

# Evolutionary Conflicts of Interest between Males and Females Review

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Sexual conflict arises from differences in the evolutionary interests of males and females and can occur over traits related to courtship, mating and fertilisation through to parental investment. Theory shows that sexual conflict can lead to sexually antagonistic coevolution (SAC), where adaptation in one sex can lead to counter-adaptation in the other. Thus, sexual conflict can lead to evolutionary change within species. In addition, SAC can — through its effects on traits related to the probability of mating and of zygote formation — potentially lead to reproductive isolation. In this review, I discuss that, although sexual conflict is ubiquitous, the actual expression of sexual conflict leading to SAC is less frequent. The balance between the benefits and costs of the manipulation of one sex by the other, and the availability of mechanisms by which conflict is expressed, determine whether actual sexual conflict is likely to occur. New insights address the relationship between sexual conflict and conflict resolution, adaptation, sexual selection and fitness. I suggest that it will be useful to examine systematically the parallels and contrasts between sexual and other evolutionary conflicts. Understanding why some traits, but not others, are subject to evolutionary change by SAC will require data on the mechanisms of the traits involved and on the relative benefits and costs of manipulation and resistance to manipulation.

## Definition and Extent of Sexual Conflict

Sexual conflict arises when there is a difference in the evolutionary interests (i.e. fitness optima) of the two sexes [1]. Such differences are created by the differential investment made by males and females in reproductive processes, which is usually predicted by anisogamy. For example, generally speaking, males often have more to gain from obtaining a mating and more to lose by not mating than do females [1–3]. Whenever the different optima for males and females cannot simultaneously be realised, there will be sexual conflict [4]. The existence of different optima underlies the widespread existence of, and sex differences in, costs of reproduction and the many instances in which each partner can gain by investing less while their partner invests more [5–7]. Sexual conflict can occur over traits that are encoded by the same or different loci in males and females (intra- and inter-locus sexual conflict, respectively). It is exacerbated by the typically low relatedness of mating partners [8] and by mating

systems that promote divergence in the genetic interests of males and females in their current versus future offspring (e.g. due to promiscuity).

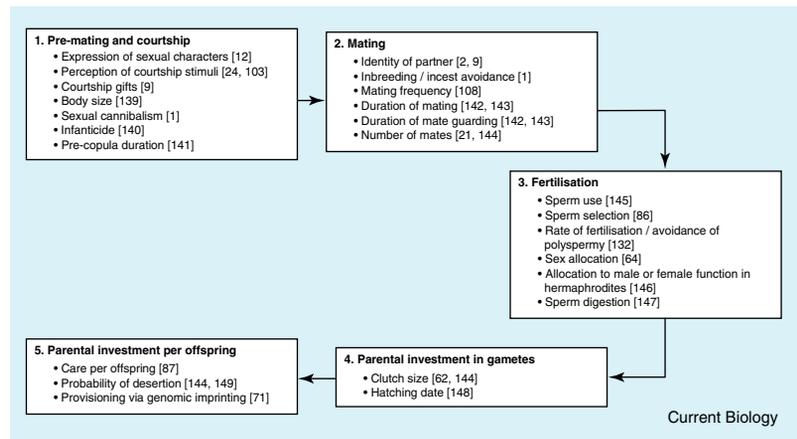
Sexual conflict is ubiquitous and encompasses processes from courtship, mate choice and mating, through to fertilisation and parental investment (Figure 1). The importance of sexual conflict is that it has the potential to drive evolutionary change via sexually antagonistic coevolution (SAC) [9]. This is because sexual conflict provides the potential for selection on each sex to try to reach its preferred optimum for a given ‘conflict trait’ [10] (Box 1), even though this will result in the other sex being moved further away from its optimum for this same trait. The sex most adversely affected by SAC may counter-adapt to try to minimise the fitness reduction caused by its being moved further away from its own optimum (the ‘conflict load’ [10], Box 1). This adaptation and counter-adaptation can drive evolutionary change in conflict traits.

In terms of evolutionary change within species, SAC driven by sexual conflict is the most cogent explanation for observations in which actions of one sex seem to result in costs to the other, or in which one sex seems to act against its best interests, in both cases without counter-balancing benefits [9]. Evidence for the existence of intra-locus conflicts comes from studies of traits common to males and females on which there is opposing selection. For example, in birds there is evidence for sexually antagonistic selection on tarsus length [11], beak colour [12] and survival [13], and in *Drosophila melanogaster* there is evidence for sexually antagonistic selection on lifespan [14]. Evidence for intra-locus sexual conflict also comes from selection experiments with *D. melanogaster* that reveal the existence of sexually antagonistic, female benefit–male detriment alleles [15] and from the discovery of sexually antagonistic genetic variation for fitness in adult *D. melanogaster* [16]. Evidence for inter-locus sexual conflict appears to be widespread [8,9,17–19]. It is, for example, the most convincing explanation for the drowning of dung fly females in dung as a result of the receipt of courtship and mating attempts from males [1], for the evolution of grasping and antigrasping mating adaptations of waterstriders [20], for variability in the social system of Dunnocks [21], and for the evolution of benign males under monogamous conditions [22] as well as for the existence of seminal fluid-induced mating costs in *D. melanogaster* [23].

