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ORIGINAL ARTICLE

Does Large Body Size in Males Facilitate Coercive Mating? A Study in *Propylea dissecta* Mulsant (Coleoptera: Coccinellidae)

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ABSTRACT

Coercive mating, where males force copulation despite female resistance, is a common reproductive strategy in many species. But there is no such studies on Ladybirds so far. The current study aims to examine how male body size influences coercive mating and its subsequent effects on female reproductive success in *Propylea dissecta*. Specifically, the study tests the hypotheses that smaller males are more likely to engage in coercive mating, that females mated by smaller males will take longer to initiate second matings, and that fecundity will be reduced in females mated by smaller males due to the energy expended in resisting harassment. In this experiment, young female beetles were paired with either large or small males in no-choice mating combinations. After the first mating, females were allowed to remate with either a large or small male, and mating behaviour, reproductive parameters (fecundity and egg viability), and offspring development were recorded. The results indicated that females paired with smaller males took longer time to commence both first and second matings, and their fecundity was significantly reduced, though egg viability was unaffected. The findings suggest that coercive mating is more costly for females, with smaller males being more persistent in their attempts to mate, despite being less competitive in size. Larger males, on the other hand, demonstrated a clear advantage in coercive mating scenarios, as females paired with them commenced mating significantly faster and exhibited higher fecundity compared to those paired with smaller males. This study highlights the significance of male body size in shaping mating dynamics and sexual selection in ladybird beetles.

KEY WORDS: Sexual selection, coercive mating, ladybird, mating, reproductive parameters

INTRODUCTION

Sexual selection is an evolutionary process that favours traits enhancing an individual's chances of mating success. It often shapes distinct characteristics, such as body size or behaviour, which play a critical role in reproductive success. Female preferences, however, can vary widely between species, with some selecting males based on traits, like symmetry (Santos, 2001; Beck & Pruett, 2002) or vigour (Shuker *et al.,* 2002). Males, on the other hand, frequently compete for female attention and, in some cases, adopt coercive mating strategies. Such behaviours often arise from female reluctance to mate with certain males, resulting in sexual conflicts between the sexes (Gavrilets *et al.,* 2001; Arnqvistand Rowe, 2002).

Forced copulation, is a potential outcome of the conflict between males and females arising from sexual selection. In some species, it plays a role as significant as mate choice or male competition in determining reproductive success for both sexes (Markow, 2000; Brennan & Prum, 2015). This male reproductive strategy has been observed across a wide range of taxa, including nonhuman primates and other mammals (Cunningham *et al.*, 2015), vertebrates, such as fish (Pilastro *et al.*, 2003; Bisazza *et al.*, 2001; Bertram *et al.*, 2015), reptiles (Gogliath *et al.*, 2010; Moldowan *et al.*, 2020), and birds (Low, 2004; Low *et al.*, 2005; Adler, 2010), as well as invertebrates, like molluscs (Allen *et al.*, 2017) and insects (Markow, 2000; Cordero & Andrés, 2002; Eberhard, 2002; Vahed, 2002; Dukas & Jongsma, 2012a).

There is increasing interest in understanding the costs borne by females due to forced copulations and the strategies they adopt to counteract male coercion (Pilastro

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*Corresponding author email: omkar.lkouniv@gmail.com *et al.*, 2003; Dukas & Jongsma, 2012b). In coercive matings, males often employ tactics, such as manipulation, harassment, intimidation, or physical harm to overcome female resistance. Body size is a significant quantitative trait that is continuously shaped by evolutionary forces (Borgia, 1979). It has a profound influence on an organism's fitness and is frequently modified by environmental conditions (Schmidt-Nielsen, 1984). In the context of sexual selection, male body size often evolves due to female preferences or competition among males (Dugatkin & Godin, 1998). In many species, larger males tend to achieve greater mating success, and female preference for larger body size is particularly prevalent in insects (Choe & Crespi, 1997). Larger males often have an advantage in forced copulation, as they are more likely to overcome female resistance, either through physical dominance or by harassing females more persistently (Eberhard, 2002; Eberhard & Cordero, 2003). Conversely, smaller males may succeed by being less conspicuous, giving them a stealth advantage in approaching females.

