

RESEARCH ARTICLE

Pre- and post-copulatory sexual selection increase offspring quality but impose survival costs to female field crickets

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Abstract

Whether sexual selection increases or decreases fitness is under ongoing debate. Sexual selection operates before and after mating. Yet, the effects of each episode of selection on individual reproductive success remain largely unexplored. We ask how disentangled pre- and post-copulatory sexual selection contribute to fitness of field crickets *Gryllus bimaculatus*. Treatments allowed exclusively for (i) pre-copulatory selection, with males fighting and courting one female, and the resulting pair breeding monogamously, (ii) post-copulatory selection, with females mating consecutively to multiple males and (iii) relaxed selection, with enforced pair monogamy. While standardizing the number of matings, we estimated a number of fitness traits across treatments and show that females experiencing sexual selection were more likely to reproduce, their offspring hatched sooner, developed faster and had higher body mass at adulthood, but females suffered survival costs. Interestingly, we found no differences in fitness of females or their offspring from pre- and post-copulatory sexual selection treatments. Our findings highlight the potential for sexual selection in enhancing indirect female fitness while concurrently imposing direct survival costs. By potentially outweighing these costs, increased offspring quality could lead to beneficial population-level consequences of sexual selection.

KEYWORDS

 fitness, *Gryllus bimaculatus*, pre- and post-copulatory, sexual selection, survival

1 | INTRODUCTION

Sexual selection is an evolutionary process that arises from fitness differences associated with non-random success in the competition for access to gametes for fertilization (Andersson, 1994; Darwin, 1871; Shuker & Kvarnemo, 2021). It operates through mechanisms occurring before and/or after mating (hence, pre- and post-copulatory selection) (Birkhead & Pizzari, 2002; Evans & Garcia-Gonzalez, 2016). These include pre-copulatory male–male competition (i.e. males fighting for breeding territories or access to females; Andersson &

Iwasa, 1996) and female choice (i.e. females selecting one or multiple partners) (Andersson & Simmons, 2006) as well as post-copulatory sperm competition (i.e. sperm of multiple males competing to fertilize the female's eggs) (Parker, 1970; Simmons, 2019) and cryptic female choice (i.e. females biasing fertilization towards a preferred male) (Eberhard, 1996; Pizzari & Birkhead, 2000). Whether sexual selection increases or decreases the fitness of individuals, ultimately affecting the mean fitness of the population, is still under debate (Candolin & Heuschele, 2008; Holman & Kokko, 2013; Kokko et al., 2003; Whitlock & Agrawal, 2009) and fuels research

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interested in understanding to which extent natural and sexual selection align (Locke Rowe & Rundle, 2021). Theory postulates that reproductive success is biased towards individuals of overall higher genetic quality ('good genes models'; Hamilton, 1982; Houle & Kondrashov, 2002; Kokko et al., 2002; Whitlock & Agrawal, 2009; Zahavi, 1975), through mechanisms of mate choice and/or competition. The process of sexual selection may hence allow females to derive indirect benefits to their progeny, by siring offspring that are themselves more successful in survival and reproduction. The net effects of sexual selection on fitness may also be enhanced by the direct benefits derived from the transfer of resources (e.g. nuptial gifts, parental care) from the mating partner, acting on female's fecundity and ability to rear offspring (Kelly & Alonzo, 2009; Rooney & Lewis, 2002). Maternal effects may also be at play as females that mate with preferred high-quality males may also increase their reproductive investment in offspring ('differential allocation hypothesis'; Burley, 1988), for example by providing more resources to their offspring (Kotiaho et al., 2003) or to their eggs (Kolm, 2001). Finally, if individuals with higher mating and/or fertilization capacity are also those with higher fecundity and survival-related traits that elevate their progeny's lifetime reproductive success (when, for example, there is genetic variation for genes that determine 'quality'), sexual selection would increase population fitness via correlated responses (Tomkins et al., 2004). At the population level, through good gene processes sexual selection may allow selecting for beneficial mutations or purging of harmful alleles, bringing large fitness benefits to both sexes (Rowe & Houle, 1996; Singh et al., 2017; Whitlock & Agrawal, 2009).

On the other hand, if there is conflict over reproduction, one sex (generally males) may increase their reproductive efficiency through harmful harassment (Gay et al., 2009), and/or seminal proteins (Wigby & Chapman, 2005) at the other's (generally females) expense (Chapman et al., 2003; Gavrilets et al., 2001; Rankin et al., 2011). Not only sexual conflict can lead to reduced female survival (Wigby & Chapman, 2005), but by resisting male harm females may suffer energetic costs, investing in defensiveness rather than offspring (Perry & Rowe, 2018). Successful males may also transfer sexually antagonistic genes that elevate their sons' reproductive success while lowering their daughters' (Brommer et al., 2007; Foerster et al., 2007). In this scenario, higher reproductive capacity of males reduces female productivity, with sexual conflict potentially decreasing the benefits of sexual selection (Pischedda & Chippindale, 2006). A key aspect in sexual selection studies is therefore understanding whether the costs to females inflicted by sexual conflict are countered by the benefits of sexual selection (Cordero & Eberhard, 2003; Garcia-Gonzalez & Simmons, 2010; Head et al., 2005; Rundle et al., 2007; Stewart et al., 2008).