SAC also has the potential, through its effects on traits related to the probability of mating and zygote formation, to result in reproductive isolation between allopatric populations and hence speciation [3,18,24]. This is because SAC may cause rapid adaptation and counter-adaptation in reproductive traits, which as a side-effect, could increase the chance of reproductive incompatibilities between different populations. The empirical evidence in support of this idea is somewhat

Figure 1. The extent of sexual conflict.

Sexual conflict can arise because of differences between males and females in the optimum value of traits related to courtship, mating, fertilisation and parental investment. Some examples of each in the context of sexual conflict are given; for numerous further examples, see [9]. See also [139–149].



mixed, though it highlights the potential of sexual conflict to drive rapid evolutionary divergence [15,22,25–27] and reproductive isolation [28]. The data that show rapid evolution in fertilisation traits (e.g. [29–32]) and in traits related to sperm or pollen competition [33,34] are consistent with the operation of SAC but also with sexual selection (i.e. either male-male competition or female choice). However, both positive associations [35–37] and no associations [38,39] between species richness and indices of the strength of sexual conflict (and sexual selection) have also been reported.

A significant problem in studying sexual conflict is that observation alone is often not enough, because SAC may be hidden from the observer. An example of crypsis in the context of conflicts arising from sex ratio distortion is found in *Drosophila simulans*. It had been assumed that, because equal sex ratios were observed in natural populations, this species had not been subject to invasion by sex ratio distorters. However, upon crossing different populations, the existence of multiple distorters and suppressors was discovered [40]. Hence, previous and ongoing conflict was entirely hidden (see other examples in [15,25]). In contrast, apparently overt conflict does not necessarily prove the existence of sexual conflict, unless any costs incurred outweigh any gains in inclusive fitness [41]. It is important to avoid subjectivity, because — especially in the study of evolutionary conflicts — organisms may often behave in a way that is inconsistent with gains or losses in their inclusive fitness [42].

The theory and data supporting sexual conflict have recently been reviewed in depth by Arnqvist and Rowe [9] and will not be covered in detail here. Instead, I explore the relationship between potential and actual sexual conflict [43] and discuss the factors, such as the balance between the benefits and costs of the manipulation of one sex by the other, which determine whether actual sexual conflict is expressed (Box 1). I review insights from sexual conflict theory and address the relationship between sexual conflict and conflict resolution, adaptation, sexual selection and fitness. I also explore some of the parallels and contrasts between sexual and other evolutionary conflicts.

### The ‘Spread’ of Sexual Conflict

The idea of contests and discords over mate choice decisions has been central to the study of sexual selection since the time of Darwin [44]. However, the idea of sexual conflict in terms of a more widespread ‘battle of the sexes’ came later [5]. Trivers [45], Dawkins [6] and most importantly Parker [1] developed the concept of sexual conflict. Following the prescient work of Parker [1], there was a hiatus before sexual conflict again received significant attention [15,24,25]. Since then, the investigation of sexual conflict has proceeded with an ever-increasing pace [4,18–28,46–49]. The increased interest in sexual conflict in the 1990s may have been partly due to technical advances in model systems that allowed previously untackled questions to be addressed [25]. This coincided with a renewed emphasis on the potential of SAC to result in damage or harm to females [23–25,50,51]. This re-emphasis promoted the discussion of seemingly hard to explain mating adaptations, such as toxins or spikes, but has had the unfortunate effect of obscuring the wider breadth and importance of sexual conflict [4,52]. Furthermore, the use of the term ‘harm’ tends to suggest a special feature of sexual conflict, i.e. the damage that is inflicted only on females and that is perhaps in addition to, or different from, the antagonistic selection over conflict traits. The focus on sexual conflict in relation to mating biases also led to a collision with the study of sexual selection [19,52–55]. To a large extent the sexual conflict versus sexual selection debate makes a false dichotomy as there are areas of overlap (see below).

### Potential versus Actual Sexual Conflict

I suggest that it is important to emphasise the distinction between potential and actual sexual conflict (Figure 2; [4,43,56]). Potential sexual conflict is present whenever the sexes have different optima for fitness-related conflict traits. However, conflict traits will only evolve if actual sexual conflict is expressed, which will depend upon the factors outlined in Figure 2. Actual sexual conflict may also shape traits at equilibrium. Potential conflict will be much more frequent than actual conflict [57] and, hence, SAC is likely to occur less frequently than the ubiquitous nature of sexual conflict might suggest. The recognition of the

**Box 1**

**Key concepts of sexual conflict.**

Sexual conflict	Occurs when there is a difference in the evolutionary interests (i.e. fitness optima) of the two sexes.
Sexually antagonistic coevolution (SAC)	The coevolution between males and females that is driven by sexual conflict.
Potential sexual conflict	When the sexes have different optima for fitness-related traits, but the sexual conflict is not expressed.
Actual sexual conflict	When the sexes have different optima for fitness-related traits, and the sexual conflict is expressed.
Conflict trait	Any fitness-related trait over which there is sexual conflict, i.e. for which there is a difference in the optimum value in males and females. Conflict traits may or may not be encoded by the same genes in males and females, hence this definition can cover conflict traits subject to intra- and inter-locus sexual conflict [4,10,99].
Conflict load	The reduction in fitness caused by each sex not being at its optimum for any conflict trait [4,10]. Note that this term does not measure the cost of bearing antagonistic traits [99].
Intra-locus sexual conflict	When a conflict trait is encoded by the same gene in males and females.
Inter-locus sexual conflict	When a conflict trait is encoded by different genes in males and females.
Value of winning	The relative size of the benefits of manipulation in males as compared to the benefits of resistance in females [4,10].
Power	The relative size of costs of manipulation in males as compared to the costs of resistance in females [4,10].

