Behavioural Processes 235 (2026) 105324

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Sex differences in locomotor recovery across mating contexts in *Drosophila melanogaster*

Rui Han [a,*,1], Jun Zhang [b,*], Xin-Hui Chen [b], Jing-Wen Duo [b], Yi-Yi Li [b], Yi-Ran Chen [b], Si-Tong Chen [b], Lin-Xiang Liu [a], Xiang-Haoran Lin [a]

[a] Tan Kah Kee College, Xiamen University, Zhangzhou, Fujian 363105, China
[b] School of Life Sciences, Xiamen University, Xiamen, Fujian 361102, China

ARTICLE INFO

Keywords:
Locomotion
Sex difference
Mating context
Social interaction
Drosophila melanogaster

ABSTRACT

Mating behaviour plays a key role in animal reproduction and profoundly affects the physiological state and behavioural performance of individuals. Although numerous studies have focused on the behavioural responses of single-sex groups of *Drosophila melanogaster* under mating contexts, systematic comparisons of male and female fruit flies across different mating contexts are still relatively limited. This study investigated the locomotion of 86 male and female fruit flies under different mating contexts, including virgin, continuously exposed to the opposite sex (mated), beginning cohabitation with the opposite sex on the 8th day of the experiment (virgin-mated), and opposite-sex cohabitation on the 8th day and switching to same-sex cohabitation (mated-deprived). The results showed that virgin males exhibited the highest overall movement speed and that continuous exposure to the opposite sex led to a transient reduction in male movement speed. In contrast, females displayed a temporary increase in movement speed under opposite-sex cohabitation but rapidly returned to levels comparable to virgins. These sex-specific and time-dependent changes indicate that mating context exerts dynamic effects on movement speed. Moreover, in contrast to the negative effects of social isolation reported in previous studies, our findings suggest that mating status and social environment jointly shape locomotor performance under non-isolated conditions. Overall, this study highlights how males and females dynamically adjust locomotor strategies in response to changing reproductive and social contexts, providing an evolutionary perspective on behavioural plasticity and sex-specific trade-offs in insects.

1. Introduction

Mating plays a crucial role in the life cycle of animals, ensuring reproductive success while also influencing physiology and behaviour (Chapman et al., 1995; Dixson and Anderson, 2004; McGraw et al., 2004; Simmons, 2019). Across taxa, mating patterns vary widely: in mammals, mate choice and courtship often involve complex competitive strategies (Clutton-Brock and Parker, 1992; Preston et al., 2001); in birds, many species exhibit long-term pair bonding (Griffith, 2019; Møller, 2003); and in insects, mating behaviours are generally less elaborate but encompass a broad diversity of strategies, ranging from mate guarding and sperm competition in beetles (Saeki et al., 2005; Simmons et al., 1999) to Sex Peptide (SP)–mediated post-mating responses in fruit flies (Chapman et al., 2003; Wolfner, 2002). Importantly, in insects, mating induces marked physiological and behavioural changes—for example, alterations in activity, feeding, and reproductive investment—that are particularly pronounced and can be quantitatively assessed (Avila et al., 2011; Gillott, 2003; South and Lewis, 2011). Thus, mating serves not only as the initiation of reproduction but also as a trigger for dynamic changes in physiology and behaviour, with sex-specific differences in both the magnitude and nature of these effects (Arnqvist and Nilsson, 2000; Bath et al., 2017; Gillott, 2003).

Fruit flies (*Drosophila melanogaster*), as classical model animals in behavioural genetics and systems biology, are highly valuable references for understanding insect mating patterns (Han et al., 2024; Sakai et al., 2002). Females exhibit pronounced post-mating changes—such as increased egg laying, reduced receptivity, and altered locomotion and feeding (Isaac et al., 2010)—largely mediated by seminal fluid proteins such as Sex Peptide (SP) transferred during copulation (Chapman et al., 2003; Liu and Kubli, 2003; Wolfner, 2002). On the other hand, male fruit

* Corresponding authors.
E-mail addresses: hanrui@lolab-nthu.org (R. Han), jzhang@xmu.edu.cn (J. Zhang).
[1] ORCID: 0009–0009-4984–0493

https://doi.org/10.1016/j.beproc.2025.105324
Received 25 October 2025; Received in revised form 23 December 2025; Accepted 28 December 2025
Available online 29 December 2025

flies perform a series of fixed courtship behaviours before mating, such as chasing, wing vibration, and licking, which consume considerable energy. Energy expenditure and investment of seminal resources during mating may also cause changes in their behaviour and physiological state (Dew-Budd et al., 2016; Dukas, 2008; Villella and Hall, 2008). Overall, previous studies have tended to emphasise changes within a single sex, systematic comparisons between males and females under comparable experimental conditions remain limited. This omission is critical because males and females often exhibit divergent reproductive strategies and physiological investments (Arnqvist and Nilsson, 2000; Bath et al., 2017; Swanson, 2003), and overlooking sex differences can obscure the distinct ways in which mating shapes behaviour and physiology in each sex.

Moreover, existing studies also face two important limitations. First, most studies use behavioural measurements at a single time point, making it difficult to reveal the dynamic process of mating effects (Carvalho et al., 2006). Since mating effects may be transient, cumulative, or reversible, focusing only on one time window may lead to incomplete or even misleading conclusions about how behaviour changes across the reproductive timeline (Wigby and Chapman, 2005; Wolfner, 2002). Second, existing studies have focused mostly on the comparison between the two end states of "virgin vs. mated context," and lack attention to transitional states during the mating process (such as switching from virgin to mated, or from mated to same-sex cohousing after the interruption of mating) (Carvalho et al., 2006; Wigby and Chapman, 2005).

To overcome these limitations, locomotion is a suitable behavioural index. Activity level reflects overall engagement in movement, while movement speed indicates the intensity of locomotor output, together offering a sensitive readout of physiological state and reproductive costs (Han et al., 2024, 2021). Locomotion is tightly linked to reproductive strategies: males invest substantial energy in courtship movements, whereas post-mating females adjust locomotor activity in relation to oviposition and resource acquisition (Isaac et al., 2010; Wicker-Thomas and Hamann, 2008). Thus, locomotion offers a powerful framework for sex-comparative analyses of mating effects.

In our previously published study (Han et al., 2024), we investigated how different mating systems influence locomotor behaviour in male and female fruit flies. That study systematically compared behavioural differences across four static mating regimes—virgin, monogamous pairing, repeated pairing with virgins, and repeated pairing with mated partners—and revealed significant sex-specific responses under different pairing contexts. However, flies were housed individually during behavioural tracking, raising potential confounds of social isolation, and the design did not address transitions in mating contexts. Building on that work, the present study systematically investigates both sexes under dynamic social and mating contexts, thereby disentangling the immediate and longer-term effects of reproductive and social experiences on behaviour.

Therefore, this study redesigned the experimental paradigm and systematically examined the locomotion of male and female fruit flies under different mating contexts: virgin, continuously cohoused with the opposite sex (mated), switched to an opposite-sex cohousing context in the middle of the experiment (virgin-mated), and interrupted opposite-sex cohousing followed by same-sex cohousing (mated-deprived). Based on previous evidence that mating imposes sex-specific physiological and energetic costs, we hypothesised that changes in mating context would differentially affect locomotor performance in males and females. Specifically, we predicted that males would exhibit a transient reduction in locomotion following mating due to increased energetic expenditure, whereas females would show short-term post-mating increases in locomotion associated with reproductive investment, with these effects diminishing over time. By measuring individual movement speed and activity level at multiple time points before and after transitions in mating contexts, we adopted a within-subject (pre–post) approach to assess how different social experiences influence behavioural performance across sexes and developmental stages, and to further explore the interaction between social environment and mating status, thereby providing a new perspective for understanding the plasticity of animal behaviour.