A powerful empirical approach for studying the fitness effects of sexual selection has been manipulating the presence and absence of selection, with females having access to many mating partners (i.e. polyandrous matings) or only one (i.e. breeding through enforced monogamy; Partridge, 1980). Many of these studies are often originally aimed at understanding the evolution and maintenance

of female mate choice, nevertheless allowing the operation of both mechanisms of sexual selection (Wong & Candolin, 2005). Using experimental evolution to measure differences in female reproductive output between breeding lines differing in mating systems (Cally et al., 2019; Edward et al., 2010; Power & Holman, 2014) has yielded mixed results, with sexual selection shown to elevate certain fitness traits (e.g. offspring viability (Partridge, 1980; Petrie, 1994; Power & Holman, 2014; Simmons & Garcia-González, 2008); and adult survivorship (Promislow et al., 1998)), but not others (e.g. offspring emergence (Martin & Hosken, 2003)). Analysing these findings with a meta-analytic approach revealed a general positive effect of sexual selection on fitness, with yet only a trend for direct measures of female reproductive success, such as number of offspring and proportion of viable offspring (Cally et al., 2019). Single-generational experiments have also been pivotal in contributing to our general understanding of the fitness consequences of sexual selection. For example, numerous studies investigating the fitness benefits of mating multiply with different males or repeatedly with the same male, have highlighted the fitness-enhancing role of post-copulatory sexual selection (Arnqvist & Nilsson, 2000; Simmons, 2005). Nevertheless, costs to females from exposure to multiple matings are extensively described (Chapman et al., 1995; Crudginton & Siva-Jothy, 2000; den Hollander & Gwynne, 2009; Martin et al., 2004). Pre-copulatory sexual selection has also shown to affect female fitness. For example, females mated to attractive males benefit from elevated offspring fitness (Head et al., 2005). Other studies instead have shown that, despite male attractiveness being heritable, there is no association with fitness traits (Prokop et al., 2012), and mating with preferred males may even be detrimental for females (Friberg & Arnqvist, 2003).

When investigating the fitness consequences of sexual selection, distinguishing simultaneously between the specific effects of pre- and post-copulatory sexual selection on reproductive output is rarely applied, despite many studies have focused on male fitness-related traits (Evans et al., 2015; Gasparini et al., 2019; McDonald et al., 2017; Travers et al., 2016, but see Gómez-Llano et al., 2021). Mechanisms operating before and after mating may contribute differently to the overall variance in reproductive success (Evans & Garcia-Gonzalez, 2016; Simmons et al., 2017), with growing evidence reporting either a higher contribution of pre-copulatory selection (Pélissié et al., 2014; Pischedda & Rice, 2012; Rose et al., 2013), of post-copulatory selection (Arnqvist & Danielsson, 1999; Marie-Orleach et al., 2021) or an equal contribution (Danielsson, 2001; Devigili et al., 2015; Filice & Dukas, 2019). The above-mentioned studies (Marie-Orleach et al., 2021; Pélissié et al., 2014; Pischedda & Rice, 2012; Rose et al., 2013) address variance partitioning by statistically evaluating the relative contribution of pre- and post-copulatory mechanisms of selection to fitness, rather than documenting absolute fitness values. Hence, interestingly, how each episode of selection relates to fitness output remains largely uncovered.

In this study, we test the assumption that sexual selection can enhance female reproductive success (Cally et al., 2019), and specifically test for differential effects of pre- and post-copulatory sexual

selection by experimentally varying the potential for sexual selection before and/or after mating. We used the two-spotted field cricket *Gryllus bimaculatus* to estimate the fitness consequences of mating either under exclusive pre- or post-copulatory mechanisms of sexual selection, compared to mating with weakened or no sexual selection. The field of reproductive biology in this species is well-studied (Alexander, 1961; Gage & Barnard, 1996; Judge & Bonanno, 2008; Parker, 2009; Simmons et al., 2006; Sturm, 2011; Tuni, Beveridge, & Simmons, 2013; Wagner & Reiser, 2000). Pre-copulatory selection occurs in the form of aggressive male–male combats when competing for access to sheltered breeding territories (i.e. cracks in the ground and gaps under stones), from where they perform long-distance calling songs to attract females (Simmons, 1986; Tachon et al., 1999). Females wander in search for sedentary calling males and exert mate choice based on the quality of male calling or courtship song (Rantala & Kortet, 2003; Verburgt et al., 2011), as well as male body condition (Bateman et al., 2001; Simmons, 1986). Field crickets are polyandrous (Bretman & Tregenza, 2005; Simmons, 1987b), hence post-copulatory sexual selection occurs in the form of sperm competition where ejaculates from multiple males are stored in the female sperm storage organ, and females bias fertilization towards preferred males by controlling such stores of sperm (Bretman et al., 2009; Tregenza & Wedell, 2002). Pre- and post-copulatory traits, respectively male body mass, aggressiveness and ejaculate size, are positively correlated on a genetic level, indicating the existence of genetic variation in male quality (Tuni et al., 2018). Previous studies show that pre-copulatory selection contributes to female fitness as egg laying is increased in females that are allowed to choose their mating partners compared with those allocated to mates (Simmons, 1987a) and in females mating with dominant males (Bretman et al., 2006). We also know that multiple mating leads to increased offspring-hatching success (Tregenza & Wedell, 1998). However, since the relative contribution of pre- and post-copulatory processes to selection has not been resolved, we refrain from giving a priori predictions on whether selection occurring before or after mating should lead to higher fitness.

