

Article

Evolutionary basis of male same-sex sexual behavior by multiple pheromone switches in *Drosophila*

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SUMMARY

Male same-sex sexual behavior (SSB) is widespread among animal species, but its proximate (mechanistic) and ultimate (evolutionary) explanations remain unclear. A prevailing view is that SSB reflects impaired sex recognition, especially in insects. By unbiased behavioral screening, we identified a *Drosophila* species, *D. santomea*, in which males seldom attack and spontaneously court males vigorously, in addition to females. Behavioral, chemical, and optogenetic neuronal manipulations indicate that *D. santomea* males can distinguish conspecific sex and retain functional aggression circuitry. Instead, male SSB reflects three evolved pheromonal changes affecting two separate signaling systems, resulting in both reduced pheromone production and behavioral valence reversal. One of these occurs unexpectedly in females and may have evolved to prevent hybridization with an interfertile, geographically overlapping sibling species. Remarkably, male SSB and similar pheromonal changes also selectively co-occur in *D. persimilis*, a geographically and phylogenetically distant species and member of another sympatric sibling pair, implying evolutionary convergence in the two young taxa. The results identify a pheromonal mechanism for rapid social evolution in *Drosophila* and suggest a plausible evolutionary origin for male SSB as arising in concert with female adaptations that ensure reproductive isolation during speciation.

INTRODUCTION

Social behaviors, including aggression, courtship, mating, parenting, and cooperation, are remarkably diverse in the animal kingdom¹ and can vary greatly between entire orders² or even closely related sibling species.³ The fitness benefits of social behaviors have received considerable theoretical attention,^{4–6} and underlying genetic, hormonal, neural circuit, pheromonal, and sensory mechanisms have been identified in several model organisms.^{7–9} Among insects, species of the genus *Drosophila*¹⁰ have provided powerful model systems for studying social behaviors,^{11–16} as exemplified by a comprehensive understanding of the biology of male courtship and mating in *D. melanogaster*.^{17–19} The study of interspecies variation

between *Drosophila* species has identified flexible genetic^{20–23} and neural^{24–27} substrates of rapid courtship evolution and revealed general principles of reproductive function and isolation.²⁸ However, this fruitful approach has rarely been applied to other social behaviors.

Aggression is a highly adaptive and virtually universal intrasexual social behavior among males and females of sexually reproducing metazoan species.²⁹ It serves to establish and maintain dominance in social hierarchies; protect resources, such as mates, food, or nesting sites, from conspecific competitors³⁰; and in humans, promote individual professional or social success as well as defend against territorial incursion.³¹ Interestingly, aggression is tightly linked to courtship and mating at the behavioral as well as neural circuit levels³² (e.g., in vertebrates,

