

BOOK REVIEWS

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SEXUAL TENSION: DOES CONFLICT LEAD TO COSTLY MATE CHOICE?¹

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Sexual Conflict is an enthusiastic introduction to sexually antagonistic coevolution. This is not surprising given that the authors are key promoters of its importance; however, their treatment is also remarkably well balanced. They begin by noting that although sexual conflict can be defined in many ways, it always boils down to the same fact. Evolutionary theory predicts that there are potential conflicts of interest whenever genetically distinct entities interact. This is demonstrably true even for such seemingly cooperative ventures as a mother feeding her child. Sexual reproduction offers no exception because it requires two participants, and potential mating partners are normally genetically unrelated. Consequently, genes that increase the reproductive success of males can be selected for even if they code for traits that are detrimental to genes expressed in females (and vice versa). The only exception to this interlocus sexual conflict is when there is strict monogamy and the genetic interests of parents exactly coincide. Even here, however, the potential for sexual conflict prior to pairing still exists if there is competition for mates. Love is truly a battlefield.

Sexual Conflict begins by tracing the history of views on sex to identify when it went from being seen as a cooperative act to a conflict-ridden ordeal. The authors argue that sexual selection theory is still widely read as implying that mate choice reinforces natural selection and improves population fitness. This contrasts with their opposing view that sexual conflict can lead to mate choice for fecundity-reducing partners. Unfortunately, this distinction is somewhat forced. The first image that sexual selection invokes is usually of profligate excess—cue the peacock's train—and the evolution of beautiful but "arbitrary" traits. Well before sexual conflict became a buzzword, Helena Cronin (1992) documented that since the inception of sexual selection theory, researchers have been classified according to whether they think that mate choice opposes or reinforces natural selection. What is true, however—and the authors argue this extremely convincingly—is that the extent of direct selection on female mating preferences due to sexual conflict has been ignored. This creates a central motif, initially promoted by Holland and Rice (1998), that is replayed in numerous scenarios throughout the book: mate choice as a by-product of sexually antagonistic coevolution. When males impose costs on females that decrease their reproductive output (e.g., by inducing them to mate inopportunistly), females that evolve resistance to males' advances do better. Ultimately, only males that

evolve techniques to overcome female resistance will mate. Females will choose (fail to resist) persistent males and, because males need not share the same long-term interests as their mates, they may (or may not) have a more detrimental effect on female fecundity than the average male. Mate choice could be a by-product of a general cost-cutting strategy.

A historic landmark that the authors identify is the chapter entitled "Battle of the Sexes" in Dawkin's *The Selfish Gene*. Thirty years have passed since then, so why has interest in sexual conflict suddenly surged now? One answer is provided by the authors' emphasis on the bizarre natural history of sexual asphyxiation in snakes and body-piercing genitalia in ricefish. They are too tactful to say so directly, but they make the case that sexual selection studies are stifled by an excessive bias toward searching for genetic benefits to mate choice. The associated models are intellectually satisfying, but their predominance may have caused us to neglect a more prosaic explanation for choosiness: males harass and harm females and continually cajole them to mate. Female resistance to reduce these costs may result in mate choice as a by-product. It is fair to say that, given the effort expended, the empirical evidence for genetic benefits of choosiness is rather paltry. Whether a focus on direct selection on mating preferences will be more fruitful is an open question, but the authors offer a well-reasoned argument that it is time to do so. This is an old plea packaged in the new framework of sexual conflict. To me, it offers a more convincing explanation for mating biases than male exploitation of female sensory systems constrained by natural selection for everyday tasks. Male coercion is an ever-present and unavoidable selective force. In contrast, if females prefer red fruit, it would seem to require only the slightest of neural adjustments to switch off this preference when assessing a male's plumage.

Readers hoping for detailed mathematical models of sexual conflict will be disappointed. Given other papers by the authors (e.g., Gavrilets et al. 2001), they might expect a formal modeling framework, such as the recent one of Moore and Pizarri (2005), to match conventional Fisher-Zahavi models. In fact, not a single equation is presented. This is no loss, though, because the models are well described without the need for mathematics. However, the limitations of the model of Gavrilets et al. (2001), which is often cited in support of an endless arms race between the sexes, were understated. This model assumes that female resistance can only evolve through shifts in mating thresholds. When sensitivity (preference slopes) can also evolve, females may rapidly evolve insensitivity to, or even actively avoid, more persistent males. This makes arms races less likely than initially thought. This

¹ *Sexual Conflict*. G. Arnqvist and L. Rowe. 2005. Princeton University Press, Princeton, New Jersey. xii + 330 pp. PB \$39.50, ISBN 0-691-12218-0.

model, only recently published by Rowe et al. (2005), is briefly referred to but should probably be read in conjunction with this book.

Although sexual conflict is the book's focus, conventional sexual selection models are not neglected. The authors provide a refreshingly concise and equation-free review that is a handy primer for new students of sexual selection. The bulk of the book is, however, devoted to a litany of case studies of apparent sexual conflict. We are taken on a tour of sex in the animal and, more briefly, plant kingdoms; even hermaphrodites are given loving attention. It was a pleasure to read about real animals and a timely reminder that there is nothing stranger than reality. The well-chosen examples have been selected to illustrate sexual interactions, occurring either before or after copulation, that seem to be costly to females. Measurements of the relevant costs are, however, usually unavailable. Some critics therefore dismiss this as unsubstantiated storytelling (e.g., Eberhard 2005). For example, just because males transfer seminal substances that promote egg laying, does this mean that there is conflict? When better to lay eggs than after successfully mating? Is there really a cost? The authors are in a catch-22. To promote a view you need to muster evidence, but in a new field, evidence is always scant and will remain so until other researchers decide to conduct the relevant studies. It is to the authors' credit that they do not hide the limitations of the data and, with a few exceptions, they offer alternative explanations.