We established three mating treatments, with potential for exclusive (i) pre-copulatory sexual selection, (ii) post-copulatory sexual selection and (iii) weakened or no sexual selection. We are aware that pre-mating competition is unlikely to prevent post-mating selection (Fisher et al., 2016) as there is no mate monopolization in this system. Yet, our aim was to experimentally fully disentangle the effects of pre- and post-copulatory selection on female reproductive success by varying the potential for sexual selection to occur before or after mating. This inevitably entailed mating system manipulation. While standardizing the number of matings, pre-copulatory sexual selection was ensured by allowing multiple males to interact with rivals (i.e. fight) and court females (i.e. sing), females to exert mate choice for one of them and breed monogamously; post-copulatory sexual selection was enabled by preventing any pre-copulatory interactions (male–male fights and/or female choice) and breeding females sequentially with multiple males, hence, polyandrously; and sexual selection was minimized through enforced monogamy, by

breeding females to one male only repeatedly. We measured direct fitness by estimating female lifetime survival, the likelihood of reproducing and the number of offspring produced, as well as indirect fitness by estimating offspring growth rates and survival. Females that experience repeated courtship and copulation are known to suffer from reduced longevity (Bateman et al., 2006), yet we predict that the benefits of sexual selection may offset these costs. We expect an overall reproductive benefit for individuals mated with the potential for sexual selection as choice and/or competition may lead to males of superior quality (Tuni et al., 2018; Wedell & Tregenza, 1999) to produce higher quality offspring, and explore the differences derived by selection being pre- or post-copulatory with no strong a priori expectation. However, given that our experimental procedure also manipulates the mating system (polyandry vs. monogamy) we expect indirect fitness to be higher following polyandrous matings, hence with post-copulatory selection.

2 | MATERIALS AND METHODS

2.1 | Animal breeding

Approximately 200 nymphs of *Gryllus bimaculatus* were collected from a large wild population in Tuscany (Giardino, 42°26'18.5"N 11°20'16.3"E, Italy) in July 2018 and transported to the laboratory at LMU Munich (Germany). Nymphs (20–30 individuals each) were placed in several large plastic tanks (23 × 15 × 17 cm) furnished with pieces of egg carton for shelter and provided with *ad libitum* food consisting of dry cat food (Ja! Knusper-Mix Rind & Gemüse), dry fish flakes (sera® Pond flakes Flockenfutter) and fresh apple slices, and water through plastic water vials plugged with cotton stoppers. Once animals reached adulthood, small plastic cups (5 × 7 × 7 cm) containing moist soil were provided for mated females to lay eggs (2 per tank). Cups were removed after 1 week and replaced with novel cups for oviposition. Removed cups were placed in new tanks provided with food and water and were left for eggs to hatch. Offspring were mixed and new tanks were formed, for rearing and breeding. This procedure generated a large, outbred population. Animals were housed in a climate room with 60% relative humidity under a 12:12 h light:dark photoperiod that was kept at 26°C for two generations, and then 28°C.

After three generations, when nymphs reached their penultimate or last instar, we transferred approximately 600 males individually to containers (10 × 10 × 9 cm) equipped with shelter, water and dry cat food. Males were housed individually to control for mating and social (e.g. fighting) experience until sexual maturation. Last instar females (approximately 400) were instead kept in small tanks (12 × 14 × 23 cm) in groups of 5. All animals were checked twice a week for moults to determine whether they reached adulthood, and hence age post-eclosion. On these occasions, females were relocated to all-adult tanks of same densities and feeding conditions. Approximately 2 weeks after reaching sexual maturity animals were allocated to the treatments described below. For logistic reasons,

age at mating was not strictly standardized and therefore controlled statistically. The day before the mating, males and females were weighed using a digital scale (KERN & SOHN GmbH, Balingen, 208 Germany, accurate to 0.001g), and males had their spermatophore removed to standardize sperm age, as males produce replacement spermatophores (McMahon et al., 2021). Females were individually isolated as described for males.

2.2 | Experimental treatments

We established the following treatments: (i) Pre-copulatory sexual selection and monogamous matings (PRE-M), in which each female was placed together with three random males inside an arena sized $32 \times 15.5 \times 13$ cm. Males were left to fight against each other and court (i.e. sing) the female. Once females exerted mate choice, meaning they successfully mounted the male and the latter transferred a spermatophore, the other males were removed from the arena, and the pair was mated again twice. In this species, dominant crickets tend to achieve higher mating success (Bretman et al., 2006; Rantala & Kortet, 2004; but see Tunj et al., 2016; Vedenina & Shestakov, 2018). (ii) Post-copulatory sexual selection and polyandrous matings (POST-P), in which each female was randomly paired to one male inside a $16 \times 15.5 \times 13$ cm sized arena, until successful mounting and spermatophore transfer, for a total of three matings with three different males. (iii) Weakened sexual selection and enforced monogamy (NO-SEL), in which each female was randomly assigned to a male inside a $16 \times 15.5 \times 13$ cm arena until successful mounting and spermatophore transfer. The pair was mated again twice. We standardized number of matings (i.e. three) across treatments not only to exclude sperm limitation but also to balance potential direct benefits females could gain from multiple matings (e.g. nutritious ejaculates) and males were not used interchangeably between treatments. Due to logistics (i.e. handling of a large number of individuals), not all trials were conducted simultaneously, with those from the NO-SEL treatment being conducted once the previous were completed. Identical conditions for animals of all treatments were ensured by maintaining identical temperature and humidity settings within the climate room at all times (for rearing, mating and fitness measurements).

In all the trials, males and females were left together for 10 min after mating to allow mate guarding and prevent females from removing the spermatophore sooner (Simmons, 1986). They were then briefly returned to their individual housing containers, and mated for two additional times as described above, at 2 h intervals to allow males enough time to produce a novel spermatophore (Parker & Vahed, 2010). Individual sperm traits (e.g. number and viability) appear to be repeatable across spermatophores in this species (Gage & Morrow, 2003; McMahon et al., 2021), likely minimizing sperm depletion effects in PRE-M and NO-SEL males. Only animals that successfully completed three matings were included in the study, resulting in a total of 133 females (and 133 males) for the PRE-M treatment, 88 females (and 264 males) the POST-P, and 103 females

(and 103 males) the NO-SEL (whereas 3 POST-P, 3 PRE-M and 3 NO-SEL females were excluded).

