J. Appl. Biosci., 50(2): 111-121, December, 2024
doi: 10.61081/joab/50v2i106

ISSN (Print) 0975-685X
ISSN (Online) 0975-864X

ORIGINAL ARTICLE

Coercive Copulation in the Ladybird Beetle *Propylea dissecta* Mulsant (Coleoptera: Coccinellidae)

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ABSTRACT

Sexual coercion is defined as the use of force or threat by a male to increase mating opportunities with a fertile female while limiting her options for mating with other males. The mechanism is critical to shaping mate selection dynamics since it influences female resistance strategies and leads to the evolution of male characteristics which facilitate successful copulation despite female preferences. This study investigates the impact of coercive mating on reproductive parameters in the ladybird beetle, *Propylea dissecta* (Mulsant), focusing on the interaction between male size, female resistance, and subsequent mate choice. We conducted experiments to assess the time to commence mating, mating duration, fecundity and viability of eggs laid by young and old females subjected to coercive matings with varying male sizes. The results indicated that in instances of coerced first matings, the time to commence mating was shorter when females were coerced by larger males. While the duration of mating was unaffected by the size of the coercive males, both fecundity and egg viability were significantly influenced by their body size. The observed preference for larger males indicates a role for cryptic female choice in enhancing reproductive outcomes. Furthermore, while coercive mating by smaller males initially reduced fecundity and egg viability, subsequent mate choice by females served as a compensatory mechanism. This study is the first attempt to examine the impact of sexual coercion in ladybird beetles on female reproduction and mate choice.

KEY WORDS : Sexual coercion, mate choice, *Propylea dissecta*, forced copulation, Fecundity, %egg viability

INTRODUCTION

Animal mating strategies can vary from cooperative to conflict-driven interactions. Males typically increase reproductive success by mating frequently with multiple partners, utilizing their abundant, low-cost gametes (Pilastro *et al*., 2003; Gowaty *et al*., 2010). In contrast, females produce fewer, energetically costly gametes and require fewer matings to optimize reproductive success (Wedell *et al*., 2002; Hayward & Gillooly, 2011).

Sexual coercion disrupts the indirect benefits of mate choice and may drive the evolution of female resistance while also favouring male traits that help them overcome this resistance (Brennan & Prum, 2012). However, studying female responses to coercion and the balance of costs and benefits has been challenging. Preference and resistance in females are often viewed as interconnected, influencing mate choice simultaneously (Arnqvist & Rowe, 2005b; Kokko*et al*., 2006).

Forced copulations, where females are denied choice and exhibit rejection behaviours, occur in numerous species, including humans (Pilastro *et al*., 2003; Gibson *et al*., 2008; Muller *et al*., 2009; Dukas & Jongsma, 2012; Bertram *et al*., 2015; Allen *et al*., 2017). Andersson (1994) even suggested coercion as a third mechanism of sexual selection, possibly driving male trait evolution across taxa (Clutton-Brock & Parker, 1995). Sexual coercion is defined as the use of force, or threat, by a male to increase mating likelihood with a fertile female while limiting her options to mate with others, often at a cost to the female (Smuts & Smuts, 1993). This tactic is widespread across animals, including monarch butterflies (Solensky, 2004), water striders (Arnqvist & Rowe, 1995, Fu *et al.,* 2024,), bed

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*Corresponding author email: omkar.lkouniv@gmail.com bugs (Yan *et al*., 2024), garter snakes (Shine & Mason, 2005), bush crickets (Vahed, 2002), and macaques (Cooper & Bernstein, 2000).

Insects have been pivotal in advancing theories of sexual selection and conflict between males and females (Arnqvist & Rowe, 2005a). Among arthropods, sexual coercion is reported in several insect groups (Cordero, 1999; McLain & Pratt, 1999; Markow, 2000; Cordero & Andrés, 2002; Eberhard, 2002; Vahed, 2002; Dukas & Jongsma, 2012) restricts female mate choice and includes forced copulation, harassment, and intimidation. Traits, like larger body size, are often favoured in coercive interactions (Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995), impacting gene flow patterns (Chesser & Baker, 1996) and genetic diversity (Zeh & Zeh, 1997). Studies reveal the fitness consequences of coercion (Solensky, 2004; Head & Brooks, 2006; Hettyey *et al*., 2009; Wallen *et al*., 2016).

