

## Sexual Conflict

### Distinguish intra- and inter-locus sexual conflict

Intralocus sexual conflict arises between male and females of the same species when different alleles at the same locus are preferred in one sex but not the other (*Rice & Gavrillets, 2014*). This means that selection favours different values of a phenotypic trait depending on which sex it is acting upon. This causes evolutionary conflict because if the expression of a given allele moves one sex towards the optimum phenotypic value, it is moving it in the opposite direction for the other sex. Therefore, said trait is under sexually antagonistic selection whereby an evolutionary ‘tug-of-war’ means that neither sex will be able to reach its adaptive peak. However, due to the observational evidence of widespread sexual dimorphism, it can be inferred that sex-limited gene expression is possible and therefore the constraint of sharing a genome is not absolute in limiting the expression of different traits at the same locus between sexes (*Rowe & Armqvist, 2005*).

In contrast, interlocus sexual conflict arises when alleles at different loci in males and females are selected for in the evolutionary interest of the sex that bears said alleles, to the cost of the other. It occurs when there is discord between the interest of males and females over the result of their reproductive interactions arising due to the disparity in cost and benefit. It often results in coevolutionary ‘arms-race’ dynamics, whereby the spread of male alleles at one locus enforces the spread of female alleles at another, and vice versa (*Rice & Gavrillets, 2014*).

## Discuss The Causes and Consequences of Interlocus Evolutionary Conflict between Males and Females

Sexual conflict was and its potential implications were first identified by Parker who stated that sexual conflict occurs if the interests of the different sexes with regard to aspects of reproduction differ (Parker, 1979). Twenty years later, interest in the topic grew as empirical studies on *Drosophila melanogaster* suggested that the conflict could lead to sexually antagonistic coevolution between males and females (Rice, 1996). This essay focuses on one of the two forms of conflict known as interlocus sexual conflict, which occurs when there is an interaction between males and females in which the optimal outcome differs between the two (Rowe & Arnqvist, 2005). The essay will first assess the cause and mechanism by which the conflict takes place, and the direct consequences in terms of coevolutionary dynamics. It will then discuss evolutionary consequences of the conflict by using two examples of adaptations from different sexually reproducing organisms, leading onto how it can result in different evolutionary consequences than historical studies suggest. Finally, the wider consequences of interlocus sexual conflict will be assessed.

Interlocus conflict is fundamentally caused by the presence of a particular type of sexual asymmetry and promiscuous behaviour. Sexual reproduction requires a number of coordinated interactions between males and females. These occur at different scales, from cellular interactions to complex whole-organism behavioural mechanisms. Such interactions have costs and benefits, which differ between the two sexes, causing sexual asymmetry. In truly monogamous species, where individuals only undergo matings with one partner in their entire lifespan, the pair act as a single reproductive unit and thus the benefits and costs are symmetrically shared (Rice & Gavrillets, 2014). However, promiscuity is widespread in sexually reproducing species. For example, polygamous species exhibit mating systems, either polygynous, polyandrous or polygynandrous, that involve at least several percent of non-monogamous matings (Andersson, 1994). Although not all sexual species show a high degree of polygamy, most are promiscuous to some extent. This disrupts the symmetrical share of the costs and benefits in reproductive interactions, leading to a reduction in correlation of lifetime fitness between two mating partners (Rice & Gavrillets, 2014). This aspect of the biology of sexual organisms causes the potential for interlocus sexual conflict to arise, because the two sexes aim to maximise the benefits, and decrease the costs, in all reproductive interactions. For example, in the dung fly *Sepsis cynipsea*, males have armoured genitalia that injure females internally during copulation. Therefore, the costs and benefits during such interactions differ between the two sexes, meaning the reproductive interaction that is 'mating rate' has a different optimum value for each sex (Blanckenhorn et al, 2002).

