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EVOLUTIONARY BIOLOGY

Brotherly love benefits females

Mating competition between males often has harmful consequences for females. But it seems that fruit flies alter their behaviour among kin, with brothers being less aggressive and females reproducing for longer as a result.

SCOTT PITNICK & DAVID W. PFENNIG

The romantic notion of sexual reproduction as a cooperative endeavour has been trampled on by a growing number of cases in which sexual competition between males results in harm to females[1]. Examples include spiny-beetle penises that punch holes in the female reproductive tract, female frogs drowning as several males struggle to mount them, and toxic ejaculate proteins that reduce a female fruit fly's desire to re-mate and can cause her early death. Such costs incurred by females represent the collateral damage of male–male competition for access to successful reproduction[2]. But the picture is complicated when the competing males are related, because of the evolutionary benefit to an individual if a relative reproduces. Theory suggests that male relatedness should reduce sexual harm to females. In a paper published on *Nature*'s website today, Carazo *et al.*[3] show experimentally that this is indeed the case in the fruit fly *Drosophila melanogaster*.

Sexual harm to females is a 'reproductive tragedy of the commons' that may reduce a population's productivity and even lead to local extinctions[4]. But conflict and cooperation in social interactions lie along a continuum, and resolving the evolutionary pressures that move populations along this continuum is a major challenge. One such pressure is genetic relatedness among males. Natural selection favours individuals that are most successful at propagating their distinctive genes; these individuals are said to have the highest 'fitness'. However, an individual's overall ('inclusive') fitness is the sum of its direct fitness, which is the number of offspring it produces, and its indirect fitness, which includes the number of offspring produced by the individual's genetic relatives as a result of its behaviour. Essentially, by helping its genetic relatives to reproduce, an individual indirectly propagates copies of some of its own genes[5].

It has been proposed that kin selection — natural selection that increases indirect fitness — can explain why males sometimes reduce the harm incurred by their mates[4,6]. Specifically, when kin compete, any harm imposed on a female should detrimentally affect the males' inclusive fitness by reducing the reproductive output of their male relatives. So, by favouring reduced competition between related males, kin selection should limit collateral harm to females. Although sexual cooperation between related males has been extensively studied in vertebrates[7,8], the fitness consequences for females have received little attention.

In a series of experiments, Carazo *et al.* paired one female with three males that were unrelated to the female, but that varied in relatedness to one another. The authors found that females paired with male triplets that were full siblings (AAA) had greater lifetime reproductive success than females paired with three males that were unrelated to each other (ABC). This difference was not a result of AAA-treatment females having higher fecundity or a longer lifespan, but rather because they exhibited reduced reproductive senescence — that is, their rate of offspring production declined with age more slowly than did that of females exposed to unrelated males. The researchers show that this pattern was attributable, at least in part, to a significantly slower decline in the survival of offspring as AAA- compared with ABC-treated females aged (Fig. 1).

The authors next sought to uncover the mechanisms underlying the reduced reproductive senescence of females when paired with brothers, by quantifying how males interact with the female and with one another. Again, females were randomly assigned to AAA or ABC trios of males, with the addition of a third, intermediary treatment of two full siblings and one unrelated male (AAB). As predicted by kin-selection theory, fighting between males was more common in ABC triplets than in either of the other conditions (Fig. 1). ABC males also courted females more intensely than AAA males. However, there were no treatment-related differences in mating rates. These observations suggest that harm to females is mediated by the aggressive behaviour

