Sexual conflict

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Evolutionary conflict arises from differences in the fitness interests of replicating entities and has its roots in relatedness asymmetries. Every replicator is related to itself by 100%, but in most cases is less related to other replicators, which generates selfishness and conflicts of interest. Since this basic condition is the norm at many levels of biological organization, conflict is rife in biological systems. Sexual conflict, on which we focus here, is the evolutionary conflict that occurs between males and females because of their divergent fitness interests. Sexual conflict occurs despite sexual reproduction requiring some level of cooperation between males and females because the fitness interests of the sexes are nevertheless never perfectly aligned. In other words, males and females may agree on where they are going, but not necessarily on how to get there. Sexual conflict is a vast topic with relevance to many areas of biology and so here we restrict our focus to matters we think are of broadest interest.

Although the ‘battle of the sexes’ had been studied in various guises earlier, and explicitly so in game theory, the study of sexual conflict per se really began in the 1970s, with the publication of two papers deserving special mention, one by Richard Dawkins and John Krebs, and one by Geoff Parker. The former focused on arms races and did much to introduce the idea that these could occur within a species, particularly between males and females. Parker’s contribution focused purely on conflict between the sexes and pretty much defined the logic and the evolutionary expectations and implications of this conflict.

In retrospect, the logic was elegantly simple — a male benefit allele (trait) can spread even if costly to females, as long as the benefit to males exceeds the female cost. Parker also explained that the evolutionary outcomes depend on how conflict is manifest. In cases of sexual attrition, where resource levels determine how long males and females can engage in conflict (the duration of persistence), evolutionary solutions (evolutionary stable strategies) can be found. However, in some cases, for example when costs are fixed independently of what opponents are doing, unresolvable evolutionary cycles can ensue and males and females can become trapped in cycles of adaptation in one sex followed by counter-adaptation in the other. Parker also pointed out that while selection may be stronger on males to win conflicts, females often wield greater power to determine outcomes. Therefore, predicting the evolutionary outcomes of sexual conflict a priori is difficult.

While much research touched on sexual conflict after Parker's defining work, the field accelerated with the 1996 publication of an ingenious experimental evolution study by Bill Rice. Rice's study design, based on experimental evolution in Drosophila, prevented females from coevolving with males. In short, females were removed from the evolving populations and replaced with new females from outside the experimental populations at each generation. This meant that females effectively became evolutionarily static and males could adapt to target them. As a result, males evolved to manipulate the fixed female phenotype, and females mated to these males suffered reduced fitness. The work offered empirical support for some implicit predictions of Parker's earlier model. More than that, it captured the collective imagination and initiated a major surge in sexual conflict research that continues to the present.

Two sexual conflicts

Rice and colleagues also clarified two fundamental types of sexual conflict: intra- and inter-locus sexual conflict. The former results from the sexes sharing an autosomal genome, coupled with sex differences in selection. Therefore, optimal trait values, such as size or weight, can differ between males and females, and the optimal allele at a locus can therefore differ between the sexes. This means each sex can prevent the other from reaching its phenotypic optima for shared traits.

Intra-locus sexual conflict is epitomized by widespread sexual dimorphism, which shows males and females are selected to perform at least some different tasks, or some tasks differently (Figure 1). For example male deer might develop large antlers for use in male–male mating contests and females develop more rudimentary structures purely as a correlated response to selection in males. Thus, antlers could be good for male fitness but a wasted resource for females. Sexually antagonistic selection over optimal trait values is likely to be common and hence allele frequencies at a locus can fluctuate depending on the sex an allele finds itself in.

Inter-locus conflict occurs when a trait in one sex interacts with a different trait in the other sex and hence different gene loci are involved. Here conflict occurs over the outcome of an interaction between the sexes. For example, the sex-peptide (SP) in Drosophila melanogaster seminal fluid benefits males by decreasing female receptivity and increasing egg laying, but also reduces female longevity (Figure 2). So the outcome of SP transfer to females is higher male fitness and lower female fitness, unless females adapt to resist this manipulation.

Detecting conflict

Deciding whether there is sexual conflict over a trait is in principle easy via a simple thought experiment: ask what would happen to trait values if control over their expression were completely determined by one sex. So for example, if females had control over seminal fluid composition in D. melanogaster, would it be different? The answer is yes. The SP found in D. melanogaster semen would no longer harm females — it would not be present or it would be altered into a non-toxic form. Similarly, if males controlled female parental investment, it would probably increase because it is in a male's interest for his mate to invest as heavily as possible in his offspring in promiscuous mating systems, even if this is at the expense of a female's future reproductive success.

