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RESEARCH PAPER

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Female mating experience and genetic background independently influence male mating success in fruit flies

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Abstract

When the reproductive interests of males and females conflict, males can evolve traits that are harmful to females, and females can coevolve traits to resist this harm. In the fruit fly, *Drosophila melanogaster*, there is genetic variation in female resistance traits, which can affect the pre- and post-mating success of males that try to mate with them. However, it is not clear to what extent the expression of these phenotypes can be modified by environmental factors such as sociosexual experience. Here, we tested how the genetic background of a female and her previous mating experience interact to affect the mating success of focal males. In the experience phase, we placed females from 28 distinct genetic backgrounds individually either with a single male (low conflict) or with three males (high conflict) for 48 hr. In the subsequent test phase, we measured the mating and post-mating fertilization success of focal males paired individually with each female. We found that focal males paired with females from the high-conflict treatment were less successful at mating, took longer to mate when they were successful, and had a lower proportion of paternity share. Furthermore, we identified significant female genetic variation associated with male mating success. These results indicate that female experience, along with intrinsic genetic factors, can independently influence different fitness components of her subsequent mates and has implications for our understanding of plastic female mating strategies and the evolution of sexually antagonistic traits in males and females.

KEYWORDS

Drosophila melanogaster, female resistance, mate choice, phenotypic plasticity, sexual conflict, sperm competition

1 | INTRODUCTION

In many species, the reproductive interests of males and females conflict, resulting in the evolution of sexually antagonistic traits. Such traits may increase the fitness of the individual expressing them at the expense of members of the opposite sex (Arnqvist & Rowe, 2005; Chapman et al., 2003). Understanding the genetic and ecological underpinnings of sexually antagonistic traits is a key question for evolutionary biologists, as these traits can exaggerate the evolution of dimorphisms between the sexes and even lead to speciation (Arnqvist, 1998; Gavrilets & Waxman, 2002; Martin & Hosken, 2003; Parker & Partridge, 1998). In mating systems where males have evolved harmful traits, females are expected to coevolve traits that resist these traits. Although recent studies have quantified the impact of ecological factors on male induced harm, few have focused on the potential consequences for female resistance (Rostant et al., 2020).

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Many early studies of sexual conflict have been conducted in uniform environments, and although evolutionary biologists are beginning to recognize the importance of environmental influences when quantifying the outcomes of sexual interactions, much of our understanding of flexibility in sexually antagonistic traits is limited to the water strider system (Arbuthnott et al., 2014; Fricke et al., 2009; Perry & Rowe, 2018; Rowe et al., 1994). In the fruit fly, *Drosophila melanogaster*, factors such as temperature (García-Roa et al., 2019), spatial complexity (Yun et al., 2017) and degree of male–male competition (Filice et al., 2020) have all been shown to influence the magnitude of male-induced harm and thus female fitness. Given this, we expect that socioecological effects would similarly influence female resistance strategies and consequently, the reproductive success of males as it is now well known that females play an active role in determining the outcomes of sexual interactions (Clark & Begun, 1998; Kokko et al., 2003; Laturney et al., 2018; Travers et al., 2015). Recent theoretical work predicts that plasticity in response to socioecological factors should improve female resistance and thus decrease the effect of sexual conflict on the evolution of sexually antagonistic traits (McLeod & Day, 2017). For example, in fruit flies, mated females upregulate proteases that degrade male accessory gland proteins (Acps) (Pilpel et al., 2008). The transfer and activation of these proteins are essential for success in male sperm competition and fertilization, and yet the fitness consequences of this upregulation for subsequent male mating partners are unknown. To the best of our knowledge, no one has directly tested if the changes brought on by differences in a female's social experience influence the reproductive success of her subsequent prospective mates.

In fruit flies, the optimal mating frequency and competition for access to mates for males is greater than it is for females, resulting in the evolution of harmful male traits expressed during courtship and copulation and the coevolution of female traits that attempt to minimize this harm. The genetic basis of female resistance is well documented. There is standing genetic variation associated with a female's ability to resist male harm (Friberg, 2005; Linder & Rice, 2005), and researchers starting with a baseline population could experimentally evolve increased female resistance by manipulating the intensity of sexual conflict over many generations (Wigby & Chapman, 2004). Furthermore, the genetic background of female fruit flies influences male reproductive success in the form of females' mating propensity (Travers et al., 2015) and males' fertilization success (Clark & Begun, 1998). While the current knowledge about heritable variation in female resistance traits is highly pertinent, it is equally important that we elucidate how socioecological factors such as females' experience with males influence their subsequent resistance to males in order to understand the relative contribution of genetic and environmental factors towards female post-mating phenotypes (Lüpold et al., 2020).