‘potential’ versus ‘actual’ distinction has proved particularly useful in the study of social insects in allowing tests of, for example, conflicts over reproductive division of labour, over sex allocation and over within-colony nepotism [57–59]. In the field of parent–offspring conflict, a distinction similar to the potential/actual conflict is made, namely between ‘battleground’ and ‘resolution’ models [60–63].

Sexual conflict will be more likely to lead to SAC when there are large differences in the fitness optima for conflict traits in males and females. This will tend to result in a large conflict load for one or both sexes, and consequently determine differences in the relative extent of the benefits of manipulation or resistance for males and females (i.e. the ‘value of winning’; **Box 1** and **Figure 2**). For example, as the benefits of increased manipulating ability show diminishing returns, manipulation driven by SAC becomes less likely. The relative costs of manipulation and resistance (i.e. ‘power’; **Box 1**) are also important. An additional factor is that the opportunity, or mechanism, for manipulation and resistance must be present. An example of such a lack of opportunity is found in the haplodiploid social

hymenoptera. In addition to the well-known queen-worker conflicts, there is also sexual conflict over the optimal sex ratio. Haploid males that mate with the queen generally have low relatedness to the sons that she produces from unfertilised eggs and, therefore, favour a sex ratio that is more female-biased than that favoured by the queen [58]. However, despite the sexual conflict, the power of males to enforce their interests is low [64] — they die after mating; sex ratio is probably controlled by the queen by either allowing or preventing the passage of sperm for fertilisation.

**Conflict Resolution**

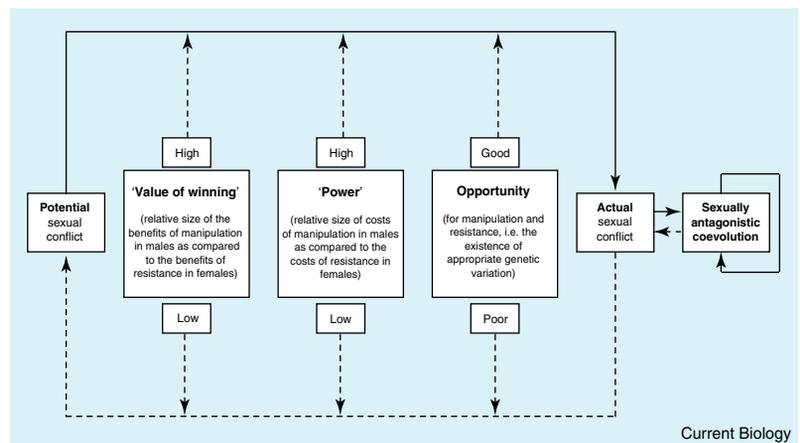
The incidence of actual sexual conflict in extant populations may also be lower than expected because of conflict resolution (**Figure 2**). Selection to reduce the effects of male and female adaptations undergoing SAC is expected, when the extent by which one sex reduces its own fitness by manipulating the other reaches a certain threshold. Here, resolution does not mean that the potential sexual conflict is removed, but just that its actual expression is reduced. Conflict resolution could theoretically be followed by the initiation of subsequent, novel conflicts [65].

SAC driven by intra-locus sexual conflict could be resolved by the evolution of sex limitation, i.e. the expression of traits by only one sex. The existence of many examples of sexually dimorphic traits suggests that sex limitation, and hence the liberation of genes from intra-locus conflicts, is widespread. Given this, it is unclear why evidence of intra-locus sexual conflict appears to be accumulating and hence it is also unclear to what extent adaptation is constrained by such conflicts [56,66,67]. More information on the effect of SAC on the genetic architecture of such traits would be welcome [67,68].

Another route for the resolution of intra-locus sexual conflicts is via genomic imprinting, which may allow both sexes to approach their conflict trait optima [69]. In mice, for example, the paternal copy of the IGF2 fetal growth factor gene and the maternal copy of the IGF2 receptor gene, whose product acts as a sink to remove IGF2, are transcribed [70]. The conflict hypothesis for the evolution of genomic imprinting [71] suggests that the interests of the male parent are best served if offspring carrying his imprinted genes grow to a large size at the expense of other litter mates — i.e. through expression of IGF2 at the paternal optimum. The interests of the mother are best served by a lower and more equitable provisioning of resources among all her offspring — i.e. expression of the IGF2 receptor at the maternal optimum. So, while imprinting could have been selected in the context of intra-locus contests over provisioning levels, a current inter-locus conflict is revealed by what happens when the imprinting is disrupted. Maternal imprinting of the IGF2 growth factor leads to small offspring, while paternal imprinting of the IGF2 receptor leads to oversized offspring [72]. Genomic imprinting is not thought to be a universal mechanism for conflict perpetuation or resolution (but, see [69]), as it is restricted to embryos that are directly provisioned from maternal tissues, such as in flowering plants and placental mammals (**Figure 2**). Consistent with this is the finding that imprinting has not been

Figure 2. From potential to actual sexual conflict resulting in sexually antagonistic coevolution (SAC).