Male coercion has significant impacts across many animal species (Clutton-Brock & Parker, 1995). By inflicting mating-related harm, males may compel females to invest in reproduction similar to terminal investment. In cases of intense sexual conflict, males may override female resistance through forced copulation (Peretti & Aisenberg, 2011). When females develop resistance tactics, males often evolve counter-strategies, such as sensory exploitation or stimulatory behaviour, especially within the context of an evolutionary arms race. Heightened conflict of interest between sexes typically intensifies this arms race, especially where increased female selectivity is linked to greater maternal investment (Chapman *et al*., 2003). Females actively resist male mating attempts in some insects (Allen & Simmons, 1996; Lauer *et al*., 1996; Crean *et al*., 2000).

Female mate preference tends to evolve more readily than in males; however, females often face forced copulation with unwanted mates, which can significantly influence female mate choice evolution (Iwasa *et al*., 1991; Arnqvist & Nilsson, 2000). Male-imposed copulation pressure shapes the development of morphological and behavioural traits related to mating, impacting tactics in both sexes (Clutton-Brock & Parker, 1995). Active female resistance may arise to reduce the costs associated with unnecessary mating or to "screen" males, allowing only high-quality partners (Eberhard, 2002; Cordero & Eberhard, 2003). Regardless of its purpose, female resistance can drive the evolution of male traits that help overcome this resistance, thereby promoting male mating success through sexual selection.

The sexual dialectics theory (Gowaty, 1997) delves into these fitness dynamics, examining how female resistance to male control over reproduction might evolve. Some studies suggest that females could gain indirect fitness benefits by selecting males who can overcome resistance, potentially producing "sexy sons" with strong competitive traits (Zeh & Zeh, 2003; Taylor *et al*., 2007). This preference might secure "good genes" in offspring, enhancing reproductive success across generations. For instance, in scorpionflies (*Panorpa latipennis*), females mated consensually with nuptial gifts laid more eggs than those subjected to forced matings without gifts, highlighting the benefits of mate choice (Thornhill, 1984). Additionally, immature females tend to resist forced copulations more vigorously than mature ones, resulting in longer latencies and reduced offspring, showing potential fitness costs of coercion (Seeley & Dukas, 2011). Forced matings with immature females have also been associated with increased physical harm, mortality rates, and reduced progeny for the coercive males compared to consensual matings with mature females (Blanckenhorn *et al*., 2002; Dukas & Jongsma, 2012; Biaggio *et al*., 2016).

While forced copulation is widespread, its full consequences remain poorly understood. Research so far has mostly documented physical injuries across species (Smuts & Smuts, 1993; Thornhill & Palmer, 2000). Ladybirds serve as a valuable model to experimentally examine the neurogenetic, behavioural, and evolutionary impacts of forced copulations. Majerus (1994) proposed two hypotheses on how female ladybirds may distinguish potential mates: (i) the "test hypothesis," where a female assesses male quality through rejection behaviour, accepting him only if he overcomes it; and (ii) the "rape hypothesis," where mating occurs if the male is strong enough to subdue female resistance.

In insects, sexual selection drives the evolution of specific traits, often shaping male courtship behaviours and female strategies to avoid non-beneficial copulations. Female insects may express reluctance through behavior, like mating refusals, a type of sexual conflict where one partner declines to engage in copulation. In the ladybird, *Propylea dissecta* (Mulsant), newly emerged or younger females display notable resistance to mating attempts, though this resistance can be overcome by more mature males. Female *Harmonia axyridis* (Pallas) ladybirds show mating refusals by moving away, shaking males off, or raising their abdomens (Obata, 1988). Mating refusals may arise from male harassment or sexual conflict, especially when mating benefits are unbalanced, leading to increased coercion (Khan, 2020; Harano, 2015). In insects, such as butterflies and beetles, females exhibit mate refusal, selectively avoiding certain males, which contributes to sexual selection through mate choice and cryptic choice mechanisms (Fukaya, 2004; Obara *et al*., 2011).