Here, we tested how the intensity of early-life sexual conflict that females of distinct genetic backgrounds experience influences the reproductive success of subsequent male suitors. Specifically, we wanted to test how female experience and genetics influence a focal male's success in (1) a premating context where reproductive success was determined by successful mating and the latency of these successful matings and (2) a post-mating context where reproductive success was determined by measuring the paternity success of the focal males. We predicted that, in both contexts, focal males paired with females that previously experienced high intensity sexual conflict would have lower reproductive success compared to focal males paired with females that previously experienced low intensity sexual conflict. We were also interested in quantifying the effect of female genetic background on focal males' pre- and post-mating success and predicted that male mating success would significantly vary with female genotype, given the documented variation in female mating propensity and resistance traits (Clark & Begun, 1998; Linder & Rice, 2005; Travers et al., 2015). Finally, we were interested in quantifying any potential interactions between female experience and genetic background, as this would indicate that females respond differently to the same experiences depending on their genotype (i.e. genetic variation in phenotypic plasticity).

2 | METHODS

2.1 | Fly stocks and general

All the females in this experiment were derived from 28 randomly selected lines from the *Drosophila* Genetic Reference Panel (DGRP) (Mackay et al., 2012). These lines were derived from wild flies caught in Raleigh, North Carolina, USA, and repeatedly inbred for 20 generations. To alleviate the deleterious phenotypic effects associated with inbreeding, we generated hybrids by crossing each line to a single standardized reference line, thereby creating unique hybrid clones (hereafter referred to as hybrid genotypes) (Filice & Dukas, 2019; Scott et al., 2018). Within hybrids, individuals are genetically identical, but between hybrids, individuals share an identical clonal haplotype inherited from their mother, and a unique clonal haplotype inherited from their father, allowing us to quantify the degree of genetic variation associated with phenotypic differences expressed from this unique haplotype. In order to reduce the potential for nongenotypic sources of variance to the observed phenotypic variation across our DGRP lines, the lines that made up our 28 hybrid genotypes were selected from a set that had been verified to be free of Wolbachia infection (Huang et al., 2014). Furthermore, each hybrid genotype was reared in multiple vials to reduce the confounding effects associated with vial sharing.

All males were derived from the *Ives* population (hereafter IV) obtained from the Long Lab (Wilfrid Laurier University). The IV population was originally collected in South Amherst, MA, USA, in 1975. In 1980, a lineage of these flies was established at large census size (>1,000 adults/generation) on a standardized culture protocol with nonoverlapping generations (Rose, 1984). Since then, this same lineage of IV has been maintained under identical conditions and used extensively as a model for studying evolutionary fitness and sexual conflict (Filice & Long, 2016; Martin & Long, 2015; Rose, 1984). The males used in the sexual conflict

experience phase were descendants from the standard wild-type IV population. Focal males in the testing phases were descendants of a sub-population of the IV line that had the *bwD* (hereafter, brown-eye) mutation introgressed via repeated backcrossing for 10 generations (Long et al., 2006). This mutation results in a brown-eye phenotype (as opposed to the wild-type red-eye phenotype). This mutation is an autosomal dominant marker, allowing us to determine the paternity of all offspring produced by focal brown-eye males that mated with females previously inseminated by red-eye males during the experience phase.

We reared all experimental flies at a standardized density of 100 eggs per vial containing ~ 5 ml of standard fly medium made of water, sucrose, cornmeal, yeast, agar and methyl paraben, and stored all flies in an incubator at 25°C and 60% relative humidity with a 12:12h light:dark cycle. We collected all flies as virgins (within 8h of eclosion, as females are not sexually receptive prior to 18 hr in this population) under light CO_2 anaesthesia. Following their initial collection, we handled all flies using gentle aspiration.

