https://doi.org/10.33307.entomon.v49i1.1040
ENTOMON 49(1): 75-86
Article No. ent. 49108

Diet and body size modulate the remating behaviour of a predaceous ladybird, *Coccinella transversalis* (Fabricius) (Coleoptera, Coccinellidae)

Mumtaj Jahan[1] and Ahmad Pervez[2*]

[1]*Department of Zoology, Radhey Hari Govt. P.G. College, Kashipur, Udham Singh Nagar 244713, Uttarakhand, India.*
[2]*Biocontrol Laboratory, Department of Zoology, Pt. L.M.S. Campus, Sri Dev Suman Uttarakhand University, Rishikesh 249201, Uttarakhand, India.*
Email: ahmadpervez@yahoo.com

ABSTRACT: The nutritional condition and body size influence the mating and female remating behaviour of a predaceous ladybird, *Coccinella transversalis*. When well-fed males were provided with females of three different dietary conditions, *viz*. (i) well-fed, (ii) food-deprived and (iii) honey-fed, the well-fed ones were most fecund with highest percentage of egg-viability and least preoviposition period and remating refusals, while food-deprived ones showed vice-versa. However, honey-fed females laid unfertile eggs after coercively mating with males, and resisted the most to remate, which gets strengthened in the second mating trial. This indicates females' nutritional condition modulates the females' mating behaviour and post-mating outcomes. The adult body size was directly proportional to reproductive output with heavier females showing high fecundity and percentage of egg viability with least preoviposition period than the lighter ones. Large females resisted the least to remate with larger males than with smaller males, while large males coercively mated with smaller females. Regardless of body-size, the females' remating resistance was enhanced in the second mating trial. Both diet and adult body size modulate the re-mating behaviour of female *C. transversalis*, as the food-deprived and large females greatly resisted to re-mate with smaller males. © 2024 Association for Advancement of Entomology

KEY WORDS: Reproduction, dietary conditions, fecundity, egg viability, aphidophagous

INTRODUCTION

Food gives direction to sexual selection by affecting sexual development, adult phenotype, and reproduction during the early development stage (Richardson and Smiseth, 2019). Both quality and quantity of food affect the growth, development and reproduction, at individual, species, and interspecific levels (Yuan *et al*., 2020). Stressful food conditions may allow adult survival with hampered reproduction (Dmitriew and Rowe, 2007), while an enriched early diet may lead to quantitative and fitter progeny (Li *et al*., 2020). Mating is associated with high energy consumption, where males expend energy in mate-search (Evans, 2003) and ejaculate production (Shandilya *et al*., 2021), while females in egg production (Perry, 2011). Thereby, the females can modify their nutrition acquisition as per the energy demand (Camus *et al*., 2018), sometimes by modulating the mating

---

[*] Author for correspondence

duration during nuptial feeding (Monalisa *et al*., 2020) or by increasing forage that enhances their nutritional state to increase fecundity (Fox and Moya-larano, 2009). As reproduction is affected by the dietary state during adult development, the food-limited environment can reduce feeding potential that directly reduces offspring production with mate choice and remating frequency (Auer *et al*., 2010).

It is widely held that body size influences the reproductive success of predaceous ladybirds (Pervez and Singh, 2013; Singh *et al*., 2021). It indicates individual fitness (Beukeboom, 2018), as larger adults have higher fitness levels (Singh *et al*., 2021). Larger body size also supports sexual coercion (Wallen *et al*., 2016). The female ladybirds mate more though the behavioural resistance towards remating is also prevalent (Obata, 1988; Perry *et al*., 2009; Pervez *et al*., 2022). This female reluctance to remating could be associated with heavy costs, like reduced foraging opportunities (Perry and Rowe, 2015), risk of physical damage (Ronn *et al*., 2007), elevated mortality (Ronn *et al*., 2007; Perry and Rowe, 2015), and increased risk of sexually transmitted diseases (Fiedler and Nedved, 2019). There are also benefits, like improved offspring fitness when potential mates are of high quality (Perry *et al*., 2009), however this female choosiness may create sexual conflict (Burke *et al*., 2021).