Male size relative to female size is a significant factor influencing mating success, with larger males often dominating access to high-quality females, especially in dense populations. However, this dominance can be costly for females, as larger males are more persistent and capable of imposing higher costs. These costs may include (i) increased energy expenditure, (ii) reduced feeding time, (iii) limited access to higher-quality food, (iv) physical injuries, (v) increased vulnerability to predators, (vi) decreased reproductive output, and (vii) reduced ability to recognize environmental cues (Rossi *et al.*, 2010; Köhler *et al.*, 2011; Reinhardt *et al.*, 2015). Consequently, females adjust their mating rates to mitigate these costs and balance the detrimental effects of male persistence.

Females typically resist forced mating attempts but often cooperate once successfully overpowered by males, even if not fully sexually mature, suggesting that resisting male coercion may be costlier than accepting mating (Thornhill & Alcock, 1983). The intensity of female resistance varies with male quality; larger males face less resistance, as they may offer benefits to females (Ryan *et al.*, 2001), while smaller males are often more persistent and harassing. To mitigate these costs, females actively resist mating attempts, as observed in arthropods (Allen & Simmons, 1996; Lauer *et al.*, 1996; Crean *et al.*, 2000). This resistance may serve to avoid excessive matings or to screen for high-quality mates (Chapman *et al.*, 2003; Eberhard, 2002; Cordero & Eberhard, 2003). Traits that enable males to overcome female resistance are likely to be favoured by sexual selection.

Ladybird beetles (Coleoptera: Coccinellidae) have been extensively studied for traits, such as body size, development, mate choice, and reproduction (Perry *et al.*, 2009; Dubey *et al.*, 2016). However, this group has not previously reported the phenomenon of coercive mating. While females generally prefer larger males due to potential fitness benefits (Dubey *et al.*, 2016), behavioural observations suggest that smaller males may employ persistence and harassment tactics to achieve copulation, which could negatively impact female reproductive success.

In *Propylea dissecta*, mating occurs soon after emergence, even with females that possess unhardened elytra and incomplete pigmentation, though previous studies indicate that males are often unresponsive to such females in other species due to their lack of pigmentation and incomplete development (Majerus, 1994b). Male physiological readiness and age play crucial roles in mating dynamics, with middle-aged males (20-30 days old) being particularly efficient in recognizing and mating with females (Mishra & Omkar, 2004, Pervez & Omkar, 2005). Interestingly, male persistence and coercion have been observed in other insects as strategies to overcome female resistance, often leading to decreased reproductive output and egg viability in females due to increased energy expenditure, physical injuries, and harassment. While coercive mating strategies are well-documented in other taxa (McLain & Pratt, 1999; Pilastro *et al.*, 2003; Muller *et al.*, 2007), this remains an unexplored aspect of ladybird beetles. The current study hypothesizes that coercive mating in *Propylea dissecta* is influenced by the body size and age of males. The study tests three key hypotheses: first, smaller males are likely to engage in more coercive mating attempts, despite being relatively inferior to larger males. Second, the time taken for females to initiate a second mating is expected to be negatively correlated with the size of the males in the first mating. Lastly, it is hypothesized that fecundity will be reduced in

Table 1: Mann Whitney U test and Paired sample t-test analyses showing the effect of male body size on mating performance in *Propylea dissecta*

	Time to commence mating (in minutes)	Mating duration (in minutes)
U Value; Z Value; P-Value	U=1002.5; Z=-4.196; P <0.0001	–
t Value; P-Value; df	–	t=-1.38; P=0.172; df=1, 107

Table 2: Two way ANOVA and Friedman test analyses showing the effect of male body size on mating and reproductive parameters post second mating in *Propylea dissecta.*