2.2 | Experiment 1: Mating success of focal males

We started each replicate by collecting 4 virgin females from each of the 28 hybrid genotypes and placing each into a food vial with a dash of live yeast (~5 mg). Immediately after being placed into vials, we randomly assigned half the females of each hybrid genotype into a low-conflict treatment and half into a high-conflict treatment. Each female vial contained a single male in the low-conflict treatment and 3 males in the high-conflict treatment. These males belonged to the IV population and were virgins collected within 8h of eclosion. Manipulating the sex ratio is a standard way to generate variability in the intensity of sexual conflict (due to both more harassment and/or matings, and increased male–male competition in more male-biased environments) (Holland & Rice, 1999; Wigby & Chapman, 2004). For females housed in individual vials, exposure to three males results in a significantly reduced lifespan and lifetime reproductive success compared to females exposed to a single male, so we chose to manipulate this number of males to generate high and low sexual conflict experiences, respectively (García-Roa et al., 2019). After 48h of male exposure, we removed all males from the vials and allowed females to remain isolated for 24h prior to testing. In each replicate, we aimed to have 2 females from each of the 56 hybrid × treatment combinations for a total sample size of 112 trials.

On the morning following the experience phase, we added a focal brown-eye male to each female vial and measured the latency and duration of any matings that occurred to the closest second (Figure 1). Any pairs that did not mate within four hours were considered to have not remated. We conducted 7 identical replicates that each took place on an independent day. While we aimed to have 784 trials, our actual sample size was 727. The 57 missing trials included cases where we were unable to collect enough hybrid females, and cases where females escaped or died within the three-day experience phase. Overall, our sample sizes ranged between 10 to 14 for the 28 hybrid genotypes and treatment combinations.

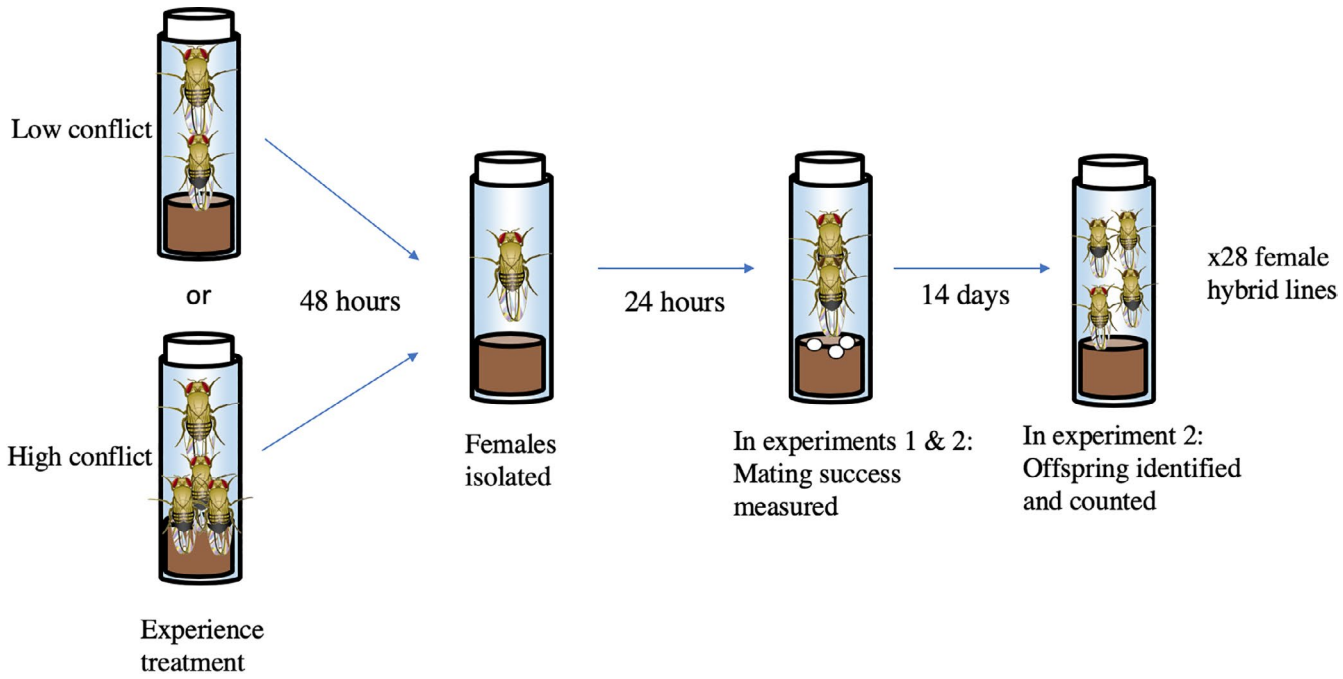

FIGURE 1 An illustration of the experimental design for both our experiments. Females were exposed to either a single male or three males for 48 hr and then housed in isolation for an additional 24 hr. After this experience phase, each female was paired with a brown-eye focal male for 4 hr and mating behaviours were scored. In experiment 2, females remained in these vials for 24 hr to lay their eggs, and the resulting offspring were counted two weeks later