After mating, females were kept individually in small tanks ($12 \times 14 \times 23$ cm) equipped with water, food, egg carton and a small plastic cup ($5 \times 7 \times 7$ cm) filled with moist soil, to lay eggs in. After 1 week the cup was placed in a new box ($6 \times 12 \times 12$ cm) with food and water for the offspring to hatch and was replaced with a new one to allow females to prolong oviposition in a novel substrate without simultaneous hatching of eggs. Similarly, the second cup was removed after 1 week and females returned in their housing containers.

2.3 | Fitness estimates

The likelihood of reproducing of each female was assessed based on whether any offspring from the two egg batches (oviposition cups 1 and 2) had hatched or not. Latency to hatching was scored as the time from providing an oviposition substrate to the female until hatching of the first offspring. After 2 weeks of egg laying, females were inspected twice a week to score lifetime survival. Approximately 3 weeks from hatching, the number of offspring produced by each female was counted by gently transferring the offspring to new containers using a paintbrush.

After counting, offspring of females within the same treatment and egg batch were mixed. We randomly selected nymphs off egg batch 1 from the PRE-M and POST-P treatments ($n = 64$ nymphs each) and from NO-SEL treatment ($n = 48$) and placed them individually in containers ($10 \times 10 \times 9$ cm) equipped with shelter and *ad libitum* water and food. Their body mass was measured twice a week until maturation (i.e. final eclosion to adulthood) and three additional times after maturation. Age at maturation was recorded, and all individuals were then inspected twice a week in their housing container to score offspring lifetime survival.

2.4 | Statistical analysis

To test whether our experimental treatments (PRE-M, POST-P and NO-SEL) affected female fitness we used generalized linear models with binomial distribution (glm-b) for likelihood of female reproduction (i.e. likelihood of producing any viable offspring) and negative binomial distribution (glm-nb, accounting for overdispersion) to investigate the total number of offspring hatched (i.e. sum of total number of offspring from oviposition cup 1 and 2) and mean latency to hatching (i.e. number of days from providing the oviposition cup to hatching, averaged for both oviposition cups). Treatment, female mass (mean-centred within treatment) and female age at mating were fitted as factors in the model. In case of a significant treatment effect, we used Tukey post hoc tests to understand differences between the treatments. Given the unintended variation in female age at mating (mean number of days from adult enclosure, PRE-M 22.73 ± 0.5 , range = 14–37, $n = 96$; POST-P 22.3 ± 0.5 ,

range = 14–30, $n = 78$; NO-SEL 9.8 ± 0.4 , range = 8–17, $n = 84$; Kruskal-Wallis, $\chi^2 = 166.84$, $df = 2$, $p < 0.0001$) we excluded females younger than 1 week ($n = 16$ females from the NO-SEL) from our analyses of female fitness and survival (i.e. a 6 day pre-oviposition period is also recommended to ensure reproductive maturity (Simmons, 1987b) and reference within). We also mean-centred age at mating by treatment to account for all variation among and within treatments before introducing it as a covariate in the models (Enders & Tofighi, 2007). We additionally ran a sequential ANOVA (Type II) on estimates of latency to hatching and number of offspring to specifically test the effect of treatment subsequent to the effect of female age as well as their interaction. Since reproductive success is represented by binomial data, sequential ANOVA was not possible here.

To analyse whether lifetime survival probabilities of females were affected by our experimental treatments, we carried out a Kaplan–Meier survival analysis to create survival curves and tested significance using a multivariate cox regression analysis on our lifetime data. Time (in days) was defined as the response variable with treatment (PRE-M, POST-P and NO-SEL), female mass and female age at mating as the independent variables. This is a non-parametric test to estimate the probability of survival at any given time interval in the data.

To test whether our experimental treatments (PRE-M, POST-P and NO-SEL) affected offspring growth we used a generalized linear mixed model (GLMM) with gaussian distribution, including body mass measured over time as response variable. Treatment and age (timepoint of each measurement) as well as their interaction were fitted as fixed effects (Model 1), as the latter will give information about differences between treatments across the entire growth period (=growth rates). To test whether offspring growth was further affected by sex, we conducted a second model including sex as well as the interactions between sex, treatment and age as fixed effects. Cricket ID was fitted as random effect in both models.

To test whether offspring body mass at maturation differed between treatments and sexes, we used analysis of variance (ANOVA). Kruskal–Wallis test was used to test for treatment differences in offspring age at maturation.

All analyses were conducted in R (version 4.1.1, R core Team, 2021) using the package ‘MASS’ for negative binomial generalized linear

models (logistic regression), the package ‘DHARMA’ (Hartig, 2020) for checking model assumptions, the package ‘multcomp’ for conducting Tukey post hoc testing and the package ‘survminer’ (Kassambara et al., 2021) for survival analysis. Data in the text are reported in mean \pm standard errors.

3 | RESULTS

3.1 | Likelihood of female reproduction

The likelihood of successfully reproducing in females (i.e. females with viable offspring) was significantly affected by the experimental treatment, as it was 99.1% ($n = 130$) in the PRE-M treatment, 100% ($n = 85$) in the POST-P treatment and 92.8% ($n = 84$) in the NO-SEL treatment (Table 1, Figure S1). However, post hoc analyses revealed no significant differences between treatments (Tukey Post-Hoc; POST-P – PRE-M: $p = 1.0$, NO-SEL – PRE-M: $p = 0.11$, NO-SEL – POST-P: $p = 1.0$). We also found a marginal positive effect of female body mass, with heavier females being more likely to successfully reproduce, but no effect of age at mating (Table 1).

