

Sexual conflict

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Sexual conflict occurs when the genetic interests of males and females diverge. Recent evidence supporting the view that male and female genomes are in conflict has now revolutionized the way in which we interpret interactions between the sexes, and suggests that sexual conflict is a potent force in male–female coevolution. Here, we consider the nature of sexual conflict and what distinguishes it from models of coevolution by sexual selection. There are advantages and pitfalls to the various experimental and comparative approaches now used. More precise predictions derived from theory are essential to evaluate much of the empirical data in support of sexually antagonistic coevolution. Equally, there needs to be a mechanistic understanding of the traits underlying sexual conflict to formulate and test these predictions.

Males and females have divergent interests in reproduction that are rooted in anisogamy and lead to distinct roles, where traits favoured by one sex might be costly to the other. Broadly defined as ‘differences in the evolutionary interests between males and females’ [1], sexual conflict is, in principle, pervasive among sexual species [1–3], and can occur between the same or different genes, that is when there are different optima for a trait expressed in both sexes (intralocus conflict) or when there is conflict over the outcome of a male–female interaction (interlocus conflict) (Box 1). Here, we focus on how interlocus conflicts drive evolutionary change and how this process differs from that predicted by other models of coevolution.

The traditional view of reproduction was one of cooperation and harmony between the sexes. This view resulted, in part, from an overestimation of the frequency of life-long monogamy in nature. Yet, the uneasy alliance between the sexes was recognized by some. Trivers concluded that ‘even when ostensibly cooperating in a joint task male and female interests are rarely identical’ [2] and Dawkins commented that ‘if there is conflict of interests between parents and children, who share 50 percent of each others’ genes, how much more severe must be the conflict between mates, who are not related to each other?’ [4]. Parker [1] provided the first formal treatment of the arms race between the sexes that can be generated by sexual conflict, citing the example of yellow dung flies *Scathophaga stercoraria* (Box 1).

How is sexual conflict different from other forms of sexual selection?

Models of coevolution by sexual selection can broadly be classified into those where the female preference is favoured indirectly and those where it is favoured directly. In indirect models, the preference evolves because it becomes genetically associated with genes that confer sexy sons (the Fisher process) and/or high-viability offspring (the good genes process) [5,6]. Such indirect effects probably play at least some role in most coevolution by sexual selection (Box 2), even if the preference is under strong direct selection [5,7]. In direct models, the preference itself is under natural selection. Females expressing the preference might gain resources (e.g. nuptial gifts), greater male parental care, fewer parasites transferred at mating, and so on [8]. The few verbal and formal models of sexually antagonistic coevolution that we have fall into the direct selection class. However, the force driving the evolution of the preference is better described as a general female avoidance of male-imposed costs, rather than, as in traditional direct models, acquisition of benefits from preferred males (e.g. [1,9–11]). Here, the preference is resistance (Box 2). The boundary, if there is one, between traditional models of sexual selection and those of sexual conflict has not yet been carefully explored theoretically.

Sexual conflict theory

Sexual conflict arising from differences in costs and benefits of mating

In addition to Parker’s [1] original treatment (Box 1), many other game theoretical models show that asymmetries in interests can generate male–female coevolution (reviewed in [12]). A promising new modelling strategy, using artificial neural networks, addresses male–female coevolution under nonequilibrium conditions. These simulations suggest that females exhibit hidden preferences that can be exploited by males [13], and that neither sex can be said to ‘win’ a conflict because evolutionary equilibria between male signals and female receptors are never reached [11,13,14].