When assessed at an intragenomic scale, the genetic mechanisms of such reproductive interactions can be used to infer the direct consequences. Suppose there is a reproductive interaction which is determined by a gene at locus A in males but locus B in females, for example, mating rate. The optimal outcome of the interaction is different for the two sexes, as explained above. Alleles at locus A that increase mating rate are favoured and thus spread through the population over generations. While this is adaptive for males, it is maladaptive for females, because their optimum mating rate that maximises fitness is an intermediate value due to the negative effects too many matings bear. Therefore, the presence of the particular alleles at locus A exerts selective pressure at locus B for alleles that decrease mating rate. Spread of alleles at this locus then affects selection of alleles at locus A, and so on (Rowe & Arnqvist, 2005).

This theory is integral in understanding the male-female coevolutionary dynamics that result as a consequence of interlocus conflict. Over time, the selective pressure exerted between loci can lead to suites of sexually antagonistic adaptations that biases the outcome of the interactions towards the evolutionary interest of the bearer of the alleles for said adaptations. Furthermore, this results into arms-race dynamics where ‘persistence adaptations’ in males interact with ‘resistance adaptations’ in females to determine the outcome of the interaction, and the existence of these traits reinforce the evolutionary escalation of each other (*Rowe & Arnqvist, 2005*).

Sexually antagonistic coevolutionary dynamics have lead to the development of complex and exaggerated phenotypes in many species. One example can be observed in invertebrate species where males have evolved a process known as traumatic insemination. It is a form of mating that relies on the evolutionary modification of male genitalia such that they are needle-like in shape. This hypodermic penis is then used to penetrate resisting females’ body walls during copulation, and the male ejaculates directly into the haemocoel. Females have antagonistically responded to this phenomenon by coevolving the ability to digest haemocoelic sperm with enzymes (*Tatarnic, Cassis & Siva-Jothy, 2014*).

Another example of how interlocus conflict is manifested is in the context of the reproductive interaction that is parental care (*Rowe & Arnqvist, 2005*). Parental care can be thought of as any form of parental behaviour that appears likely to increase the overall fitness of the parents’ offspring (*Sheldon B, 2018*). Sexual conflict exists in the evolution of parental care due to the sexual asymmetry in the optimum provision that males and females would ideally provide to maximise their own fitness. This depends on the method by which the species copulate, which has caused a vast array of differing parental care strategies to evolve. One of these strategies includes the abandonment by males following copulation (*Davies NB et al, 2012*) which is beneficial to males as they need not reduce their own fitness by caring for offspring, but still gain fitness provided the offspring are cared for by the mother. In mammals, 95% of species exhibit female-only care with no cases of male-only care, because males often have the trait of desertion (*Clutton-Brock TH, 1991*). This was able to evolve in male mammals because they have evolutionarily taken advantage of the strategy of internal fertilisation. Gametes desiccate when exposed to air, which historically caused terrestrial animals to evolve a mechanism by which fusion of gametes happens internally in aqueous. This is significant because it means following copulation, the female will physically be left in possession of the zygote, rendering it impossible for her to desert it while the male still can (*Dawkins R & Carlisle TR, 1976*). This biological phenomenon forces females into Trivers’ “cruel bind”, whereby the parent that is abandoned by its mate does not, or cannot, desert the offspring (*Trivers RL, 1972*). Therefore, one would expect high incidences of male desertion to evolve in internally reproducing organisms, as demonstrated by the data that confirms these high frequencies in birds and mammals.

In a paper by Barta et al, a mechanism by which females might respond to the adaptive trait of male desertion was identified. The theory behind this mechanism was that if the threat of a female deserting following male desertion was not credible, then males will desert due to the relative costs and benefits of the reproductive interaction. However, if there is a credible threat that the female may not be able to provide sufficient care by herself, then males may be forced to care for the offspring, thus lessening the costs of fitness to females. Using state-dependent models, the authors were able to demonstrate that females may be able to circumvent the intended behaviour of males by keeping her energy reserves below the threshold level required for uniparental care, thus providing a credible threat (*Barta et al, 2002*). The model

therefore predicts that an evolutionary stable solution may evolve whereby the strategic regulation of body mass in females might have an important role in the outcome of this interlocus conflict in the context of parental care.