Coccinella transversalis (Fabricius) is an aphidophagous ladybird (Coleoptera, Coccinellidae) of the Oriental region with a wide prey range (Omkar and James, 2004) and biocontrol prospects (Michaud *et al*., 2013). It suppresses the population of aphid, *Hysteroneura setariae* (Thomas) (Pervez and Sharma, 2021), and can survive on non-aphid foods during aphid scarcity (Maurice *et al*., 2011). During aphid scarcity, females have pressure to optimally forage (Kindlmann and Dixon, 1993) and males to search for potential mates (Dixon, 2000), which probably depends on body-size. Considering the wide distribution and biocontrol potential of *C. transversalis*, we investigated the influence of dietary conditions and body size on the females' remating and reproductive behaviour.

MATERIALS AND METHODS

Stock culture

Adults of *C. transversalis* were collected from the agricultural fields near the suburbs of Kashipur, India (29.2104° N; 78.9619° E) and brought to the laboratory. They were paired in separate Petri dishes (2.0cm x 9.0cm) containing *ad libitum* quantity of aphids, *Aphis craccivora* (Koch) infested on cowpea, *Lablab purpureus* (L.) twigs. These Petri dishes were then kept in an Environmental Test Chamber (*Remi, Remi Instruments*) maintained (at 25±1°C; 65±5 % R.H.; 12L: 12D photoperiod). The adults mated and the females laid fertile eggs, which were reared from egg-hatch till adult emergence on the above diet, and F_1 virgin adults thus obtained were sexually identified by carefully examining their genitalia under Stereoscopic trinocular (*Lyzer*) and were isolated. These F_1 adults were used in the experiment carried out from 10:00 to 18:00 hours.

(i) Effect of nutritional conditions on female re-mating resistance

To find out the effect of nutritional condition on female resistance towards first and second mating, one hundred individuals of *C. transversalis* were reared from egg-hatch to adult-emergence on a sufficient quantity of *A. craccivora* in hundred Petri dishes (size and prey as above; one larva per Petri dish). After emergence, the adult ladybirds were sexed by carefully examining the genitalia under a spectroscopic trinocular. The newly emerged adult males continued on the same diet. However, the newly emerged females were split into three different groups, *viz.,* (i) excess aphid diet (Food-satiated females), (ii) one-tenth of aphid diet (Food-deprived females) and (iii) non-aphid sufficient quantity of honey-diet for the next five days (Honey-fed females). It is known that adult males and females become sexually mature in less than five days after emergence (Pervez *et al*., 2022). Five -day-old females were paired with respective 5-day-old males fed *ad libitum* aphids in ten replicates (n=10) in dietary statuses. The entire behavioural activities including mating refusal incidences, the time required to commence mating, latent period (*i.e.,* duration between the establishment of genital contact and first mating bout), number of bouts, and mating duration, were observed using stereoscopic trinocular at 40X and 100X magnifications with computer attachment. After the mating was terminated, the adult male and female ladybirds were taken out and kept in different Petri dishes (size and food, as above). These were again paired on the next day to record the same parameters in the second mating trial. Thereafter, the females were isolated in Petri dishes (size and food, as above) and monitored for oviposition for the next five days to record their pre-oviposition period, fecundity, and percent egg viability.