Using a genetic model, Rice [15] predicted that sexually antagonistic genes should be located on the sex chromosomes, and recent empirical work supports this prediction [16]. Rice showed that alleles of sex-linked genes can spread even when the cost to one sex outweighs the benefit to the other. Gavrillets *et al.* [10] used a quantitative genetic model to address the situation in which female

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Box 1. Intra- and interlocus sexual conflict

Two main forms of sexual conflict can be distinguished. When the fitness optima for a trait expressed in both sexes are different in males and females, this is referred to as intralocus conflict. Here, antagonistic selection in males and females, coupled with a genetic correlation between the two sexes, will lead to each sex impeding adaptive evolution in the other [a]. However, selection for sex-limited gene expression could result in independent evolution in the two sexes, thus enabling each sex to reach its adaptive peak [b,c]. Intralocus conflicts are potentially very common, although their evolutionary importance is debated [d,e]. Recently, Chippindale and co-workers provided strong evidence for such conflicts in laboratory stocks of *Drosophila melanogaster* [f]. They found a strong positive genetic correlation between male and female fitness at the larval stage (when the interests of the two sexes are concordant), but a strong negative genetic correlation between adult male and female reproductive success (when the sexes are expected to have different genetic interests). This remarkable result suggests that there is substantial antagonistic adult fitness variation, with genes that benefit males being simultaneously detrimental to females and *vice versa*. However, it is possible that much of the adult fitness variation attributable to unconditionally deleterious mutations have been removed from these laboratory populations with their rather constant environments. This would have the effect of inflating estimates of the contribution to fitness variation by sexually antagonistic alleles. However, studies of genotype \times sex interactions for adult fitness components do provide evidence for intralocus conflict [g]. More studies of this nature will enable us to determine how common such loci are.

By contrast, interlocus conflicts occur when there is conflict over the outcome of male–female interactions, so that the optimal outcome is different for the two sexes [h]. Such conflicts can occur over mating frequency, fertilization, relative parental effort, female remating behaviour, female reproductive rate and clutch size. Both sexes are expected to evolve suites of sexually antagonistic adaptations that bias the outcome towards their own interests [i]. The result is sexually antagonistic coevolution between interacting traits in males and females. It was Parker [j] who first pointed to the general importance of such coevolutionary processes. He cited as an example, the drowning of yellow dung fly *Scathophaga stercoraria* females caught up in struggles between male suitors. In this example, males are presumably subject to intrasexual selection for competitive ability. However, this has the side-effect of selecting for sexually antagonistic adaptations in

females to lessen the deleterious effects of becoming casualties in battles between males. Parker considered what would happen when a novel male trait, favoured in males by sexual selection, conveyed a cost to females. In spite of the fact that females could benefit from mating with males carrying the novel trait, because of a ‘sexy sons’ effect, the novel trait was often favourable to males but harmed females. When a male trait and female response were allowed to coevolve under sexual conflict, ‘unresolvable evolutionary chases’ often occurred. Parker’s early work illustrated that sexually antagonistic coevolution can lead to rapid, directionless and unpredictable evolutionary change.

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choice arises from avoidance of direct mating costs. The model assumed an optimal female mating rate and that male fitness increased with increasing mating frequency. The model predicted that the resulting conflict over mating patterns can result in rapid antagonistic coevolution, where male display traits are exaggerated as a consequence of female resistance (Box 2). In this formulation, the costs of resistance to females at equilibrium can be substantial (Box 2; [17,18]).

Parental care and sexual conflict

Trivers stressed that sexual conflict is central to the evolution of parental care [2]. Although outside the main scope of this review, it should be noted that various forms of sexual conflict over parental care occur: each sex should generally prefer the other to ‘work harder’, because the evolution of increased care by one sex will enable reduced care in the other [14,19,20]. We thus often expect sexually antagonistic coevolution between traits that function to increase provisioning by the other sex, and those that function to resist such manipulations (Box 3). A rich body of game theory models centres on this general prediction,

but also point to the social complexity of such conflicts (reviewed in [21,22]). Genomic imprinting is another possible evolutionary consequence of conflicts over offspring provisioning in mammals (reviewed in [23,24]).