This study aims to investigate sexual coercion in

Table 1: General linear model showing the effect first and second coercive matings on mating and reproductive parameters in *Propylea dissecta*

Mating Treatments*	Time to commence mating (in minutes)	Mating duration (in minutes)	Fecundity (no. of eggs laid)	Egg viability (%)
F (YL.YS.OC) (P-Value); df	F=3.01 (P=0.054);1,89	F=0.97 (P=0.382);1,89	F=44.99 (P<0.0001);1,89	F=4.22 (P=0.018);1,89
F (YL.YLC) (P-Value); df	F=2.00 (P=0.163);1,59	F=0.10 (P=0.756);1,59	F=308.75 (P < 0.0001);1,59	F=51.60 (P<0.0001); 1,59
F (YS.YSL) (P-Value); df	F=9.18 (P=0.004);1,59	F=0.64 (P=0.427);1,59	F=496.46 (P < 0.0001);1,59	F=37.46 (P<0.0001);1,59
F (OC.OCC) (P-Value); df	F=0.03 (P=0.858);1,59	F=0.81 (P=0.372);1,59	F=355.75 (P < 0.0001);1,59	F=51.30 (P < 0.0001);1,59

*YL=Young ♀×Large♂ (No choice); YS=Young ♀×Small♂ (No choice); O=Old ♀×Large♂ / Small ♂ (mate choice during 1st mating) YLC=Large ♂/ Small ♂ (mate choice during 2nd mating); YSC=Large ♂/ Small ♂ (mate choice during 2nd mating); OCC=Large ♂/ Small ♂(mate choice during 2nd mating)

ladybird beetles, an important step toward understanding how forced mating behaviour impact female reproductive strategies, mate choice, and the evolutionary dynamics of sexual conflict in ladybird beetle, *P. dissecta*. Specifically, this study will examine: (i) whether females genuinely lose reproductive conflict, shown by pressures favouring increased resistance, (ii) if indirect benefits arise from coercion, and (iii) coerced females' behaviour in subsequent matings. We hypothesize that coercion may lead females to limit or delay reproduction, shedding light on the costs of forced copulation and the evolution of female resistance.

MATERIALS AND METHODS

Experimental Model

Propylea dissecta is an aphidophagous ladybeetle of Oriental origin and is quite common in the agricultural and horticultural landscapes of North India, preying commonly on aphids, *Aphis gossypii* Glover and *Aphis craccivora* Koch (Omkar & Pervez, 2000a). It is a polymorphic ladybird beetle with three morphs: pale, intermediate and typical. The elytra of the typical morph possessesthree dark black streaks with expanded ends, while the pale morph lacks these black markings completely. There is a prominent sexual dimorphism in *P. dissecta* with sex-specific characteristic black markings on the head and pronotum (Omkar & Pervez, 2000b).

Collection and Rearing Conditions

Adults of mixed body sizes were collected from the agricultural fields surrounding Lucknow, India (26°50'N, 80°54'E) and brought to the laboratory for rearing. Field collected adults were paired and placed in transparent plastic Petri dishes (9 × 2 cm, one pair per dish) with *ad libitum* daily replenished bean aphid, *A. craccivora* (reared on host plant *Vigna unguiculata* L. in a greenhouse maintained at 27 ± 2°C, 65 ± 5% R.H. and 14L: 10D photoperiod). Petri dishes were placed in BOD incubators (Yorco Super Deluxe, YSI-440 New Delhi, India) (abiotic and biotic conditions as above). The pairs were checked daily for oviposition. The eggs laid were collected every 24 hours and incubated under the above abiotic conditions until hatching. Each larva was reared till pupation to adult emergence individually in plastic Petri dishes (size as above) and provided with *ad libitum* aphids till the age of 10 days. The adults were taken from this stock only to perform experiments.

Optimization of Female Age

To standardize the appropriate ages of the females for this study, females of different ages (newly emerged, 1, 3, 6, 9, 12, 18, 20, 22 and 24 hours) were paired with the middle aged males (20-30 days old) under the similar laboratory conditions mentioned above and data were recorded. The results revealed that newly emerged females of 18 hours (young) and 22 hours (older) had significant differences (t value = -6.89, P = 0.000) in their mating success. Thus, for this study, the females of 18 hours were considered as young and of 22 hours as old females and were randomly selected from the stock. All selected females had a body mass (16 ± 2 mg). The natural body mass variation in stock culture ranged from 5-12 mg for males. Males of 11 ± 2 mg were considered large while those of body mass 6 ± 2 mg were considered small.