Analyses	Time to commence mating (in minutes)	Mating duration (in minutes)	Fecundity (no.of eggs laid)	Egg viability (%)	Total development period (in days)
F $_{\text{First mating male size}}$ (P-Value); df	F=2.47 (P = 0.118); 1,119	---------	---------	--------	---------
F $_{\text{Second mating male size}}$ (P-Value); df	F=69.58 (P<0.0001); 1,119				
F $_{\text{First mating male size} \times \text{Second mating male size}}$ (P-Value); df	F=1.13 (P=0.289); 1,119				
χ^2 Value; P-Value; df		χ^2=1.818;P=0.611; df = 3, 117	χ^2=50.96;P<0.0001; df = 3, 117	χ^2=5.08;P=0.166; df=3, 117	χ^2=83.88,P<0.0001, df=3, 117

females that were first mated by a smaller male, likely due to the energy expended in resisting harassment.

MATERIALS AND METHODS

Experimental model

Propylea dissecta is an aphidophagous ladybird beetle that is quite common in the agricultural and horticultural landscapes of India, preying commonly on aphids, *Aphis gossypii* Glover and *Aphis craccivora* Koch (Omkar & Pervez, 2000a).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 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 then placed (abiotic factors as above) in BOD incubators (Yorco Super Deluxe, YSI-440 New Delhi, India). The pairs were checked daily for the number of eggs laid. 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). The adults were taken from this stock only to perform experiments.

Experimental Protocol

For the experiment, young females of 18 hours old were chosen and were subjected to coercive mating with a male of 20 days. The young females were subjected to mating with large and small males in no choice combinations. The mating combinations were: (i) Young ♀ × large ♂, and (ii) Young ♀ × small ♂. Post-termination of their first mating; each treatment was divided into two groups. The first group was allowed to mate again with the new large sized males while the second group was allowed to mate with small sized males. After the termination of the second mating, males and females were separated. The mating behaviour, which includes contacts involving frequent touch, running, moving apart, mounting, elytral fanning and establishment of mating was observed. The pronounced rejection behaviour, which involves shrinking the abdomen, retracting legs and making the body round, circling motion in one place and kicking was also observed. Mating parameters, such as time to commence mating (from the cohabitation to mounting on female) and mating duration (time from intromission until dismounting) were recorded. Reproductive parameters including fecundity (number of eggs laid) and percent egg viability (number of eggs hatched ×100/ number of eggs oviposited) were recorded for the next 10 days. The females were checked for egg laying at each 24 hours and the number of eggs was counted and marked; and females were placed in new Petri dish of the same size with the *ad libitum* food for the

Table 3: Paired t-test showing the comparative output of mating parameters during first and second mating in *Propylea dissecta.*

Mating Treatments	Time to commence mating (in minutes)	Mating duration (in minutes)
t Value; (P-Value); df	t = -2.65, P = 0.009; df =1, 107	t = 3.77, P < 0.0001; df =1, 107

next 24 hours. This was repeated until the tenth day of oviposition. Each Petri dish was properly marked and the number of eggs was counted and checked for viable eggs. The development duration of offspring from each treatment was also recorded and analyzed. Each treatment was replicated 30 times.

Statistical Analysis

Data on 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. The data of time to commence first coercive mating and second mating and mating duration (1st mating) were found normally distributed, while the data on mating duration (2nd mating), fecundity and percent egg viability were found to have non-normal distribution.

The data on time to commence mating, recorded during the first mating, were subjected to Mann Whitney U test while the data on mating duration of the first mating were subjected to a two-sample t-test. Data of time to commence mating recorded from the second mating were subjected to two-way ANOVA. Data of mating duration, fecundity, percent egg viability and total development duration were subjected to the Friedman test. The comparison of pooled data of time to commence mating and durations of first and second coercive matings were subjected to paired t-test. All statistical analyses were conducted using SPSS statistical software (version 20.0, SPSS Company, Chicago, USA).