In practice, it can be more difficult to assess sexual conflict over trait values, partly because any selection it generates, or the conflict itself, can be ephemeral, and may not be detectable at a specific point in evolutionary time. With this caveat in mind, measuring the sex-specific fitness optima for a shared trait can easily be done using standard selection analysis to test whether male–female fitness peaks overlap (Box 1). If peaks do not overlap, selection is tugging trait values in different directions in each sex and there would be conflict over the shared trait. Similarly, the intersexual genetic correlation for fitness can be measured. A negative correlation suggests widespread intra-locus conflict, as the allelic combinations that make for good females produce less fit males and vice versa (but for one caveat see Duffy et al. (2019) Ecology & Evolution). Conversely, for specific traits (rather than fitness), strong positive intersexual genetic correlations coupled with sex differences in trait optima indicates that the sexes are not free to evolve to their sex-specific optimum. Measuring the direct selection on mate-preference can also be undertaken. If preferred mates cause direct fitness reductions, this suggests manipulation and conflict-driven mate-choice.

However, because measuring fitness in natural systems can be challenging, experimental evolution can also offer a tractable way to assess sexual conflict. It also has the advantage that it is possible to experimentally create extreme scenarios that rarely, if ever, occur in nature. By restricting evolution to one sex, or by imposing strict monogamy, one can alter the balance of power between males and females, or even eliminate conflict entirely. Comparisons can then be made to treatments where these conditions have not been imposed to assess impacts of sexual conflict. Similarly, manipulations that alter the balance of power in sexual interactions, by altering how well females can resist males for example, can reveal latent conflict.

Recently, approaches have made inroads into identifying specific loci under sexually antagonistic selection. Ideally, genome-wide association studies are combined with phenotypic data, including fitness estimates, in order to directly identify the genes involved in conflict. These approaches have identified key conflict alleles, such as alleles for DDT resistance in Drosophila, and for early maturation in salmon, both of which influence male and female fitness in opposing directions.

In the absence of phenotype data, it is still possible to scan for genomic signatures of sexual conflict. Intra-locus conflict can result in balancing selection, where alleles are subject to fluctuating selection depending on whether they are present in males or females. Population genomic scans for loci exhibiting signatures of balancing selection are becoming increasingly possible given the availability of sequence data from a wide variety of organisms. Without associated fitness data from both sexes, this approach cannot be used to identify conflict loci directly because there are many potential causes of balancing selection. Additionally, estimates are influenced by a range of other genomic factors, such as local recombination rate, which preclude using this method to identify putative conflict genes without associated fitness data. However, the approach can be used to compare the potential for sexual conflict across large groups of genes with different phenotypic implications. Results have been mixed, with some showing that sexual conflict is rife within the genome, and others suggesting that conflict has been largely resolved.

Some theory

Sexual conflict has been the subject of considerable theoretical investigation since Parker's early exploration and much of this has focused on inter-locus sexual conflict. Inter-locus models have verified many of Parker's initial insights, and expanded them in a remarkable number of directions. There has simply been too much work to go into great detail here, so we will limit ourselves to a few key insights.

First, theory has confirmed that endless cycles of male–female adaptation and counter-adaption are only rarely expected to occur. Additionally, it is clear that male harming of females can be advantageous for males if harm educes female remating, or increases female investment in current reproduction. That is, if making sex damaging reduces the likelihood that a female will mate with a rival male, or increases how much a female invests in the harmful male's offspring, then harm can be advantageous for males.

Models also suggest that conflict can affect evolution in a range of ways, depending for example on initial conditions and the genetic detail assumed (e.g. allele number, dominance relationships, effect sizes). Importantly, the manner of female response to male manipulation is important. For example, if females evolve to become less sensitive to attempted male manipulation, arms races are unlikely. In one sense this reflects models of sexual selection more generally — outcomes depend critically on female preference, particularly the shape of preference functions, and how preferences evolve.

Finally, information asymmetries — whether or not both sexes are equally informed about a sexual interaction — can also alter model outcomes. For example, if males have to choose a strategy (e.g. how much to ejaculate) before females have to decide how to respond (how much sperm to store), females have more information about the interaction than males and conflict solutions tend toward female optima. This harks back to Parker's point about power residing with females.