Experimental Protocol

To assess the effects of forced copulations on the fitness of females of *P. dissecta*, the females were taken from the prepared laboratory stock and subjected to forced matings in the following combinations: (i) Young ♀ × Large ♂ (no choice), (ii) Young ♀ × Small ♂ (no choice), (iii) Old ♀ × Choice of Large ♂ and Small ♂. Young females were 18 hours old and old females were 22 hours old. The behavioural observations were made, which included female resistance through fast movements, curving abdomen, kicking and loss of balance, and stridulating rapidly. Whereas males made frequent attempts to commence mating. When first coercive mating terminated, these combinations were further divided into two groups after the termination of the mating. One group was given the opportunity of second coercive mating and the others were not. In the group subjected to second coercive mating, the once mated females including both young and old were given the choice of unmated large and small males. All males were 20 days old. The mate preferences, mating parameters, time to commence mating and mating durations were recorded for each mating pair. Once the pairs disengaged naturally, males were removed and females were transferred into the new Petri plates and provided with *ad libitum* aphids. Daily oviposition and percent egg viability were recorded for the next 10 days. Each treatment was replicated 30 times.

STATISTICAL ANALYSIS

The chi-square (χ^2) goodness-of-fit analysis was used to test the null hypothesis of coercive mating and to compare the mate preference in all treatments given in the study. Data of time to commence mating, mating duration, fecundity, percent egg viability and total development duration (dependent factors) were first tested for normality of error distribution (Kolmogorov-Smirnoff test) and homogenous (Bartlett's) distribution. Data on time to commence mating, mating duration, fecundity and percent egg viability were subjected to the generalized linear model. All statistical analyses were conducted using Minitab-16 statistical software (Minitab Inc., State College, Pennsylvania, USA).

RESULTS

Effect of First Coercive Mating on Mating Performance

The time to commence mating was significantly influenced by the male mating treatments (F=3.01; P=0.054; df=1, 89; Table 1). In the first mating treatment, a higher time to commence mating was recorded in the young females that mated with the small body sized males and young females that mated with large males showed a smaller time duration (Fig. 1a).

First coercive mating had insignificant effect on mating duration (F=0.97; P=0.382; df=1, 89; Table, 1), it was found to be similar in all groups (Fig. 1b).

Fecundity showed significant variation in all the mating groups. Male body size during their first mating appeared to affect female fecundity significantly (F = 44.99; P < 0.0001; df = 1, 89; Table 1). In the first mating treatment, the highest fecundity was recorded in the pair where old females were given mate choice, followed by the young females that mated with large males, and young females that mated with small males. Older females were more fecund than younger females (Fig. 2a).

In the first coercive matings, male mating treatments influenced the percent egg viability significantly (F=4.22; P=0.018; df = 1, 89). In the first mating treatment, the highest percent egg viability was recorded in the pair where old females were given mate choice and the lowest percent egg viability was recorded by young females that mated with small males. The percent egg viability differed significantly across all the treatments (Fig. 2b).

Forced Copulation and Female Mate Choice

A statistically insignificant result was observed for the first mating when older females were given mate choice ($\chi2$ = 3.724, P = 0.054). In trials with young females, larger males achieved higher mating success than smaller males during both the first mating and the second coercive mating ($\chi2$ = 5.085, P = 0.024). Large males were also more successful when paired with young females who had previously mated with small males ($\chi2$ = 6.665, P = 0.010). Similarly, when older females were given a choice between large and small males in the second mating, large males were more successful ($\chi2$ = 5.085, P = 0.024; Fig. 3). Thus, in ladybird beetles, larger males demonstrate greater reproductive success, suggesting that male size positively influences mating attractiveness.

Effect of Second Coercive Mating on Mating Performance

The time to commence mating did not differ significantly (F = 2.00; P = 0.163; df = 1, 59) between young females during their first coercive mating with large males and their second mating, where males were selected by the females. In contrast, young females coerced by small males in their first mating showed a significant difference in time to commence mating compared to those given mate choice in the second mating (F = 9.18; P = 0.004; df = 1, 59). Among older females given mate choice in both first and second matings, there was no significant difference in time to commence mating (F = 0.03; P = 0.858; df = 1, 59). The highest time to commence the second mating was observed in young females initially coerced by large males, while the lowest time of mating was seen in those initially coerced by small males. Both young females that mated with large males and older females given mate choice in both matings showed similar times to establish mating (Fig. 1a).