3.2 | Latency to hatching

Offspring of PRE-M and POST-P females hatched significantly sooner than offspring of the NO-SEL group (Table 1, Figure 1; Tukey Post-Hoc; NO-SEL – PRE-M: p -value = 0.001; NO-SEL – POST-P: p -value = 0.002), but there was no difference between POST-P and PRE-M offspring (Tukey *post hoc*: p -value = 0.99). Latency to hatching was not affected by female body mass or age at mating (Table 1). The sequential ANOVA provided similar results (Table S1).

3.3 | Number of offspring

The total number of offspring hatched from each female was not affected by the treatments (mean number of total offspring, PRE-M 187.3 ± 8.7 , $n = 118$; POST-P 182.7 ± 13.5 , $n = 79$; NO-SEL 200.2 ± 16.2 , $n = 77$; Table 1) nor by female body mass and age at

TABLE 1 Results from the GLMs testing the effects of treatment, female body mass (mean-centred within treatment), female age at mating (mean-centred within treatment), on (i) female reproductive success (hatching probability of entire egg batch, binomial), (ii) latency to hatching (negative binomial) and (iii) number of offspring (negative binomial).

	Reproductive success			Latency to hatching			N offspring		
	GLM-Binomial			GLM-NB			GLM-NB		
	χ^2	df	p -Value	χ^2	df	p -Value	χ^2	df	p -Value
Treatment	10.87	2	0.004	15.48	2	<0.001	0.59	2	0.74
Female body mass	3.89	1	0.048	0.11	1	0.74	2.68	1	0.1
Female age at mating	2.29	1	0.13	0.39	1	0.53	0.5	1	0.48

Note: Significant effects are shown in bold.

mating (Table 1), which was supported by results from the sequential ANOVA (Table S1).

3.4 | Female survival

Survival probabilities were significantly higher for NO-SEL females compared with PRE-M (HR = 2.76, $df = 2$, $p = 0.0001$) and POST-P females (HR = 2.91, $df = 2$, $p < 0.0001$, Figure 2) but did not differ between PRE-M and POST-P females. They were neither affected by female age at mating (HR = 0.98, $df = 2$, $p = 0.14$) nor by female mass (HR = 1.25, $df = 2$, $p = 0.6$). The average age at death was 61.3 ± 1.7 days ($n = 80$) for NO-SEL females, 53.7 ± 1.1 days ($n = 95$) for PRE-M females and 53.4 ± 1.2 days ($n = 77$) for POST-P females.

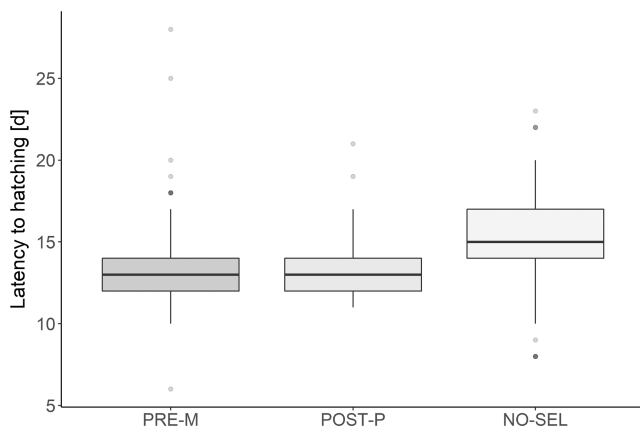
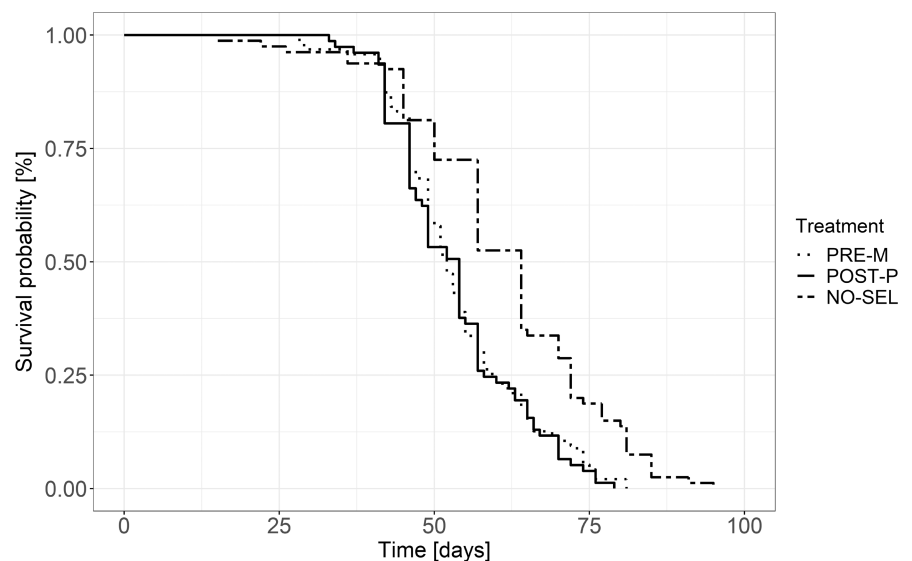


FIGURE 1 Differences across treatment (PRE-M = pre-copulatory sexual selection and monogamy; POST-P = post-copulatory sexual selection and polyandry; NO-SEL = no sexual selection and enforced monogamy) for latency to hatching of offspring, with NO-SEL offspring hatching significantly later compared with PRE-M and POST-P offspring.

FIGURE 2 Survival probability for females of the parental generation across treatments (PRE-M = pre-copulatory sexual selection and monogamy; POST-P = post-copulatory sexual selection and polyandry; NO-SEL = no sexual selection and enforced monogamy). POST-P (straight line) and PRE-M (dotted line) treatments died sooner compared with NO-SEL the treatment (dashed line).



