

Trick or treat: the battle of the sexes

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Males and females differ in many ways due to their distinct roles in reproduction. A fundamental asymmetry, that in fact defines the genders, occurs over initial investment in gametes, with males producing many, tiny and females few, large gametes. Another very general asymmetry concerns the intensity of selection for multiple mating between the sexes: while males can maximize their reproductive output by obtaining as many partners as possible, females need fewer partners to achieve their maximum reproductive output (Bateman, 1948). That these distinct roles can generate a 'battle of the sexes' or 'sexual conflict' and can affect the evolutionary dynamics of reproductive traits and behaviours has been recognized since the 1970s, and has now developed into an exciting and major area of investigation in evolutionary biology. Evolutionary conflict between the sexes, or sexually antagonistic selection, can affect either traits encoded by the same locus in both sexes (intra-locus conflict), where different phenotypic values will be favoured, or male and female traits governed by different loci (inter-locus conflict). While intralocus conflict may result in the evolution of sex limitation and sexual dimorphism (*de facto* becoming an interlocus effect), interlocus conflict gives wide scope for continual evolution of traits in males that manipulate female reproduction, and of female resistance to manipulation. The recent rise of interest for this field was particularly stimulated by this insight that antagonistic selection on male and female traits can fuel chain reactions of reciprocal evolutionary change, i.e. lead to an 'intra-specific Red Queen' process analogous to coevolutionary arms races between hosts and parasites (Rice & Holland, 1997).

The timely monograph by Arnqvist & Rowe (2005) synthesizes research on sexual conflict, embeds it in the historical and conceptual context of sexual selection research, explores many natural history examples across taxa, and questions both the conceptual stringency and the empirical testability of hypotheses emanating from the idea of diverging evolutionary optima in males and females, thus paving the way for future directions. One of the strengths of this book is the comprehensive look at studies completed by a wide variety of scientists

(on 75 pages, the reference list comprises over one-fifth of the book).

As a young field of broad interest to biologists from different sub-disciplines, sexual conflict is not free of conceptual heterogeneity. The possible meanings of metaphors such as 'conflict resolution' or 'battle of sexes' are fitted into the framework of intraspecific coevolution, where average male and female fitness cannot be independent of each other. The authors are honest about the fact that there are often identical expectations under a sexual selection and sexual conflict scenario; for example, correlated male-female evolution. They note the difficulties this presents in determining the force at work in any given system. However, they also discuss the theoretical contributions that sexual conflict theory has made, including the distinction between a male trait experiencing sexually antagonistic selection vs. sexual selection. Under sexually antagonistic selection, the male trait is advantageous to the male but simultaneously disadvantageous to the female. In contrast, a male trait under traditional sexual selection is advantageous to both the male and the female. Thus, in the latter case the male trait can spread by female preference for the trait. Despite this theoretical distinction, there currently is no golden rule to demonstrate conflict in any given system. For empiricists, the authors advocate a combined approach, encompassing economic studies to measure costs and benefits of sexual interactions, phenotypic manipulation, experimental tests of optimality modeling, experimental evolution, genetic experiments, and comparative studies. They also discuss how to measure the strength of sexual conflict by the phenotypic selection gradient approach of Shuster & Wade (2003), and through inference of the cost of sexually antagonistic adaptations to population fitness. The honesty in discussing how far empirical studies can discriminate among hypotheses, and in identifying where empirical evidence or theoretical developments are lacking, is one of the strengths of this book. Such honesty both promotes further thought and discussion among readers and avoids the pitfalls of overinterpretation.

The conflict between the sexes can affect traits expressed both before and after mating. Pre-mating sexual conflict is illustrated by examples as diverse as

diving beetles, bedbugs (a group of organisms where insemination is through the body wall, bypassing female resistance to mating), and water striders. The analysis of pre-mating conflict is one of the authors' areas of expertise, in particular their work on water striders. Accordingly, the section on identifying adaptations for male persistence (a term coined by Parker, 1974) in obtaining matings and female resistance to multiple matings is thorough. Similarly, the sexes can disagree over copulation duration, as suggested by male and female genital morphology and female physical struggles during mating in many species. While the 'good genes' hypothesis predicts that females struggle to test males and choose those with the greatest endurance, the sexual conflict hypothesis predicts that males impose copulation durations beyond a point that is beneficial for females (for example, to transfer manipulative seminal proteins) and females will struggle to avoid the cost.

Again Parker's work was groundbreaking for recognizing that sexual selection continues after mating in polygamous mating systems. Post-mating processes include sperm competition, where the gametes of multiple males compete for access to the ova of a female, and cryptic female choice, where females bias the fertilization success of one male over another (Parker, 1970; Eberhard, 1991, 1996; Thornhill, 1983). Parker's (1970) review on sperm competition has been cited over 1000 times, and this demonstrates how post-mating sexual selection became a major topic of research in zoology (Smith, 1984; Birkhead & Møller, 1998; Simmons, 2001). Some of the most interesting and far-reaching work in sexual conflict has been the discovery that female interests can be compromised by male adaptations to sperm competition. Compromises can occur from both defensive adaptations in males such as those that cause increased female refractoriness to remating and offensive adaptations such as those geared towards removing or otherwise incapacitating previously stored sperm. Potential costs to females induced by defensive male traits (e.g. traits that delay female remating) include direct material or genetic costs, incidental side effects (e.g. due to mate guarding), and harm solely for the sake of delaying remating. Offensive male traits can be costly to females due to damaging ejaculates (increasing risk of polyspermy, infertility or injuries following traumatic insemination) and because they may restrict the female's ability to exert cryptic female choice. The authors discuss some lines of evidence consistent with costs to females from damaging copulation but temper this with a list of other hypotheses that could account for the observations. For example, a reproductive tract immunologically hostile to sperm may be due to selection on females to avoid infection. As to the cost of denying females the opportunity of cryptic choice the authors are convincingly skeptical.