2. Material and methods

2.1. Fly strains

Wild-type *Drosophila melanogaster* (*Canton-S* strain) was used in this study. Flies were obtained from the Bloomington Drosophila Stock Centre (BDSC, RRID: BDSC_64349). Flies were maintained on standard cornmeal–agar media composed of 33.53 g of cornmeal, 5 g of agar, 12.5 g of yeast, 20 g of sucrose, and 3 ml of propionic acid, with double-distilled water added to a final volume of 500 ml (corresponding to ~425 ml of water). The medium was dispensed at 10 ml per 95 × 24 mm culture vial. Flies were reared at 25 °C under a 12:12 h light: dark cycle (lights on at 8:00 a.m. and off at 8:00 p.m.). In total, 86 flies were used in this study, including 41 males and 45 females.

2.2. Tracking apparatus

Locomotion levels were recorded via a video tracking system (Han et al., 2024). Individual flies were transferred into clean, empty fly tubes with plastic stoppers. Before recording, flies were given a 5-min acclimation period: at 13:55, each pair of flies from the same tube was separated and placed individually into fresh tubes. This short acclimation was chosen to minimise stress while allowing the flies to adapt to the new environment. Recording duration was set to 1 min per fly. Recordings were performed sequentially between 14:00 and 15:00, a period when flies are normally active but outside their peak mating time, in order to reduce interference with potential reproductive behaviours.

The tubes were horizontally placed on a white paper background and visually separated via triangular barriers to prevent mutual visual interference. A Huawei P50 Pro smartphone camera mounted on a fixed stand at approximately 15–20 cm above the tubes was used to record the videos. Raw videos were standardised to 1920 × 1080 resolution (MP4 format, muted) at 15 fps, which subsequent automated analysis using custom Python scripts.

2.3. Experimental design

Newly eclosed flies were collected within 8 h under light CO_2 anaesthesia, sexed under a stereomicroscope, and confirmed as virgins. All experimental flies were derived from the same cohort and allocated at a density of two flies per vial with food medium. Flies were then assigned to five experimental groups: (1) virgin male and (2) virgin female, each maintained in same-sex pairs throughout the experiment; (3) mated, opposite-sex pairs housed together continuously; (4) virgin-mated, initially housed in same-sex pairs and switched to mixed-sex pairs on Day 8; and (5) mated-deprived, initially housed in mixed-sex pairs and separated into same-sex pairs on Day 8. For clarity and brevity, these descriptive labels are used throughout the manuscript, omitting the term “context.” Movement speed and activity level were measured on Days 4, 9, and 15, and flies were subsequently maintained until death (Fig. 1).

2.4. Data analysis

All behavioural recordings were obtained via a smartphone camera positioned above the test area. The videos were then analysed offline via a custom Python 3.8 script to extract the position of each fly frame by frame. The resulting movement trajectories were recorded as sequences of x–y coordinates over time. From these coordinates, frame-to-frame Euclidean distances were calculated. A frame was classified as “active”

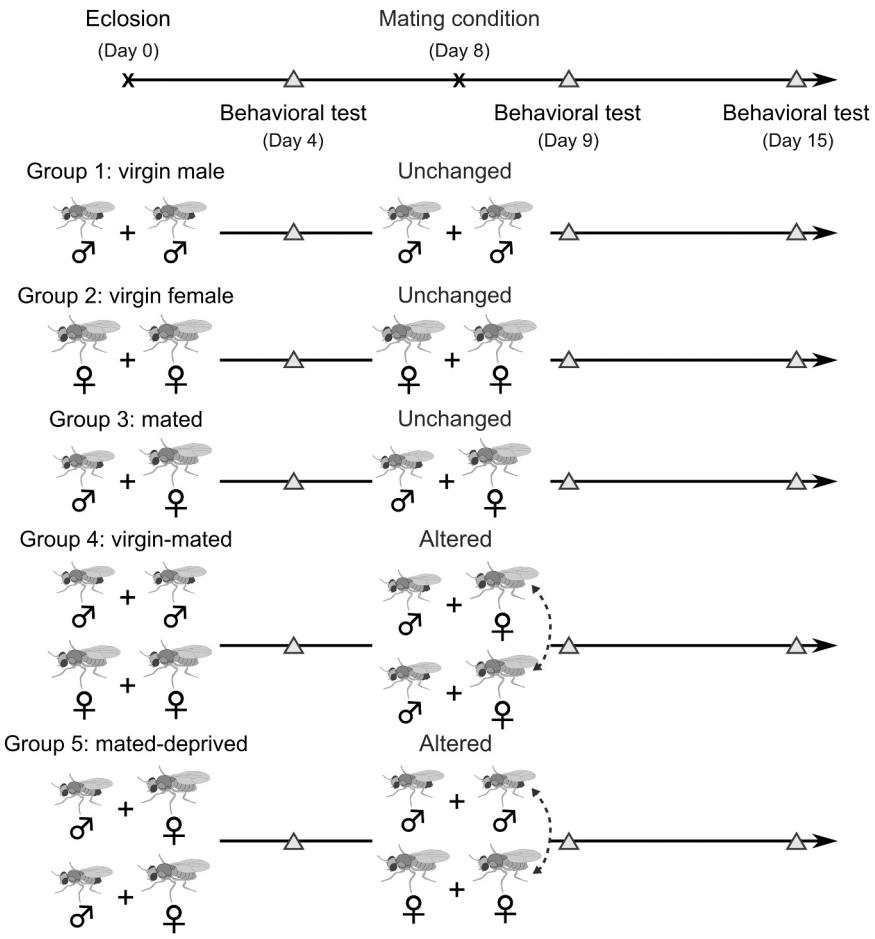

Fig. 1. Schematic diagram of the experimental design. Flies were assigned to five groups with different mating contexts: virgin male and virgin female groups were maintained in same-sex pairs throughout the experiment; mated flies were kept in continuous male-female pairs; virgin-mated flies were initially housed in same-sex pairs and switched to mixed-sex pairs on Day 8 to allow mating; and mated-deprived flies were initially kept in mixed-sex pairs and separated into same-sex pairs on Day 8 to terminate mating interactions. Locomotion levels were assessed on Days 4, 9, and 15.

if the displacement between consecutive frames was greater than zero. The activity level was then defined as the proportion of active frames relative to the total number of frames.

To quantify movement speed, the total path length (sum of all Euclidean distances) was divided by the fixed recording duration (60 s). This definition emphasises the fly's overall locomotor capacity per unit time under standardised recording conditions, rather than instantaneous speed during active periods. Conceptually, "actual locomotor speed" could also be defined as the total path length divided by the time spent moving; however, this metric can be derived by dividing our movement speed by the activity level. We deliberately adopted the fixed-duration approach here because it more directly reflects the fly's ability to generate movement within a standardised timeframe, which was the aspect of locomotion we were most interested in.

Thus, the coordinate data were directly converted into two quantitative measures of locomotion—activity level and movement speed (Han et al., 2025a,b, 2024, 2021). In this study, we use the term "locomotion levels" to collectively refer to these two measures. Locomotion levels were analysed to evaluate sex differences (virgin male vs. virgin female) as well as the effects of different mating contexts across three time points (Days 4, 9, and 15).

