



The evolution of insect mating systems, thirty years after

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The title of the new book edited by David Shuker and Leigh Simmons will sound familiar, at least to evolutionary biologists with gray hair on their temples. And so it should: the title, and the entire book, is a deliberate homage to Randy Thornhill and John Alcock's classic of 1983. It is intended to "update the empirical and conceptual scope of the original book" to "reveal many new questions to inspire a new generation of insect behavioural researchers . . .". Indeed, a retrospective volume such as this compels the reader to ask an obvious question: What have we learned over the past three decades? Dusting off my copy of Thornhill and Alcock and leafing through it side by side with the new, eponymous volume, I am struck by how much has changed, and how much has not.

The 15 chapters, all written by leading authorities in the field, present succinct syntheses of information and ideas on a variety of topics related to insect mating systems. Some chapters address topics that were central to the original book, and provide a guide to the basic ideas as well as recent advances (e.g., David Shuker's chapter on sexual selection theory, Hanna Kokko, Hope Klug, and Michael Jennions' chapter on mating systems, and John Hunt and Scott Sakaluk's chapter on mate choice). Other chapters focus on topics that received scant attention back in 1983 (such as Ben Normark's chapter on modes of reproduction, or Boris Baer's chapter on sexual selection in social insects). This book will, no doubt, be a valuable resource for graduate students beginning their careers in evolutionary ecology, as well as established researchers seeking an up-to-date synthesis. Indeed, a number of

chapters—Goran Arnqvist's chapter on cryptic female choice, Marlene Zuk and Nina Wedell's chapter on the role of parasites, Boris Baer's chapter on social insects, Doug Emlen's chapter on weaponry, and others—are outstanding examples of clear writing and thinking, and will serve as valuable guides for future research. The brief final chapter, by John Alcock and Randy Thornhill, provides an interesting overview of the entire book, and highlights some areas of notable progress.

The new book clearly reflects the monumental technical advances made since the early 1980s. Like all branches of biology, behavioral ecology has been transformed by technological innovations that have furnished a much more detailed knowledge of the mechanistic basis of physiological, morphological, and behavioral variation. One example is the bewilderingly complex blend of chemicals discovered lurking inside male ejaculates, and the potential for this sinister seminal soup to influence female physiology, reproduction, and life history. Such cryptic factors in sexual coevolution were unknown in 1983, but are discussed in several chapters of the new book, including Mike Ritchie and Roger Butlin's chapter on the genetics of mating systems, Leigh Simmons' chapter on sperm competition and Boris Baer's chapter on social insects. Another area of notable progress is the developmental biology of secondary sexual traits, including the role of endocrine signaling, highlighted in Ritchie and Butlin's chapter, as well as Patricia Moore's chapter on reproductive physiology. And, of course, we now know vastly more about the genetics and genomics of male sexual traits and female preferences—a topic addressed at length in Ritchie and Butlin's chapter and Hunt and Sakaluk's chapter. These advances show that behavioral ecology has come of age as a science. Where researchers once had to settle for observations of morphology and behavior, they are now able to

connect a great deal of phenotypic variation with the underlying biochemical processes.

Yet, evolutionary biology is primarily concerned with the ultimate questions: Why does evolution proceed along certain trajectories? Why do organisms look and behave as they do? I picked up this book hoping, most of all, to get a sense of the progress that behavioral ecology has made over three decades on this ultimate front. And, of course, there have been important advances, many of which are reflected in this book. For example, we now have a far greater understanding of the role that parasites and their devious machinations can play in sexual coevolution, and recognize that even genomes are teeming with parasites (selfish genetic elements)—the topic of Zuk and Wedell's chapter. We have also gained a much deeper appreciation of the pervasiveness of sexual conflict, an insight that is implicit on every page of the new book, and treated at length in Rhonda Snook's chapter on polyandry. Disappointingly, there is almost no mention of recent advances in the study of maternal and paternal effects, even though such nongenetic effects, rather than "good genes," could account for indirect benefits of mate choice in some systems. On the other hand, I am excited by ongoing efforts to re-examine our most basic assumptions about the evolution of mating systems, reopening such seemingly straightforward questions as which sex should search for mates or invest in offspring, or for that matter whether mating should play any role in reproduction at all. It is refreshing to see these fundamental issues considered in the chapters on modes of reproduction (by Ben Normark), mating systems (by Hanna Kokko, Hope Klug, and Michael Jennions), and parental care (by Per Smiseth).

Nonetheless, I cannot escape the impression that behavioral ecology is still wrestling with many of the same old puzzles. Indeed, although the intervening years have yielded countless new examples and witnessed many reductionistic triumphs, the jury is still out on a number of key questions posed in Thornhill and Alcock's book. For example, although behavioral ecologists have demonstrated beyond any doubt that females can be choosy (thus settling a long-standing dispute between Darwin and Wallace), there is as yet no broad consensus on the factors that drive the evolution of female choice—in particular, the role of "good genes," and genotype–environment interactions. Likewise, why do females of many species mate with multiple males? How important is sexual conflict in natural populations? What are the principal causes of diversification in mate preferences and secondary sexual traits? Clearly, behavioral ecologists still have a great deal of work to do.

But it is not really surprising that so many basic questions remain to be answered. Evolutionary biology is difficult, and behavioral ecology tackles some of its most challenging problems. Besides highlighting new questions that arise from recent advances in knowledge and understanding, this book will make an important contribution by re-focusing attention on the old questions that still hang over our heads, seemingly just out of reach. This is a challenge that is sure to inspire the next generation of brave and inventive insect researchers.

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