Both reproductive behaviour and physiology in females are regulated by a complex endogenous system that makes male exploitation possible. Indeed male

ejaculates often contain substances similar or identical to those signals endogenous to females. Mating induces egg maturation and ovulation in most animals (Eberhard, 1996) and in insects this effect has been shown to be due to male-transfer of gonadotropins. For example, the vitellogenesis-stimulating hormone itself (Juvenile Hormone, JH) is packaged into the spermatophore and transferred to females during mating in the silk moth *Cecropia*. In other insects, males transfer a substance that induces endogenous JH production in the female. Because under polygamy males may increase their fitness by causing females to produce offspring (prior to remating) at higher rates than favoured by natural selection in females, these male-transferred substances are candidate traits for sexual conflict. Because of life-history trade-offs, male manipulation of female reproductive rate may have costs for females, such as faster senescence. While female mortality schedules were at the start of exciting discoveries on sexual conflict (e.g. in *Drosophila*), this discussion suggests that the investigation of additional life-history consequences may be one of the promising future directions in sexual conflict research.

Beyond the fascinating diversity of natural history, comparative tests have made clear that sexual conflict has potentially important evolutionary implications. In particular, sexually antagonistic coevolution can generate fast local co-adaptation between the sexes and promote speciation both in allopatry and sympatry. Comparative tests support the role of intersexual selection in speciation, and sometimes in extinction. How this implication can be tested on a micro-evolutionary scale, in particular through inferences from between-population crosses, has been a topic of a recent debate among several scientists including the authors. While Arnqvist used this approach experimentally, Rowe unveiled the weaknesses with respect to interpretation using theoretical models. Inferences from between-population crosses often reveal significant interactions between the sexes but cannot on their own conclusively demonstrate sexually antagonistic coevolution.

Evidence of sexual conflict is available mainly for insects, yet sexual conflict is expected to apply to all sexually reproducing species. The authors explore this taxonomic breadth and use examples from hermaphroditic animals where sexual conflict can be overt (e.g. hypodermic insemination in leeches or flatworms, sperm digestion and love darts in molluscs). Overt conflict of this type may result from the fact that in hermaphrodites sexual conflict is not only expected after mating (with the special twist that manipulations could increase female allocation in the partners), but can also involve mating roles (donate/receive sperm). The latter may be resolved in a *tit-for-tat* manner by gamete trading. A few idiosyncrasies are discussed: hermaphroditism prevents the evolution of sex-limited expression that can resolve intra-locus conflict, it may be favourable in conditions where mates are scarce and pre-mating sexual selection is

weak, and may be associated with an even sex allocation optimum, not fulfilling Bateman's principle. Despite this, the authors provide arguments that there is no strong reason to assume less potential for post-mating sexual conflict and sexually antagonistic coevolution in hermaphrodites. This is tantalizing news for those studying another major group of sexually reproducing and typically hermaphroditic organisms, the flowering plants. Although plants are sedentary and rely on vectors for 'mating', making pre-mating sexual selection unlikely, pollen competition occurs after pollen deposition, and could generate consequences similar to those of sperm competition. Selection on pollen tubes for rapid growth may result in traits that inhibit competing pollen but also in suboptimal fertilization of the pollen recipient. In fact, double fertilization itself may have evolved in response to parental conflict over offspring provisioning. The authors point out that the study of plant and animal reproduction has traditionally been conducted in different contexts, i.e. avoidance of selfing vs. sexual selection (Barrett, 2003; Bernasconi *et al.*, 2004). A unified view of sexual conflict theory across diverse taxa may lead to exciting novel insights.

On the other hand, plants can inspire new ideas to zoologists. This was the case for the interpretation by Haig & Westoby (1989) of genomic imprinting as a conflict between paternally and maternally inherited genes. This hypothesis, despite some controversies, was successful in predicting patterns of imprinted gene expression during early development of mammalian embryos as well as in the triploid endosperm of flowering plants. It is quite possible that the scientific impact of this widely known idea also contributed to making sexual conflict an influential topic. As the authors briefly discuss, the conflict hypothesis of genomic imprinting has implications touching on cancer and developmental failures and raises the possibility that sexual conflict may have evolutionary costs even impacting on human health. Parental evolutionary interests can diverge not only for investment during early embryonic growth, but also when offspring need parental care, a costly undertaking that can decrease future survival and reproduction of the caregiver. Strategies in the tension field between increased parental care in the parent of one sex and more selfish behavior in the other are illustrated by case studies in birds (penduline tits, European starlings, collared and pied flycatchers) and insects (burying beetles).

In sum, *Sexual Conflict* is a pleasant read, and the wealth of examples, ideas and useful discussions of methodological approaches will appeal not only to researchers in the field, but to anyone with an interest in evolution. For undergraduate biologists just learning about this field, in future editions it would be convenient if some of the

main concepts, models or major case studies were explained in distinct and easy-to-retrieve explanatory boxes. Suggestions in the book towards demonstrating sexual conflict and understanding its implications more deeply are (1) to pay more attention to selection acting on females, in particular to measure fitness costs to females arising from adaptations in males, (2) to include more taxa, and (3) to develop theory. Our guess is that novel genomics approaches may also take an enlightening part in future studies. It will be exciting to witness the impact this book will undoubtedly have on future research in this field.

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