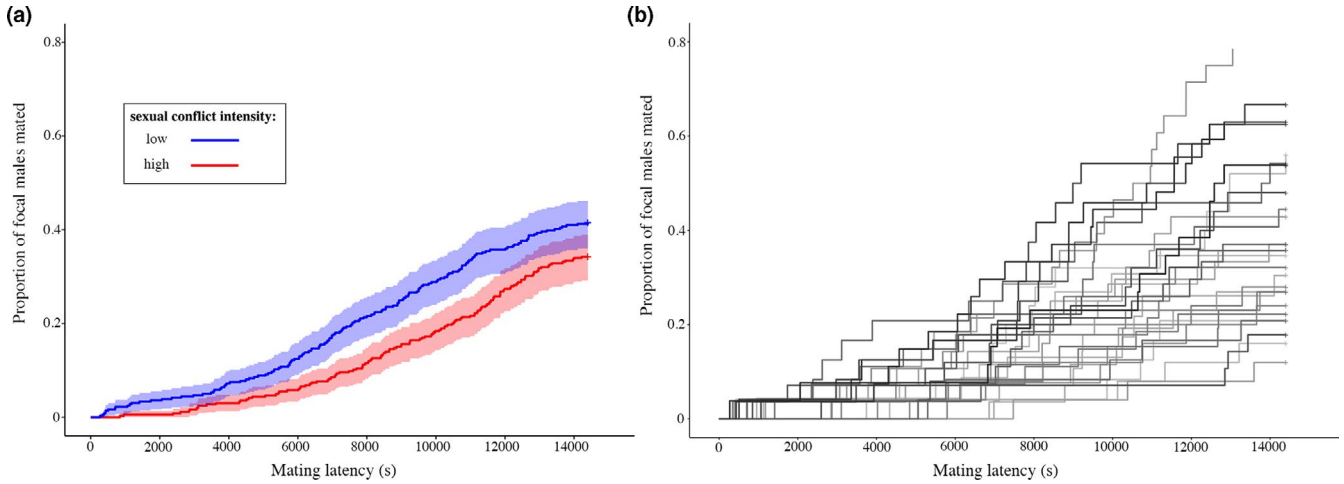

FIGURE 2 (a) Effect of female sexual conflict experience on the subsequent mating success of focal males in experiment 1. Each Cox-regression curve represents the cumulative proportion of matings by focal males paired with females that previously experienced either low (blue) or high (red) sexual conflict. (b) Effect of female genetic background on the subsequent mating success of focal males in experiment 1. Each Cox-regression curve represents the cumulative proportion of males that mated over time. The varying shades of grey represent the 28 different hybrid female genotypes that were tested

2.3 | Experiment 2: Paternity success of focal males

Testing the paternity success of focal males required a replication of the steps conducted in experiment 1. Hence, we took the opportunity to test again the mating success of males as we did in experiment 1. We started each replicate by collecting 10 virgin females from each of the 28 hybrid genotypes and randomly placed half into a low-conflict treatment and half into a high-conflict treatment as detailed above. Simultaneously, we collected 280 brown-eye males and placed them in individual vials.

On the day following the 72h experience phase (48h with males, 24h alone), we placed each female into a fresh vial containing a focal brown-eye male and recorded all matings. Since our paternity analysis required that the females remate, recording the matings ensured that the focal male had a chance to inseminate the experienced females and also provided an additional block of mating success data that could be compared with the data from experiment 1. Females that did not remate within four hours were excluded from further analysis. Two weeks later, we counted all the adult offspring from the female vials and quantified paternity based on the proportion of brown-eye offspring in each vial (Figure 1). We conducted 3 replicates but had only 558 trials owing to cases where we were unable to collect enough hybrid females, and cases where females escaped or died within the three-day experience phase. Out of the 558 trials, 224 females remated during the test for the paternity analysis. Overall, our sample sizes of remated females ranged between 1 to 11 for the 28 hybrid genotypes and treatment combinations. The large variation in sample sizes per genotype is consistent with the large genetic variation in remating rates documented in experiment 1 (Figure 2b).