A number of models have also investigated elements of intra-locus sexual conflict. Many of these have assessed how well the sexually antagonistic selection under-pinning this conflict can generate balancing selection and maintain genetic variation. How genetic variation is maintained in the face of selection and drift is a major question in evolutionary biology, and intra-locus sexual conflict could potentially be an additional, very general mechanism that helps resolve this issue. Outcomes are mixed in terms of how generally or easily variation is maintained, but there is increasing support for intra-locus conflict as a mechanism maintaining genetic variation when fitness landscapes are complex and heterozygote advantage is significant. Moreover, when parameterized with data from a DDT resistance locus in Drosophila with known sexually antagonistic effects, models (and experimental populations) suggest polymorphism is maintained. Basically, allele Y performs best in females, and allele y does best in males, and therefore both alleles at the y-locus are maintained in the population because there is no ‘best’ variant — the allele ‘quality’ is sex dependent.

Sexual conflict and sexual selection

Sexual conflict is not sexual selection and sexual selection is not sexual conflict. However, sexual selection may cause conflict and responses to sexual conflict may generate sexual selection. Sexual selection results from reproductive competition and is formally defined as the non-random (with respect to phenotype) variance in mating or fertilization success. Therefore, if a male trait confers a mating advantage but also harms females, then it both is the product of sexual selection and generates sexual conflict. For example, penis spines in seed beetles induce damage in the female reproductive tract, and are thought to increase sperm competitiveness and reduce female fecundity. Spines are therefore the product of sperm competition, and thus sexual selection, and they also generate sexual conflict. Broadly similar results in terms of female damage have been reported in the fly Sepsis cynipsea, although here it is not entirely clear how males benefit from harming females. Kokko and Jennions discuss this at length in the 2014 book edited by Rice and Gavrilets.

Conflict resolution

How can sexual conflict be resolved? This depends on the type of conflict. For inter-locus conflict, resolution (or avoidance) can in principle be achieved by perfectly aligning the evolutionary fitness interests of the sexes through indissoluble monogamy. However, this never occurs in nature because there are always alternative pathways to fitness — even in monogamous systems other potential partners always exist. However, perfect inter-sexual fitness correlations can be achieved experimentally by imposing strict genetic monogamy with no possible access to other mates. This design ensures that male fitness is entirely dependent on his female mate, and therefore male and female fitness interests are perfectly correlated.

Intra-locus conflict arises from shared genetic architecture, and therefore the potential for resolution is ultimately governed by the degree to which genetic architecture can be decoupled between males and females. Theory suggests sex-limited trait development, gene duplication, and sex-specific gene regulation can all resolve intra-locus conflict. Moreover, the evolution of sex-specific dominance effects can mitigate conflict, as shown in salmon.

Several lines of evidence also suggest that genetic architecture of males and females are often distinct. Recent work in mice suggests that a surprisingly large proportion of autosomal knock-out mutations affect only one sex. Similarly, genome-wide association studies in humans reveal that the genetic architecture for many traits is significantly different between males and females. Both these findings suggest that the potential for intra-locus conflict resolution exists, and experimental work in Silene suggests that resolution of conflict can occur with just a few generations of antagonistic selection.

However, inter-sexual genetic associations can constrain the resolution of intra-locus conflict. For example, Harano and colleagues showed in flour-beetles that selection on male mandibles, which are sex-limited in development, reverberated through the male phenotype (because of intra-male genetic covariances) and bled over into females via inter-sexual genetic correlations of non-sex limited characters — selecting on the male-limited trait resulted in a masculinized female phenotype because of other shared traits. Thus, sex-limitation need not always result in resolution of this conflict. Similarly, pleiotropy in terms of expression breadth has been shown to constrain the evolution of gene expression differences between the sexes.

Outstanding questions

Many conflict matters require additional research, not least of which is the need to identify specific sexually antagonistic alleles. At present only a handful of examples are known, and all are loci of major effect. In order to address key issues such as the efficacy of conflict at maintaining genetic variation, as well as the potential and route(s) of conflict resolution, additional data are sorely needed in a diverse array of species and mating systems.

Furthermore, theories of good-genes sexual selection rest on the assumption that a good male genotype represents a good female genotype. Intra-locus conflict casts doubt on this possibility. Therefore, understanding the incidence and resolution of sexual conflict becomes important for understanding models of sexual selection.