Power and value of winning are defined in [1,3,4,10]. Potential sexual conflict is set in motion by the difference in the optimum value of ‘conflict traits’ for males and females. The conversion of potential sexual conflict into actual sexual conflict that can drive SAC depends upon the benefits and costs of adaptation and counter-adaptation and the opportunity (or mechanism) for doing so. Parker [4] suggests that the sex with the higher power–value ratio may be under stronger selection to win or adapt faster in coevolutionary chases. Solid lines show routes to actual sexual conflict. Dotted lines show routes leading to conflict resolution and repression of competition. SAC may be self-reinforcing and lead to a variety of different coevolutionary outcomes or alternatively select for de-escalation and hence conflict resolution.



found in species where this type of provisioning is not possible [73].

Inter-locus sexual conflicts could be resolved by the evolution of insensitivity of the female to the male stimulus [74]. Rowe *et al.* [74,75] described models that allow both the threshold and the sensitivity of female resistance to mating to evolve. Such models made sexual conflict less likely because of conflict resolution, i.e. de-escalation and desensitisation of the female to the male manipulation. This could, however, lead to subsequent selection for a different pathway to be used by males and a new conflict to be initiated. The models of Gavrillets and Hiyashi [76] also indicate conflict resolution in examples where monandrous populations evolve from polyandrous ones and where random mating evolves from non-random mating. The evolution of males that impose lower mating costs on their mates under monogamy [22], and the evolution of resistance to mating costs in females in empirical studies [27] suggest that such conflict resolution can occur.

The theory and reality of genetic conflicts and their resolution have been studied in most detail in social insects (e.g. [58,77]). Kin conflict theory, first applied to the study of parent-offspring conflicts [45,78], has been particularly useful in illustrating how co-operation and conflict should coexist [57]. For example, conflict theory predicts obvious conflicts of interest over reproductive division of labour, sex allocation and within-colony nepotism [58,59]. In the case of sex allocation, there is evidence that conflict is actually expressed. The asymmetry of relatedness between queens and sexual forms, as opposed to between workers and sexual forms selects for workers of some species to bias colony sex ratios towards their optimum [64] — in some remarkable instances via ‘split sex ratios’ [79]. In contrast, the predicted conflicts over colony nepotism in social insects seem to be quite rare, due to the effectiveness of conflict resolution mechanisms [58]. Colony nepotism potentially exists when, for example, multiple mating by the queen creates multiple patrilineages within a single colony. These different lineages may

each have different genetic interests. However, the odour recognition mechanisms by which different patrilineages might be distinguished appear to be relatively ineffective [80,81]. Workers may also act in ways that facilitate the mixing up or scrambling of their odour cues to prevent the recognition of the different patrilineages and thus reduce the likelihood of actual conflict [59,82]. Conflict resolution may be selected for because it increases colony productivity. However, this resolution could initiate novel conflicts, because the increased colony productivity increases the potential benefits of manipulation for any newly arising conflict gene [65]. This repression of competition exactly parallels mechanisms that act to decrease some types of intra-genomic conflict [83], e.g. the evolution of suppressors of sex ratio distortion. The benefits of suppression of sex ratio distortion are in increased productivity, i.e. through the production of larger numbers of gametes, as none are removed through the actions of the distorter. Haig and Grafen [84] suggest that recombination may produce a similar end result as odour cue scrambling and may, therefore, have partly arisen to repress intra-genomic competition by mixing up genes.

#### Insights from Sexual Conflict Theory

Models of sexual conflict have tended to fall into three types (Box 2): game theory models (e.g. [1,3,85–87]), population or quantitative genetic models (e.g. [88–90]) and neural network models (e.g. [91,92]). In terms of which is the best approach to use, the key question is whether the findings of game theory, genetic and neural network models are consistent with each other; or, whether there are genetic details (e.g. dominance, number of loci, etc.) which, when known and incorporated into genetic models, would invalidate the inclusive fitness approach taken by game theorists. In the field of parent-offspring conflict such a synthesis of approaches has proven that a considerable diversity of models are largely consistent with each other [63], hence allowing general rules to be deduced. For example, in parent-offspring conflict, two main messages

