area of research understandable, by giving key examples, elucidating problems, reviewing mechanisms (when known), and providing insights for future work.

In summary, the author has succeeded in bringing the disciplines of microbial and disease control into sharp focus, listing their advantages, disadvantages, as well as discussing the interrelationships between "pure" and "applied" biology. Finally, I envy the students at the University of Edinburgh who have had the opportunity to attend Dr. Deacon's classes. His enthusiasm, clarity, and understanding of these areas comes through quite clearly in this enjoyable book.

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Sexual Selection: Biology and Behavior

The Evolution of Insect Mating Systems
Randy Thornhill and John Alcock

This book contains a compendium of the current literature on insect reproductive biology and behavior, especially relating to sexual selection. Although the book concentrates on insect mating systems, one does not have to be an entomologist or ethologist to understand the theories and examples used. In fact, vertebrate behaviorists and evolutionary biology students would do well to read it in order to appreciate the diversity and complexity of animal reproductive systems so vividly apparent in the world of insects. The text is well written; it is concise and the theoretical orientation easy to follow. Opposing views are often discussed together with the arguments supporting the authors' own theoretical reasoning. Thornhill and Alcock have amassed many good examples in various insect orders from the entomological literature so as to illustrate and support the logic of their approach to insect mating systems.

Chapter 1 (Evolution hypotheses and tests) presents the authors' approach; searching for the underlying function and mechanism to the evolution of animal reproductive behavior, especially sexual selection. The book's theme is one of natural selection, as a mechanism for evolutionary change, acting on the individual and its
genes in ways that are adaptive. Male-male competition and selective mate choice by females and their role in sexual selection are central to insect reproductive behavior. The logic of adaptationist selection and the forming of hypotheses with testable predictions is presented; a trait is adaptive if its functional benefits exceed the costs as individuals attempt to maximize genetic contribution to their progeny. At the outset the stage is set for continual arguments against the group selectionist approach to reproduction, at some points in the book this seems excessively belabored. In chapter 2 various methods of reproduction are discussed including asexual reproduction, the adaptive values of sexual selection, and especially the increased genetic diversity and flexibility of sexual individuals. The theory of sexual selection (chapter 3) concerns the importance of females being the limited, thus selective, resource for which males develop often elaborate adaptive behavior to promote successful reproduction. Sexual selection has both intrasexual and intersexual (epigamic) types Reproduction consists of investments from each sex towards the mating effort and the parental effort. The most common type of mating system in insects is polygynry in which males copulate with more than one female in a breeding season, whereas less commonly either sex has only a single mate (monogamy).