Additionally, sexual dimorphism, although widespread, need not indicate that conflict has been fully resolved, although it may indicate a partial resolution. What are the constraints on conflict resolution and where do we find them? In cases of sexual dimorphism, how much conflict remains unresolved, and why?

Finally, is mate choice generally rational? In other words, do preferred mates enhance fitness? Or are preferred partners those best able to manipulate their mates for selfish benefit? These are just some outstanding but important questions.

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Box 1. Mapping Sexual Conflict

Fitness landscapes are one way to visualize fitness variation with respect to some phenotype of interest. They usually map the relationship between fitness and traits that vary on a continuous scale, such as body mass or mating speed. These landscapes can reveal whether the sexes are subject to contrasting patterns of selection, and therefore reveal the presence of sexual conflict.

By way of illustration, consider a simple hypothetical case testing for sexual conflict over body mass and colour in some population. Larger females are more fecund and colourful males are more sexually attractive but greater colour increases predation risk in both sexes. To create landscapes, male and female body size and colourfulness are measured along with fitness (e.g. lifetime reproductive success) for a sample of individuals. For each sex, colour and size are plotted, and fitness is then layered over this. The resulting 3D fitness surface is analogous to a contour map, with mountains for fitness peaks (trait combinations favored by selection) and valleys for trait combinations that reduce fitness (and are selected against).

Statistical techniques can be then used to describe the topography of these landscapes and characterize patterns of selection. If fitness peaks differ across the sexes for shared traits (i.e. peaks are in different locations), this is consistent with sexual conflict. This is what we show here — female fitness is maximized with large, less colourful females, but male fitness peaks at intermediate size and colour (hotter colours (more red) = higher fitness).

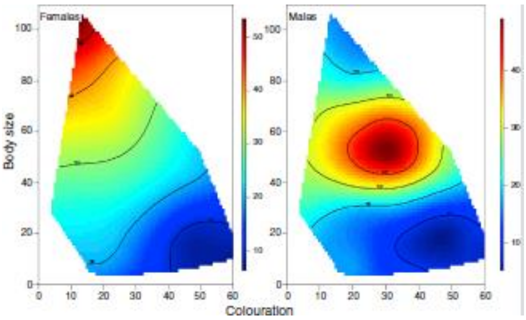

Figure 1. Examples of sexual dimorphism in beetles, ducks and fish.

Sexual dimorphism like this is very common in nature and indicates selection for maleness and femaleness is widespread. It is unclear whether this dimorphism indicates resolved or on-going intralocus sexual conflict for shared traits. Research on the beetles shown here indicates that despite sexual dimorphism (in mandibles) sexual conflict is unresolved. Images courtesy of Tom Houslay, Frank Van Veen and Matthew Silk.

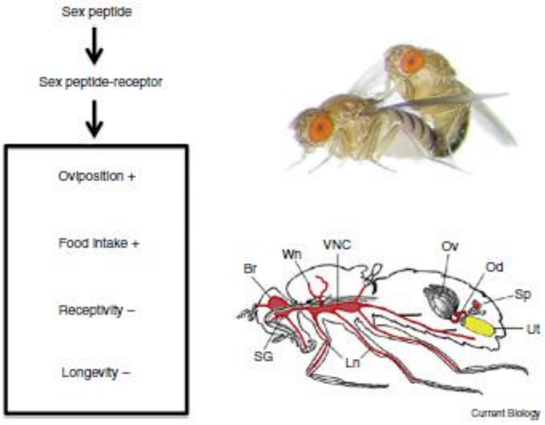

Figure 2. Drosophila seminal fluid generates inter-locus sexual conflict.

During copulation (top right; photo credit: Amy Xinyang Hong and Cedric Tan) male D. melanogaster transfer a suite of seminal proteins to females and one of these, sex-peptide, has sexually antagonistic effects. It increases male fitness by increasing egg-laying (Oviposition +) and decreased female remating (Receptivity -), but reduces female longevity (Longevity -) while increasing feeding (Food intake +). Sex-peptide acts on the female nervous system (bottom right) in the brain (Br), legs (Ln), oviduct (Od), ovary (Ov), suboesophageal ganglion (SG), spermathecae (sperm stores: Sp), ventral nerve cord (VNC) and wings (WN), all shown in red. Sex-peptide binds in the uterus (yellow: Ut), but there do not appear to be receptors there. Redrawn from Kubli, E. (2008) Curr. Biol. 18, R210–R212.