Mating duration showed no significant variation across treatments. For young females mated with large males in their first coercive mating and given mate choice in the second, mating duration remained similar (F = 0.10; P = 0.756; df = 1, 59). Similarly, young females that mated with small males first and had mate choice in the second mating also showed no significant variation in mating duration (F = 0.64; P = 0.427; df = 1, 59). Among older females provided with mate choice in both matings, no significant difference was observed either (F = 0.81; P = 0.372; df = 1, 59). The mating duration was highest for older females with mate choice in both matings, while the lowest duration was observed in young females first mated with large males and given mate choice in the second. No significant differences in mating duration were found across all treatments (Fig. 1b).

Fecundity differed significantly across treatments. Young females that mated with large males in their first coercive mating and were given mate choice in the second mating showed significant variation in fecundity (F = 308.75; P < 0.0001; df = 1, 59). Similarly, young females that initially mated with small males and later had mate choice in the second mating also exhibited significant fecundity variation (F = 496.46; P < 0.0001; df = 1, 59). Among older females with mate choice in both matings, fecundity varied significantly as well (F = 355.75; P < 0.0001; df = 1, 59). Following the second coercive mating, fecundity was highest in older females given mate choice in both matings and lowest in young females initially mated with small males and given mate choice in the second mating. Older females demonstrated higher fecundity in both coercive matings compared to young females (Fig. 2a).

Percent egg viability showed significant variation across treatments. For young females that mated with large

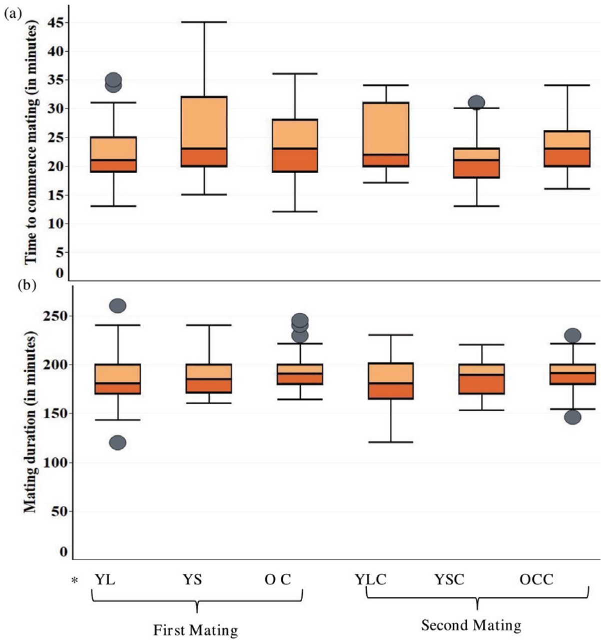

Fig. 1: Box and Whisker plots showing the effect of coercive matings on mating parameters (a) time to commence mating, and (b) mating duration in *Propylea dissecta.* The center horizontal line is drawn at the median. The vertical lines extending from the boxes are 1.5 times the length of the box. Circles represent outliers.

*On the X- axis in the given mating combinations, Y= Young ♀; O= Old ; L= Large ; S= Small ♂; C= Mate choice between large and small ♂