Sample sizes varied across treatments due to the initial allocation of individuals, mortality during the experiment, and the application of exclusion criteria. At the outset, virgin males (8 pairs, 16 flies) and virgin females (7 pairs, 14 flies) were assigned relatively larger sample sizes because they served as reference groups for comparison. Mated-deprived flies (15 pairs, 15 males and 15 females) were also allocated more individuals based on our previous findings (Han et al., 2024) suggesting potential post-mating effects on locomotion. In contrast, mated flies (8 pairs, 8 males and 8 females) and virgin-mated flies (10 pairs, i.e., 10 virgin males and 10 virgin females) were initiated with fewer individuals. During the experiment, mortality further reduced the number of flies available for testing. In addition, data points were excluded if either activity level or movement speed on a given day exceeded two standard deviations from the group mean; once excluded, all subsequent measurements from that individual were omitted, even if the fly remained alive. As a result, sample sizes differed across days and mating contexts. Missing values in the deposited dataset indicate either mortality or data exclusion. The exact sample sizes for each group at each time point are provided in the dataset and detailed in the accompanying figure legends.

2.5. Statistical analysis

All valid data were analysed using generalised linear mixed models (GLMMs) in SPSS (version 22.0). For both activity level and movement speed, GLMMs were specified with a normal distribution and identity link function. Fly identity (ID) was included as a random intercept to account for repeated measures across Days 4, 9, and 15. Fixed effects included treatment (sex or mating context), time (Day 4, 9, 15), and their interaction.

To examine sex-specific effects, we compared virgin male and virgin female fruit flies across time. For mating context effects, we compared virgin, mated, virgin-mated, and mated-deprived flies within each sex.

Estimated marginal means (EMMs) were obtained, and simple effects analyses were conducted at each time point when main effects or interactions were significant (or when time-specific comparisons were of particular interest).

Post hoc pairwise comparisons of EMMs were adjusted for multiple testing using the Holm–Bonferroni (sequential Bonferroni) correction. This approach controls the family-wise error rate while maintaining greater statistical power than the classical Bonferroni correction. Unless otherwise stated, all p values presented in the manuscript correspond to Holm–Bonferroni–adjusted post hoc comparisons.

Sample sizes for each group and time point are provided in the corresponding figure legends, and reflect the exclusion criteria described above (see Data Analysis for details). Unless otherwise indicated, data are shown as mean ± *SEM*. *P* values < 0.05 were considered statistically significant; exact p values are reported where possible, and results with $0.05 \leq p < 0.1$ are described as trends.

Model fit was evaluated using corrected Akaike's Information Criterion (AICc) and Bayesian Information Criterion (BIC). Because the GLMMs were specified with a normal distribution and identity link function, equivalent linear mixed-effects models were fitted to obtain these model fit indices.

Post hoc power analyses were conducted to assess whether the available sample sizes were sufficient to detect the observed effects. Power was estimated for the primary model effects (sex and mating context on movement speed) based on the observed F statistics and corresponding degrees of freedom. Effect sizes derived from the model outputs were entered into G*Power (version 3.1) to calculate achieved power, indicating that the main effects underlying the central conclusions of this study were detected with adequate statistical power.

3. Results

3.1. Virgin male flies exhibit greater movement speed than virgin female

To assess sex differences in locomotor performance, virgin males and virgin females were maintained unmated throughout the experiment, and their movement speed and activity level were measured on Days 4, 9, and 15 (Fig. 1). Generalised linear mixed models revealed a significant main effect of sex on movement speed, with virgin males moving faster than virgin females ($F(1, 57) = 9.467$, $p = 0.003$; Fig. 2a). Post hoc analyses indicated that this difference was significant on Day 4 and Day 9, but not on Day 15. Model fit indices based on AICc and BIC were used to evaluate the mixed-effects models applied across all analyses (Table S1).

In contrast, activity level did not differ significantly between virgin males and virgin females, either as a main effect ($F(1, 57) = 0.053$, $p = 0.819$) or at any individual time point (Fig. 2b). Thus, the observed sex difference in locomotion was driven entirely by movement speed. Notably, virgin male speed declined with age, whereas virgin female speed remained relatively stable. However, as age increases, the movement speed of virgin male gradually decreases, whereas that of virgin female remains relatively stable.

3.2. Temporary decline and recovery of movement speed in male flies exposed to mated context

We next examined the effects of mating context on movement speed and activity level in male flies (Fig. 3; Fig. S1). For movement speed, a significant main effect of group was detected among virgin male, mated, virgin-mated, and mated-deprived males ($F(3, 94) = 5.056$, $p = 0.003$; Fig. 3a). Post hoc comparisons showed that virgin males moved significantly faster than both mated males and mated-deprived males.

In addition, time-specific analyses revealed that group differences in movement speed were most evident at earlier time points. On Day 4, the virgin-mated group exhibited higher movement speed than both the mated and mated-deprived groups, and virgin males also moved faster than mated-deprived males, while the comparison between virgin males and mated flies approached significance ($p = 0.055$; Fig. 3b). By Day 9, group differences in movement speed were no longer statistically significant and similarly approached significance ($p = 0.052$; Fig. 3c), and by Day 15, no group differences were detected (Fig. 3d).

On the other hand, in terms of activity level, there was a significant main effect of group among virgin male, mated, virgin-mated, and mated-deprived flies ($F(3, 94) = 3.314$, $p = 0.023$). Post hoc comparisons revealed that the mated group had significantly lower activity levels than all the other groups did (Fig. S1a). However, post hoc comparisons at individual time points did not reveal consistent or statistically significant differences after correction (Fig. S1b–d). Taken together, these results indicate that exposure to a mated context in males primarily affected movement speed in a transient manner, while effects on activity level were weak and inconsistent.

3.3. Temporary increase and recovery of movement speed in female flies exposed to mated context

We then examined the effects of mating context on locomotor performance in female flies (Fig. 4; Fig. S2). For movement speed, the main effect of group was not statistically significant ($F(3, 94) = 1.190$, $p = 0.318$; Fig. 4a). Nevertheless, time-specific analyses revealed transient differences on Day 4, when mated-deprived females moved significantly faster than both virgin females and virgin-mated females, and mated females also moved faster than virgin-mated females (Fig. 4b). These differences were no longer present on Day 9 or Day 15 (Fig. 4c–d).

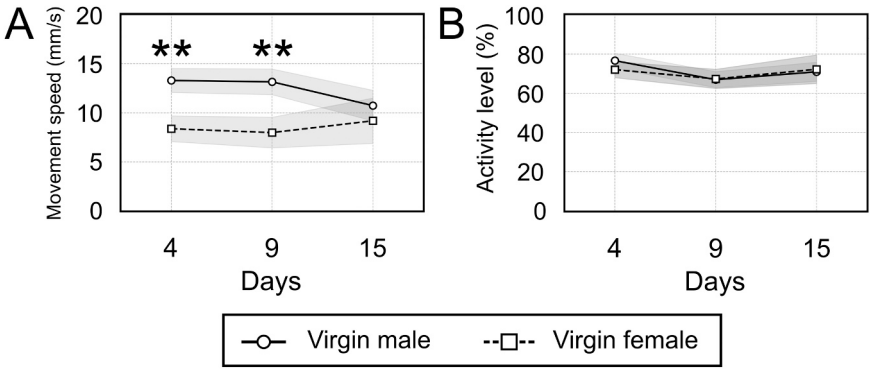

Fig. 2. Locomotion levels of virgin male and virgin female fruit flies on Days 4, 9, and 15. **a** Movement speed of virgin male (blue line) and virgin female (red line) flies. **b** Activity levels of virgin male (blue line) and virgin female (red line) flies. The shaded areas represent the standard error of the mean. The data are presented as the means ± *SEM*s. Statistical comparisons between groups at each time point were conducted via GLMM. Asterisks indicate statistically significant differences between groups at the corresponding time points (**$p < 0.01$). Sample sizes (Day 4 / Day 9 / Day 15): virgin males, n = 15 / 13 / 9; virgin females, n = 13 / 9 / 4.