Sexual conflict and speciation

Sexual conflict clearly has the potential to promote allopatric divergence [25,26]. During allopatry, males and females are expected to coevolve at different rates along separate coevolutionary trajectories, assuming that there are multiple perceptual, mechanical or biochemical biases in females that males can exploit [11,13]. Two recent models have examined situations in which compatibility between males and females determines the outcome of sexual interactions (i.e. reproductive state ‘matching’), and have found that sexual conflict promotes both allopatric [27] and sympatric [28] divergence in reproductive traits. In a series of game theory models, Parker and Partridge [29] considered the likelihood of reinforcement when partly diverged populations meet. They showed that sexually antagonistic coevolution could drive increased rates of speciation under some scenarios, but, under

Box 2. Female resistance to reduce mating rate or to 'screen' males?

Substantial evidence demonstrates that females can suffer significant direct costs of mating (e.g. [a]) that are sufficient to explain the frequently observed resistance of females to mating as well as the evolution of male traits functioning to overcome this resistance. Experimental reductions in the level of female resistance can lead to longer and more frequent copulations [b,c]. Moreover, variation in female resistance and resulting sexual selection can be predicted, based on direct fitness tradeoffs [d–f]. In contrast to the view that female resistance is favoured because it decreases the magnitude of direct costs is the suggestion that such costly behaviour is maintained by indirect selection for genetic benefits (e.g. [g]). Under this scenario, female resistance evolved and is maintained as a result of selection to screen among males of different genetic quality. Males that are most persistent in mating attempts are assumed to be the fittest. Females should therefore elevate their levels of resistance to mate with the persistent males, and thus gain greater genetic benefits for their offspring.

However, the increasing evidence that females suffer substantial costs of physical resistance, including death [d,h,i], is inconsistent with the idea that they resist matings with males to screen them. The magnitude of indirect genetic benefits required to offset such costs in females would seem prohibitively high. Even if resistance becomes genetically correlated with male persistence owing to linkage disequilibrium, such indirect benefits are expected to be a weak force in the face of direct selection on resistance (cf. [j]). Although no studies have yet demonstrated indirect selection on resistance, we might expect such effects to occur. Yet, any beneficial screening effect that might be detected (i.e. more resistant females producing fitter offspring) is more likely to represent a reinforcing side effect rather than being the main selective benefit of resistance.

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others, it led to increased gene flow between populations. The contribution of sexual conflict to speciation depended upon the intensity of selection on males *versus* females and the scope for evolutionary change in each sex, both variables that are difficult to determine.

Detecting sexual conflict and its consequences

It was originally thought that sexual conflict would be difficult to study because of problems in accurately measuring relative costs and benefits in males and females [1] and in identifying the underlying genes involved. Adaptation followed by balancing counteradaptation also makes coevolutionary trajectories difficult to observe unless populations are perturbed [3,30]. However, an increasing number of studies have measured the costs and benefits of mating interactions in males and females, and molecular genetic tools have revolutionized the study of sexual conflict in model systems such as *Drosophila melanogaster*. Here, we briefly review such studies, with a focus on more recent advances. Nevertheless, we wish to emphasize that, in the absence of a clear functional understanding of the traits involved, it is currently not possible to isolate sexual conflict as the force leading to a pattern of rapid evolution of reproductive characters or to speciation.

The economics of mating and the evolution of antagonistic traits

A basic requisite for sexual conflict over mating interactions is that optimal outcomes differ for males and females, a finding documented in several recent studies

(e.g. [31–35]). The existence of morphological adaptations in both sexes, which give an advantage to the bearer at the expense of the other sex, suggests the potential for an evolutionary arms race. There is clear evidence of such sexual antagonism in the evolution of morphological adaptations of water striders ([30], reviewed in [31,36]). A recent comparative analysis of 15 congeneric species of these insects showed that evolutionary changes in the balance of armaments between males and females (i.e. clasping and anticlasping adaptations), but not in the absolute level of armament escalation, resulted in evolutionary change in the outcome of sexually antagonistic mating interactions [30].