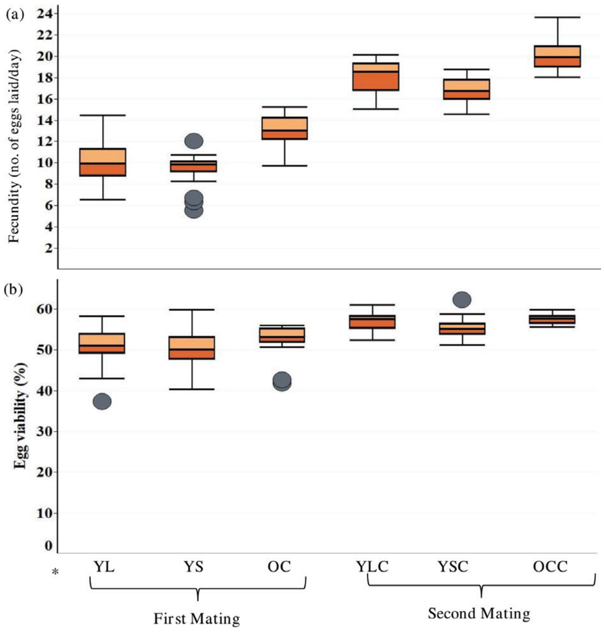

Fig. 2: Box and Whisker plots showing the effect coercive matings on repridcutive parameters (a) fecundity, and (b) percent egg viability in *Propylea dissecta.* The center horizontal line is drawn at the median. The vertical lines extending from the boxes are 1.5 times the length of the box. Small circle represent outliers.

*On the X- axis in the given mating combinations, Y= Young ♀; O= Old ; L= Large ; S= Small ♂; C= Mate choice between large and small ♂

males in their first coercive mating and had mate choice in the second, egg viability varied significantly (F = 51.60; P < 0.0001; df = 1, 59). Similarly, young females initially mated with small males and given mate choice in the second mating also showed significant variation in egg viability (F = 37.46; P < 0.0001; df = 1, 59). In older females with mate choice in both matings, percent egg viability varied significantly as well (F = 51.30; P < 0.0001; df = 1, 59). The highest percent egg viability was recorded in older females, while the lowest was observed in young females previously mated with small males. Significant variation in egg viability was present across all treatments (Fig. 2b).

DISCUSSION

The results revealed that in the case of coerced first matings, the time to commence mating was shorter when the females were coerced by large males. The mating duration was not affected by the male body size and the fecundity and percent egg viability were significantly influenced by the body size of the coercive males.

The delay in time to commence first mating in coercive treatment that coercion imposes fitness costs on females, leading to heightened resistance. Similar responses occur in female *Drosophila melanogaster*, where early mating rejection is common post-eclosion to avoid costs that could limit reproductive success over their lifetime (Manning, 1967). Age and sexual maturity significantly influence mating behaviour in insects, including ladybird beetles, with younger, sexually immature females generally resisting mating attempts (De Luca & Cocroft, 2008; Tinzaara *et al*., 2011; Omkar & Mishra, 2009; Omkar & Pervez, 2005). This resistance may be due to the ability of young females to partially control post-mating physiological and behavioural changes, a mechanism observed in several insect species (Omkar & Mishra, 2005; Haddrill *et al*., 2008; Perry & Rowe, 2010). In contrast, sexually mature females are often more receptive to coercive mating attempts, readily accepting mating when ready for reproduction (Omkar & Pervez, 2005). For males, coercive mating with younger, less agile, immature females may enhance their fitness by exploiting this stage of female vulnerability (Seeley, 2010).

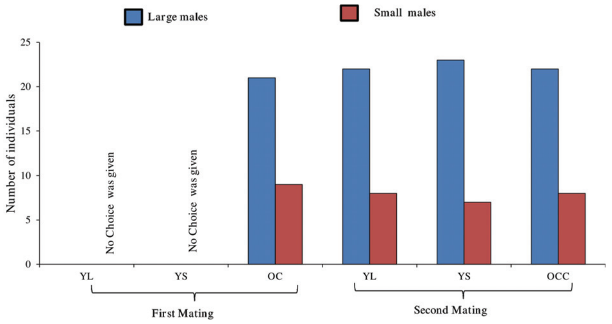

Fig. 3: Mate choice in female *Propylea dissecta* during both first and second coercive matings.

Behavioural observations suggest that young females are more vulnerable than older ones, allowing males to exploit this weakness. These younger females are less agile and slower than older, sexually immature females, making it easier for males to capture and force them to mate. Their ongoing resistance before and during copulations likely accounts for the longer latencies and shorter mating durations compared to those of mature females reported previously. This indicates that female resistance traits serve as a counter-adaptation to male persistence in mating. Despite this resistance, males frequently attempt to mate, possibly to enhance female investment in reproduction. During forced copulations, males may leverage their body mass to overpower females, particularly in restricted environments like laboratory Petri dishes. Successful mating occurs when females become less resistant or when males succeed in overpowering them despite their active resistance.Results from subsequent coercive matings show that the size of the male during the first mating influences the timing of the second mating, as well as the fecundity and egg viability of the females. This aligns with the "winning by losing" hypothesis, where females that capitulated to larger males or chose them in their first mating experienced greater overall offspring production in subsequent matings.