RESULTS

Effect of male body size on mating and reproductive performance

The time to commence mating was significantly affected by male body size (U = 1002.50; Z = -4.196; P < 0.0001; Table 1) during their first coercive mating. The results showed that females paired with smaller males took significantly longer to commence mating compared to those paired with larger males. However, when the females were given second coercive mating male body size had a

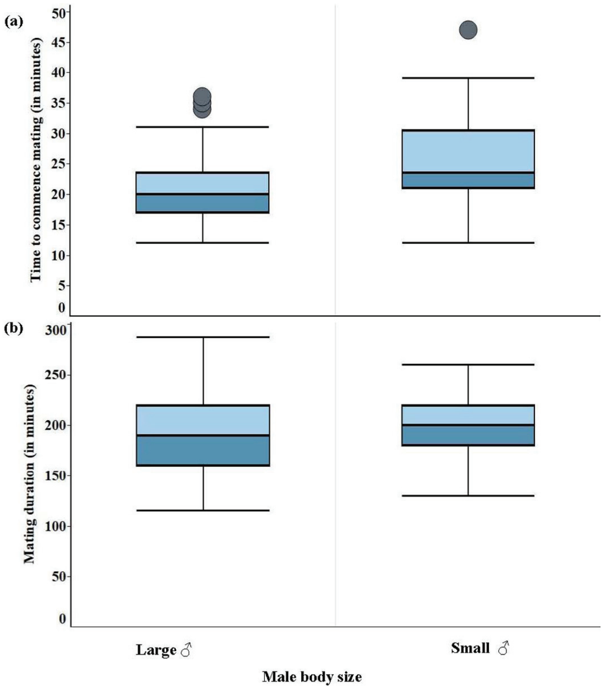

Fig. 1. Box and Whisker plots showing the effect of male body size on (a) time to commence mating, and (b) mating duration in *Propylea dissecta.* The center horizontal line is drawn at the median. The vertical lines extending from the boxes are 1.5 times the length of the box. Circles represent outliers.

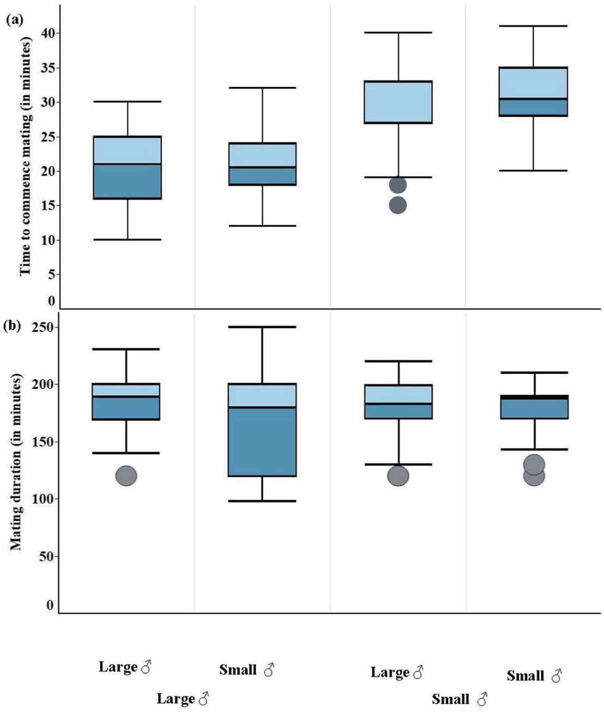

Fig. 2. Box and Whisker plots showing the effect of male body size during second mating on (a) time to commence mating, and (b) mating duration in *Propylea dissecta.* The center horizontal line is drawn at the median. The vertical lines extending from the boxes are 1.5 times the length of the box. Circles represent outliers.

significant effect (F = 69.58; P <0.0001; df = 1, 119) on time to commence mating. The interaction among both these factors was found to be insignificant (F = 1.13; P = 0.289; df = 1,119; Table 2). The pairs involving smaller males took the longest time to commence mating in both mating treatments, while pairs with larger males recorded the shortest time. Females that experienced their first coercive mating with smaller males took significantly longer to establish second matings, a trend not observed in females that mated with larger males (Figures 1a and 2a). These findings align with our hypothesis that mating with smaller males is more taxing for females, likely due to increased harassment.

