

Katydids and Bush-Crickets: Reproductive Behavior and Evolution of the Tettigoniidae

Darryl T. Gwynne
 Cornell University Press
 Ithaca, New York 2001
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OUR APPRECIATION OF biological diversity owes much to the collective efforts of a special cadre of scientists who become thoroughly captivated by particular organisms, recognize those central issues that can be studied with greatest precision in their favorite species, and enthusiastically advertise their findings to the biological community. The Canadian behavioral ecologist Darryl Gwynne is among this breed, and his efforts have put katydids (bush-crickets, should you reside outside the Western Hemisphere) on the behavioral ecology and evolution map. True, by mid 20th century, katydids (Tettigoniidae) had already acquired some status in the natural history of North America through their mating songs, especially the variable syllables sung by *Pterophylla camellifolia* (true katydid). In addition, entomologists were becoming aware of the importance of these songs in species recognition, sexual advertisement, and male rivalry. But it was Darryl Gwynne's studies of mating systems in North American and Australian tettigoniids over the past 20 years – which have taught us so much about the evolution of courtship behavior and how ecological factors may influence the roles assumed by the sexes – that earned this family a central place in biology. These landmark studies, accompanied by concise reviews of the evolution, anatomy, physiology, and ecology of tettigoniids, are now presented in an eminently readable book, "Katydids and bush-crickets: reproductive behavior and evolution of the Tettigoniidae" (D.T. Gwynne, 2001, Cornell Univ. Press, 317 pp.).

In nine chapters, Gwynne introduces us to the global diversity of the Tettigoniidae and its phylogenetic relationships to other Orthoptera, describes the basic biology of this family, and then focuses on five topics in reproductive behavior: pairing of the sexes as facilitated by acoustic and vibratory signals, courtship feeding and the evolution of spermatophore attachments, sexual selection, risks incurred by the signaler and receiver, and sexual roles in courtship. The last topic is given special attention, as some tettigoniids are noteworthy for variation and reversals in sexual roles. Thus, we learn about ardent and aggressive females, coy and discriminating males who donate as much or more material investment to their offspring as their female partners do, and the circumstances under which the insects may revert to habits more befitting their gender. Gwynne writes in a personal style, almost chatty in places, but he does not treat these observations as mere natural history oddities. Rather, he makes exemplary use of "the exception probes the rule" tactic to test and refine our understanding of the

relationships between the sexes in animal mating systems.

"Katydids and bush-crickets: reproductive behavior and evolution of the Tettigoniidae" is not, nor did its author intend it to be, an encyclopedic coverage of these insects. Readers desiring in-depth treatment of specific subjects including tettigoniid systematics, acoustic behavior, and neurobiology may be better served by consulting the (slightly out-of-date) edited volume "The Tettigoniidae: biology, systematics and evolution" (W.J. Bailey and D.C.F. Rentz, [eds.], 1990, Springer-Verlag, 395 pp.). Instead, Darryl Gwynne's recent book guides the reader through the complex interplay among ecology, evolution, and behavior that has shaped courtship interactions, mating systems, and sexual differences. Sexual selection theory is clearly a prevailing theme, and its nuances are carefully explained so that one may evaluate the various hypotheses derived from its application. Such application is particularly well developed for analyzing the evolution of the tettigoniid spermatophore, which is accounted for by no fewer than 10 potential explanations based largely on sexual selection. Importantly, the explanation that emerges from current analysis as most likely in general (ejaculate protection) is not that which the author favored in his initial research (paternal investment).

As indicated above, "Katydids and bush-crickets" is not a book about mechanisms. Given its stated focus, this is fine, but there are several places in which I would have preferred a stronger physiological or genetic approach: biomechanical and neurophysiological factors, in addition to ecological ones, do constrain the sorts of songs that katydids can sing and hear, and genetic aspects of signaling, mating preferences, and changes leading to speciation deserve more attention. Similarly, could better understanding of development and nutritional biochemistry provide new insight to the katydid spermatophore? The book includes a number of valuable comparisons with other insects, but several critical ones were not made. For example, gregarization in the decticine katydid *Anabrus simplex* (Mormon Cricket) is discussed, but there is scant mention of the "locust phenomenon" in Old World Acrididae. Could information on factors regulating locust populations and their movement help explain how tettigoniid hordes periodically form and march across the Great Basin?