**Box 2**

**Relevant theoretical concepts.**

Game theory model	A model where each player's payoff depends upon the strategy and/or frequency of the strategy of the opponent. At the evolutionary stable strategy, each player is optimising its payoff [1].
Population genetic model	A modelling approach that examines the conditions for the spread of an allele into a population [88].
Neural network model	A modelling approach that uses an artificial neural network to simulate the sensory perceptions of individuals and hence predict their behaviour and responses to stimuli [91].
Fisher's runaway model of sexual selection	Models in which the mate choice exerted by females is for attractive males. The benefit of choice is indirect, and accrued through the production of sons that are highly attractive mates (sexy sons) [100].
Indicator/Good Genes models of sexual selection	Models in which the mate choice exerted by females is for males that indicate their viability. The benefit of choice is indirect, through the increased viability or reproductive success of offspring [101].
Sensory exploitation	Models in which the sensory biases of females (e.g. sensitivity to specific sound frequencies for efficient predator avoidance) are subsequently used ('exploited') by males in mate choice (e.g. use of the same frequency for courtship song) [102].
Indirect and direct benefits	Indirect benefits are the genetic advantages (e.g. the acquisition of superior genes) accrued by the offspring of parents exercising reproductive decisions. Direct benefits (or costs) are those visited directly upon the individuals that exercise the decisions [98].

are that there is no general rule as to whether parents or offspring will win such conflicts [61,62,93] and that relatedness does not always predict the outcome of the conflict [61,94].

Although it is not yet clear whether the diversity of approaches employed to model sexual conflict is reaching a consensus, important insights have been made nevertheless. For example, Parker's [1] original theoretical treatment showed the potential for sexual conflict to result in the spread of alleles encoding male reproductive traits that have potentially harmful effects on females. This prediction is supported by subsequent models [24,89]. Modelling has also been extremely useful in showing whether potential signatures of sexual conflict are likely to be reliable. For example, there has been considerable interest in whether

the pattern of results achieved when crossing allopatric populations can show the operation of sexual conflict [95–97], although current theory suggests that they cannot [3,75].

**Female Mating Bias**

A key contribution of sexual conflict theory is the examination of how female mating biases may evolve, and whether this contrasts with the predictions from models of sexual selection. For example, under SAC, females are predicted to be under direct selection to avoid costs of mating [9,19]. Theory predicts that there need be no indirect benefits of mating biases — although they may occur — nor any adaptive consequences of mating choices at the population level [89,98,99]. In contrast, in Fisherian runaway and 'good genes' models [100,101] (Box 2), selection on female preferences is indirect and arises because of a genetic correlation between the preference and the male trait, the latter being under direct selection for increased male mating success or high viability (see the review by Cotton *et al.* in this issue). The direct selection of female mating biases under SAC also contrasts with the expectations of sensory exploitation models. In such models, female mating preferences arise because of pleiotropy, due to direct natural selection on females in a context other than in mate choice, e.g. predator avoidance (Box 2; [102]). It is conceivable, however, that sensory exploitation may often kick-start SAC [24,103], because it can select for mechanisms in males that can exploit the sensory preferences of females. Females may then find themselves in a 'sensory trap' [102] from which it is difficult for them to escape, because if they evolve insensitivity, they also lose the naturally selected benefit of their preference.

**Indirect Genetic Benefits**

Theory is essential in tackling the issue of whether the indirect genetic benefits can balance the direct costs of mating [98] (Box 2). This is important in terms of sexual conflict over traits related to mate choice. If indirect genetic benefits gained by females through the production of sexy sons are large enough to offset any direct costs, then this form of sexual conflict becomes synonymous with existing models of mate choice [52]. Costs of female choice are, by definition, part of models of SAC. In contrast, models of sexual selection vary in their capacity to incorporate them; for example, costs incurred by females due to their choice of mate cannot easily be explained by models of the Fisher runaway process [104,105]. On the other hand, 'good genes' models can incorporate female mating costs, because costs are offset as female preference becomes associated with fitness, which is under directional selection to increase [9]. However, theory predicts that, because of the much stronger selection acting on them, direct effects should be larger than indirect effects and therefore outweigh them [46,105–107]. Hence, the theory shows that indirect genetic benefits need play no role in evolution by SAC [98].

**Predicting Traits Likely to Be Subject to SAC**

In order to determine why SAC shapes some traits and not others, it will be crucial to determine the value of

winning and the power of conflict traits (Box 1; Figure 2). Lessells [10] considered this issue for traits related to remating interval, mating probability, fecundity and parental investment. In terms of the remating interval, the optimum for females will often be an intermediate interval [108] and lower than the optimum for males, thus rendering manipulation for males potentially highly beneficial [10]. For traits related to the probability of mating, the benefits of male manipulation are also potentially high, as males that do not mate gain no fitness [1,3]. In contrast, females can benefit from not mating because they may subsequently gain matings with alternative mates of higher value. In terms of fecundity, there are potential benefits of manipulation for males because their fitness will increase in proportion to the number of eggs produced. In contrast, for traits related to parental investment, the benefit of manipulation is predicted to be small, because the value of winning decreases with increasing manipulation [10]. In addition, trade-offs between parental investment per offspring and fecundity [109] can further decrease or even eliminate potential sexual conflict, because the female's increased investment would lead to decreased fecundity and, hence, cause fitness costs for the male [10].