The mating duration was, however, not significantly (T = -1.38; P = 0.172; df = 1,107; Table 1) affected by male body size during the first coercive mating. When females were allowed to mate with small sized males, they mated for a longer duration than large sized males in the first coercive mating. During second coercive mating, males show a decline in their mating duration. The mating duration was affected insignificantly ($\chi^2 = 1.818$; P = 0.611; df =3, 117; Table 2) when a second opportunity was given to males to mate in no-choice conditions. The longer mating duration was found in the pairs where females mated with large males during both matings. Both coercive matings were around 190 minutes while normal matings of similar aged sexually mature adults continue for around 250-300 minutes indicating either lesser energy to continue mating in smaller males or earlier termination by females or a limit on mating duration (Fig. 1b, 2b).

Fecundity was significantly affected by male body size ($\chi^2 = 50.96$; P < 0.0001; df =3, 117; Table 2). The higher fecundity was recorded in the pairs that included larger males in both the coercive matings and the lowest fecundity was recorded in the pairs where a large male mated in first mating and a small male during the second mating (Fig. 3a). The effect of body size on the first mating male was evident as females mated with small sized males during their first coercive mating laid a smaller number of eggs than females mated with large sized males.

The percent egg viability was found to be affected insignificantly ($\chi^2 = 5.08$; P = 0.166; df =3, 117; Table 2) by the male body size. No significant difference was observed among all treatments given in this experiment (Fig. 3b).

Comparative analysis of mating parameters during first and second mating

The comparative analysis of data shows male body size had a significant (T = -2.65; P = 0.009; Table 3) effect on time to commence mating. The results revealed that when the males were allowed to a second coercive mating; they took longer time to commence mating than the first coercive mating. The result shows that during the first coercive mating, the individuals mated for a longer duration than the second coercive mating. Thus, the individuals in the first coercive mating established mating earlier and mated for a longer duration (Fig. 4a, 4b). The comparative analysis of mating duration was also affected significantly (T = 3.77; P < 0.0001; Table 3) by the male body size.

Effect of male body size on offspring total development duration

The results revealed that male body size had a significant (χ^2= 83.88, P < 0.0001, df = 3, 117) effect over offspring development duration. Longer offspring development duration was observed where young females mated with the small sized males and shorter development duration was found when females were allowed to mate with larger males (Fig. 5).

DISCUSSION

The current study found that smaller males took longer to commence mating during both the first and second matings. The size of the first male also influenced the time to commence the second mating, while mating duration was not affected by male size. Additionally, female fecundity and egg viability were significantly impacted by the size of the mating males.

The increase in time to commence mating by small sized males is likely due to increased harassment by smaller males than larger males. The current findings also indicate that males do not have full control over the mating outcome, a pattern that has been observed in previous studies (Fedorka & Mousseau, 2004; Bretman *et al.*, 2013). Males are expected to attempt to mate indiscriminately and persistently to maximize their reproductive success, while females are expected to avoid superfluous matings showing resistance towards mating. Smaller males were more likely to attempt forced copulation in *P. dissecta;* probably suggests that forced copulation might be a condition dependent alternative mating tactic used by small males (Dukas, 2006). The result also revealed that the time to commence the second mating was affected by the size of the first mated male with the female. In this condition, the large males were likely to have a size advantage in their endeavours, as they were more vigorous courters and forced female cooperation. While the small males exhibited more sneak, persistent and persuasive behaviour towards females to combat reproductive success (Malamuth *et al.*, 2005; Watters, 2005). If so, the female mating rate is expected to be plastic and to co-vary with the male ability to copulate. Thus, females might modulate their resistance and that may alter the relative costs and benefits of mating. Here one possibility is that females adjust their mating rate to balance the costs imposed by male harassment. Harassment of females and coercive mating occur in many organisms (McLain & Pratt, 1999; Pilastro *et al.*, 2003; Muller *et al.*, 2007), but they are typically mediated by brute force associated with larger male body size.