(ii) Effect of adult body size of both sexes on the female re-mating resistance

To find out the effect of small and large adult body size on the mating behaviour and refusals, the adult males and females were isolated in the Petri dishes (size as above) containing *ad libitum A. craccivora* infested on the twigs of *L. purpureus* immediately after emergence. Thereafter, these adults were weighed using an electronic balance (*SHIMADZU*, Model ATX-224 at 0.1mg precision) and segregated into two categories (small and big) in accordance with their body size (*i.e.* large female ~ 27.0–28.0mg, small female ~ 17.0 - 18.0mg, large male ~ 20.0 – 21.0mg, small male ~ 15.0 – 16.0mg). After 5 days post-emergence, these adults were grouped into four mating-pair groups, *viz*. (i) large male × large female, (ii) large male × small female, (iii) small male × small female, and (iv) small male × large female, and were allowed to mate. The mating behaviour was observed using stereoscopic trinocular, as above and the time of mating commencement, latent period, bouts in copula, mating duration, and steps taken by the adult females showing mating refusals were recorded (space and food as above). The mating pair was isolated if mating did not commence and they were again re-paired at 10:00h on the next day until the mating commenced. After mating was terminated, the adult male and female ladybirds were isolated and again paired on the next day to record the same parameters in the second mating trial. After the two mating trials, the females were isolated and observed for the next five days to record the pre-oviposition period, fecundity, and percent egg viability. The experiment was replicated ten times.

The data of both experiments were subjected to the Kolmogorov–Smirnov test for the normality distribution check and Bartlett's test for the homogeneity of variances using statistical software (SAS 9.0, 2002). The data on mating refusals, mating commencement duration, latent period, number of bouts, mating duration, post-oviposition period, fecundity, and percent egg-viability were subjected to one-way ANOVA and means were compared using Tukey HSD on SAS 9.0 (2002). All the studied mating parameters were further subjected to two-sample t-test using SAS 9.0 (2002) to determine the effect of first and second mating on them.

RESULTS AND DISCUSSION

(i) Effect of nutritional conditions on female re-mating resistance

The nutritional condition during mating significantly affects the female remating behaviour, as the first and second mating commenced earlier by a food-satiated female than food-deprived and honey-fed females with fewer mating refusals (Fig. 1). The honey-fed females mated coercively and longer in first and second trials than satiated and food-deprived females (Table 1). Latent periods varied significantly in both first and second mating trials. Similarly, bouts also varied significantly in first and second trials. The males forcefully tried to mount on food-deprived females and latter responded by frequently bending their abdomens downwards and dislodging the males, thereby displaying refusals. These males moved away after a few attempts (5 -10) and thereafter showed no interest in mating. Food-satiated females exhibited significantly the least number of mating refusals (0.9±1.10) compared to food-deprived (2.1±1.37) and honey-fed (2.2±1.14) females during the first trial. The mating refusals by food-satiated (4.20±1.48), food-deprived (9.10±3.07) and honey-fed (2.2±1.14) females increased significantly during the second trial (Table 1).

Table 1. Mating duration, mating commencement, latent period and bouts in copula of females of *C. transversalis* at different dietary statuses

Mating trial	Nutritional state	Duration (in minutes)	Commencement (in minutes)	Latent period (in seconds)	Bouts (no.)
First	Satiated	18.23±1.8^{b}	2.80±1.14^{b}	3.7±0.82^{a}	238.70±26.80^{a}
	Food deprived	15.62±1.35^{c}	6.60±7.69^{ab}	2.1±1.52^{b}	214.50±14.55
	Honey fed	25.57±1.24^{a}	9.50±5.48^{a}	3.4±1.17^{a}	221.40±7.76^{ab}
Second	Satiated	18.43±2.08^{b}	1.90±1.45^{b}	3.4±1.17^{a}	221.40±7.76 b
	Food deprived	15.06±2.06^{c}	11.90±4.86^{a}	2.30±0.48^{b}	245.60±27.19^{b}
	Honey fed	28.27±1.70^{a}	14.20±3.71^{a}	3.70±0.82^{a}	289.40±25.60^{a}

Data are Mean ± S.D.; Tukey's Range = 3.51; d.f. = 2, 27; Different letters in the column denote that data is significantly different