The magnitude or likelihood of costs of manipulation and of resistance may also differ for traits related to mating versus those related to parental investment. Such differences will impact on the likelihood of SAC shaping these processes [10]. The magnitude of the costs is likely to be extremely sensitive to the mechanism by which manipulation and resistance are achieved. For example, costs of resistance via physical contests may be different to those in which resistance is effected by a change in the shape or affinity of a hormone receptor [10]. The costs of resisting a mating may also be less than those of imposing a mating [1,3]. The availability of mechanisms to manipulate and resist may vary in traits related to mating through to parental investment. For example, there are a multitude of signalling pathways that are essential for controlling the female sensory and reproductive system [102], which males may be able to exploit in order to manipulate traits related to mating. However, for traits related to parental investment, any manipulation achieved during mating would have to be relatively long-lasting. This may be difficult to achieve other than by mechanisms such as epigenetic modification of DNA by genomic imprinting [110].

#### **Adaptation and Extinction**

A suggested feature of sexual conflict is that it leads to a decrease in the mean fitness of a population [55,89,98,110]. It has, therefore, been suggested that models of sexual selection and sexual conflict contrast with one another in the extent to which they do or do not promote adaptation at the population level. There is no clear expectation that the Fisher runaway process will lead to adaptation and increased population fitness — at least not in the phase after establishment. In contrast, 'good genes' models could lead to increased population fitness, or increased rates of adaptation, if the effects of the 'good genes' are strong. Although some aspects of theory are consistent with

the idea that sexual selection can lead to increased population fitness [111], other models predict both increased and decreased mean fitness [66,112], even under direct selection [113]. Models of segregation distortion also predict increased or decreased population fitness at equilibrium [114].

It seems unlikely that there would be any directional fitness benefit of mate choice under sexual conflict, unless there is a significant input of indirect selection alongside direct selection for female resistance [9]. Population adaptation would only occur by chance as the result of an unpredictable chase. Rowe and Day [99] showed that, under SAC, depressions in mean fitness may be ephemeral, small and even absent at equilibrium. They note that the origin, establishment and equilibrium phases of SAC can appear very different in terms of fitness patterns. Hence, the general message is that mean population fitness gives an unreliable indication of the underlying coevolutionary process [3,75,88,90,99].

A related issue is whether any decreased population fitness that might result from sexual conflict or sexual selection is strong enough to lead to an increased probability of extinction. There is evidence both for [22,115,116] and against [117–119] this hypothesis in the context of sexual selection. The possibility that sexual conflict might increase the probability of extinction is a logical extension of the finding that it may sometimes lead to decreased population fitness [15,16,89], but whether it is more or less likely than sexual selection to do so is unclear.

#### **Speciation**

The importance of sexual conflict lies not only in its potential to drive evolutionary change within species, but in its potential to cause reproductive isolation, and hence speciation [3,24,110]. A recent review of sexual conflict models relating to speciation has highlighted that there are at least six different types of dynamics that can be generated [120]. Verbal treatments of sexual conflict originally assumed that sexual conflict would generate continuous coevolutionary chases [18,24]. Whilst theory shows this to be a possible outcome [88–90], there are alternatives: evolution towards an equilibrium or line of equilibria, cyclic evolution, diversification in females but not males (the so-called 'Buridan's Ass' scenario [120]) and diversification in both sexes [120]. Furthermore, Gavrillets and Hiyashi [76,120] highlight that different dynamics are possible within the same model with different initial conditions. More importantly, although all of these models predict increased genetic variation, only two types of dynamic outcome have the potential to lead to speciation: continuous evolutionary chases and diversification of traits in both sexes (sympatric speciation via the latter appears difficult [90]).

A potential contrast between models of sexual selection and sexual conflict is in their predicted importance in promoting speciation [88,90,121,122]. Arnqvist and Rowe [9] argue that sexual conflict is more likely than sexual selection to result in speciation because it will select for more rapid and divergent coevolutionary change. They suggest that this is the case because selection on females is direct and because SAC can

occur under a very wide range of conditions, due to the multiple routes that males can exploit and that females can use to evade exploitation. This is an area that will benefit from further theoretical and empirical study.

### **Equilibrium versus Non-equilibrium Dynamics in SAC**

It has been suggested that mechanistic details may determine which type of modelling is appropriate. One example for this is whether SAC is predicted to reach a point (or line) of equilibrium, or alternatively no equilibrium at all [9]. For example, if males have multiple ways of manipulating females and females have multiple ways of evading or reducing the effects of these manipulations, then SAC could be better modelled using non-equilibrium approaches [9,24,91,92]. The difficulty in modelling this situation is in trying to predict the response to novel stimuli, hence models that can incorporate mechanisms of recognition may be advantageous [91,92]. Such models show that females can be manipulated by males that exploit their recognition systems and that changes in female memory can subsequently create new biases for males to exploit [92]. Multiple signals and receiving mechanisms have also been considered in the context of sexual selection for mate choice [123]. Therefore, knowledge of mechanism is likely to be very important in determining whether the specific details matter to the evolutionary outcome and whether there is a contrast between sexual selection and sexual conflict with respect to evolutionary dynamics. The nature of the dynamics of SAC is relevant to how we interpret the output of experiments utilising replicated populations under artificial selection or experimental evolution [22,27,97]. If there are limited ways in which males manipulate and females resist the mating tactics of males, then replicates may well respond to selection in a similar way. If SAC is best described by non-equilibrium dynamics and there are multiple ways in which males manipulate and females respond, then replicates could all adopt separate evolutionary trajectories and each respond differently. It would be difficult in the latter case to distinguish genetic drift from such a non-replicated response.