2.4 | Statistical analysis

We conducted all data analysis using R version 3.5.2 (R Core Team, 2013). For the mating success test, we constructed a Cox proportional hazard model using the *Surv* and *coxme* functions from the *survival* and *coxme* packages (Therneau & Grambsch, 2000), which took into account the binomial outcome of mating success and the latency of successful matings as a survival term. Our model included experience treatment as fixed factor, and hybrid genotype and replicate as random factors. We also analysed the binomial outcome of mating success on its own by constructing a generalized linear mixed-effects model (GLMM) using the *glmer* function from the *lme4* package (Bates et al., 2014) for the data obtained in both experiment 1 and experiment 2. In both models, we included experience treatment as a fixed effect, and hybrid genotype, the crossed interaction between treatment and genotype, and replicate as random factors. To analyse male paternity success, we constructed a GLMM with a binomial response variable defined by the number of brown-eye offspring weighed by the number of red-eye offspring. We included experience treatment as a fixed effect, and hybrid genotype crossed with experience treatment and replicate as random effects. However, this initial model was overdispersed, so we added an observer-level random factor that assigns each observation a unique ID to our final model (Harrison, 2015). We calculated the *p*-value for the fixed effect in our coxme model using the *ANOVA* function from the *car* package to perform a Wald χ^2 test (Fox et al., 2014), and for all other models using the *mixed* function from the *afex* package to perform a likelihood ratio test (Singmann et al., 2016). For the random effects in our Cox model, we determined statistical significance by performing a likelihood ratio test. This involved comparing the fit

of two nested models: one that contained the random effect of interest, and one that did not (Bolker et al., 2009). For the random effects in our GLMMs, we tested the significance of each variance component using a nonparametric bootstrapping approach, which involved comparing the magnitude of our models' variance components to the distribution of 10,000 variance components that were determined from a randomized set of the experimental data (Ziegel & Manly, 1998).

3 | RESULTS

3.1 | Experiment 1: Mating success of focal males

Focal males paired with females from the high-conflict treatment were both slower and less likely to mate compared to males paired with females from the low conflict treatment ($\chi^2_1 = 8.5$, $p = .0035$, Figure 2a). The female hybrid genotype had a significant effect on the mating success of focal males ($p < .0001$, Figure 2b, Table 1) and the effect of experimental replicate was not significant ($p = .5$, Table 1). When looking at focal male success and only taking into account the binomial outcome of mating success, males paired with females from the high-conflict treatment were still less likely to mate ($\chi^2_1 = 3.9$, $p = .04$). Similarly, female hybrid genotype had a significant effect on mating outcome ($p < 0001$, Table 1), but the interaction between female treatment and genotype was not significant ($p = .65$, Table 1), nor was the effect of experimental replicate ($p = .64$, Table 1).

3.2 | Experiment 2: Mating success of focal males

Females from the high-conflict treatment were significantly less likely to remate than females from the low conflict treatment ($\chi^2_1 = 6.17$, $p = .01$, Figure 3a). The effect of hybrid genotype was significant ($p = .002$, Table 2, Figure 3a), as was the effect of experimental replicate ($p < .0001$, Table 2), but the interaction between experience and genotype was not significant ($p = .084$, Table 2). The correlation between the binary outcome of male mating success when mating with females from the same hybrid genotype in experiments 1 and 2 was strongly positive ($t_{26} = 3.3$, r = 0.54, $p = .0029$; Figure 3b). In other words, males had a similar mean mating success when paired with a female from a particular genetic background in both experiments 1 and 2.

3.3 | Experiment 2: Paternity success of focal males

Focal males paired with females from the high-conflict treatment also had significantly lower paternity success compared to focal males paired with females from the low conflict treatment ($\chi^2_1 = 22.36$, $p < .0001$, Figure 4). Both female hybrid genotype and the interaction between experience treatment and hybrid genotype did not significantly effect paternity success of the focal males (hybrid: $p = .76$, Table 2; experience × hybrid: $p = .55$, Table 2; Figure 4), nor did experimental replicate ($p = .12$, Table 2).

4 | DISCUSSION

In this study, we set out to test how a female's previous social experience and her genotype influence the subsequent reproductive success of her suitors. In both pre- and post-mating scenarios, focal males had lower reproductive success when paired with females that previously experienced high than low sexual conflict. Specifically, focal males paired with females that had experienced high conflict mated at a lower frequency, took longer to mate, and had lower paternity success (Figures 2-4). Furthermore, the genetic background of females was an important factor determining male mating success in both our premating tests (Figure 2b and Figure 3a), and the positive correlation between the premating test results in experiments 1 and 2 (Figure 3b) suggests some of these genetic effects produce replicable outcomes over time. Previous studies have documented that the genetic identity of a female influences the reproductive success of her mates (Clark & Begun, 1998; Clark et al., 1999), and we add to this by finding that the magnitude of this heritable effect can change depending on the socioecological experience of a female.