The book's main portion is concerned with the evolutionary effects of intrasexual selection, especially on male insects. In protandry (common in solitary bees and wasps) males emerge before females and fertilize females as they elope. The timing of mate locating (chapter 4) by males is influenced by whether females mate once or multiply, in the latter case males are likely to search for mates about to oviposit. Specially timed emergence into large reproductive swarms serves as a predator-swamping tactic for the periodical cicada and mayflies; restricted seasonality of mating is common. Chapter 5 treats motivation to copulate, which is usually much stronger in males than females because a male increases his genetic contribution with each female he is able to mate. Thus males are more likely to detect and pursue mates, attempt copulation, and fight for the chance to copulate; they may have elaborate behavioral or structural modifications to assist with these goals. Competition in the attraction of females is the theme of chapter 6, which is a good example of how (in most chapters) the authors are able to summarize the most important aspects and/or examples in useful concise tables. Table 6.1 presents the costs and benefits of the major mate attraction systems—chemical, auditory, visual, and tactile. The phenomenon of "cooperative" male aggregation for attracting females is treated in Table 6.2 with examples from several insect orders in which noncalling males actively seek calling males and often manage to intercept females attracted to the callers. Another aspect of this male "cooperation" is summarized in Table 6.3 concerning "joiner" aggregations of calling males that apparently benefit by attracting more females and by reducing the risk of predation. The adaptiveness of selection and defense of mating sites is thoroughly explained in chapter 7 using tables of diverse examples of insects whose males locate females for copulation at sites of: emergence; oviposition; foraging; conspicuous landmarks; and virgins prior to emergence. Male aggressive defense at these sites is common but includes risks of injury, predation, and loss of time and energy. Chapters 8 and 9 consider the ecological male mating systems (summarized in Table 8.1) as either monogamous with the male guarding or assisting the female after copulation or polygynous in which the males defend groups of females or resources for them, including territorial defense like lekking and scramble competition. Genetic mechanisms can maintain two or more mating systems within a single species that may be able to be switched under variable conditions or at special times; this flexibility is adaptive. Large male advantage is also a significant factor in these mating systems. Male protection of females during courtship and copulation (chapter 10) is necessary because fertilization of eggs is not guaranteed by just locating a mate. Males have evolved protective methods to: remove females from an area of high competitor density; counteract any female attraction signals; and prevent physical separation during copulation. The authors stress that the elaborate "lock and key" features of insect genitalia (especially the penis) as well as the diversity of copulatory positions is probably adaptive for preventing takeover of mates by male competitors. Sperm competition and the fertilization of eggs (chapter 11) follows from last chapter's discussion because of the selective advantage of males that inseminate already-mated females, if their sperm can take precedence over previous males (= sperm precedence or last-male fertilization advantage) and they can prevent other males from subsequent copulation/fertilization. Sperm precedence is illustrated by the unusual example of the Calopteryx damsel; whose males have evolved an elaborate penis structure that physically removes sperm stored in the female spermatheca from previous male mates.

The final part of the book deals with intersexual selection concentrating on females. Selective mate choice by females (chapter 12) is currently debated in vertebrate reproductive ethology. There is limited evidence and it is difficult to prove whether intersexual selection occurs when females discriminate among males or whether the effects are produced by intrasexual selection. Thornhill's own research on the scorpionfly, Hyllobittacus apticus, provides a reasonable case for female choice. Potential benefits to females from males can be either material or genetic. The authors reason that if males vary in the quality of benefits they offer and if females can discriminate among potential mates, then female choice based on materials is adaptive. Evidence for the speculation that sperm and other "mating" fluids provide nutrition to the female and her eggs is nicely supported by experimental evidence. Genetic evidence for female choice is only speculative at present and the authors over-speculate about this at certain points. The authors believe that the principle underlying female choice mechanisms (chapter 13) is that courtship enables females to assess fitness differences among males and not only to prevent hybridization (the traditional view). The female usually controls the father of her offspring although sex-role reversals do occur. The sex contributing the most to reproduction is the limited resource for the opposite sex and controls courtship. Female mating systems

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(chapter 14) are either monogamous or polyandrous. The polyandrous types are based on restricted, cyclical, or continuous female receptivity and may be beneficial for replenishing sperm supplies, nutrition, predator risk reduction, and improvement of genetic quality or diversity.

Each chapter often has a specific example of an insect whose reproductive system illustrates well the central idea. These same examples are often referred to in subsequent chapters relating to other aspects of insect mating systems. These central examples are supported with numerous other examples discussed more briefly. Although the adaptationist views are often speculative, the authors have done an excellent job of selecting corroborative evidence from their own research and that of others.

There are many appropriate figures and graphs that complement the ideas in the text. The book is well edited with only a very few mistakes, such as calling Pterostichus a tenebrionid (p. 399) or the slight confusion between the cerambycid text example (pp. 302–303) and its curculionid figure (figure 10.6). Such errors are offset nicely with bits of humor, e.g. figure 5.7 showing a “buprestid beetle trying (unsuccessfully) to copulate with a discarded beer bottle.” The authors admit the selectivity of examples to illustrate their themes; however, the diversity of the insect world may provide examples for other viewpoints as well. The book is surprisingly easy to read and contains a large amount of factual information. It is certainly the best reference for insect reproductive biology, and one I highly recommend.

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