These points notwithstanding, Darryl Gwynne has written a book that is both informative and provocative. He has combined his considerable literary panache with extensive knowledge of tettigoniid biology and a sophisticated understanding of evolution to offer us an exciting view of a magnificent group of insects. Moreover, he demonstrates how tettigoniids have served as organisms par excellence for studying diverse aspects of courtship: acoustic communication, parental investment, sexual role reversals. The book is superbly illustrated with figures, line drawings, and color plates of tettigoniids from the various continents.

For the converted, critical directions in future research are noted in most sections. Anyone interested in Orthoptera or reproductive behavior should read this book. It will be the inspiration for the next generation of tettigoniid specialists and insect behavioral ecologists alike.

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Biology, Ecology & Systematics of Australian Scelio.

Paul Dangerfield, Andrew Austin, and Graeme Baker
CSIRO publishing
Collinwood, Australia 2001
IX + 254 pp.

AS THE AUTHORS point out, *Scelio* means 'scoundrel' or 'rogue'. It is a species-rich genus of scelionid wasps, with over 225 described species. All members of the genus are parasitoids of eggs of grasshoppers and locusts, Acrididae. Many species have been used in classical biological control attempts, and they have been reared in large numbers from pest species such as *Locusta migratoria* (L.).

The primary purposes of the book are to revise the Australian fauna of *Scelio* and to support research on locust pests with an identification key to species. The book succeeds very well in these objectives, but much more is accomplished. Thirty pages are devoted to biology, ecology, and biological control, and 30 more are devoted to host relationships, morphology, and phylogeny. Finally, a materials and methods section details all that is known about collection, dissection, rearing, and surveying parasitism rates.

The nontaxonomic portions deal with the world fauna of *Scelio*, and the sections on phenology, sex ratio, mating, host finding, etc., are worth reading for all those interested in hymenopteran biology. There are numerous sections that discuss the interactions between species of *Scelio* and agricultural systems, e.g., their potential as biological control agents and the effects of insecticides. Like other chapters, the morphology chapter is comprehensive. In most publications with a taxonomic focus, morphology sections are superficial and rather dry treatments meant to help the reader work through identification keys. Not here. Dangerfield et al. go into great detail in both form and function, and it is one of the most interesting chapters. The information presented on the telescoping ovipositor system is fascinating.

The guts of the book is the taxonomic section. It is exemplary, with standardized drawings and distribution maps for every species (Fig. 1), and numerous SEM photos augment the line drawings.

I recommend the book to all those interested in grasshopper and locust control, scelionid systematics, and hymenopteran morphology and biology. Systematists cannot be all things to all people, but we would have a much wider readership if we included a wider

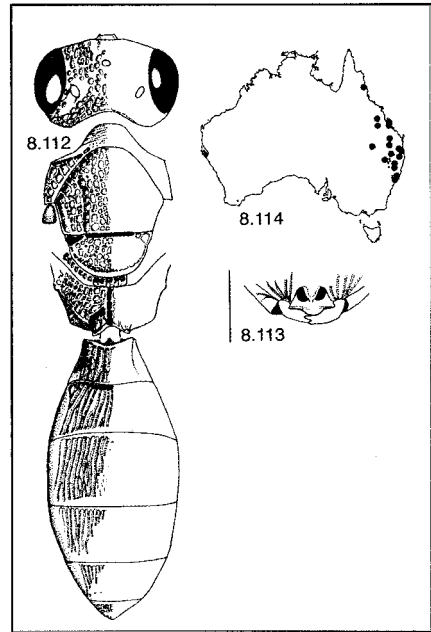


Fig. 1. *Scelio pilosifrons*, dorsal habitus, lower head, and distribution map (from Dangerfield et al., p. 149).

range of information in our revisionary studies, as Dangerfield et al. have.