In our pre- and post-mating tests, the lower reproductive success of focal males paired with females from the high-conflict treatment likely represents a combination of male and female responses to increased sexual conflict. A key problem in the current sexual conflict literature is disentangling the degree to which

TABLE 1 Variance components, standard deviation, and *p*-values estimated using a GLMM fit by maximum-likelihood (Laplace approximation) for the reproductive success of males paired with females from one of 28 genetic hybrid backgrounds from the experiment 1 data set

Response	Source of variance	Variance	Standard deviation	% of Variance explained	*p*-value
Cox hazard mating success (mating latency, proportion mated)	Hybrid	0.26	0.51	20.4	4.9×10^{-9}
	Replicate	0.012	0.11	0.94	.5
Proportion mated	Hybrid	0.32	0.57	23.4	4.2×10^{-7}
	Hybrid × experience	0.033	0.18	2.4	.65
	Replicate	0.013	0.12	0.95	.64

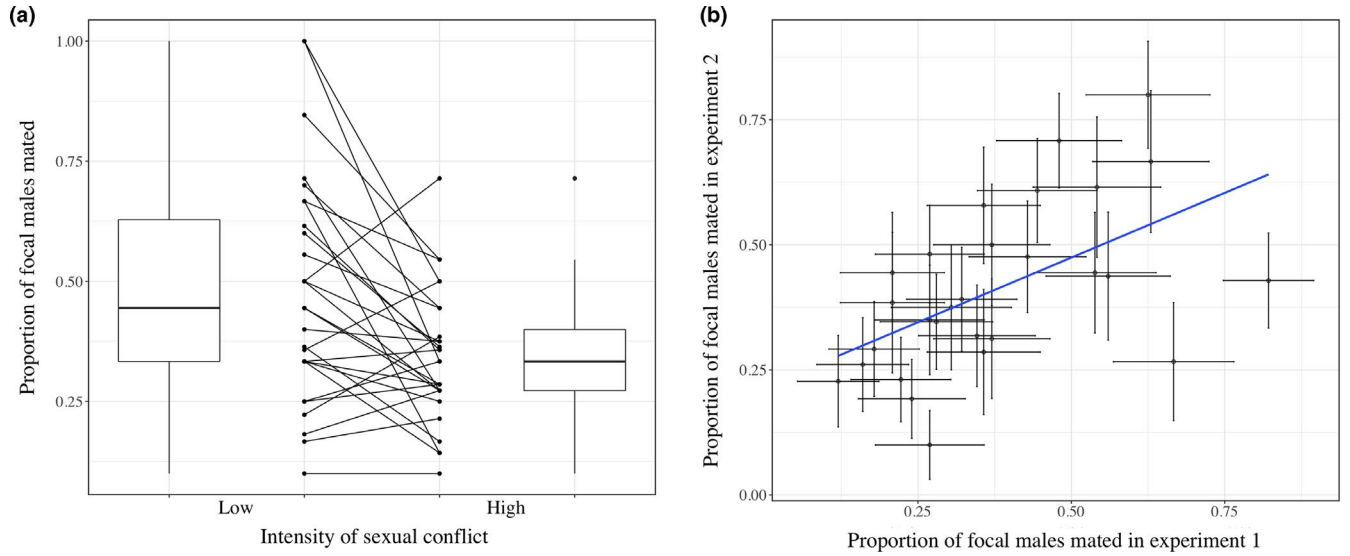

FIGURE 3 (a) Effect of female sexual conflict experience and genotype on male mating success in experiment 2. The boxes contain the middle 50% of data (interquartile range [IQR]), and the horizontal lines represent the medians. The whiskers above and below each box represent values within ± 1.5 IQR, and any values beyond this are outliers represented by closed circles. The reaction norm plot in the centre of the panel depicts the change in the mean of each female hybrid genotype across the two experience treatments. (b) Correlation between male mating success in experiments 1 and 2 when mating with females of the same hybrid genotype. Each open circle represents the mean mating success of males with a particular female genotype, and the horizontal and vertical bars represent standard errors. The blue slope represents the regression line

TABLE 2 Variance components, standard deviation, and *p*-values estimated using a GLMM fit by maximum-likelihood (Laplace approximation) for the reproductive success of males paired with females from one of 28 genetic hybrid backgrounds from the experiment 2 data set