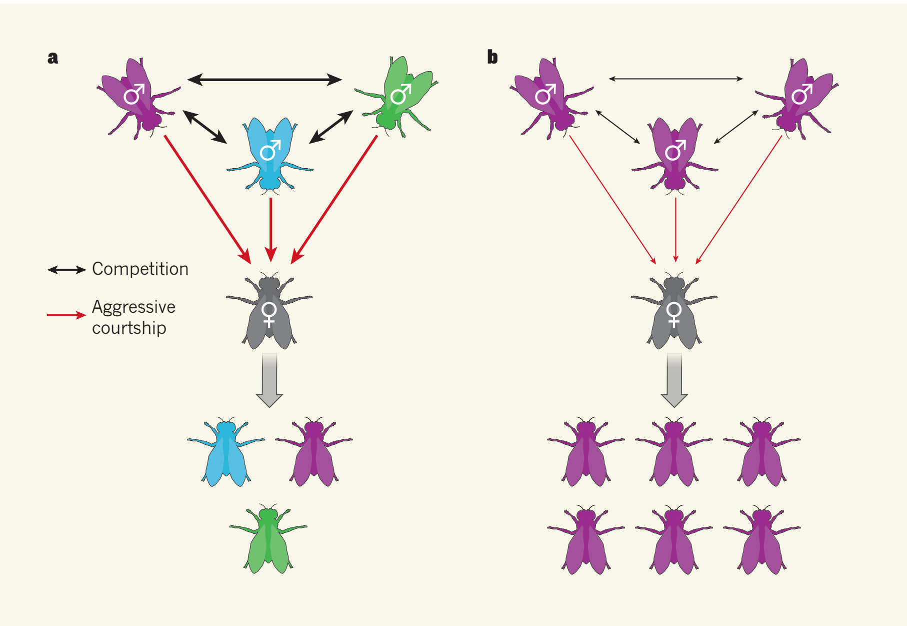

Figure 1 | Kindness to kin reduces harm to females. a, Unrelated male fruit flies compete with each other and court females aggressively. Carazo *et al.*[3] find that this behaviour harms females by causing them to age rapidly (in reproductive terms) and ultimately to produce fewer offspring. **b**, By contrast, the authors observe that brothers compete and court less aggressively; consequently, the females are reproductively successful for longer and produce more offspring. This reduced aggression between brothers also benefits the males: by helping his brothers to reproduce, a male indirectly propagates copies of some of his own genes.

of unrelated males towards each other and to females, reinforcing earlier findings[9].

One might propose that ABC males harm their mates by adjusting the contents of their ejaculate. For example, the seminal-fluid hormone Acp70A can reduce female lifespan, and *D. melanogaster* males are adept at facultatively adjusting both the sperm and seminal-fluid content of their ejaculates[10,11]. But Carazo *et al*. ruled out this explanation. They quantified female post-mating behaviours that are influenced by ejaculate content (latency to re-mating, and egg-laying rate) and found no differences between females inseminated by AAA compared with ABC males. Thus, the beneficial consequences of kin selection seem to involve pre-mating sexual selection. Nevertheless, another experiment revealed dramatic post-copulatory consequences of male competitive behaviour. By combining two brothers with one unrelated male (AAB), the authors found that the unrelated male did not court or mate more frequently than either of the brothers, yet sired on average twice as many offspring! Although the mechanism underlying this dramatic pattern remains a mystery, the evolutionary implications are clear: the gentler behaviour among brothers that reduces premature ageing of females is evolutionarily unstable. Such kindness will not be rewarded whenever selfish, unrelated males join the group.

Drosophila melanogaster has been an important model system for studying myriad topics in evolutionary biology, including sexual selection and sexual conflict, but not kin selection. Natural fruit-fly populations are typically large, and individuals are thought to disperse widely within their environment, so there would presumably be little opportunity for interaction among relatives. Yet Carazo and colleagues' findings suggest that *D. melanogaster* populations might occasionally be (or have been) structured such that they could be influenced by kin selection. We hope that this surprising and compelling study will tempt more *Drosophila* biologists to leave the laboratory to explore the ecology of this model system. ■

Scott Pitnick *is in the Department of Biology, Syracuse University, Syracuse, New York 13244, USA.* **David W. Pfennig** *is in the Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599, USA.*
e-mails: sspitnic@syr.edu; dpfennig@unc.edu

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