The mating refusals were significantly greater in second trials in food satiated (t = -5.67; P < 0.0001; d.f. = 16), deprived (t = -6.58; P < 0.0001; d.f. = 12), and honey-fed females (t = -9.25; P < 0.0001; d.f. = 11). Similarly, the mating commencement (t = -2.25; P = 0.040; d.f. = 15) and mating duration were significantly increased in honey-fed females (t = -4.05; P = 0.001; d.f. = 16). However, this increase was not significant in satiated (t = -0.24; P = 0.812; d.f. = 17 and t = 1.55; P = 0.141; d.f. = 17) and in deprived females (t = 0.72; P = 0.480; d.f. = 15 and t = -1.84; P = 0.085; d. f. = 15). The bouts in food-deprived (t = -3.19; P = 0.007; d.f. = 13) and honey-fed females (t = -8.04; P < 0.0001; d.f. = 10) also increased significantly in second trials. The pre-oviposition period of *C. transversalis* after two copulations was significantly shorter in satiated females than food-deprived and honey-fed females. The fecundity and egg viability were significantly greater in satiated females than food-deprived and honey-fed females (Table 2).

(ii) Effect of body weight of both sexes on the female remating resistance

The body size significantly affected the mating to post-mating parameters of *C. transversalis*. The time of mating commencement was greater when smaller males were used in the first and second trials. This time to commence mating in all four mating groups decreased significantly in the second trial. Similarly, latent periods of smaller males were significantly greater in both the first and second mating trials. The latent period in all four mating groups decreased significantly in the second trial. The smaller-sized males and females copulated for significantly longer duration in the first and second trials. However, the number of bouts was significantly greater when larger male and female copulated in both trials (Table 3).

The larger females resisted more to the mating advances of smaller sized males in both first

Table 2. Reproductive output of females of *C. transversalis* maintained at different dietary levels

Nutritional state	Pre-oviposition (in days)	Fecundity (no. of eggs)	Egg viability(%)
Satiated	5.00 ± 0.00^{c}	337.80±8.65^{a}	92.87 ±5.48^{a}
Deprived	5.70 ± 0.48^{b}	110.50±9.70^{b}	82.80 ±5.02^{b}
Honey fed	8.20 ± 1.03^{a}	3.00 ± 1.41^{c}	0.00 ±0.00^{c}

Data are Mean ± S.D.; Tukey's Range = 3.51; d.f. = 2, 27; Different letters in the column denote that data is significantly different

(F=32.02; P < 0.0001; d.f. = 3, 36) and second (F=21.40; P < 0.0001; d.f. = 3, 36) trials as compared to other mating groups (Fig. 2). The first and second mating trials were compared using a two-sample t-test. The mating duration and mating refusals increased, while mating commencement decreased significantly in all four groups of second trials (Table 3). The fecundity (F = 37.41; P < 0.001; d.f. = 3, 36) and percent egg-viability (F = 81.83; P < 0.0001; d.f. = 3, 36) of larger females were significantly greater than those of smaller females, irrespective of male body size (Table 4). Similarly, the pre-ovipositional periods of larger females were significantly (F = 21.60; P < 0.001; d.f. = 3, 36) shorter than those of smaller females, irrespective of male body size.

The nutritional conditions and body size influenced the reproductive behaviour of *C. transversalis*, including the female remating resistance. As expected, well-fed females readily accepted male copulatory attempts, copulated for a longer duration with higher fecundity and egg viability, and least resisted remating during both mating trials. However, food-deprived and honey-fed females took more time in accepting male copulatory attempts, mated for both longer and shorter durations, and resisted more to re-mate with lower fecundity and egg viability. The early mating commencement in well-fed females could be attributed to their satiated condition which makes them highly receptive to copulation, and increases the probability to select potential mates who have better sperm quality with accessory gland proteins and oviposition stimulants that results in better offspring (Albo *et al*., 2012; Mirhosseini *et al*., 2014). On the other hand, delay in mating commencement in food-deprived and honey-fed females indicates females' poor nutritional status hinders the mating process, as courting males need to invest more time and effort (Singh *et al*., 2021).