The longer mating durations with large males demonstrate that the influence of size appears to be particularly important when mating is costly. Prior to or during mating energy is spent on various aspects of mating, *viz.* to search for an individual or to avoid undesirable mates, mating opportunities, predation, injury, reduction in harassment and persistence of matings (Pilastro *et al.*, 2003; Muller *et al.*, 2007). Thus, the body size of male mates is possibly of prime importance in combating costs and providing more benefits. Another benefit that may be important to females is the male nutrient donation; Oberhauser (1997) suggested that an increase in female lipid reserves is *via* the transfer of male derived nutrients. Further longer matings with larger males might not only be to avoid sperm competition (Alcock, 1994) but also result from a female strategy to avoid additional male harassment (Rowe *et al.*, 1994; Ryan *et al.*, 2001).

Female reluctance to mate is dependent on the costs associated with mating (Thornhill & Alcock, 1983; Rowe *et al.*, 1994). The females resist matings by fast movement, kicking away the male with their hindlegs, curving abdomen, stridulating, running and even biting the male. The females were successful in dislodging the male before accepting the copulation. Three alternative hypotheses may account for this kind of display behaviour: (i) large males may mate more frequently with females, because of either female choice, male aggressiveness, or male life span (*e.g.* large males may mate more often as they live longer) (Maciel-de-Freitas *et al.*, 2007; Cator *et al.*, 2010), (ii) males persistence increases male reproductive success at the expense of costs associated with persistence, such as high predation risk (Rowe, 1994) and reduced foraging time (Robinson and Doyle, 1985), and (iii) females suffer costs of mating but must balance this with the direct cost of expressing (Clutton-Brock & Parker, 1995). The large size of females may also be favoured because it reduces sexual harassment by males. These alternative hypotheses are not mutually exclusive. Some workers have suggested that

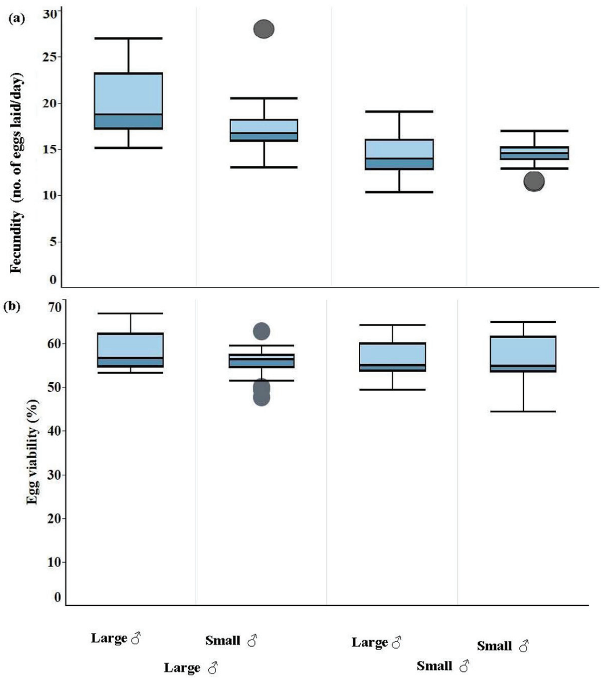

Fig. 3. Box and Whisker plots showing the effect of male body size post second mating on (a) fecundity, and (b) percent egg viability in *Propylea dissecta.* The center horizontal line is drawn at the median. The vertical lines extending from the boxes are 1.5 times the length of the box. Circles represent outliers.