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Sperm Competition and Its Evolutionary Consequences in the Insects

Leigh W. Simmons
Editors: John R. Krebs and Tim Clutton-Brock
Princeton University Press
Princeton, New Jersey, 2001
448 pp.

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ENTOMOLOGISTS AND TAXONOMISTS in particular have long recognized the diversity and often puzzling complexity of insect genitalia, but it is not until relatively recently that a conceptual framework emerged for exploring the function and evolution of such elaborate structures. In his seminal review, "Sperm competition and its evolutionary consequences in the insects," Geoff Parker (1970) was the first to outline the broad implications that the temporal overlap of competing ejaculates within the female reproductive tract holds for an organism's reproductive traits. From the evolution of complex genitalia designed for removing sperm deposited by previous males, to that of mating plugs and other accessory gland proteins preventing females to subsequently mate, not to mention the

evolution of behavioral adaptations such as mate guarding and morphological adaptations of sperm cells themselves, the venues in which sperm competition affects an organism are many and, at the time, were largely unexplored. It is therefore not surprising if in the last 30 years this area of research literally exploded. A mere dozen papers were published on sperm competition in the 1970s, about 60 in the 1980s, more than 500 in the 1990s and projections for this decade are around a staggering 2,000 (approximations compiled from the *Web of Science* for all organisms).

Leigh Simmons' "Sperm competition and its evolutionary consequences in the insects," will not strike us for the originality of his title (note that the book is dedicated to his former mentor and colleague G. Parker), but is an excellent snapshot of this rapidly expanding field of research. Where one could expect a synthesis, Simmons brings us an up-to-date review in which he underlines the complexity and multiplicity of adaptations to sperm competition and reflects on the difficulties inherent to their study. Behavioral, physiological, and morphological reproductive traits may evolve in response to intrasexual selection (competition between males), but also through intersexual selection (female-male coevolution) and natural selection. The author rightfully pinpoints the difficulties in designing experiments that allow researchers to discriminate between the respective effects of those often confounding selection pressures. Manipulating mating behavior, reproductive organs, or sex peptides of insects is often riddled with difficulties, if not impossible; hence, many studies are correlational in nature and their result cannot be interpreted easily. In some chapters, these studies and their flaws are discussed in such details that we are left with the frustrating feeling that all we have read is several pages of speculations and that the conclusive experiments remain to be done. Those interested in a less detailed introduction to sperm competition might therefore favor the chapter "Sperm competition in insects: mechanisms and the potential for selection" by the same author and co-author Michael T. Siva-Jothy, published in Birkhead and Møller's book "Sperm selection and sexual selection" (1998). In contrast, for newcomers that want to take an active part in this field of research, Simmons' book should be considered an

essential reading, offering a plethora of stimulating and critical ideas.

The book starts with two introductory chapters, one on sexual selection and sperm competition from a historical perspective, followed by an essential second chapter that introduces important concepts, models, and methods. Next, the author discusses, in turn, morphological, physiological, and behavioral aspects of sperm competition, and finishes with a chapter on mechanisms of female sperm selection and sperm competition in social insects. Although considerable advances have been made in behavior and morphology, physiology in particular offers new and promising perspectives. This is especially true, in my opinion, for topics such as the evolution of sex peptides and pheromones. The same applies to the fascinating topics of variation in sperm morphology across species, sperm polymorphism within species, and the potential for sperm selection processes by females developed in the later chapters. These are areas in which much remains to be done and in which continuing progress in molecular techniques and genomics should quickly lead to major advances. Moreover, the interface of those fields with the study of speciation is among the most exciting areas of research in evolution.

I have only one cautionary note to potential readers. As underlined above, a good share of the book discusses debatable results or very recent advances in a vast and fast expanding field of research. This treatise is therefore likely to be quickly outdated and should be read SOON.

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