When the earlier coerced females were given the opportunity to choose their mates, the preference was found towards large sized males than small sized males. The mate preference for large sized males by both young and old females during both the first and second coercive matings may probably be attributed to: (1) a competitive advantage over small sized adults (passive mate choice), or (2) distinction between mates made by females (active mate choice). Generally, females discriminate between mates through assessing their body size, which is a major indicator of fitness in most of the cases (Savalli & Fox, 1998; Thompson & Fincke, 2002; Beukeboom, 2018; Ancco Valdivia *et al*., 2020). There are two hypotheses proposed as to how a female discriminatesbetween their mates: the first is the test hypothesis, which states that females assess the quality of a male actively by showing rejection and if the male overcomes her rejection behaviour, she accepts as a mate. The second rape hypothesis suggests that even if the female does not want to accept mating but if the male is strong enough to subdue the rejection of the female, mating occurs (Majerus, 1994a). The frequent contact and mounting attempts made by small males are indicative of their strategy opted under competitive conditions where small males possibly increase their reproductive success by attempting quick matings (Gotthard *et al*., 2007). However, in this study, the rejection shown by the females towards coercive mating attempts by large and small body sized males in this ladybird beetle corroborates with the perception of being choosy and coercion mating attempts reduce females' reproductive fitness modifying their reproductive output, longevity and disturb their physiology. The delay in time to commence mating in establishing second mating is indicative of the fact that coercion is a costly phenomenon. Thus, females used to resist further matings. However, the resistance traits of females and mating preference co-evolve as long as females are able to attain some indirect benefits of mating even when both large and small sized males coerce. The coercive behaviour of males might interfere with the potential indirect benefits that females stand to gain by choosing a particular mate and this, in turn, enhances the female resistance to coercion. Mate recognition in ladybird beetles is known to use tactile cues in mate recognition as indicated by observations of male touching of female antennae, elytra and pronotum with their antennae during courtship (Hemptinne *et al*., 1998; Killian *et al*., 2006; Silk *et al*., 2011). Hodek & Ceryngier (2000) advocated the extension of such studies in coccinellids. The mating behaviour in ladybird beetles has been reported in *Harmonia axyridis* Pallas (Obata, 1987, 1988; Obata & Hidaka, 1987), *Coccinella septempunctata* Linnaeus (Omkar & Srivastava, 2002), *Coccinella transversalis* Fabricius (Omkar & James, 2005), *P. dissecta* (Omkar & Pervez, 2005) and *Coelophora saucia* (Mulsant) (Omkar & Singh, 2010). However, females may modulate their resistance based on the features of pursuing males. These features may or may not be identical to the ones used by sexually mature females to assess males. These findings altogether indicate males' willingness to mate and low mating propensity by the young females. In second coercive matings, female mating duration varied insignificantly between the treatment and females appear to prefer large males as mates in all treatments, including both young and old females, can be interpreted as forced copulation is a condition-dependent alternative mating strategy. These findings are in accord with the previous studies suggesting that sexual coercion as an alternative mating strategy (Dawkins, 1980; Cheng *et al*., 1983; Mineau *et al*., 1983; Andersson, 1994; Clutton-Brock & Parker, 1995; Alcock, 2009; Conroy & Gray, 2014). However, small males appear to be more persuasive for matings than large males. The more frequent attempts by small males could be due to their early emergence, greater agility, more rapid movements, efficient persuasion for mates, attempts to optimize mating success even through females' preference were for large males (Singer, 1982; Bulmer, 1983). Female fitness and reproductive success might increase with the male body size female mated with even in coercive conditions. The reduction in mating duration was recorded in second coercive mating that could be the result of the females obstruction through walking and kicking, while the males were copulating and making continuous attempts this might also result in reduced mating durations, as recorded in the coercive matings. The mating duration is assumed to be under males' control as reported in many insect species too (Yasui, 1994; Bretman *et al*., 2013). Thus, it is possible that the males responded to the females' resistance by terminating the matings early. Similar findings have been reported in the bean weevil, *Callosobruchus maculatus* (Crudgington & Siva-Jothy, 2000). Females may also diminish the costs of coercive matings by exercising mate choice in subsequent mating opportunities. In odonates, male harassment had a negative impact on female fitness (Ubukata, 1984; Waage, 1987), that males have the potential to coerce females and that forced copulations indeed occur (Cordero, 1999). Thus, males practice it as a condition dependent strategy to gain more reproductive fitness. The young females produced fewer eggs than old females. The likely reason for this difference is that the young females are not physiologically prepared for mating and egg laying by the frequent copulatory attempts (Moshitzky *et al*., 1996; Shahid *et al*., 2016), and this can be beneficial for males. For females, having offspring fathered by a male they did not choose, may incur additional costs, which might include injuries, reduced survival, mating success and limit or delay the reproductive output. Injuries caused by forced copulation have been documented in many species (Mineau *et al*., 1983; Thornhill & Palmer, 2000; Arnqvist & Rowe, 2005a) resulting in a reduction in female reproduction. Previous studies have indicated that early egg laying in females can be costly, potentially leading to reduced fertilization rates, lower offspring numbers, and diminished offspring quality later in life. In this study, females were not provided with food between matings, limiting their available resources for reproduction. As a result, females may incorporate nutrients from male ejaculates into their somatic and reproductive tissues for maintenance (Bownes & Partridge, 1987; Pitnick & Markow, 1994; Ravi Ram & Wolfner, 2007), which could further restrict their reproductive capacity. Consequently, males may strategically influence female receptivity to enhance their chances of fathering offspring.