### **Sexual Conflict, Fitness and Levels of Selection**

There has been debate about the effects of SAC on fitness and in particular on male versus female fitness [55,124,125]. The root of the confusion seems to lie in the fact that males and females are not independent entities and hence a male's reproductive success is tied to that of the females with which he mates. Therefore, if a male mates only with a single female, then his lifetime reproductive success is equivalent to that of his mate. But whenever a male mates with more than one female, and vice versa, the reproductive success of the two sexes is not necessarily the same. A particular male may gain an advantage by pulling the value of a conflict trait towards his own optimum and away from that of the females with which he mates, therefore increasing the relative fitness of his genotype. The relative fitnesses of the male and female genotypes undergoing SAC can diverge, even though the stable sex ratio for a population at equilibrium is 1:1 [100]

and hence at a population-wide level, the mean fitness of males and females must be equal (noted in this context by Arnqvist [125]).

It is, therefore, important to make explicit which definition of fitness is being used and to consider the appropriate level of selection. The fitness of a population, for example, may not be aligned with that of particular alleles undergoing SAC. For example, the fixation of sex-linked meiotic drivers is expected to be rare because it could lead to population extinction, if the drive is very efficient [126]. It is possible to examine the performance of a particular allele — or a chromosome — in a standard genetic background [16]. However, more often the performance of individuals in sexual conflict studies is examined by, for example, calculating their lifetime reproductive success. In the absence of segregation distortion, this measure will be equivalent to the performance of the allele under SAC. Fitness should be defined in terms of whether it is being used as a synonym for lifetime reproductive success, or used as a measure of the expandability of a population. If these considerations are not made, then statements concerning the reduction in fitness in one sex caused by the actions of the other can be flawed or imprecise (for discussion, see [55,124,125]).

### **Power of Explanation and Exclusion in Sexual Conflict Models**

It is important to consider what sexual conflict theory can explain that was not previously explained. In addition, what observations would lead us to conclude that evolutionary change arising from sexual conflict does not occur? This potentially fruitful avenue of research has recently been investigated by Eberhard [127], who conducted a comparative test on an impressive wealth of taxonomic information on insects and spiders, based on an idea suggested by Alexander *et al.* [128]. The hypothesis was that sexual conflict could be a more potent evolutionary force for diversification in species in which males and females interact directly during mating in aggregations, as compared to situations where females attract males from a distance. Following this reasoning, the diversity of genital morphology would be predicted to be more pronounced in the former scenario in which females are subject to potentially high levels of male harassment, than in the latter in which they are relatively protected. However, the taxonomic information did not uphold this prediction, leading to the suggestion that the results provided no evidence for the importance of sexual conflict in shaping the evolution of the morphological characters studied [127]. Although such tests may provide an indication of whether escalating arms races may have occurred, these are not the only possible signatures of SAC, as other dynamics are possible [120]. Hence, such tests do not exclude the possibility that SAC — or indeed other coevolutionary processes — may have been responsible for driving male–female coevolution. In a further investigation [129] an absence of female morphological characters having a potential role in female defence against mating was recorded, in situations in which they might have been expected. However, in the absence of mechanistic, experimental information, it is not possible to be certain whether the

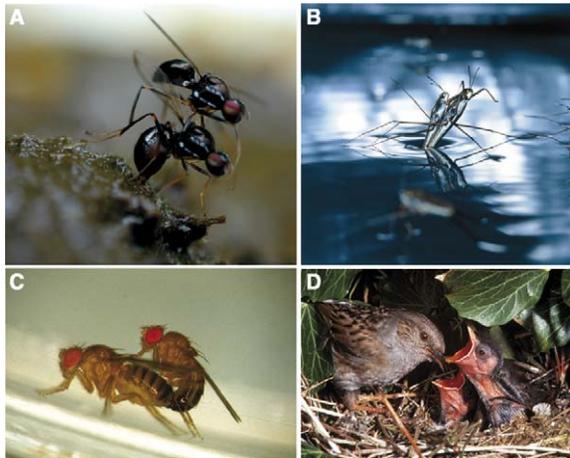


Figure 3. Model animals for the study of sexual conflict.

Sexual conflict has been described in detail in relatively few systems to date, including (A) dung flies (e.g. *Sepsis* spp.), (B) waterstriders (e.g. *Gerris* spp.), (C) fruit flies (*Drosophila melanogaster*) and (D) dunnocks (*Prunella modularis*). The task now is not just to expand knowledge of the operation of sexual conflict in other species, but to move to a more comprehensive understanding of why sexually antagonistic coevolution affects some traits and not others. Photos with permission from B. Eberhard (A), J. Rydell and I. Danielsson (B), T. Chapman (C) and W.B. Carr (D).

relevant adaptations and potential counter-adaptations are always being considered, or whether the correct functional roles have always been attributed. As also noted in [127], it may be that physiological rather than morphological traits provide a greater opportunity for SAC and so the absence of evidence for SAC in one class of traits does not preclude its importance in another. It will be very useful to try to refine this approach to devise critical tests for the operation of SAC.