Food-deprived females copulated for a shorter duration than the well-fed ones, as also reported in a ladybird, *Menochilus sexmaculatus* (Fabricius) (Singh *et al*., 2021). The food conditions during the adult stage exert an impact on reproductive behaviour and restricted food availability could act as a limiting factor by modulating mating duration to its shortest period. Nevertheless, the honey-fed females copulated for a longer duration than the other two females, which indicates their poor nutritional state leading to being easily overpowered and coerced by the males. Under coercive mating with honey-fed females, males modulated mating duration by inflicting themselves upon females and forcing them into copulation resulting in a longer mating duration. As observed in coercive mating,

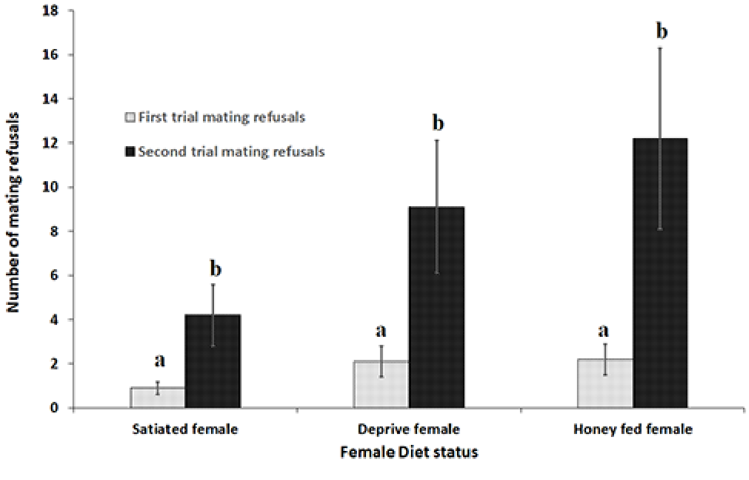

Figure-1: Mating refusals by female, *C. transversalis* during first and second mating trials with respect to the female's nutritional status. Different letters denote that data is significantly different. Data is Mean ± S.D.

Table 3. Mating duration, time of mating commencement and latent period and bouts in copula of *C. transversalis* during first and second mating trials

Mating trial	Combinations	Duration (in minutes)	Commencement (in minutes)	Latent period (in seconds)	Bouts (numbers)
First	Large Male x Large Female	20.85±1.05^{b}	4.90±0.73^{b}	4.00±0.82^{b}	325.40±8.96^{a}
	Large Male x Small Female	17.56±0.73^{c}	4.80±0.63^{b}	3.80±0.92^{b}	322.70±29.96^{a}
	Small Male x Large Female	16.05±0.71^{c}	8.10±1.19^{a}	4.40±0.52^{b}	228.30±5.25^{b}
	Small Male x Small Female	24.64±1.09^{a}	5.20±0.63^{b}	6.20±1.13^{a}	234.10±7.08^{b}
Second Large	Male x Large Female	23.16±0.79^{bc}	2.80±0.63^{b}	3.30±0.67^{b}	329.50±16.26^{a}
	Large Male x Small Female	24.86±1.40^{b}	3.00±0.82^{b}	3.50±0.53^{b}	327.60±5.46^{a}
	Small Male x Large Female	21.55±1.53^{c}	4.40±0.52^{a}	4.90±0.99^{a}	297.30±11.38^{b}
	Small Male x Small	25.70±2.16^{a}	3.50±0.53^{ab}	4.60±0.69^{a}	269.40±52.20^{c}

Data are Mean ± S.D.; Tukey's Range = 3.81; d.f. = 3, 36; Different letters in the column denote significantly difference