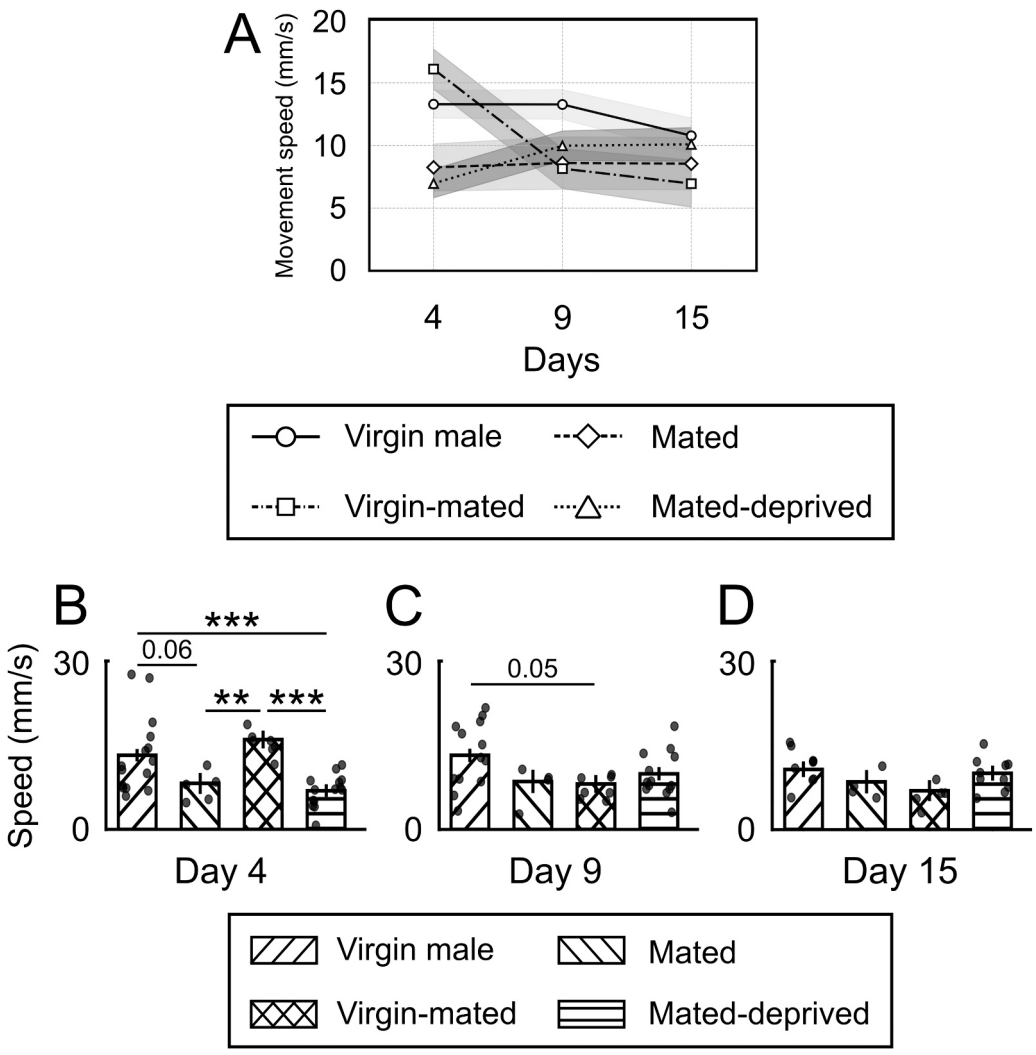

Fig. 3. Movement speeds of male fruit flies under different mating contexts across three time points. **a** Line plot showing the movement speed of virgin male (blue), mated (red), virgin-mated (green), and mated-deprived (yellow) flies on Days 4, 9, and 15. The shaded areas represent the *SEM*. **b-d** Bar plots showing group comparisons on Day 4 (**b**), Day 9 (**c**), and Day 15 (**d**). Each dot represents an individual fly. The data are presented as the means ± *SEM*s. Statistical comparisons between groups at each time point were conducted via GLMM. Asterisks indicate significant differences between groups (**$p < 0.01$, ***$p < 0.001$, p values are shown directly when $p < 0.1$). Sample sizes (Day 4 / Day 9 / Day 15): virgin male, 15 / 13 / 9; mated, 5 / 4 / 4; virgin-mated, 7 / 7 / 5; mated-deprived, 14 / 13 / 10.

In contrast, activity level in females was not significantly affected by mating context, either as a main effect ($F(3, 94) = 0.334$, $p = 0.801$) or at any individual time point (Fig. S2). Overall, these results indicate that exposure to mating contexts induces a short-term increase in locomotion in female flies, driven primarily by movement speed. This enhancement is most pronounced immediately after mating but is transient, as females rapidly return to locomotor levels comparable to those of virgins. Although activity level showed a similar trend, these differences were not statistically significant. Furthermore, transferring mated females into same-sex housing (mated-deprived group) did not produce significant changes in their locomotor behaviour.

4. Discussion

In this study, we systematically investigated the effects of mating context on the locomotion levels of fruit flies, and specifically compared sex differences by focusing on the virgin male and virgin female groups as a baseline. Across five mating contexts—virgin male, virgin female, continuously cohabiting with the opposite sex (mated), switched to opposite-sex cohabitation midway (virgin-mated), and switched to same-sex cohabitation midway (mated-deprived)—we found that virgin males had the highest overall movement speed, and continuous exposure in the mated context led to a temporary decline in their speed. In contrast, females showed a temporary increase in movement speed in the mating context, which then returned to the level of virgins. Although copulation was not directly observed, it is highly likely that flies in mixed-sex conditions did mate. Thus, these results indicate that mating context influences movement speed in a time-dependent and sex-specific manner. Importantly, the effects of mating context on movement speed were transient and varied with recent social experience, indicating that locomotor output is dynamically adjusted rather than fixed across reproductive contexts. Such patterns are consistent with sex-specific trade-offs between reproductive investment and other performance-related demands under changing social conditions.

Notably, in the present study, sex differences in movement speed were examined exclusively through comparisons between virgin males and virgin females, rather than through direct male–female contrasts across all mating contexts. We consider this approach to be justified by the fundamentally different physiological and behavioural consequences that mating elicits in male and female *Drosophila melanogaster*. Previous studies have demonstrated that females typically undergo a period of post-mating behavioural suppression and face substantial reproductive investment costs, including egg production and associated energetic demands, whereas males primarily experience mating-related