This example shows a potential evolutionary response and consequence of interlocus sexual conflict that does not necessarily lead to antagonistic arms-race dynamics. This is because male desertion is a behavioural trait that cannot be exaggerated in the way that many morphological adaptations can. Despite the interaction being under control of genes at different loci in males and females, the potential responsive evolution of the females by regulating body mass to provide credible threats will not necessarily result in a feedback dynamic of reinforcing coevolution. This is because the selective pressure that the credible threat exerts does not pull the male desertion trait in the direction of exaggeration, but more likely males will evolutionarily compromise in deciding when to desert or care for offspring. This suggests that the consequences of interlocus sexual conflict need not necessarily result in coevolutionary arms-race dynamics.

A paper by Rowe, Cameron and Day discusses other potential outcomes of interlocus sexual conflict, challenging the traditional theory that it always leads to suites of coevolving 'persistence' and 'resistance' sexually antagonistic adaptations. Their paper used state-dependent models whereby the sensitivity of female resistance traits were allowed to evolve as opposed to the thresholds alone. The results suggested escalatory arms-races need not occur in all cases depending on the nature of genetic variation in female preference functions and the form and strength of natural selection acting on said functions in contexts unrelated to mating. In short, the differences in the evolutionary lability of male and female traits under interlocus conflict can have significant effects on the outcome. Different outcomes include, for example, an increase or decrease in female fitness, or an escalatory or retreating trajectory in male traits (Rowe, Cameron & Day, 2005).

Discussion in this essay thus far has revolved around the direct effects that interlocus conflict has over evolutionary dynamics, however the question that remains is what wider ecological effects can be expected from these dynamics? Although some research suggests that the conflict may result in population extinction due to the direct costs the antagonistic adaptations have on the other sex (Rankin, Dieckmann & Kokko, 2011), most suggests that it will lead to speciation. Coevolution of 'persistence' and 'resistance' traits may incidentally lead to differing allopatric populations diverging in these traits rapidly, thus losing mutual reproductive compatibility leading to the production of new species (Gavrilets, 2014). A perspective on this classical scenario of speciation was added in 1998 by Parker and Partridge when they added an evolutionary component into the process of reinforcement. This occurs when two partially diverged populations hybridize and their hybrids have reduced fitness. It then follows that selection would favour the evolution of reinforced pre-mating isolating mechanism, so as to decrease the frequency of unfit hybrids. However, although females are selected to resist this, some males may benefit despite the offspring's reduced fitness as they generally invest less. Therefore, this sexual conflict with regards to acceptance of matings in interpopulation encounters plays an important role in the rate of evolution of the reinforcement of isolation mechanisms, and thus the rate of speciation (Parker & Partridge, 1998).

A further wider ecological consequence is the role interlocus conflict plays in the co-optimization of sexual adaptations for viability-related functions. Bonduriansky identified three mechanisms by which this can take place. Firstly, sexual conflict can displace populations from their ecological optima as the sexually selected traits become maladapted for their

environment. Secondly, the traits may serve as preadaptations for novel ecological functions making it possible to exploit new niches. Finally, traits that may originally be sex-limited, such as horns in beetles, may be transferred between the sexes (*Bonduriansky, 2011*). These demonstrate how interlocus selection might lead to the ability for populations to explore wider phenotypic space leading to diversification and potential speciation.

In conclusion, interlocus conflict is caused by the evolutionary dispute over the outcome of male-female reproductive interactions. This often leads to the direct consequence of coevolutionary sexually antagonistic arms-race dynamics where ‘resistance’ and ‘persistence’ adaptations in the two sexes will interact to determine the outcome of said conflicts. However, as discussed, further dynamics and outcomes are possible depending on the conditions during evolution. The wider ecological consequences are most prominent in the conflict’s role in speciation. It is clear that interlocus sexual conflict has wide implications and is of great importance in shaping the diverse behaviours and morphologies observed in the sexually reproducing taxa.

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