manual for those interested in incentive-based tools for conservation on private lands. Hopefully, in the near future we can collectively develop similar instruction manuals for other conservation tools.

NICK SALAFSKY

*Nick Salafsky (e-mail: nick@FOSonline.org) is codirector of Foundations of Success, an organization in Bethesda, Maryland, that aims to improve the practice of conservation through adaptive management by working with practitioners to test assumptions, adapt, and learn.*






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