

## ANIMAL BEHAVIOUR

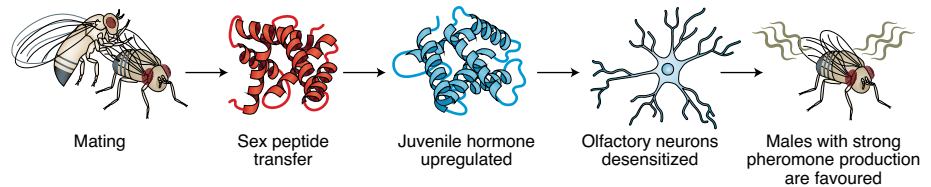
## Escaping the choosiness trap

Behavioural experiments and genetic manipulations reveal the mechanisms by which *Drosophila* females plastically alter their choosiness in response to mating, resolving trade-offs of mate choice.

Jennifer C. Perry and Ben R. Hopkins

In Sylvia Plath's novel *The Bell Jar*, the narrator sits beneath an imaginary fig tree. Each branch of the tree represents a path her life could take, each juicy fruit an inviting future: poet, professor, traveller, athlete. But as she sits, unable to decide which fruit to pick, the figs begin to darken, wither and drop to the ground. And so she remains figless — such are the perils of indecision. The polyandrous *Drosophila* female faces a similar dilemma, one that has been called the 'fundamental trade-off of mate choice'<sup>1</sup>. On the one hand, females want a high-quality partner, both for his good genes that offspring will inherit and for any direct material benefit he can offer, such as good territory. But setting high standards presents serious risks<sup>2,3</sup>. Conspicivics might be few and far between, or all males encountered might fall short of a female's standards, setting her up for mating and reproductive failure. The risk is real: in some populations, >15% of females go un-mated, whether through an excess of choosiness or other factors<sup>4</sup>. Writing in *Nature Ecology & Evolution*, Kohlmeier et al.<sup>5</sup> describe how *Drosophila melanogaster* females navigate this choosiness trap.

In a series of beautifully controlled experiments, the authors demonstrate that mating induces a switch-like increase in female choosiness. As virgins, females exhibited no preference between males from two established wild-type strains, *Tai* and *Netherlands*. But after mating, females preferred *Tai* males. This change in preference held in both competitive and non-competitive trials, allowing the authors to exclude the alternative hypothesis that *Tai* males simply outcompete *Netherlands* males with mated females (for example, because they are better able to overcome any increased resistance to re-mating). *D. melanogaster* females store sperm for weeks and second-mating males displace most sperm from storage. As a result, this plastic modulation of choosiness allows females to first get sperm in the bank, and subsequently enact choosiness to 'trade up' for sperm from higher-quality mates if they come along<sup>6</sup>.



**Fig. 1 | *D. melanogaster* females become more selective when choosing a mate after mating.** This increase in selectivity is brought about by a post-mating increase in the release of juvenile hormone, which is likely stimulated by the male seminal protein sex peptide. Juvenile hormone desensitizes OR47b olfactory neurons to the male aphrodisiac pheromone palmitoleic acid. This leads mated females to prefer pheromone-rich males.

But is this a true increase in choosiness or just an increase in female information about variation in male quality and female skill in assessing males? To distinguish between these two explanations, the authors next tested whether female receipt of sex peptide, a male seminal protein that induces a catalogue of post-mating changes in female behaviour<sup>7</sup>, was required for the post-mating increase in choosiness. They found that in the absence of sex peptide (or its receptor) the post-mating increase in choosiness was reduced, suggesting that it's largely independent of experience and, in fact, a novel sex-peptide-dependent post-mating response.

The next part of the puzzle was to discover how mating stimulates a change in female choosiness. Using single-sensillum recordings in virgin and mated female antennae, the authors found that in mated females, OR47b olfactory receptor neurons show a 50% reduction in sensitivity to the male aphrodisiac pheromone palmitoleic acid. They further showed that desensitization is a downstream consequence of a post-mating increase in juvenile hormone. Juvenile hormone is implicated in an extensive range of reproductive processes, and its biosynthesis is thought to be triggered by sex peptide. Crucially, the authors showed that a consequence of the desensitization of OR47b neurons was a preference for males with more palmitoleic acid, which, it turns out, is exactly what *Tai* males have.