Bumble bee *Bombus terrestris* females benefit from multiple mating [37,38]. Yet, both genetic and behavioural data show that females mate only once in their lifetime [39]. This is due to male transfer of mating plugs and seminal substances that prevent female remating [40]. Males can apparently successfully prevent female remating in spite of the detrimental effects of monandry to females. In *D. melanogaster*, a negative tradeoff between a component of sperm competitive ability in males and early female mortality was identified [41], suggesting that genes which conferred a sperm competition advantage on males had a deleterious pleiotropic effect on females [3].

Another powerful means of demonstrating the existence of sexual conflict and the function of the underlying traits involved is to manipulate them genetically (Box 4). For any study of the costs and benefits of mating to provide evidence of sexual conflict, net costs and benefits for each sex must be precisely defined and measured. For example,

Box 3. Sexual conflict over parental care

The genetic interests of males and females often differ with regards to parental care. Fundamental conflicts over mate desertion, over the relative amount of care invested in offspring and over the number of simultaneous mates are common [a]. This sets the stage for sexually antagonistic coevolution between various behavioural adaptations in both sexes. For example, among biparental species with a variable mating system, it is commonly in the interest of a female to monopolize the reproductive effort expended by her mate. Whereas paired males often spend considerable effort on attracting more or additional females, we expect females to exhibit sexually antagonistic adaptations aimed at keeping their mates monogamous. Such female strategies occur in birds, fish and insects, and include: (1) interference with male mate attraction by soliciting superfluous copulations [b] or by directly attacking or otherwise obstructing displaying males [c]; and (2) general aggression towards other females, particularly during the pair formation period [d,e]. Males could, however, reduce female interference by, for example, signalling at some distance away [f,g] or by physically intervening in aggression from females directed towards new potential mates [h]. Such coevolutionary 'tug of wars' between the sexes can sometimes result in highly dynamic mating systems [i], and can generate evolution of mating system components even in the absence of any change in the ecological setting [j].

Sexually antagonistic coevolution between male and female reproductive behaviours that affect parental care is in theory very similar to coevolution between other types of sexually antagonistic traits. Research of sexual conflict should benefit from better integration of theory from different fields and from the incorporation of results from different taxa.

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a detected reduction in female longevity could be a consequence of rescheduling the timing and scale of reproduction without necessarily representing a net fitness cost.

Artificial selection

An important line of evidence for detecting sexual conflict comes from studies of experimental evolution in *D. melanogaster*. The first evidence for sexually antagonistic genes was described by Rice [17]. Chromosomal regions were confined to either females (experimental lines), or to both sexes (control lines). Sexual conflict predicts that the gene regions confined to females would be released from any counterselection during expression in males and should therefore accumulate 'female benefit–male detriment' alleles. Fewer males containing these gene regions emerged from cultures than from control lines, suggesting that males from the experimental lines contained alleles that were detrimental for them. The nature of the genes involved remains unclear and it is not known how they benefit females or harm males. Rice [42] also studied the evolutionary consequences of release from sexual antagonism. He used a stock of *D. melanogaster* with chromosomal translocations to provide a standard female phenotype against which males could evolve. Females were discarded every generation and could not counter-evolve to the adapting males. Consistent with a beneficial effect of release from sexual antagonism, adapting males scored more highly in fitness assays compared with controls. Test females also suffered higher mortality when mating with males from one replicate of the adapting

male lines relative to females mated to the other adapting or control line males.

The evolutionary consequences of reduced opportunity for sexual conflict (and sexual selection) have also been studied in *D. melanogaster* by imposing monogamy [18]. Using experimental evolution, monogamous (one male and one female) or polyandrous (one female and three males) lines were created. After 47 generations, females mating with monogamous males had higher subsequent survival than did those mating with polyandrous males. Monogamous females had lower survival than did polyandrous females when paired with polyandrous males. The short-term fecundity of monogamous females was also lower than that of polyandrous females when both were exposed to ancestral, base-stock males. These results suggest that monogamous females were more susceptible to the potentially deleterious effects of mating with males, and that monogamous males were less able to inflict harm to females. Monogamous populations also exhibited a greater net reproductive rate, suggesting a cost to sexual conflict. Pitnick *et al.* [43,44] tested the same lines after 80-plus generations of selection and several differences between regimes were consistent with sexual conflict. However, there were also some unexplained differences between lines within treatments.