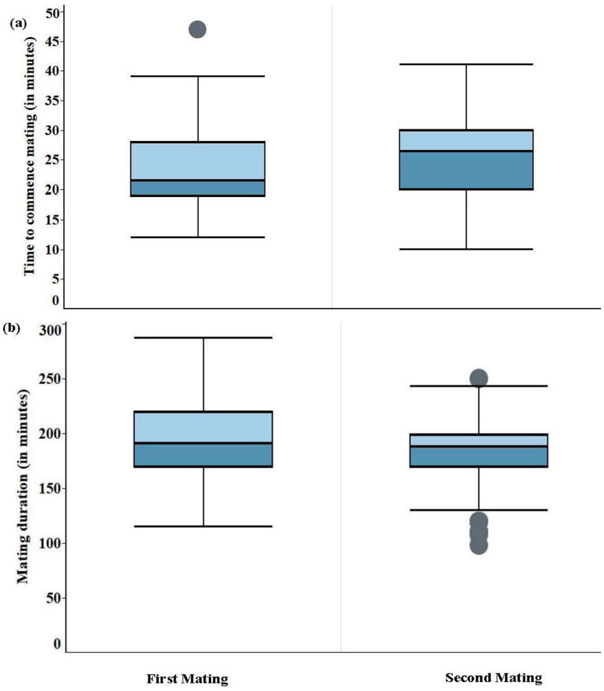

Fig. 4. Box and Whisker plots showing the comparison of (a) time to commence mating, and (b) mating duration between first and second mating in *Propylea dissecta.* The center horizontal line is drawn at the median. The vertical lines extending from the boxes are 1.5 times the length of the box. Circles represent

small males, being relatively inconspicuous and more agile, may be more successful than larger males by using this tactic, they use to compensate for their mating success (Hughes, 1985; Pilastro *et al.*, 1997). One important complication with forced copulation is that the smaller and weaker females are less able to resist forcible insemination than most other females within the population. Therefore, they are less likely to reproduce and more likely to produce smaller or less viable offspring. Thus, the ability to forcibly inseminate females may not increase the number of offspring that a male sires as much as it enhances the number of copulations that a male obtains. Females often struggle against submission by males and sometimes escape or run before genital contact occurs. By resisting the males during mating, the females perhaps reduce the mating duration and as a result receive less sperm and other accessory stimulants. Because both sperm and accessory gland proteins in the seminal fluid influence a female's propensity to remate and reproduce (Gromko *et al.*, 1984; Ram & Wolfner, 2009). Thus the females' resistance could increase their propensity to remate with a male of their choice once they reach sexual maturity.

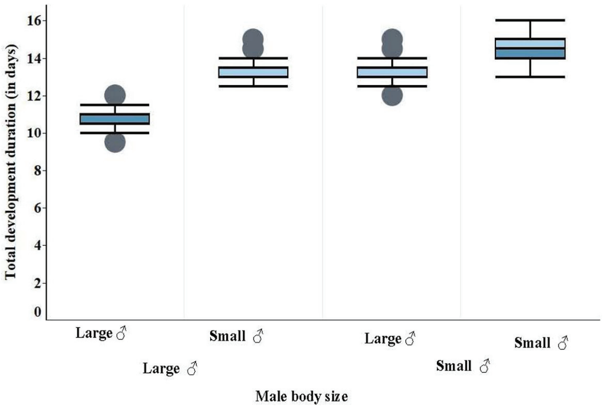

Fig. 5. Box and Whisker plots showing the effect of male body size post second mating on total developmental duration in *Propylea dissecta.* The center horizontal line is drawn at the median. The vertical lines extending from the boxes are 1.5 times the length of the box. Circles represent outliers.