Response	Source of variance	Variance	Standard deviation	% of Variance explained	*p*-value
Proportion mated	Hybrid	0.27	0.52	17	.002
	Hybrid × experience	0.08	0.29	5	.084
	Replicate	0.26	0.51	16.1	1×10^{-7}
Paternity success	Individual	1.77	1.33	62	.99
	Hybrid	8.6×10^{-9}	9.3×10^{-5}	<0.0001	.76
	Hybrid × experience	0.04	0.2	1.4	.55
	Replicate	0.045	0.21	1.6	.12

female post-mating responses represent male manipulation and/or mutually beneficial responses that females play some part in (i.e. via phenotypic plasticity). In the case of premating outcomes, the delaying of a female's remating interval has clear benefits from a male standpoint as it can reduce the risk of sperm competition and is driven by the transfer of Acps in the ejaculate that are shaped by natural selection, as males that strategically invest into the transfer of Acps tend to have higher reproductive success (Alonzo & Pizzari, 2013; Hopkins et al., 2019; Johnstone & Keller, 2000; Wolfner, 2002). During the experience phase, females in the high-conflict treatment likely mated more (García-Roa et al., 2019), and the males they mated with likely upregulated the expression of competitive traits such as seminal fluid transfer and harassment due to the presence of male–male competition (Bretman et al., 2009; Hopkins et al., 2019). This means the females in the high-conflict treatment were likely subjected to more male manipulation and may have more to lose from a subsequent remating, which could explain the lower mating success of the focal males. On the other hand, we do not know the conditions for which it is in a female's best interest to strategically increase her own resistance to multiply mating. This is because polyandry can sometimes increase female reproductive success due to an increased short-term reproductive output from either nuptial gifts (Arnqvist & Nilsson, 2000) or other male effects (Rubinstein & Wolfner, 2013). However, matings past the optimal degree of polyandry can have deleterious effects and reduce the longevity and lifetime reproductive output of females (Chapman et al., 1995; Stewart et al., 2005). Therefore, mated females can potentially gain from either accepting future prospective mates or modulating their mate choice in order to avoid exploitative males that may decrease their

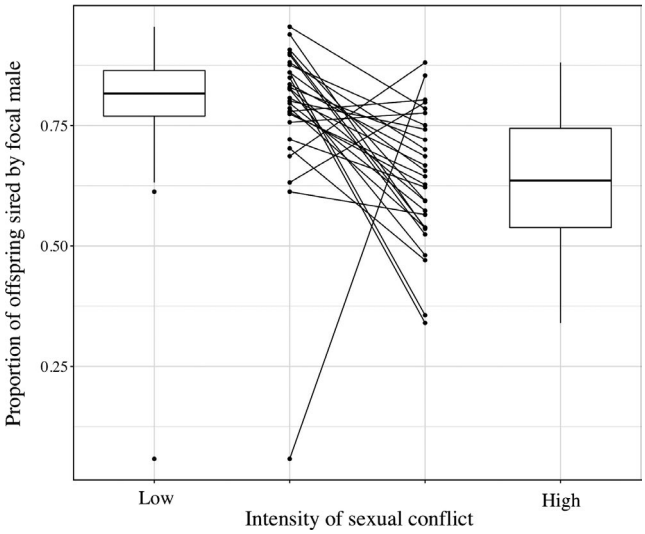

FIGURE 4 Effect of female sexual conflict experience and genotype on subsequent male post-mating success. The boxes contain the middle 50% of data (interquartile range [IQR]), and the horizontal lines represent the medians. The whiskers above and below each box represent values within ± 1.5 IQR, and any values beyond this are outliers represented by closed circles. The reaction norm plot in the centre of the panel depicts the change in the mean of each female hybrid genotype across the two experience treatments

fitness (Filice & Long, 2017; Holland & Rice, 1998). Given that the direct and indirect benefits of polyandry in fruit flies vary across time and with body condition (Long et al., 2010; Long Pischedda & Rice, 2010), we should expect that females may regulate their mating rate based on previous mating experience. Furthermore, it may be that the perception of male density in a previous environment influences mating propensity (Rowe et al., 1994). When a female experiences a high male-density environment, it may make sense to increase mating resistance in order to adequately sample all available males before making a choice (Atwell & Wagner, 2014), but on the other hand it may be beneficial to reduce receptivity in order to avoid the costs of high male harassment (i.e. convenience polyandry) (Rowe, 1992). The fact that females in our study appear to increase their mating resistance in response to increased male density may suggest a lack of convenience polyandry in this species. Overall, in our tests, it is likely that male manipulation and female-driven remating behaviours are both in part responsible for the lower mating success of focal males paired with females that had experienced high conflict. In order to further disentangle the relative contributions of male-induced effects and female volition towards various female post-mating responses such as remating delay, future studies should continue to systemically determine how the volume and constitution of male Acps influence female remating propensity.