Sexual conflict has occasionally been presented as though it is a fundamentally new concept distinct from conventional sexual selection theory. This book should do much to dispel this false dichotomy. To quote, "In fact, the fit is so good that it is entirely unclear whether a distinct boundary even exists between what we refer to as sexual conflict and the body of theory on sexual selection" (p. 14). The simple truth is that male-imposed costs on females due to sexual conflict are only one of many selective forces that potentially affect mating preferences. Whether this selection is more important than, say, natural selection for foraging or locomotive efficiency, or is stronger than compensatory genetic benefits of costly mate choice, remains to be seen. That said, there is a growing presumption that the indirect genetic benefits of choice are too small to outweigh any direct costs, especially if preferred males impose greater costs on females than the average male. Perhaps this is true, but appropriate studies that measure direct costs of choice and offspring lifetime fitness are still surprisingly rare (Head et al. 2005). There are also some major unresolved questions about what constitutes a cost of choosiness (e.g., compare the methods of Head et al. 2005; Stewart et al. 2005).

In my view, the best outcome of the current emphasis on overt sexual conflict is that it has raised new questions: What is the optimal mating rate for females? Do males gain by decreasing female longevity? This has spawned several ingenious studies. Bill Rice's group has, for example, conducted a set of innovative experiments that graphically illustrate sexual conflict in fruitflies (e.g., Rice 1996; Stewart et al. 2005). It has also produced datasets that might otherwise have gone uncollected, such as comparative studies of male and female morphology and mating rates (Arnqvist and Rowe 2002). Many of these studies are described in detail in the

book. Readers may be frustrated that some contradictory results are not discussed (e.g., Eberhard 2004), but this is simply testimony to the steady output of new papers published since this book went to press. The authors did an excellent job of reviewing the evidence available to them.

Unfortunately, there are now also many papers that invoke sexual conflict unnecessarily. Why discuss sexual conflict at length to describe a dataset that shows a familiar large-male mating advantage? One could, of course, say the same about papers making the tenuous argument that female choice has evolved for genetic benefits because larger males have acquired more resources and thereby indicated their superior genetic quality. This argument is no better than the counterclaim that choice is due to sexual conflict because only large males are able to overcome female resistance traits. The authors are aware of these problems and the need to measure actual costs and benefits. Interestingly, however, they seem to conclude that sexual conflict explanations are less amenable to definitive experiments than ones invoking benefits of choice. They suggest that accumulation of confirmatory evidence from multiple sources will be required to demonstrate convincingly a role for sexual conflict in the evolution of specific traits (p. 226). In contrast, definitive experiments to falsify the claim that female choice is maintained by genetic benefits are possible and, indeed, essential. The difference may be that sexual conflict explanations seem to require evidence about traits' origins (i.e., a history of sexually antagonistic coevolution), while Fisher-Zahavi model explanations are ahistoric. The latter require only that choosiness is currently maintained because greater net offspring fitness compensates for any reduction in female fecundity to increase the net production of descendants. Sexual conflict explanations should be held to the same standard. This means that sexual antagonistic selection must be shown in extant populations. Although sexual conflict may be "hidden" in observational studies (like the static pose of evenly matched arm wrestlers), phenotypic manipulation can test whether reducing putative female resistance traits increases direct fitness costs. If this is not possible, then there is no real progress. No matter how convincing the indirect evidence that sexual conflict maintains mate choice, it will be no superior to, say, the equally plausible claim that genetic benefits must maintain extrapair copulations in birds if females actively seek out mates on distant territories during their peak fertilization period (e.g., Double and Cockburn 2000).

The abuse of sexual conflict arguments will be diminished by the clear-headed explanations of concepts provided in *Sexual Conflict*. In the penultimate chapter, the authors undertake a housekeeping exercise to define terms and clarify theoretical issues. They do a great job of dispelling the myth that either sex can "win" the battle—only specific alleles can. I was, however, confused by their argument that sexual conflict should not be invoked when males attempt to "override" female choice. This view clashes with widespread usage. Parker (1979) defined sexual conflict as a conflict of evolutionary interest between individuals of the two sexes. Why does this not fit with a situation in which a male cricket prevents premature removal of his spermatophore (a form of cryptic choice) if such retention is costly to the female? The authors argue, for example, that although there is sexual con-

flict over the mating rate itself, a female deciding whether to mate with a particular male because of his genotype/phenotype is in the domain of the traditional topic of sexual selection (p. 224). Earlier in the book, however, the authors also note that sexual conflict may be male phenotype dependent (i.e., males vary in the costs that they impose) and phenotype independent (i.e., mating excessively is costly regardless of male identity). To be internally consistent, this implies that the authors are suggesting that when a male's ability to "override" female choice is phenotype dependent, this should be discussed without invoking sexual conflict. I suspect that many readers will need more convincing on this point.

In sum, *Sexual Conflict* is a well-written book that is extensively researched and full of quirky biological facts. As I read it, I began to think of new experiments and interesting species that I would like to study. I am less sure that a monograph on mainstream mate choice theory would have evoked the same response. New angles lead to fresh insights. The occasional polemic statement aside, there is every reason to believe that sexual conflict will soon be integrated into sexual selection theory. The authors have provided a valuable resource, and I hope that it will be widely read.

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