3.5 | Offspring growth

Individuals of the NO-SEL treatment ($n = 41$) grew significantly slower than individuals of the PRE-M ($n = 59$) and POST-P ($n = 63$) treatment (Table 2 Model 1, Figure 3). Overall, females grew faster than males, with this effect being strongest in the PRE-M treatment compared with the NO-SEL treatment (Table 2 Model 2).

Offspring body mass at maturation was significantly lower for offspring of NO-SEL treatments (ANOVA; $F = 9.01$, $df = 2$, $p = 0.0002$; mean body mass at maturation [g] PRE-M 0.94 ± 0.03 , $n = 59$; POST-P 0.91 ± 0.03 , $n = 63$; NO-SEL 0.78 ± 0.03 , $n = 41$), as well as for males compared with females (ANOVA; $F = 28.8$, $df = 1$, $p < 0.0001$; mean body mass [g] males 0.81 ± 0.02 , $n = 83$; females 0.97 ± 0.02 , $n = 79$) (Figure S2). Offspring age at maturity neither differed between treatments (Kruskal-Wallis; $\chi^2 = 0.76$, $df = 2$, $p = 0.69$; mean offspring age [d] PRE-M 31.4 ± 1.2 , $n = 59$; POST-P 31.6 ± 0.8 , $n = 62$; NO-SEL 31.2 ± 1.5 , $n = 41$), nor between sexes (Kruskal-Wallis; $\chi^2 = 2.02$, $df = 1$, $p = 0.16$; mean offspring age [d] females 32.6 ± 0.9 , $n = 79$; males 31 ± 0.9 , $n = 83$).

3.6 | Offspring survival

Survival probabilities of offspring did not differ between NO-SEL and PRE-M offspring (HR = 1.48, $df = 2$, $p = 0.12$) or POST-P offspring (HR = 1.38, $df = 2$, $p = 0.16$) nor were they affected by sex (HR = 0.9, $df = 1$, $p = 0.57$) or size at maturity (HR = 1.42, $df = 2$, $p = 0.46$) (Figure S3). The average age at death was 88 ± 2.7 days ($n = 46$) for PRE-M offspring, 86 ± 3.2 ($n = 49$) for POST-P offspring and 93.6 ± 3.5 days ($n = 42$) for NO-SEL offspring.

4 | DISCUSSION

We measured reproductive outcome of females exposed to treatments allowing for exclusive pre-copulatory and post-copulatory

	Model 1: Treatment*age	Model 2: Treatment*age*sex
Fixed effects	β estimate (95% CI)	
Intercept	0.021 (-0.026, 0.07)	-0.039 (-0.112, 0.032)
Treatment PRE-M	0.025 (-0.04, 0.09)	0.099 (0.001, 0.195)
Treatment POST-P	-0.02 (-0.08, 0.041)	-0.019 (-0.075, 0.115)
Age	0.018 (0.017, 0.019)	0.021 (0.02, 0.023)
TreatmentPRE-M:Age	0.009 (0.008, 0.01)	0.007 (0.005, 0.009)
TreatmentPOST-P:Age	0.011 (0.01, 0.013)	0.011 (0.009, 0.013)
Sex Male		0.11 (0.01, 0.212)
TreatmentPRE-M:SexMale		-0.134 (-0.262, 0.0003)
TreatmentPOST-P:SexMale		-0.059 (-0.192, 0.076)
Age:SexMale		-0.005 (-0.007, -0.003)
TreatmentPRE-M:Age:SexMale		0.003 (0.0002, 0.006)
TreatmentPOST-P:Age:SexMale		0.0001 (-0.003, 0.003)
Random effects	σ^2 (95% CI)	
Cricket ID	0.028 (0.026, 0.03)	0.028 (0.026, 0.031)
Residual variance	0.021 (0.02, 0.022)	0.02 (0.019, 0.022)

Note: Significance shown in bold.

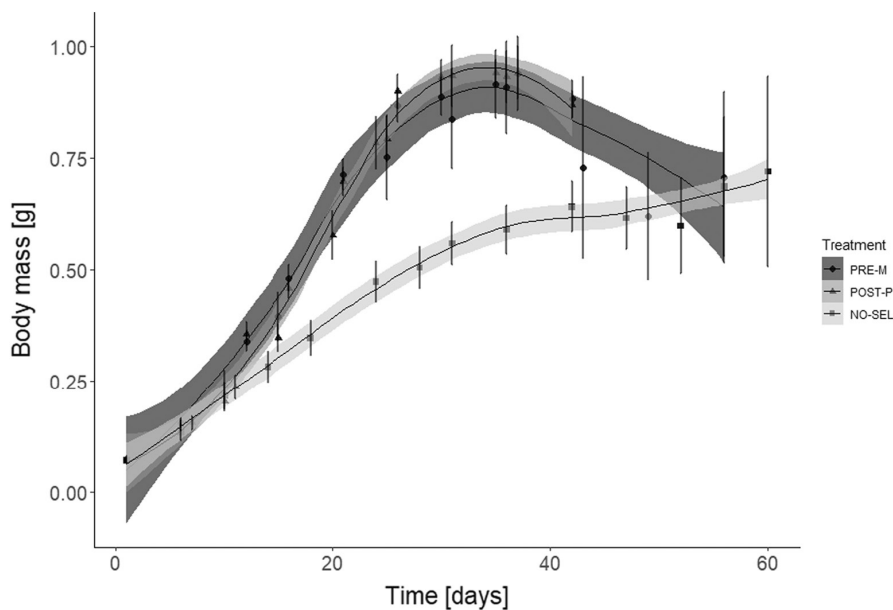


TABLE 2 Estimated effect sizes and 95% credible intervals around the mean of predictors of body mass; predictors model 1: Treatment (PRE-M, POST-P and NO-SEL), age (timepoint when body mass was measured) and their interaction; model 2: Treatment, age and sex (male or female) and their interactions; treatment effects are indicated as contrasting PRE-M and POST-P against NO-SEL (intercept); random effect: Cricket ID.