The experimental design employed in the *Drosophila* experiments [18], and in similar studies of *Scathophaga* [45], results in higher inbreeding in the monogamous versus polygamous lines. This is a potential problem because both sexual conflict and higher inbreeding predict that monogamous males should reduce investment in

Box 4. Sexual conflict and the evolution of male accessory gland proteins in *Drosophila*

In *Drosophila melanogaster*, the major male reproductive tract proteins are the 80 or so accessory gland proteins (Acps) [a] which are transferred to the female with the ejaculate during mating. Such proteins directly affect female behaviour and physiology after copulation in many insect species and their evolution appears to be influenced by sexual conflict, at least in *D. melanogaster*. Acps show high levels of amino acid polymorphism and interspecific divergence, and are estimated to evolve at twice the rate of nonreproductive tract proteins [a]. There is evidence for directional selection on 12 different *Acp* gene sequences. High rates of evolutionary change in loci encoding seminal fluid proteins appear to be common both within and between *Drosophila* species (reviewed in [b]). This is predicted by sexually antagonistic coevolution, but is also consistent with other models of sexual selection.

The Acps involved in conflict in *D. melanogaster* [c] were identified using males genetically engineered to lack them [d]. These males were used to demonstrate that main-cell Acps are necessary for sperm transfer [e] and cause the female cost of mating [f] which appears to result from sexual conflict in this species. Males that lack specific Acps have been used to determine *Acp* function and involvement in sexual conflict (e.g. [f–i]) by comparing the performance of a knockout mutant with that of a wild-type gene control. Another manipulation for studying function is the overexpression of specific Acps. Using this technique, it was recently shown that overexpression of *Acp62F* (but not seven other Acps) caused a reduction in adult *D. melanogaster* life span [j]. *Acp62F* is therefore a candidate for causing the *Acp*-mediated cost of mating in females. This *Acp* is one of several protease inhibitors that may protect sperm and/or seminal fluid substances from enzymatic attack in the female reproductive tract [j]. Its deleterious side-effect might be due to interference with essential enzymatic processes inside the female body cavity, as this *Acp* enters the female haemolymph through the vaginal wall [j].

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reproduction and evolve to become more benign to females, relative to polyandrous males [46]. This leads to potentially confounding effects of monogamy and inbreeding.

Comparative studies

Comparative studies provide some evidence that sexual conflict has played a direct role in the evolutionary diversification of natural populations. Sexual conflict is predicted to promote rapid evolutionary change in the underlying genes involved [25,47]. Data consistent with this prediction are now coming from sequence analyses of male reproductive tract proteins, some of which appear to be involved in sexual conflict [48] (Box 4). Unfortunately, we know much less about rates of evolutionary change in the receptors of these proteins. However, unidentified ovary proteins do show elevated levels of divergence in *D. melanogaster*–*Drosophila virilis* species group comparisons, relative to nongonadal proteins [49]. Sequence analysis of the receptors to three mammalian fertilization proteins in a range of different mammalian species has also recently uncovered higher rates of evolutionary change relative to control genes [50]. It will be necessary to identify more of the genes involved in sexual conflict, in both sexes, if we are to understand the role of conflict in genetic divergence.

Two recent studies of morphological traits also support a role for sexual conflict in the rapid coevolution of antagonistic reproductive characters between species. The first study, noted above, provides good evidence for an

arms race in water striders [30]. The second study, in diving beetles, suggests antagonistic coevolution of male grasping and female antigrasping traits [51]. Both are notable because they feature traits in both sexes, the function of which in sexual conflict is understood. The degree of evolutionary divergence in genitalic traits of male insects is also significantly elevated in polyandrous relative to monogamous species, as is predicted by the increased potential level of conflict under polyandry [52]. It should be noted however, that it is difficult to make precise inferences about coevolutionary processes from molecular and morphological data that describe trait divergence in one sex only.

