PUBLISHED: 15 MAY 2017 | VOLUME: 1 | ARTICLE NUMBER: 0174

news & views

REPRODUCTIVE BEHAVIOUR

Make love, then war

Female aggression is enhanced after mating. Genetic manipulation and behavioural observation show that the receipt of sperm, and a seminal fluid protein, enhances female *Drosophila* aggression towards other females.

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Anyone who has come face-to-face with a mother bear and her cubs knows to tread lightly, or get out of the way, fast! Females of many species can be aggressive to one another over resources, mates, breeding or to reduce or prevent reproduction by other females[1] — but a highly aggressive female defending her progeny or reproductive capacity is particularly dangerous. Understanding the triggers that change the intensity or quality of female aggressive behaviours associated with reproduction can help to reveal the underpinnings of the behaviours themselves. And what better way to dissect this than with the powerful model system, *Drosophila melanogaster*, whose aggressive behaviour was first described over 100 years ago by Sturtevant[2]. Writing in *Nature Ecology & Evolution*, Bath *et al.*[3] show that the extended duration of female aggression in fruit flies is caused by receipt of sperm and, in part, by receipt of a seminal fluid protein, known as the sex peptide (SP), during mating. Therefore, their results show that aggressive behaviours in one sex can be influenced significantly by chemical messages from the other, and open up many questions regarding the function and adaptive value of female aggressive behaviour. If you thought fighting, head butting and shoving were exclusively male pursuits, then think again!

Aggressive behaviour overall, and mating competition in particular, have typically been studied in mammals and are less well understood in invertebrates. A particular gap in our knowledge, tackled by Bath *et al.*, is how aggression responds to cues signalled during mating. In flies, females show aggressive behaviours[4] and mated females have been reported to fight for longer and to retreat less often than virgins[5]. Bath *et al.* asked how this change in female–female aggression is modulated by mating, by comparing aggressive interactions among wild-type and mutant strains of *D. melanogaster*. The team placed pairs of females in observation chambers with limited food resources, to catalyse aggressive interactions. Interactions between two virgins, or two mated females, or a virgin and a mated female were filmed and the total duration of aggressive interactions (head butts and shoving) and amount of time spent feeding were quantified. The results were clear: the amount of time spent in aggressive behaviour significantly increased when at least one female of a pair had mated.

Aggressive behaviour in females is expected to show high plasticity, associated with specific reproductive events. Hence, there was a strong rationale for testing the dependence of post-mating aggression in females upon aspects of mating. The authors picked apart the contributions of mating *per se*, sperm, and an important seminal fluid protein, SP, which elevates fecundity and decreases remating receptivity[6,7], using molecular genetic tools such as spermless males, and males that did not produce SP. They found that increased aggression by mated females depended on receipt of sperm: aggression did not increase following mating with spermless males. Receipt of SP accounted for part of the elevated aggression in mated females, although the intermediate levels of aggression seen in SP-null mated females suggest that other seminal proteins might also contribute to modulating female aggression.

The authors hypothesized that increased aggression can be mediated directly upon females, or indirectly through demands for food or other effects of the increased egg production induced by mating. The authors examined the contribution of egg production to female aggression by testing females whose oogenesis was arrested at an early stage. Aggression was elevated by mating even in females that could not complete oogenesis (though this strain of females was less aggressive overall). Hence, increased aggression in mated females was not mediated simply through the direct agency of maturing or laying eggs *per se*. Fighting over food may be a general part of female–female interactions[1,5], so Bath *et al.* also recorded the flies' feeding behaviour to determine whether it was related to the increased aggressiveness of mated females. If aggression functions primarily to defend or acquire limited food resources for post-mating egg production, then one might predict that elevated aggression following mating should be linked to elevated egg production or feeding. However, neither effect was consistently observed.

The emerging picture is that mating, receipt of sperm and SP can elevate aggression by a female against other females (Fig. 1), but that the relationship between post-mating aggression and food acquisition is less clear. A better understanding of the temporal sequence of the expression of these different post-mating behaviours might provide clues. The findings also prompt many wider questions.

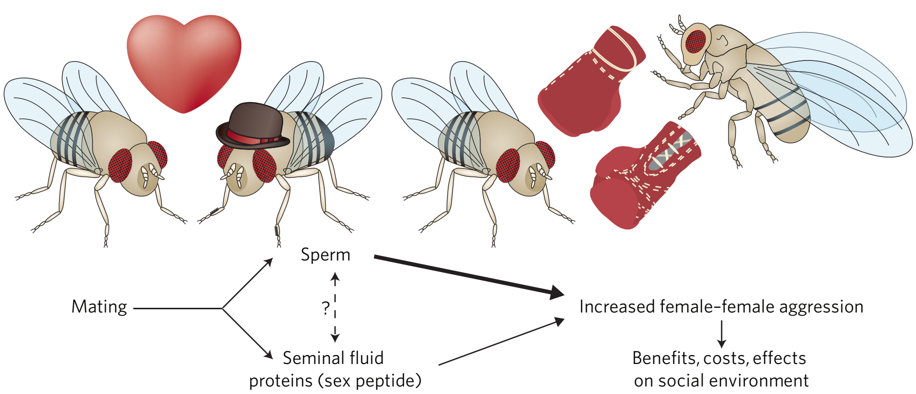

Figure 1 | Diagram to illustrate inducers and potential outcomes of mating on post-mating female–female aggression.

It will be interesting to determine the fitness benefits and costs of increased post-mating aggressive behaviours by females, including whether those behaviours are sex specific or have transgenerational consequences. There are several possibilities: (1) that heightened female aggressiveness is an example of sexual conflict, with males inducing this behaviour in their mates as part of a strategy to increase their offspring's survival despite potential costs to the mother; (2) that the increase in aggression benefits mated females through the acquisition of more nutrients and oviposition sites and hence more offspring; or (3) that high aggression is costly to females, hence they 'use' mating cues from the male, to turn up aggression only when needed.

There are additional implications for how aggression expressed by individual mated females might interact with the wider social and sexual environment[8]. It will be interesting to examine the extent to which all females respond to this heightened aggressive environment and whether the elevated aggression is focused towards other females, potential suitors, or towards all flies. As a result of contributions from the mating male, individuals of both sexes will experience a markedly different social environment when encountering mated versus virgin females, which could in turn change their behaviours[9].

The study also prompts questions about the mechanism by which sperm and SP increase post-mating aggressive behaviours, including how female aggression varies as a consequence of food limitation, and the significance for aggression of the alteration of the hormonal milieu of females upon mating. Finally, it will also be fascinating to uncover the neuronal pathways that are stimulated to increase female–female aggression by mated females. Octopamine and dopamine pathways have been implicated in aggression in male flies and can also be modulated in females after mating (for example, refs [10,11–14]), making these neuromodulators and neurotransmitters good candidates to test for roles in post-mating aggression.

In conclusion, the study by Bath *et al.* adds new depth to our understanding of the regulation of aggressive behaviours in response to reproductive cues. Their finding that receipt of sperm and seminal proteins during mating cause *D. melanogaster* females to become more aggressive towards other females opens up new avenues to discover how aggression can be modulated, and how selection and sexual conflict can tune this modulation. ❐

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Competing interests

The authors declare no competing financial interests.