FIGURE 3 Differences across treatment (PRE-M = pre-copulatory sexual selection and monogamy; POST-P = post-copulatory sexual selection and polyandry; NO-SEL = no sexual selection and enforced monogamy) for growth curves of average weight measurements per days.

sexual selection or weakened sexual selection. We expected fitness benefits to arise when sexual selection was present, with no a priori expectation for pre-copulatory selection weighing more than post-copulatory selection on fitness outcome. Yet, when considering the different mating systems (monogamy vs polyandry) that were experimentally applied to obtain the two treatments, we hypothesised polyandry, and hence post-copulatory selection, to provide fitness advantages to the offspring (Arnqvist & Nilsson, 2000; Tregenza & Wedell, 1998). We found that, despite suffering higher survival costs, females benefit from sexual selection as those from the no-selection

treatment were less likely to reproduce, had offspring that hatched later in time, development was slower and body mass at maturation lower. There was, however, no difference in how either pre- or post-copulatory selection affected the fitness estimates studied. We can exclude an effect of the mating system, as monogamy was present in treatments with (i.e. pre-copulatory treatment) and without selection (i.e. no selection treatment) and these nevertheless yielded different reproductive outcomes. These findings suggest that sexual conflict may potentially be at play, negatively affecting female lifetime reproductive success but not offspring fitness given that sexual

selection, regardless of whether it occurs before or after mating, appears to provide indirect reproductive benefits in the form of faster and higher quality offspring development.

The likelihood of females reproducing was overall high in our study, and given that we controlled for sperm limitation, reproductive failure may derive from naturally non-viability of gametes (Simmons, 1987b) or incompatibility (García-González, 2004; Zeh & Zeh, 1996, 1997). Yet, it was lowest in females that did not exert mate choice. Female crickets that have a choice may have the means to avoid mating with unfertile and/or incompatible partners. By mating with preferred males these may also invest more in their offspring (Burley, 1988), as previously shown by Simmons (1987a; but see also Arnqvist & Danielsson, 1999; Kotiaho et al., 2003; Sheldon, 2000). It is possible that females use certain male traits as quality indicators, such as body size (Simmons, 1986) and/or song traits (Rantala & Kortet, 2003; Verburt et al., 2011) to assess relative male quality, including fertility and allocate resources to reproduction accordingly. Female crickets of *Gryllus lineaticeps* mating to males producing preferred song types are, for example shown to live longer, produce more eggs and these have higher hatching success (Wagner & Harper, 2003). Although there is contrasting evidence, female preference for dominant males has also been reported (Bretman et al., 2006) and dominance has been identified as eliciting higher egg production in *G. bimaculatus* females in some studies (Bretman et al., 2006), but not others (Tuni et al., 2016). In our study, mate assessment could take place either with many partners present simultaneously in pre-copulatory selection treatments, or sequentially in post-copulatory selection treatments. Given that only females that successfully mated were included in our study, assessment and choice may have potentially translated into post-copulatory allocation to increase offspring quality in terms of sooner hatching, faster and better development. The positive genetic correlations between multiple reproductive traits in males of this system (Tuni et al., 2018) also suggests that females may be selecting for the same overall male phenotype. For example, dominance could be assessed in only one of our treatments, the one with pre-copulatory selection, but given that aggressive individuals are those with larger body mass (Tuni et al., 2018), these may have been preferred even in the absence of contest competition when assessed sequentially. In the case of *G. bimaculatus*, larger males (i.e. with higher body mass), which are also the most aggressive, possess ejaculates of greater size (i.e. sperm numbers; Tuni et al., 2018).

Increased maternal investment when sexual selection had the potential to occur may have led to the more successful offspring reported in our study. A study on *G. bimaculatus* indeed shows that offspring of females allowed to choose their mates developed faster and had higher survival compared with those that were allocated mates (Simmons, 1987a). Developing faster at higher growth rates brings large reproductive advantages to the offspring as these individuals will be able to reproduce sooner and will possess superior body condition at the time of mating. Opposing to this, offspring with delayed growth might be disadvantaged when females are choosing to mate with fully developed males in better body

condition (Bateman et al., 2001; Simmons, 1986). Given that females mating without sexual selection were also the youngest, we cannot fully exclude that the differences documented between the treatments with and without selection are driven by differences in female age at mating. Specifically, younger (no-selection) females may have been delayed in their oviposition if egg development was not complete, leading to later hatching of offspring. Maternal age effects are also known to potentially influence offspring development and performance (Mousseau & Fox, 1998). Whereas numerous studies report negative transgenerational effects of senescing mothers (e.g. offspring of older females hatch later), develop more slowly or have shorter lifespan (Benton et al., 2008; Bock et al., 2019; Lind et al., 2015; Priest et al., 2002), others report positive effects due to an increase in investment in reproduction by older mothers (Froy et al., 2013; Kroeger et al., 2020; Part et al., 1992; Poizat et al., 1999; Travers et al., 2021). In the case of field crickets, a recent study on *Gryllus bimaculatus* shows that offspring of older females experience longer latencies to hatching and have lower hatching success; these were bigger at adulthood but had shorter lifespans (Noguera, 2021). While these findings may suggest that the effects reported in our study are unlikely driven by the younger female age, maternal age effects should be explored further.

Not all of our estimates of fitness differed between treatments, in particular offspring number. A study from Gómez-Llano et al. (2020) on the fruit fly *Drosophila melanogaster*, which to our knowledge is the only other study using an experimental design that attempts to simultaneously discriminate between the effects of pre- and post-copulatory selection on fitness, similarly found that the number of emerging adults per female did not differ among different sexual selection regimes, although in the context of adaptation to novel thermal environments, evolving with pre-copulatory sexual selection proved beneficial.