Population crosses

A promising line of investigation into the role of sexual conflict in early divergence is to cross closely related allopatric populations. Sexually antagonistic coevolution is predicted to result in differential rates of evolution between different populations and, under some scenarios, evolution along separate coevolutionary trajectories. Although the latter prediction is also a feature of other models of sexual selection, it should be possible to identify conflict as a force in population divergence using predictive theory and careful crosses between populations [29]. For example, females might lack resistance to allopatric males with which they have not coevolved. Several recent studies have crossed populations to investigate interactions between responses in reproductive traits and population

origin [53–58]. Andrés and Arnqvist [55] crossed three strains of the housefly *Musca domestica* in all combinations. Males crossed within two of the three strains induced a lower proportion of their mates to oviposit than did males crossed between strains. There was thus a tendency for weaker responses of females to males with which they had coevolved, but this was not entirely consistent across strains. Brown and Eady [56] compared the results of crosses within and between two populations of *Callosobruchus maculatus* beetles. Males in within-population crosses had higher sperm competitive ability, and induced a longer period of nonreceptivity and higher fecundity in their mates than did males in between-population crosses. The lowered fitness of males in crosses between populations contrasted with the results of Andrés and Arnqvist [55]. Two similar studies, in *Drosophila* [57] and in *Tribolium* [58], also generated partly inconsistent results. In spite of the conflicting results of all these studies, many of the data were interpreted as support for sexual conflict. This suggests that current theory is not sufficient to specify a clear null hypothesis and separate patterns predicted by sexual conflict from those predicted by other processes. One feature currently missing from these studies is a measure of population genetic differentiation. The accumulation of reproductive incompatibilities is eventually expected to lead to reproductive isolation [25,28] and could complicate interpretation of results. Sexually antagonistic traits that vary either quantitatively or qualitatively are also predicted to lead to different outcomes in male–female interactions within and between populations [55]. A mechanistic understanding of conflict is therefore essential to indicate the identity and nature of the relevant traits to study.

Prospects

There is widespread evidence that interactions between the sexes are often characterized by conflict. There is also good evidence that sexual conflict influences the evolution of reproductive traits. We see research along the following lines as being particularly important in the near future.

We need to develop better, generally applicable frameworks and predictive theory for male–female coevolution under interlocus sexual conflict. It is, for example, unclear exactly what is meant by the intensity or strength of sexual conflict, whether and how it can be quantified and manipulated, and how it relates to the rate of sexually antagonistic coevolution. It is a particularly difficult concept, because past conflict can be hidden by adaptation [3,30]. We also need theoretical models that explicitly incorporate female resistance generated by antagonistic coevolution into existing models of female choice, to understand the relative importance of these processes [6, 59].

Self-reinforcing coevolution of armaments, even in the absence of other types of selection, is a central prediction of sexual conflict theory [1,25,60]. But, as yet, we lack a comprehensive understanding of the role of sexually antagonistic coevolution in trait diversification. Although sexually antagonistic coevolution can promote divergence, it is not always predicted to do so, and we need models that will enable us to use patterns of divergence to better

distinguish among alternative coevolutionary processes. We need to understand genetic mechanisms to enable us to probe conflict with standard genetic tools. We also need thorough comparative studies, based on traits in both sexes with known function to investigate the role of conflict in trait diversification, and in speciation and extinction.

Finally, much of the research has been confined to a handful of taxa and traits. The taxonomic breadth and range of phenotypic traits that are involved in sexual conflict therefore remain unclear. There is a need for further in-depth empirical studies of sexual conflict, preferably combining economic, functional and comparative studies at the organismal level with studies of the molecular and genetic mechanisms underlying conflict.

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