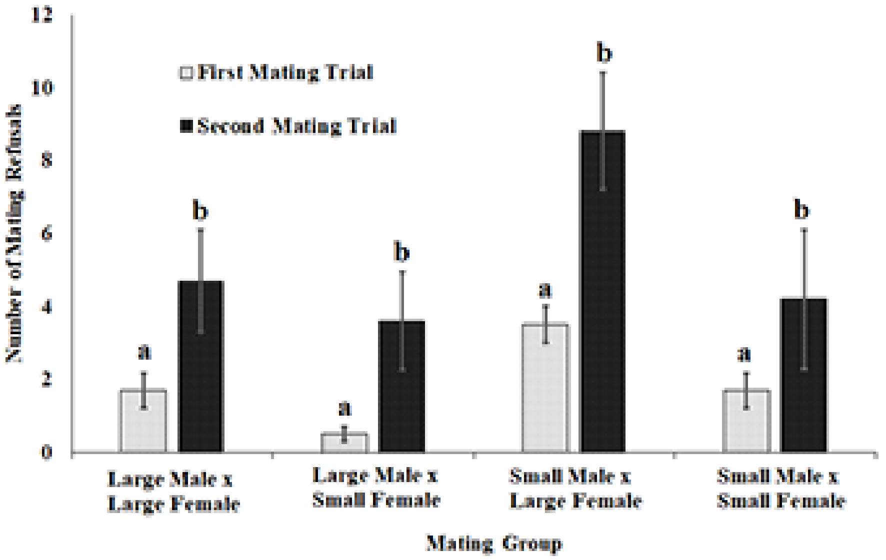

Figure-2: Mating refusals by female, *C. transversalis* during first and second mating trials with respect to the adult body-size. Different letters denote that data is significantly different. Data is Mean ± S.D.

males may harm the females, override their resistance by forced copulation and try to copulate with immature females (Peretti and Aisenberg, 2011). The latent period and bouts in a copula were male dependent and as the dietary condition was only applied to females and males were reared on *ad libitum* food the latent period was almost similar when copulation occurred with females of different dietary conditions under both mating tests. The number of bouts was mating duration-dependent, reported more under longer mating. However, if applied to both sexes the post-emergence nutritional conditions could influence mating performance due to increased latent period resulting in decreased vitality (Agarwala *et al*., 2008).

The findings support the hypothesis that the females under stressful food conditions resist more male copulatory attempts compared to those reared in favourable food condition. This could be attributed to the reproductive costs associated with mating, avoidance of superfluous mating, hindrance in female foraging capacity, increased risk of predation, increased risk of sexually transmitted diseases, and physical damage leading to declining fecundity (Ronn *et al*., 2007; Fox and Moya-larano, 2009; Perry *et al*., 2009). The energy requirements vary in both sexes, as males expend energy in copulatory and pre-copulatory processes, while females invest energy in search of suitable oviposition sites, laying eggs, controlling oviposition timing and using maternal effects to tailor progeny (Sipos *et al*., 2012; Mirhosseini *et al*., 2014) hence lower nutritional state (Perry *et al*., 2009) and sexual immaturity of females (Khan, 2020) also trigger re-mating resistance.

Nutritional status was an important determinant of post-mating response, more fecundity with shorter pre-oviposition and a higher percentage of egg viability were observed when mating was reported in well-fed females. However, the deprived and honey-fed females had a more preoviposition period with lesser fecundity and the lowest percentage of egg viability. The higher energy consumption during the early stage enhances the reproductive capacity and females reared on a favourable diet from egg to adult stage have higher fecundity with more egg hatchability and early oviposition in comparison to the females who had a restricted diet after their emergence (Li *et al*., 2020). The higher hatching success in well-fed females is attributed to the suitable feeding conditions of both sexes, having more available resources to invest in reproduction (Ernande *et al*., 2004). Thus, egg viability is determined by both female nutritional status and male ejaculate quality and quantity with the accessory gland protein (Pervez *et al*., 2004; Perry and Rowe, 2008; Vargas *et al*., 2012; Michaud *et al*., 2013; Singh *et al*., 2016). Reduced fecundity in food-deprived and honey-fed females was attributed to their poor nutrition state negatively affected egg development and oogenesis acceleration (Behmer and Nes, 2003) and showed oosporation by reallocating resources for survival instead of reproduction (Moore and Attisano, 2011). The restricted diet may also limit female reproductive output by decreasing egg number, downregulating immune response, and reducing longevity (French *et al*., 2007; Karl *et al*., 2007) thereby to attain maximum egg viability abundant food conditions should be mandatory for all life stages of an individual. The body size significantly influenced the mating behaviour and female remating refusals. When mating was reported the large males took the least time to commence mating than the smaller males. This shows the effect of (i) mating urge in which large males vigorously court and force females for copulation (Partridge and Farquhar, 1983) and (ii) advantage of large body proportion that provides males higher fitness for more offspring production (Dubey *et al*., 2016). However, smaller males who work more sneakily invest more time in mating attempt thereby their persistence in mating lead females to engage in copulation that increases their reproductive success and produces more offspring (Watters, 2005).