In our post-mating tests, the lower paternity success of males paired with females that had experienced high conflict may also be explained by a combination of factors driven by both males and females. In many mating systems, the last male to mate typically has an advantage in securing the most paternity, a pattern known as last-male sperm precedence. However, the strength of this effect can break down when a female mates multiply, which could potentially be explained by increased male sperm competition (Zeh & Zeh, 1994) or female-driven effects that modulate male paternity success (Laturney et al., 2018). Specifically, Laturney et al. (2018) identified a positive relationship between the penultimate to last mating interval and the paternity success of the last male, suggesting that by modulating remating latency, females have some control over the outcomes of last-male sperm precedence. This lends to the argument that polyandry can be adaptive if females gain direct benefits in the form of increased short-term offspring production, or indirect benefits in the form of increased genetic quality and/or variety (Arnqvist & Nilsson, 2000). It could be that in our study, females from the high-conflict treatment that mated more frequently during the experience phase could balance any direct costs of multiple mating by reducing the paternity share of their last mate and thus increase the genetic diversity of her offspring. A potential mechanism of this may be related to the fact that mated females upregulate proteases that degrade male Acps, which are important for success in sperm competition (Pilpel et al., 2008). However, it may also simply be that the upregulation of Acps degrading proteases is a response to mitigate the direct harm associated with the receipt of some Acps (Chapman et al., 1995). As such, it is critical that future studies should investigate the relationship between the expression of Acps degrading proteases, the number of times a female has mated, and her fitness. If, for example, females that positively upregulate these proteases in response to more matings have higher fitness than those who express less in response to the same number of matings, this could suggest that the degradation of Acps is an adaptive response to gain indirect offspring benefits and/or to reduce the direct harm associated with the receipt of these Acps.

Finally, our results, which indicated that the premating success of focal males was affected by female genotypes (Figure 2b, Figure 3a), confirm that some of the decision to remate is due to female-specific effects. This also agrees with previous studies with similar outcomes (Filice & Long, 2017; Simmons, 2003; Travers et al., 2015). Genetic variation in remating rate may represent adaptive variation in female reproductive strategies associated with trade-offs between survival and maximizing early-life reproductive output (Filice et al., 2020; Travers et al., 2015). Additionally, such genetic variation may represent variation in females' choices to either remate with or reject the single focal male type we presented to them, which may operate as a strategy to resist the harm of subsequent matings (Linder & Rice, 2005). However, contrary to previous studies that have found significant female genetic variation in the effect of last-male paternity success (Clark & Begun, 1998; Clark et al., 1999), we failed to identify a similar outcome. One possibility is that a small sample size in some of our experience × hybrid groups resulted in insufficient statistical power to detect differences attributable to female genotype. It is also possible that the outcomes of post-copulatory male–male interactions such as sperm competition largely drown

out female-specific effects in determining last-male paternity success. Such female-specific effects include cryptic choice, sperm storage and upregulation of proteases (Avila & Wolfner, 2017; Birkhead, 1998; Pilpel et al., 2008). In this case, females can still rely on the precopulatory rejection of males to modulate their reproductive outcomes. Future studies should continue to investigate this by identifying female genotypes that vary in their post-mating responses and test the mechanisms that underlie such differential responses.

Taken together, our results have important implications for our understanding of how social experience can determine the expression of sexually antagonistic traits. Specifically, we found that females who experience high levels of sexual conflict can modify their phenotypes in a way that reduces the pre- and post-mating success of their future suitors and that these outcomes also depend on females' genetic background. We propose that these effects represent adaptive mechanisms to offset the costs of male-induced harm by allowing a female to modulate her remating rate in a way that is best for her own fitness and thus have important consequences for our understanding of how socioecological factors can influence the evolution of sexually antagonistic traits. Future studies should continue to untangle the relative contribution of female-driven effects in mating interactions in order to improve our understanding of adaptive female mating behaviours, which may have major consequences for the outcomes of sexual selection and evolution.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

DCSF and RD designed the experiments. DCSF and RB carried out the experiments. DCSF wrote the first draft and performed the statistical analysis, and all authors were involved in the revision process.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.n2z34tmvc

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