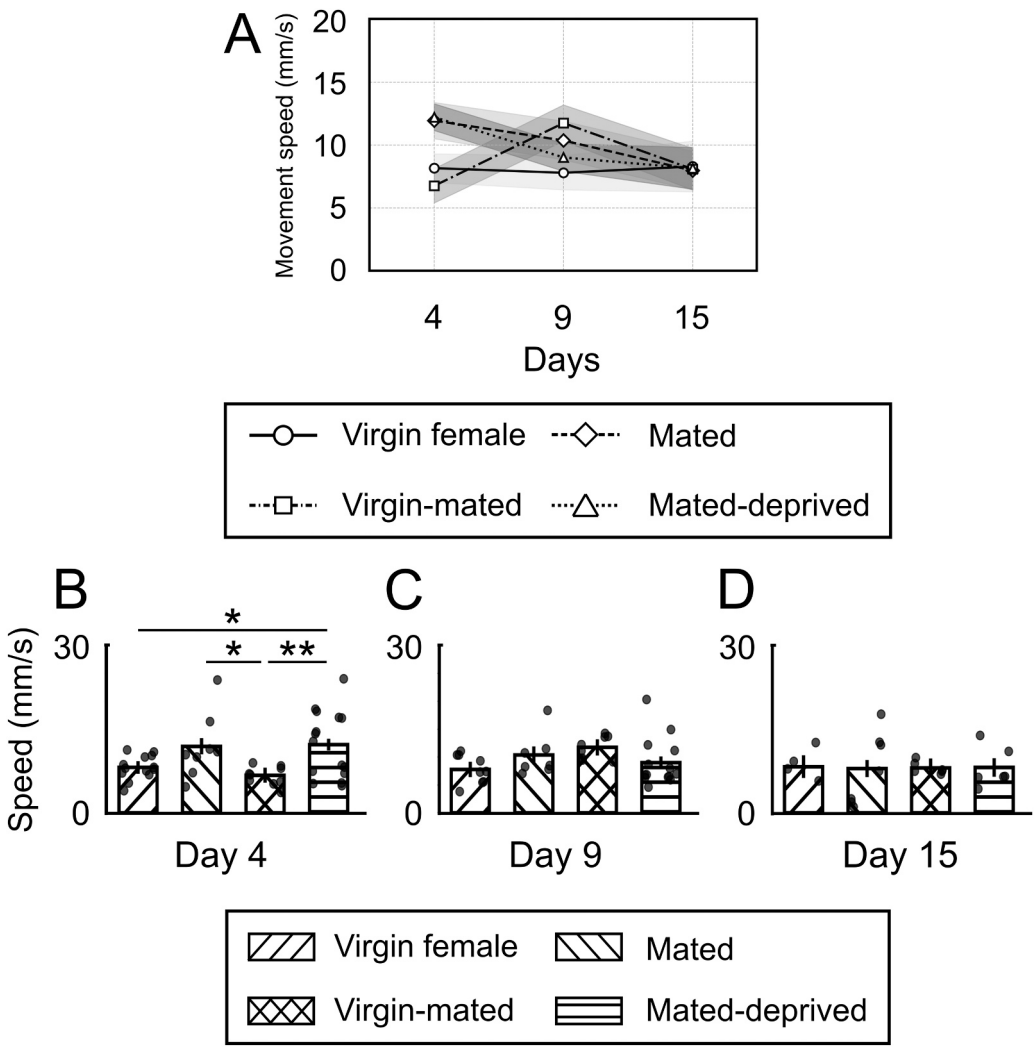

Fig. 4. Movement speeds of female fruit flies under different mating contexts across three time points. **a** Line plot showing the time course of movement speed on Days 4, 9, and 15 in virgin female (blue), mated (red), virgin-mated (green), and mated-deprived (yellow) flies. **b-d** Bar plots showing group comparisons at each time point with individual data points overlaid. Same measurements and analysis method as in Fig. 3 (GLMM; $*p < 0.05$, $**p < 0.01$). Sample sizes (Day 4 / Day 9 / Day 15): virgin female, 13 / 9 / 4; mated, 8 / 7 / 7; virgin-mated, 9 / 8 / 6; mated-deprived, 15 / 14 / 6.

energy expenditure linked to courtship activities and ejaculate production (Chapman et al., 2003, 1995; Liu and Kubli, 2003; Wigby and Chapman, 2005). Consequently, behavioural changes observed under post-mating conditions reflect not only inherent sex differences, but also sex-specific reproductive states and trajectories. Under such conditions, any male–female difference detected after a given mating context could arise from a combination of intrinsic sex differences in speed and the sex-specific consequences of mating, making it difficult to disentangle these two sources of variation. By focusing on virgin males and virgin females, we aimed to establish a clear baseline for intrinsic sex differences in locomotor performance prior to mating. This baseline then served as a reference framework for interpreting how different mating contexts modulate locomotion within each sex. Accordingly, the primary emphasis of this study was placed on within-sex comparisons across mating contexts, rather than on direct male–female comparisons under post-mating conditions, which could conflate baseline sex differences with mating-induced effects and obscure sex-specific mechanisms underlying behavioural modulation.

Male fruit flies exhibited reduced movement speed after mating (mated and virgin-mated groups), which may have resulted from both behavioural and physiological influences. During mating, males engage in energetically costly courtship and copulation behaviours, which may lead to a short-term depletion of energy reserves and consequently lower speed (Bretman et al., 2013; Byrne and Rice, 2006; Fricke et al., 2008; Vartak et al., 2015). In addition, continuous cohabitation with females may reduce exploratory motivation, thereby diminishing behavioural activity (Kent et al., 2008). Although we found that males transferred to single-sex groups (mated-deprived context) showed no statistically significant difference from continuously mated males, the scatter distribution in Fig. 3c indicates that a larger proportion of individuals exhibited increased movement speed after the transfer. We speculate that the suppressed locomotion observed in the mated group may be related to persistent sperm competition, which drives repeated mating attempts and sustained reproductive investment (Arbuthnott et al., 2014). Such ongoing investment likely increases energetic costs and contributes to reduced movement speed as resources are diverted toward reproduction. By contrast, the mated-deprived group may experience relief from sperm competition pressure once removed from female contact, thereby reducing reproductive expenditure and allowing some recovery of speed. Alternatively, as previously reported, males that remain with females may continue to engage in repeated copulation attempts, which could further prolonged reduction in movement speed (Reuven and Katherine, 2012). Nevertheless, these interpretations should be regarded with caution given the lack of statistical significance.

On the other hand, the behavioural characteristics of female flies distinctly differ from those of males. Our results indicate that females

exhibited a transient increase in movement speed following mating context, after which they quickly declined. In other words, the effect of mating on females followed a rise-then-fall pattern. This may be related to females rapidly entering an egg-laying state post-mating, which increases foraging and exploratory behaviours (Carvalho et al., 2006; Walker et al., 2015). Furthermore, previous research has shown that seminal fluid proteins, particularly the SP transferred from males to females during mating, can induce metabolic and behavioural changes in females (Carvalho et al., 2006). However, this enhancement was short-lived and was no longer significant by Days 9 and 15. Additionally, females that were switched to same-sex housing after mating (mated--deprived) on Day 8 did not show markedly lower movement speed compared with continuously mated females on Day 9. This suggests that the post-mating increase in movement speed is time-limited. Because movement speed was measured 24 h after females were moved to same-sex groups, residual effects of seminal fluid proteins, particularly SP, were likely still present, leading some mated-deprived females to maintain slightly elevated movement speed. Therefore, it is possible that some females in the mated-deprived group still exhibited slightly elevated movement speed on Day 9. If additional time points had been included, such as daily observations between Days 9 and 15, a clearer divergence between mated and mated-deprived females might have emerged. Unfortunately, due to technical limitations of our current video-recording setup, which required housing flies individually in vials, we had to balance minimising stress to the flies with the feasibility of continuous video recording. We acknowledge this limitation and further elaborate on methodological considerations regarding video recording later in the Discussion.

An additional point requiring consideration is the absence of significant differences between groups on Day 15. Although Day 15 does not represent an advanced age for fruit flies, this convergence may reflect a combination of temporal recovery following mating-context transitions and habituation to the experimental procedure. First, the transition in mating context occurred on Day 8, meaning that by Day 15 flies had experienced approximately seven days of recovery. Given that mating in *Drosophila melanogaster* typically occurs shortly after initial contact between sexes (Greenspan and Ferveur, 2000; Markow, 1987; Spieth, 1974), the behavioural effects associated with mating or changes in mating context are likely to be most pronounced shortly after the transition and may diminish over time. Thus, even though the flies were not senescent, a recovery period of seven days may have been sufficient for movement speed differences between groups to attenuate. Second, repeated transfer of flies to the recording apparatus may have contributed to behavioural habituation. Although considerable effort was made to minimise disturbance associated with handling and relocation, such effects are difficult to eliminate entirely. Importantly, any habituation or handling-related effects would be expected to influence all experimental groups in a comparable manner. While this factor may therefore help explain the lack of group differences observed on Day 15, it is unlikely to fully account for the clear behavioural differences detected during the earlier testing sessions. Taken together, we suggest that the convergence of movement speed on Day 15 likely reflects the combined effects of recovery from mating-context transitions and repeated exposure to the experimental procedure.

