

remate at lower frequencies. Further research on variation in both reproductive morphology and life history traits is essential.

What determines male mating rate? New research is highlighting the potential importance of variation in reproductive organ size in determining the limits of male mating frequency and reproductive success. The accessory glands provide the material required to synthesise the spermatophore in which the sperm, produced by the testes, are packaged. Male mating rate is both phenotypically and genetically correlated with the size of male accessory glands, but not of the testes. Furthermore, mating causes a significant short-term decrease specifically in accessory gland size. In other Diptera, the accessory glands produce substances that alter female behaviour and physiology, as well as structural proteins that may correspond to those forming spermatophores. Current research with stalk-eyed flies is focussed on identification of accessory gland products and evaluating their role in mediating potential conflicts of interest between the sexes.

Where can I find out more?

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Sexual conflict

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What is sexual conflict?

Sexually reproducing organisms are under evolutionary selection pressure to maximise their Darwinian fitness, but adaptations that function to increase fitness in one sex can reduce or constrain fitness in the other. Sexual conflict is the conflict that exists as a result of the divergent evolutionary interests of males and females.

Is it common? Sexual conflict is inevitable and ubiquitous because the evolutionary interests of males and females never exactly coincide. This has identifiable consequences at genomic and whole organism levels. At an intra-locus level, genes may be expressed in both males and females that may be beneficial only to one sex. Ultimately, this favours sex-limited gene expression, but because this may take time to evolve, the adaptive evolution of each sex can, at least in the short term, be impeded by counter-selection in the other sex.

Other conflicts are mediated by genes at different loci that can evolve independently in the two sexes. These ‘inter-locus’ conflicts arise over diverse aspects of reproduction, from mating decisions (how often and with whom mating should occur), to levels of parental investment (how much each parent expends on offspring production). For example, males can typically achieve high fitness by mating with many females, but females are generally unwilling to mate indiscriminately as such behaviour is not in their best interests. Similarly, where both parents care for their offspring, each could potentially achieve higher fitness if their partner were to provide more care, providing the other parent with opportunities to divert ‘saved’ investment into additional reproductive attempts. In each case, individuals could potentially achieve higher fitness if their

prospective or actual mating partners were to ‘agree’ with their strategy for doing so, but the divergent evolutionary interests of the sexes means that their optimal strategies for maximising fitness rarely coincide.

So who wins? Theory suggests several broad scenarios: male win, female win, compromise or endless evolutionary chases. Predicting outcomes can be complicated, however, and in optimality models they depend on relative power and benefits of winning. Power in these models is the relative cost of a unit of escalation: if it is relatively cheaper for a female to overcome a male adaptation than it is for a male to counter-adapt, then females have an evolutionary advantage in the conflict, and this may frequently be the case.

The benefits of winning are perhaps even more difficult to assess, but one may expect that this part of the equation is weighted more heavily in favour of males, as for them the issue will frequently be whether or not they reproduce at all, while for females it may only be an issue of who they mate with. Individuals of either sex may also attempt to shift the balance of conflict in their favour by coercion or manipulation.

An interesting example of this phenomenon is found among poeciliid fish, where males have evolved a sneak-mating strategy that completely circumvents active female mate choice. Rather than actively court females to gain female consent to copulate, males sneak up on females, insert their modified anal fin that acts as an intromittent organ, and transfer sperm. This tactic is the means by which almost all insemination occurs in the mosquito fish.

Where adaptations in one sex generate counter-adaptations in the other sex, such as increased resistance to manipulation, sexual conflict may result in prolonged or continuous evolutionary chases. Such evolutionary chases or sexual arms races can have important evolutionary consequences, and have been the subject of much recent

investigation. However, theory predicts that unresolvable sexual arms races may be infrequent, and that it is more usual for one sex or the other to gain an evolutionary advantage, halting antagonistic co-evolution, even though the underlying conflict may not be resolved, or that a balance in 'arms levels' results. Exceptions may be common at the molecular level — for example, involving seminal proteins and receptors — where costs of escalation are probably relatively low.

What's the big deal? Sexual conflict has been implicated as the driving force behind many important biological phenomena, including the rapid molecular evolution of reproductive genes and proteins, genome evolution and genomic imprinting. Conflict over reproductive investment may even explain the evolution of the sexes: proto-males may have parasitized the larger gametes of proto-females. Recently, sexual conflict has been implicated in speciation. In any evolutionary arms race between the sexes, there are potentially many different ways individuals of either sex could evolve to enhance their fitness. Any adaptation then counter-selects on the opposite sex, which again has many ways it could counter-adapt, and so on.

In any sexual arms race, it is genes involved in reproduction that are the focus of conflict, and molecular evidence suggests that many reproductive genes evolve extremely rapidly. As a result, populations can, in principle, evolve differences in almost any reproductive trait extremely rapidly through sexual conflict, and it is largely this feature that has prompted the promotion of sexual conflict as a speciation agent. It is important to note, however, that more traditional mechanisms of sexual selection can also generate rapid evolution of reproductive characters, and that distinguishing between the different selection pressures that can potentially lead to reproductive isolation is likely to be difficult.

Sexual conflict, sexual selection, what's the difference? The two concepts are intimately related. Sexual selection, selection in exclusive relation to securing matings (more strictly fertilizations), inherently generates sexual conflict because, for example, females will mate with some males, but not with others. Additionally, sexual conflict can be thought of as a sexual selection mechanism, as adaptation to win sexual conflicts can increase variance in reproductive success. Traditionally, sexual selection via female choice was seen to be generated by either direct or indirect benefits to females. In contrast, recent formulations of sexual selection generated by sexual conflict give primacy to direct costs, and female mating decisions are viewed as an attempt to minimise costs rather than maximise benefits. The importance of various mechanisms is currently being debated, but it seems likely that all play some role in sexual selection, although their relative importance may vary.

Where can I find out more?

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Primer

Fidelity in protein synthesis

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The flow of genetic information from DNA to RNA to protein constitutes the basis for cellular life. DNA replication, transcription and translation, the processes through which information transfer occurs, are the result of millions of years of evolution during which they have achieved levels of accuracy and speed that make modern life possible. All three processes have base complementarity at the core of their mechanisms. DNA replication and transcription both depend on complementarity of the incoming nucleotide to the DNA template, whereas translation depends on the complementarity of the anticodon of the incoming transfer RNA (tRNA) to the codon in the template messenger RNA (mRNA). Fidelity of genetic information transfer thus relies heavily on discrimination between complementary, Watson-Crick (and in a few cases wobble) base pairs and non-complementary ones.

To ensure high selectivity, the macromolecular machines that carry out replication, transcription and translation — DNA polymerase, RNA polymerase and the ribosome, respectively — have evolved specific substrate recognition strategies. These strategies exploit the stability arising not only from the hydrogen-bonding and stacking capacity of Watson-Crick base pairs but, more importantly, from their distinct geometry. Both polymerases and the ribosome have chemical groups that directly monitor the geometry of the template-substrate base pair. In the case of DNA polymerases, this 'geometric selection' is estimated to contribute three orders of magnitude or more to selectivity, while hydrogen bonding only provides 7-40-fold selectivity.