#### Sexual and Other Evolutionary Conflicts

Sexual conflict is one of a series of evolutionary conflicts that include those between selfish genetic elements and their DNA hosts, between nuclear and cytoplasmic genes, between parents and offspring, between parasites and their hosts, predators and their prey and between individuals within social groups. It will be very useful in the future to examine systematically in what ways change by SAC may or may not differ from these other types of conflict and specifically to examine any homology between the models put forward to explain them. I note here a few examples of differences and shared features.

It seems clear that there are at least many qualitative similarities between different types of genetic conflicts. The common features of these processes and models are that conflicts arise because different alleles are unequally distributed between interacting parties, and because not all alleles receive equal benefits [130]. For example, there may be useful similarities between theory of preference alleles in models of mate choice, and of modifiers of segregation distortion [130]. These models make similar predictions for increased or decreased equilibrium population fitness [114]. Similarities between models of segregation distortion and

parent-offspring conflict have also been noted by Haig [131].

Another example comes from Frank's [132] models of sexual conflict over fertilisation rates in egg-sperm interactions. The models examine the conflict that arises because selection in males acts to increase the rate at which sperm penetrate the egg, while selection in females acts to decrease or diversify these rates in order to reduce the incidence of polyspermy. The models show that in males, the outcome can be diversifying or stabilising selection depending upon the value of an exponent, in a way that parallels models of host-parasite coevolution [133].

Parker [1] highlights an example in which sexual conflict may be similar to parent-offspring conflict [78]. In trying to predict which sex might gain the upper hand, the important parameters are the strength of selection and the different aims of the interactants. It may be easier, for example, for males to attempt matings than it is for females to resist matings, because some level of mating is essential and hence the resistance of mating may not always be adaptive. In this sense the comparison to parent-offspring conflict is apparent, as it may be easier for offspring to beg for more parental investment than it is for parents to resist being deceived and stop supplying parental investment [1,134].

There may be contrasts between sexual and other conflicts in the expected dynamics of each process. For example, as in sexual conflict, predator-prey interactions are characterised by unequal selection pressures operating on the participants, or the 'life-dinner' principle, according to which one party is 'running for their life' and the other merely for their dinner [42]. However, the respective fitness of predators and prey is unlikely to be linked in the same way as it is in males and females and will instead vary according to the degree of specialisation of the predator. Similar arguments can be made for coevolution between parasites and their hosts, with hosts potentially gaining fitness in the absence of the parasite. Exactly how coevolutionary change will differ in these cases as compared to those driven by sexual conflict is unclear, but it seems highly likely that the dynamics of adaptation and counter adaptation will differ significantly.

To place sexual conflict in a wider evolutionary context, it may be profitable to consider levels of selection theory in relation to genetic conflicts [58]. This should help to illuminate when co-operation ends and conflict begins [135-137]. A useful concept is the 'evolution of individuality', where an individual is any entity in which the within-individual conflicts are less strong than the between-individual conflicts. Individuals can then exist because genetic conflicts at lower hierarchical levels have been sufficiently suppressed to allow them to do so. This raises the question of what processes lead to the suppression of the various within-genome conflicts and why do actual conflicts sometimes break out? A consideration of these concepts led Bourke and Franks [58] to propose some general principles for the acquisition of individuality, based on either the suppression of selfishness by rivals (e.g. through policing or through greater power being in the hands of rivals) or on the self-suppression of

selfishness (e.g. through self limitation because of costs or frequency-dependent fitness).

It will also be important to compare, across all different levels and types of interactors, the emergent properties of mutualistic versus antagonistic coevolutionary systems. For example, antagonistically coevolving systems may select for rapid geographic and temporal divergence [138]. It will be interesting to determine whether this is indeed restricted to this mode of evolutionary change.

## Conclusions

In the future, it will be useful to refine the empirical and theoretical study of sexual conflict, to move from documenting the existence of actual sexual conflict in an increasing range of species, to asking how and why sexual conflict is fuel for evolutionary change in some instances and not others (Figure 3). For this we will need a much better understanding of why conflicts persist or de-escalate and a quantification of the benefits and costs of manipulating and being manipulated. For example, although males may stand to gain more by mating than females have to lose, the costs of imposing a mating may be larger than the costs of resisting a mating, so the net balance is unclear [1,3]. We also need data on mechanisms in both sexes. For example, what is the number of loci involved in adaptations or counter-adaptations and is it different for physiological versus morphological traits? Do males have a larger population size of reproductive genes from which to draw for SAC because of the fact they generally engage in more within-sex competition for matings than do females? We are also lacking measures of antagonistic selection and lacking functional studies of antagonistic traits. It will be useful to examine in more detail the genetic architecture of traits involved in intra- and inter-locus sexual conflicts. A demonstration of the power of sexual conflict in natural populations is the ultimate aim [20]. However, unless there is detailed knowledge of mechanism in both sexes, then the actual targets of sexual conflict cannot be identified and measured.

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