Moreover, in the present study we examined behavioural changes under non-isolated housing conditions, with particular attention to sex-specific effects of mating status. In contrast, our previous work showed that males kept alone after successive mate replacements exhibited a gradual decline in both activity level and movement speed (Han et al., 2024). In the current study, however, males in the mated-deprived group did not show such a decline, likely due to the absence of social isolation in the experimental design. Research has shown that social isolation can reduce locomotion levels in fruit flies (Yost, 2023). These findings suggest that mating status may interact with the social environment. Notably, in our "mated-deprived" context, flies transitioned from a heterosexual mating state to same-sex cohabitation, which constituted a change in social context. However, social interactions in *Drosophila melanogaster* are also known to vary with age (Leech et al., 2017), suggesting that the effects observed here may be further modulated by the age of the flies, an aspect that warrants future investigation. Future studies could therefore examine how both age and housing conditions (comparing individually housed vs. group-housed flies) interact with mating status to shape behavioural plasticity, thereby providing a more comprehensive understanding of how the social environment modulates locomotor and social behaviours in the fruit fly.

Regarding the mechanisms underlying mating-induced behavioural changes in fruit flies, we believe that the behavioural alterations observed in males and females after mating may be regulated by a variety of molecular and neural mechanisms. In males, the post-mating decline in movement speed may result from seminal fluid synthesis, sperm depletion, and regulation of accessory gland protein (Acp) expression, together with the substantial energetic costs of producing and transferring seminal fluid components. In addition to SP, recent studies have identified novel seminal fluid proteins such as venerose, a large glycoprotein that enhances female fecundity but imposes heavy biosynthetic and metabolic demands on males (Kim et al., 2024; Singh and Soller, 2025). The repeated investment in these energetically costly ejaculate components suggests that males face pronounced trade-offs, as allocating resources to reproductive expenditure may constrain somatic maintenance and movement speed. This is particularly relevant in our study, where continuously cohabiting males—presumably investing persistently in ejaculate production—exhibited a more marked decline in movement speed compared with males transferred to same-sex groups. These physiological processes not only demand considerable energy but also may influence energy allocation (Chapman et al., 2003; Findlay et al., 2008). From a neural regulation perspective, males engage neural circuits associated with motivation, reward, and motor control during courtship—such as dopaminergic neurons and P1 neurons—which may undergo modulation following mating, consequently altering behavioural output (Keleman et al., 2012; Kohatsu et al., 2011; Philipsborn et al., 2011; Yamamoto and Koganezawa, 2013; Zhang et al., 2016). These neural circuits may also be reshaped when males are transitioned to same-sex cohabitation. On the other hand, in females, the observed post-mating enhancement in movement speed is typically attributed to systemic behavioural changes induced by SP. SP acts through its receptor in both the female reproductive tract and central nervous system, triggering increased feeding, elevated oviposition, and reduced receptivity to remating (Chen et al., 1988; Dukas and Dukas, 2012; Haussmann et al., 2013; Yapici et al., 2008). During this process, neuronal activity in central brain regions is likely restructured—for instance, pC1 neurons and their associated circuits have been implicated as key mediators in post-mating behavioural plasticity (Wang et al., 2020; Zhou et al., 2014).

One limitation of this study is that flies were only recorded for 1 min per day over 3 days. We acknowledge that such a short recording duration may increase variability, as fly behaviour at any given minute could be strongly influenced by transient states such as courting, feeding, resting, or mating, and may therefore introduce additional measurement noise. However, recording conditions were strictly standardised across all experimental groups, and the use of mixed-effects models partially mitigates the influence of short-term behavioural fluctuations on the overall analysis. This limitation arises from our current video-tracking approach, which only permits accurate measurement when flies are recorded singly in individual tubes. Recording multiple flies simultaneously would generate substantial tracking errors, as overlapping trajectories make it impossible to reliably reassign individual identities once the flies separate. Consequently, flies originally housed in pairs had to be temporarily separated for recording. To minimise interference with the flies' normal behavioural state, we adopted a compromise between increasing measurement noise and reducing experimental disturbance, keeping both the number of recording sessions and the duration of each separation as short as

possible. Future research should focus on developing improved measurement approaches that allow accurate assessment of locomotor performance in multiple flies within the same tube, while minimising measurement noise and preserving natural behavioural and social contexts.

A second limitation concerns sample sizes, which were relatively small and uneven across groups and time points. Because the recording duration was short, some flies exhibited extremely low activity or movement speed throughout the entire 1-min session, which led to their exclusion under our strict criterion (values exceeding two standard deviations from the group mean in either locomotor measure were removed). Once a fly's data were excluded at a given time point, subsequent measurements for that individual were treated as missing. While this conservative procedure ensured that only reliable data were retained, it further reduced the available sample sizes and created imbalances between sexes and across days, particularly at later time points such as Day 15, which may have limited statistical power for certain comparisons. Future work will require optimising existing video-tracking systems to continuously and accurately quantify locomotion without altering the flies' original housing contexts, as well as developing improved data-filtering strategies to achieve more stable and representative results. In addition, future studies should aim to employ larger sample sizes to improve statistical power and obtain more precise estimates of locomotor differences across mating contexts.

Finally, this study did not incorporate molecular or genetic tools to verify mechanisms, nor were neural activity data collected. Consequently, the pathways and signalling processes underlying behavioural changes remain unresolved. Other limitations also warrant consideration. We did not record the frequency or duration of mating events, making it difficult to distinguish between single versus multiple mating experiences. Observations were restricted to the first 15 days post-eclosion, leaving long-term behavioural and lifespan effects unexplored. Moreover, only the *Canton-S* wild-type strain was used, although previous work suggests strain-specific differences in mating effects on locomotion (Helfrich-Förster, 2000). Future research should integrate multiple genotypes, long-term behavioural tracking, neural activity monitoring, and molecular manipulations to clarify the regulatory processes and adaptive mechanisms underlying sex-specific locomotor changes in different mating contexts.

In this study, we found that exposure to different mating contexts induces time-dependent changes in movement speed, with clear sex-specific patterns. Male flies showed a transient reduction in movement speed followed by recovery, whereas females exhibited a temporary increase that subsequently returned to virgin levels. Collectively, these findings highlight the importance of reproductive context in shaping movement speed and reinforce the value of *Drosophila melanogaster* as a model for linking social experience with motor regulation. From an evolutionary perspective, the observed sex-specific and transient modulation of movement speed is consistent with differential allocation strategies following mating, whereby males and females balance distinct reproductive costs and benefits. By incorporating dynamic transitions in mating and housing conditions, our approach captures how recent social experience shapes behavioural output over time, providing a useful framework for examining the interaction between social environment and behavioural plasticity.

Funding

This work was supported by the National Natural Science Foundation of China (Grant No. 32500921); the Fujian Provincial Natural Science Foundation of China (Grant No. 2024J08018); the Zhangzhou Natural Science Foundation Project (Grant No. ZZ2024J07); and the Young and Middle-aged Teachers' Education and Scientific Research Projects in Fujian Province (Science and Technology Category) (Grant No. JAT220508).