An increase in fecundity following the second mating may result from mating with larger males, as these males are likely transfer a greater amount of nutrients through their ejaculates. The size of the male during the first mating significantly impacts female fecundity, as size disparity often drives fecundity selection favouring larger males (Darwin, 1871; Ghiselin, 1974; Honek, 1993; Deb *et al.*, 2012, Uzma & Omkar, 2017). However, while there are benefits to mating with larger males, females may also incur costs, such as reduced mobility, interference with feeding and egg-laying activities, and disruptions to their normal physiology. Increased reproductive output may also suggest cryptic female choice, as previously reported in ladybird beetles (Carbone & Rivera, 1998; Tallamy *et al.*, 2002). Therefore, these findings could have significant evolutionary implications regarding the effects of coercion and male size on female reproduction.

Percent egg viability varied significantly across all treatments of coercive matings. Females are likely to benefit most from mating with large males in good condition due to the increased nutrient supply (Oberhauser, 1988) or the potential for higher fitness in their offspring (Charlesworth, 1987), resulting in greater egg viability. Previous studies have demonstrated a positive correlation between male size and egg viability in insects (Yadav *et al.*, 2010), including ladybird beetles (Bista & Omkar, 2013). Females subjected to double coercion laid more viable eggs, likely due to receiving larger amounts of ejaculates. It is noteworthy that most of these females were mated to larger males, suggesting a preference for larger body size, which could enhance egg viability through cryptic female choice. This phenomenon plays a significant role in post-copulatory processes among ladybird beetles (Kaufmann, 1996; Ransford, 1997; Carbone & Rivera, 1998).

Consequently, males may benefit from coercive matings while employing condition-dependent mating strategies. These findings align with previous research on coercion as an alternative mating strategy (Dawkins, 1980; Cheng *et al.*, 1983; Mineau *et al.*, 1983; Andersson, 1994; Clutton-Brock & Parker, 1995; Alcock, 2009; Conroy & Gray, 2014) and the female preference for larger males (Andersson, 1994).

In conclusion, the results suggest that coercive mating play an important role in sexual selection mechanisms related to internal fertilization, acting as an alternative tactic for competitively inferior males to enhance their reproductive success. Importantly, the findings indicate that female roles are not passive; the conflict between sexes fosters complex sexual selection dynamics. Coercive mating with large males, followed by subsequent mate choice, enhances reproductive success in ladybird beetles, while initial coercion by smaller males may reduce fecundity and egg viability, indicating that female mate choice after coercion compensates to optimize reproductive outcomes.This study is the first to investigate sexual coercion in ladybird beetles, an important step toward understanding how forced mating behaviors impact female reproductive strategies, mate choice, and the evolutionary dynamics of sexual conflict in this ecologically significant group.

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