The mating duration was significantly influenced by the body size of the mating pairs. The smaller males mated for a longer duration than large males. The prolonged mating duration in smaller males reflects their lower probability of being selected as mates, investing more time in a mating that for a period reduces the chances of their female partner engaging in copulation with another male and

Table 4. Reproductive output of *C. transversalis* in different mating combinations

Mating combination	Pre-oviposition (days)	Fecundity (no. eggs)	Egg viability (%)
Large Male x Large Female	5.00±0.00^c	333.10±1.66^a	91.89±1.05^a
Large Male x Small Female	5.30±0.48^b	247.20±2.44^b	85.84±2.92^b
Small Male x Large Female	5.00±0.00^c	327.90±1.19^a	90.90±2.20^a
Small Male x Small Female	5.90±0.32^a	241.00±0.82^b	83.40±1.76^b

Data are Mean ± S.D.; Tukey's Range = 3.81; d.f. = 3, 36; Different letters in the column denote significant difference

provides more time to small male for inseminating female with more sperms for fertilizing more eggs leading to enhancing their probability to gain more fatherhood by attaining more offspring assurance (Holwell *et al*., 2016). The longer copulation results in higher male harassing behaviour towards smaller females to engage them in longer copulation (Ryan *et al*., 2001). From the earlier study, it is been known that large males copulate for a longer mating duration (Lupold *et al*., 2011; Pervez and Singh, 2013). However, a shorter mating duration in larger males when they mated with large and small females could be related to their better ejaculate size, higher quality and quantity of sperm with accessory gland products that enhance their post-copulatory reproductive success (Avila *et al*., 2011), thereby the larger males have an advantage over smaller males (Pervez and Singh, 2013).

Multiple matings are common in insects, including ladybirds. The males and females can enhance their reproductive success through multiple mating despite female remating refusals (Obata, 1988; Perry *et al*., 2009; Pervez *et al*., 2020). In the present study, remating resistance was significantly influenced by the body size of both mating partners. This could be associated with the benefits of mating with larger males because (i) large males have higher fitness and give rise to progeny with higher survival success (ii) large males can overcome female resistance by scaring females for further harassment (Pilastro *et al*., 2003; Muller *et al*., 2007). However, the remating resistance occurred more when small males courted large females because the females discriminate the male mating success, though the females mate with smaller males, they still prefer large males for attaining higher reproductive success (Dubey *et al*., 2016). Thereby, the mating success does not solely depend on the males (Bretman *et al*., 2013) though males indiscriminately and persistently attempt to mate for more fatherhood, females show more choosy behaviour and avoid those mating who are superfluous and exert some relevant costs, and this scenario leads to a sexual conflict where the mating rate works as a strong driving force in the evolution of reproductive strategies in both sexes (Rowe *et al*., 2020).

Higher fecundity with a shorter preoviposition period was found when large females copulated than the small females, as also reported earlier (Vargas *et al*., 2012; Dubey *et al*., 2016). Large females provide more space to accommodate developing eggs, have a greater number of ovarioles, and can produce more eggs by allocating more energy resulting in higher offspring numbers (Osawa, 2005; Dixon, 2007; Singh *et al*., 2021). Smaller females were less fecund with a greater preoviposition period and lesser egg viability. Further mating with smaller males reduced their post-mating output because large males under copulation contribute more sperm with accessory gland proteins that stimulate egg production and lead to enhanced fecundity compared to small males (Mirhosseini *et al*., 2014). Thereby, the body size of both sexes shapes the reproductive success in ladybirds not only male size as stated earlier (Bista and Omkar, 2013).