We found that sexual selection also entails costs, as removal of sexual selection led to longer female survival. All females across treatments were exposed to the stress of male harassment, as males are known to court vigorously (Bateman, 2000; Bateman et al., 2006). Yet, there are some differences between the treatment groups. In our pre-copulatory sexual selection treatments these costs may have been particularly exacerbated by male behaviour, as males were aggressively fighting against each other and approaching females simultaneously. Aggressive behaviours were often observed to be directed to females (Bateman et al., 2006; Vedenina & Shestakov, 2018; personal observations). On the other hand, in our post-copulatory sexual selection treatment, being exposed to several different males may have potentially increased disease transfer (Simmons, 2005; Thrall et al., 2000) or transfer of harmful chemicals from multiple ejaculates, as known in *Drosophila melanogaster*, where males evolve seminal fluids that increase their mating success but are harmful to females and even increase female mortality (Chapman et al., 1995). This could result in reduced longevity (Friberg & Arnqvist, 2003), which is a cost that promiscuous females suffer from more likely with strong negative implications for female lifetime reproductive success. The lower survival observed

in females mated with the opportunity for sexual selection instead does not appear to be a consequence of trade-offs in resource allocation between reproduction and soma-maintenance (Roff et al., 2002; Stearns, 1992), as if for example females had increased offspring production. Variation in female age at mating, with those from the no-selection treatment being unintentionally younger, may also potentially explain our results. Younger females may better cope with costly mating, such as multiple inseminations and/or multiple encounters with courting males, when these occur earlier in life, rather than pointing to trade-offs between reproduction in early life and survival (Wilson & Walker, 2019). This is also shown in the field cricket *Gryllus assimilis* (Limberger et al., 2021), where older mated females had an increased mortality rate compared to females mated at younger age and virgin females. Limberger et al. (2021) suggest that late-mated crickets increase their resource allocation towards current reproduction, since future reproduction might not be as likely as it is for younger females, leading to an acceleration of senescence and death.

Interestingly, the direct survival costs of mating with males selected either pre- or post-mating, may be potentially compensated by the indirect offspring viability benefits gained from sexual selection. Despite contrasting theoretical arguments (Cameron et al., 2003) and empirical evidence (Pischedda & Chippindale, 2006; Stewart et al., 2008; Taylor et al., 2008), indirect benefits arising from harmful matings have been suggested to outweigh the costs imposed by males (Cordero & Eberhard, 2003). In the field cricket *Acheta domesticus*, females mating with attractive partners experience survival costs that are counterbalanced by producing offspring with greater fitness (Head et al., 2005). Similarly, in the Australian field cricket *Teleogryllus oceanicus*, females mated to males that invested more in the production of accessory glands incurred longevity costs due to harmful ejaculate-driven effects, but yet their offspring survival was improved (Garcia-Gonzalez & Simmons, 2010). Despite not being able to define the target of female choice and/or male manipulative traits, our findings are similarly suggestive of indirect benefits counteracting direct costs of sexual selection.

Overall, our findings suggest that the action of sexual selection overrides any benefit inherently linked to the mating system, monogamous or polyandrous, as we importantly uncover differences in fitness outcomes of monogamous matings occurring with and without sexual selection. Several studies investigating whether polyandry is adaptive have reported fitness benefits of mating with multiple partners (Tregenza & Wedell, 1998; Tuni et al., 2013a; Tuni & Bilde, 2010). Yet, these studies commonly compare fitness of polyandrous females to monogamous matings in which they allocate males to females, limiting female choice and resembling our enforced monogamy treatment with no sexual selection. Our findings are therefore in line with most literature, as polyandrous matings from the post-copulatory treatment yielded higher fitness outcomes compared to monogamous mating lacking selection (no selection treatment). It would be interesting to investigate whether

the magnitude of such indirect benefits would be equally high, if selection was allowed to operate.

5 | CONCLUSIONS

Whether sexual selection enhances fitness or not fuels an active field of research, with studies reporting positive effects such as increased population growth rates (Fox et al., 2019) and accelerated rates of adaptation to novel environments (Gómez-Llano et al., 2020; Parrett et al., 2019; Parrett & Knell, 2018; Servedio & Boughman, 2017), while others suggest higher extinction rates due to costly sexual traits or reduction of effective population size and genetic drift (Kokko & Brooks, 2003; Kokko & Jennions, 2008; Whitlock, 2000). Our results are in line with current literature, which states that fitness values are often higher in populations evolving under sexual selection, relative to populations where sexual selection is experimentally removed or weakened (Cally et al., 2019). Pre- and/or post-copulatory sexual selection may lead to a comparable magnitude of indirect fitness benefits to females, as revealed by measuring a range of fitness estimators encompassing offspring viability, growth and survival but impose direct survival costs to females. By outweighing the costs of reduced longevity, the increased developmental ability reported for offspring has the potential to contribute to the beneficial population-level consequences of sexual selection (Cally et al., 2019; Gómez-Llano et al., 2020; Parrett et al., 2019), highlighting the relevance of indirect benefits of sexual selection in maintaining population viability.

AUTHOR CONTRIBUTIONS

Magdalena Matzke: Data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Aurora Rossi:** Investigation (supporting); writing – original draft (supporting). **Cristina Tuni:** Conceptualization (lead); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (equal); resources (lead); supervision (lead); validation (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICTS OF INTEREST

All authors gave final approval for publication and declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available on Dryad at <https://doi.org/10.5061/dryad.wm37pvmrj> and on Zenodo at <https://doi.org/10.5281/zenodo.7340773>.

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