CRediT authorship contribution statement

Jun Zhang: Supervision, Project administration, Investigation, Conceptualization. **Rui Han:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jing-Wen Duo:** Resources, Investigation, Data curation. **Xin-Hui Chen:** Resources, Methodology, Investigation, Data curation. **Lin-Xiang Liu:** Visualization. **Yi-Ran Chen:** Resources, Investigation, Data curation. **Yi-Yi Li:** Resources, Investigation, Data curation. **Xiang-Haoran Lin:** Visualization. **Si-Tong Chen:** Resources, Investigation, Data curation.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

Acknowledgements

We are grateful to all the lab members for their suggestions and collaboration in this study. We also thank the National Demonstration Centre for Experimental Life Sciences Education (Xiamen University) for providing the experimental environment and fruit fly.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2025.105324.

Data availability

Data will be made available on request.

References

Arbuthnott, D., Agrawal, A.F., Rundle, H.D., 2014. Remating and sperm competition in replicate populations of drosophila melanogaster adapted to alternative environments. PLOS One 9, e90207. https://doi.org/10.1371/journal.pone.0090207.

Arnqvist, G., Nilsson, T., 2000. The evolution of polyandry: multiple mating and female fitness in insects. Anim. Behav. 60, 145–164. https://doi.org/10.1006/anbe.2000.1446.

Avila, F.W., Sirot, L.K., LaFlamme, B.A., Rubinstein, C.D., Wolfner, M.F., 2011. Insect seminal fluid proteins: identification and function. Annu. Rev. Entomol. 56, 21–40. https://doi.org/10.1146/annurev-ento-120709-144823.

Bath, E., Bowden, S., Peters, C., Reddy, A., Tobias, J.A., Easton-Calabria, E., Seddon, N., Goodwin, S.F., Wigby, S., 2017. Sperm and sex peptide stimulate aggression in female Drosophila. Nat. Ecol. Evol. 1, 0154. https://doi.org/10.1038/s41559-017-0154.

Bretman, A., Westmancoat, J.D., Gage, M.J.G., Chapman, T., 2013. Costs and benefits of lifetime exposure to mating rivals in male Drosophila melanogaster. Evolution 67, 2413–2422. https://doi.org/10.1111/evo.12125.

Byrne, P.G., Rice, W.R., 2006. Evidence for adaptive male mate choice in the fruit fly Drosophila melanogaster. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2005.3372.

Carvalho, G.B., Kapahi, P., Anderson, D.J., Benzer, S., 2006. Allocrine modulation of feeding behavior by the sex peptide of drosophila. Curr. Biol. 16, 692–696. https://doi.org/10.1016/j.cub.2006.02.064.

Chapman, T., Bangham, J., Vinti, G., Seifried, B., Lung, O., Wolfner, M.F., Smith, H.K., Partridge, L., 2003. The sex peptide of Drosophila melanogaster: female post-mating responses analyzed by using RNA interference. Proc. Natl. Acad. Sci. USA 100, 9923–9928. https://doi.org/10.1073/pnas.1631635100.

Chapman, T., Liddle, L.F., Kalb, J.M., Wolfner, M.F., Partridge, L., 1995. Cost of mating in Drosophila melanogaster females is mediated by male accessory gland products. Nature 373, 241–244. https://doi.org/10.1038/373241a0.

Chen, P.S., Stumm-Zollinger, E., Aigaki, T., Balmer, J., Bienz, M., Böhlen, P., 1988. A male accessory gland peptide that regulates reproductive behavior of female D. melanogaster. Cell 54, 291–298. https://doi.org/10.1016/0092-8674(88)90192-4.

Clutton-Brock, T.H., Parker, G.A., 1992. Potential reproductive rates and the operation of sexual selection. Q. Rev. Biol. https://doi.org/10.1086/417793.

Dew-Budd, K., Jarnigan, J., Reed, L.K., 2016. Genetic and sex-specific transgenerational effects of a high fat diet in drosophila melanogaster. PLOS One 11, e0160857. https://doi.org/10.1371/journal.pone.0160857.