Collectively, this careful work suggests a behavioural model whereby mating and receipt of sex peptide upregulates juvenile hormone, which desensitizes OR47b to male pheromone, effecting an increase in preference threshold that shifts mating preferences towards males that produce more pheromone (Fig. 1). The power of the study comes from the authors' ability to use phenotypic engineering to directly validate the model: they engineer females with increased choosiness (virgin females treated with a juvenile hormone analogue) and males with increased attractiveness (*Netherlands* males treated with pheromone).

Fascinating mechanistic questions now arise. What are the downstream targets that juvenile hormone acts on in female OR47b neurons? Does the increase in choosiness decay as stored sperm is depleted, such that the strength of female preference continues to wax and wane throughout life? Is preference for non-pheromonal traits, such as body size and vibrational courtship, similarly altered by mating? If so, how is information from multiple signals integrated to coordinate overall choosiness? Does choosiness continue to increase with mating experience as females gain more information about the population of males and more skill at evaluating males, and does sex peptide encode and engender effects of that experience on choosiness? The finding that female choosiness is modulated by sex peptide — a molecule strongly implicated

in sexual conflict and male manipulation of female reproduction<sup>8</sup> — opens new possibilities for exploring conflict over mate choice.

With this new model of mating-induced plasticity in choosiness in hand, the scope for significant advances in understanding the evolution of mate preference is clear. Is mating-induced choosiness a *D. melanogaster* innovation, or a general phenomenon in sperm-storing animals? Many animals show a post-mating reduction in sexual receptivity<sup>9</sup>; are they too becoming choosier? There are also interesting consequences for the operation of sexual selection if mating-induced choosiness is widespread. Most sexual selection through female choice of male ornaments is then likely to arise through mated females, and it is through mated females that the potential for coevolution and runaway selection will be strongest. By contrast, sexual selection on males through virgin females is likely to take the form of a race to locate them, and consequently to favour male traits involved

in speed, explorativeness and detection of female cues. The balance between these forces will depend on the relative frequency of virgin and mated females in a population, along with the relative paternity share males stand to gain from matings with virgin versus mated females. Finally, mating-induced choosiness might help to resolve the puzzling observation that females of many species appear not to avoid inbreeding even when costs of inbreeding depression are clear<sup>10</sup>: studies of virgin females might have missed later-life choosiness and inbreeding avoidance.

As a whole, the discovery of proximate mechanisms underlying female choosiness uncovered here — made possible by the powerful fruit fly genetic toolkit — unleashes new prospects for testing ultimate adaptive hypotheses for the evolution of mate choice. □

Jennifer C. Perry <sup>1</sup>✉ and Ben R. Hopkins <sup>2</sup>

<sup>1</sup>*School of Biological Sciences, University of East*

*Anglia, Norwich, UK.* <sup>2</sup>*Department of Evolution and Ecology, University of California Davis, Davis, CA, USA.*

✉e-mail: [jennifer.perry@uea.ac.uk](mailto:jennifer.perry@uea.ac.uk)

Published online: 21 June 2021

<https://doi.org/10.1038/s41559-021-01500-5>

## References

1. Courtiol, A., Etienne, L., Feron, R., Godelle, B. & Rousset, F. *Am. Nat.* **188**, 521–538 (2016).
2. Jennions, M. D. & Petrie, M. *Biol. Rev.* **75**, 21–64 (2000).
3. Kokko, H. & Mappes, J. *Evolution* **59**, 1876–1885 (2005).
4. Hare, R. M. & Simmons, L. W. *Biol. Rev.* **94**, 929–956 (2019).
5. Kohlmeier, P., Zhang, Y., Gorter, J. A., Su, C.-Y. & Billeter, J.-C. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-021-01482-4> (2021).
6. Halliday, T. R. in *Mate Choice* (ed. Bateson, P.) 3–32 (Cambridge Univ. Press, 1983).
7. Avila, F. W., Sirot, L. K., LaFlamme, B. A., Rubinstein, C. D. & Wolfner, M. F. *Annu. Rev. Entomol.* **56**, 21–40 (2011).
8. Perry, J. C. & Rowe, L. *Cold Spring Harb. Perspect. Biol.* **7**, a017558 (2015).
9. Hopkins, B. R., Avila, F. W. & Wolfner, M. F. in *Encyclopedia of Reproduction* (ed. Skinner, M. K.) 137–144 (Elsevier, 2018).
10. de Boer, R. A., Vega-Trejo, R., Kotrschal, A. & Fitzpatrick, J. L. *Nat. Ecol. Evol.* <https://doi.org/ggbb> (2021).

## Competing interests

The authors declare no competing interests