Results revealed that female fecundity is dramatically affected by male body size because ejaculate size is positively correlated with male body size. Male body size is also correlated with the hormonal stimulants or other accessory proteins that stimulate egg laying and potentially influence the egg size, (Stanley-Samuelson & Loher, 1986; Parrott *et al.*, 2006). In the heteropteran, *Neacoryphus bicrucis*, sexual coercion lowered female fecundity (McLain & Pratt, 1999) possibly on account of the energetic costs of female fleeing and resisting to mate. Females are generally assumed to prefer larger males with dominant and competitive abilities. There are, however, alternatives to direct female choice that deserve consideration. In some insects, the large body size is positively related to their fighting ability (Alcock, 1996; Zuk & Simmons, 1997), high energy and other resource reserves (Bangham *et al.*, 2002; Ponlawat & Harrington, 2007). The success of large males may also be attributed to their superior strength and stamina conferring an ability to mate frequently by coercion. Additionally, large males may produce larger sized ejaculates and this could be advantageous in total sperm storage. As expected fecundity was much less in the case of mating with small males and the effect of body size of the first mating male is also evident here. This could be indicative of one of two things: (i) the smaller males harass more, causing females to resist more leading to high energy expenditure, thus decreasing the female fecundity, and (ii) small males could be providing lesser benefits via accessory gland proteins. Cryptic female choice could also have a role to play here and the other possible alternatives include the fecundity advantage of large females are: (i) the advantage of early maturation in males (Bisazza, 1993), (ii) a reduced growth rate of males as a consequence of the intense sexual activity, and (iii) an energetic advantage of small males in locomotion (Blanckenhorn *et al.*, 1995). Thus, forceful insemination might favour larger body size in males because of advantages in mate quality as well as the number of matings. Additional data are needed to clarify the relative fitness benefits accruing from forcible insemination versus matings driven by female reproductive success and choice.

Percent egg viability did not differ significantly as coercive mating might be an alternative mating strategy by males (Gross, 1996) to optimize reproductive success. Females may be choosing good parenting genes if there is a negative genetic correlation between the genes that influence the male size and the genes that influence the quality as the cryptic female choice suggested in many previous studies in insects (Andrés & Rivera, 2000; Edvardsson & Göran, 2000; Albo *et al.*, 2013). There may also be a direct benefit to selecting small males. Unfortunately, larger body size may be commonly linked to performance in a wide variety of fitness-relevant tasks, so this issue cannot be ignored. Disentangling the relative importance of the fundamentally different pathways, *i.e.* female mate choice, male-male competition and forced copulation by which larger body size males enhance their mating success remains an important challenge for future work. Such systems are unquestionably complex and deserve considerably more attention to comprehend the mechanisms of sexual selection and other factors influencing male reproductive success. The effect of male body size on the developmental duration of offspring could be ascribed to better genes (Kokko *et al.*, 2006). Larger ejaculates by larger males with more numbers of sperm (Bissoondath & Wiklund, 1996), and more nutrients *via* accessory gland proteins (Avila *et al.*, 2011) probably enhance the offspring's fitness. Previous studies support our finding that offspring fitness may also change based on differential investment in eggs by females in response to variation in male quality (Cunningham & Russell, 2000; Prokop *et al.*, 2007) and accessory nutrients provided by them. The results on shorter development duration of offspring sired by large size males are indicative of the possible increased fitness they might have gained through some indirect genetic benefits.

In sum from this study, it can be concluded that: (i) smaller males took longer to establish matings both in the first and second matings, (ii) time to commence second coercive mating was affected by the size of the first male and was higher in those that had mated with smaller males in first mating, (iii) mating duration was not modified by the size of mating males but were recorded shorter than normal mating duration reported earlier, (iv) fecundity was affected by size of mating males, with lesser fecundity observed in females mated with smaller males. However, percent egg viability was not affected by male body size, and (v) offspring from large males developed faster. This study is first attempt in ladybird beetles and suggests that coercive matings appeared more costly to females than males and males gain from forced copulation. Small sized males were more persuasive to females than larger males.

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