Dixson, A.F., Anderson, M.J., 2004. Sexual behavior, reproductive physiology and sperm competition in male mammals. Physiol. Behav. 83, 361–371. https://doi.org/10.1016/j.physbeh.2004.08.022.
Dukas, R., 2008. Evolutionary biology of insect learning. Annu. Rev. Entomol. 53, 145–160. https://doi.org/10.1146/annurev.ento.53.103106.093343.
Dukas, R., Dukas, L., 2012. Learning about prospective mates in male fruit flies: effects of acceptance and rejection. Anim. Behav. 84, 1427–1434. https://doi.org/10.1016/j.anbehav.2012.09.010.
Findlay, G.D., Yi, X., MacCoss, M.J., Swanson, W.J., 2008. Proteomics reveals novel drosophila seminal fluid proteins transferred at mating. PLOS Biol. 6, e178. https://doi.org/10.1371/journal.pbio.0060178.
Fricke, C., Bretman, A., Chapman, T., 2008. Adult male nutrition and reproductive success in Drosophila melanogaster. Evolution 62, 3170–3177. https://doi.org/10.1111/j.1558-5646.2008.00515.x.
Gillott, C., 2003. Male accessory gland secretions: modulators of female reproductive physiology and behavior. Annu. Rev. Entomol. 48, 163–184. https://doi.org/10.1146/annurev.ento.48.091801.112657.
Greenspan, R.J., Ferveur, J.-F., 2000. Courtship in drosophila. Annu. Rev. Genet. 34, 205–232. https://doi.org/10.1146/annurev.genet.34.1.205.
Griffith, S.C., 2019. Cooperation and coordination in socially monogamous birds: moving away from a focus on sexual conflict. Front. Ecol. Evol. 7. https://doi.org/10.3389/fevo.2019.00455.
Han, R., Wei, T.-M., Tseng, S.-C., Lo, C.-C., 2021. Characterizing approach behavior of Drosophila melanogaster in Buridan's paradigm. PLOS One 16, e0245990. https://doi.org/10.1371/journal.pone.0245990.
Han, R., Zhang, J., Huang, H., Chen, Y.-J., Lu, Y.-Y., Wang, Y.-C., Lo, C.-C., Tan, Y.-H., Li, J.-Y., Pan, B.-W., Zhang, Y.-L., 2025b. Effects of coffee on drosophila melanogaster: concentration-dependent enhancement and sleep deprivation recovery. Ethology n/a, e70002. https://doi.org/10.1111/eth.70002.
Han, R., Zhang, J., Huang, G.-X., Yuan, R.-X., Lian, Y.-S., Zhao, M.-Y., Lu, Y.-Y., Huang, H., Wang, Y.-C., Chen, Y.-J., Lo, C.-C., Tan, Y.-H., 2025a. The effects of blue light on locomotion and cognition in early adult drosophila melanogaster. J. Exp. Zool. A Ecol. Integr. Physiol. 343, 511–520. https://doi.org/10.1002/jez.2900.
Han, R., Zhang, J., Wang, R.-X., Xu, J.-X., Weng, K.-C., Wang, A.-X., Huang, H., Lu, Y.-Y., Chen, Y.-J., Wang, Y.-C., 2024. The impact of different mating systems on locomotion in drosophila melanogaster. J. Insect Behav. 38, 2. https://doi.org/10.1007/s10905-024-09866-7.
Haussmann, I.U., Hemani, Y., Wijesekera, T., Dauwalder, B., Soller, M., 2013. Multiple pathways mediate the sex-peptide-regulated switch in female Drosophila reproductive behaviours. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2013.1938.
Helfrich-Förster, C., 2000. Differential control of morning and evening components in the activity rhythm of drosophila melanogaster—sex-specific differences suggest a different quality of activity. J. Biol. Rhythms. https://doi.org/10.1177/074873040001500208.
Isaac, R.E., Li, C., Leedale, A.E., Shirras, A.D., 2010. Drosophila male sex peptide inhibits siesta sleep and promotes locomotor activity in the post-mated female. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2009.1236.
Keleman, K., Vrontou, E., Krüttner, S., Yu, J.Y., Kurtovic-Kozaric, A., Dickson, B.J., 2012. Dopamine neurons modulate pheromone responses in Drosophila courtship learning. Nature 489, 145–149. https://doi.org/10.1038/nature11345.
Kent, C., Azanchi, R., Smith, B., Formosa, A., Levine, J.D., 2008. Social context influences chemical communication in D. melanogaster males. Curr. Biol. 18, 1384–1389. https://doi.org/10.1016/j.cub.2008.07.088.
Kim, S.-J., Lee, K.-M., Park, S.H., Yang, T., Song, I., Rai, F., Hoshino, R., Yun, M., Zhang, C., Kim, J.-I., Lee, S., Suh, G.S.B., Niwa, R., Park, Z.-Y., Kim, Y.-J., 2024. A sexually transmitted sugar orchestrates reproductive responses to nutritional stress. Nat. Commun. 15, 8477. https://doi.org/10.1038/s41467-024-52807-3.
Kohatsu, S., Koganezawa, M., Yamamoto, D., 2011. Female contact activates male-specific interneurons that trigger stereotypic courtship behavior in drosophila. Neuron 69, 498–508. https://doi.org/10.1016/j.neuron.2010.12.017.
Leech, T., Sait, S.M., Bretman, A., 2017. Sex-specific effects of social isolation on ageing in Drosophila melanogaster. J. Insect Physiol. 102, 12–17. https://doi.org/10.1016/j.jinsphys.2017.08.008.
Liu, H., Kubli, E., 2003. Sex-peptide is the molecular basis of the sperm effect in Drosophila melanogaster. Proc. Natl. Acad. Sci. USA 100, 9929–9933. https://doi.org/10.1073/pnas.1631700100.
Markow, T.A., 1987. Behavioral and sensory basis of courtship success in Drosophila melanogaster. Proc. Natl. Acad. Sci. USA 84, 6200–6204. https://doi.org/10.1073/pnas.84.17.6200.
McGraw, L.A., Gibson, G., Clark, A.G., Wolfner, M.F., 2004. Genes regulated by mating, sperm, or seminal proteins in mated female drosophila melanogaster. Curr. Biol. 14, 1509–1514. https://doi.org/10.1016/j.cub.2004.08.028.
Møller, A.P., 2003. The evolution of monogamy: mating relationships, parental care and sexual selection. In: Boesch, C., Reichard, U.H. (Eds.), Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals. Cambridge University Press, Cambridge, pp. 29–41. https://doi.org/10.1017/CBO9781139087247.002.
Philipsborn, A.C. von, Liu, T., Yu, J.Y., Masser, C., Bidaye, S.S., Dickson, B.J., 2011. Neuronal control of drosophila courtship song. Neuron 69, 509–522. https://doi.org/10.1016/j.neuron.2011.01.011.
Preston, B.T., Stevenson, I.R., Pemberton, J.M., Wilson, K., 2001. Dominant rams lose out by sperm depletion. Nature 409, 681–682. https://doi.org/10.1038/35055617.
Reuven, D., Katherine, J., 2012. Costs to females and benefits to males from forced copulations in fruit flies. Anim. Behav. 84, 1177–1182. https://doi.org/10.1016/j.anbehav.2012.08.021.
Saeki, Y., Kruse, K., Switzer, P., 2005. Physiological costs of mate guarding in the japanese beetle (Popillia japonica Newman). Ethology 863–877.
Sakai, T., Isono, K., Tomaru, M., Fukatami, A., Oguma, Y., 2002. Light wavelength dependency of mating activity in the Drosophila melanogaster species subgroup. Genes Genet. Syst. 77, 187–195. https://doi.org/10.1266/ggs.77.187.
Simmons, L.W., 2019. Sperm Competition and Its Evolutionary Consequences in the Insects. Princeton University Press. https://doi.org/10.1515/9780691207032.
Simmons, L.W., Tomkins, J.L., Hunt, J., 1999. Sperm competition games played by dimorphic male beetles. Proc. R. Soc. Lond. Ser. B Biol. Sci. 266, 145–150. https://doi.org/10.1098/rspb.1999.0614.
Singh, D.N.D., Soller, M., 2025. Venerose: a nuptial gift with implications. J. Neurogenet.
South, A., Lewis, S.M., 2011. The influence of male ejaculate quantity on female fitness: a meta-analysis. Biol. Rev. Camb. Philos. Soc. 86, 299–309. https://doi.org/10.1111/j.1469-185X.2010.00145.x.
Spieth, H.T., 1974. Courtship Behavior in Drosophila. Annu. Rev. Entomol. 19, 385–405. https://doi.org/10.1146/annurev.en.19.010174.002125.
Swanson, W.J., 2003. Sex peptide and the sperm effect in *Drosophila melanogaster*. Proc. Natl. Acad. Sci. 100, 9643–9644. https://doi.org/10.1073/pnas.1834127100.
Vartak, V.R., Varma, V., Sharma, V.K., 2015. Effects of polygamy on the activity/rest rhythm of male fruit flies Drosophila melanogaster. Sci. Nat. 102, 3. https://doi.org/10.1007/s00114-014-1252-5.
Villella, A., Hall, J.C., 2008. Neurogenetics of courtship and mating in Drosophila. Adv. Genet. 62, 67–184. https://doi.org/10.1016/S0065-2660(08)00603-2.
Walker, S.J., Corrales-Carvajal, V.M., Ribeiro, C., 2015. Postmating circuitry modulates salt taste processing to increase reproductive output in drosophila. Curr. Biol. 25, 2621–2630. https://doi.org/10.1016/j.cub.2015.08.043.
Wang, F., Wang, K., Forknall, N., Patrick, C., Yang, T., Parekh, R., Bock, D., Dickson, B.J., 2020. Neural circuitry linking mating and egg laying in Drosophila females. Nature 579, 101–105. https://doi.org/10.1038/s41586-020-2055-9.
Wicker-Thomas, C., Hamann, M., 2008. Interaction of dopamine, female pheromones, locomotion and sex behavior in Drosophila melanogaster. J. Insect Physiol. 54, 1423–1431. https://doi.org/10.1016/j.jinsphys.2008.08.005.
Wigby, S., Chapman, T., 2005. Sex peptide causes mating costs in female drosophila melanogaster. Curr. Biol. 15, 316–321. https://doi.org/10.1016/j.cub.2005.01.051.
Wolfner, M.F., 2002. The gifts that keep on giving: physiological functions and evolutionary dynamics of male seminal proteins in Drosophila. Heredity 88, 85–93. https://doi.org/10.1038/sj.hdy.6800017.
Yamamoto, D., Koganezawa, M., 2013. Genes and circuits of courtship behaviour in Drosophila males. Nat. Rev. Neurosci. 14, 681–692. https://doi.org/10.1038/nrn3567.
Yapici, N., Kim, Y.-J., Ribeiro, C., Dickson, B.J., 2008. A receptor that mediates the post-mating switch in Drosophila reproductive behaviour. Nature 451, 33–37. https://doi.org/10.1038/nature06483.
Yost, R., 2023. Recovery from social isolation in Drosophila: the role of dopamine and the autism-related gene nlg3. Electron. Thesis Diss. Repos.
Zhang, S.X., Rogulja, D., Crickmore, M.A., 2016. Dopaminergic circuitry underlying mating drive. Neuron 91, 168–181. https://doi.org/10.1016/j.neuron.2016.05.020.
Zhou, C., Pan, Y., Robinett, C.C., Meissner, G.W., Baker, B.S., 2014. Central brain neurons expressing doublesex regulate female receptivity in drosophila. Neuron 83, 149–163. https://doi.org/10.1016/j.neuron.2014.05.038.