The nutritional conditions and body size modulate the mating behaviour and female remating resistance in *C. transversalis,* and the study suggests that (i) nutritional state post-emergence shapes female reproductive behaviour, (ii) well-fed females have better reproductive output with more fecundity, percentage of egg viability and emit least remating resistance that increases in subsequent matings, (iii) poor nutritional females (deprived and honey fed) emit more remating resistance with a greater preoviposition period, lesser fecundity and percentage of egg viability, (iv) *C. transversalis* shows the size-dependent mating success and both males and females contribute to output, (v) copulation in larger pairs results into more fecundity, a higher percentage of egg viability and emit least remating resistance, (vi) small pairs show lower fecundity with least percentage of egg viability and (vii) large males took advantage of body size and harass smaller females by coercive mating, while large females show more remating refusals when paired with smaller males.

ACKNOWLEDGEMENT

AP is thankful to the Science and Engineering Research Board, Ministry of Science and Technology, Govt. of India, for the financial assistance (EMR/2016/006296).

REFERENCES

Agarwala B.K., Yasuda H. and Sato S. (2008) Life history response of a predatory ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to food stress. Applied Entomology and Zoology 43: 183–189. doi:10.1303/aez.2008.183.

Albo M.J., Toft S. and Bilde T. (2012) Female spiders ignore condition-dependent information from nuptial gift wrapping when choosing mates. Animal Behaviour 84: 907–912. doi:10.1016/j.anbehav.2012.07.014.

Auer S.K., Arendt J.D., Chandramouli R. and Reznick D.N. (2010) Juvenile compensatory growth has negative consequences for reproduction in *Trinidadian guppies* (*Poecilia reticulata*). Ecology Letters 13: 998–1007. doi:10.1111/j.1461-0248.2010.01491.x.

Avila F.W., Sirot L.K., LaFlamme B.A., Rubinstein C.D. and Wolfner M.F. (2011) Insect seminal fluid proteins: identification and function. Annual Review of Entomology 56: 21–40. doi:10.1146/annurev-ento-120709-144823.

Behmer S.T. and Nes W.D. (2003) Insect sterol nutrition and physiology: a global overview. Advances in Insect Physiology 31: 1–72.

Beukeboom L.W. (2018) Size matters in insects–an introduction. Entomologia Experimentalis et Applicata 166: 2–3. doi: 10.1111/eea.12646.

Bista M. and Omkar (2013) Effects of body size and prey quality on the reproductive attributes of two aphidophagous Coccinellidae (Coleoptera) species. The Canadian Entomology 145: 566–576. doi:10.4039/tce.2013.34.

Bretman A., Westmancoat J.D. and Chapman T. (2013) Male control of mating duration following exposure to rivals in fruitflies. Journal of Insect Physiology 59: 824–827. doi:10.1016/j.jinsphys.2013.05.011.

Burke N.W. and Holwell G.I. (2021) Male coercion and female injury in a sexually cannibalistic mantis. Biological Letters 17: 20200811. doi:10.1098/rsbl.2020.0811.

Camus M.F., Huang C.C., Reuter M. and Fowler K. (2018) Dietary choices are influenced by genotype mating status and sex in *Drosophila melanogaster.* Ecology and Evolution 8: 5385–5393. doi:10.1002/ece3.4055.

Dixon A.F.G. (2000) Insect Predator- Prey Dynamics: Ladybird Beetles and Biological Control. Cambridge University Press Cambridge U.K. pp257.

Dixon A.F.G. (2007) Body size and resource partitioning in ladybirds. Population Ecology 49: 45–50. doi:10.1007/s10144-006-0019-z.

Dmitriew C. and Rowe L. (2007) Effects of early resource limitation and compensatory growth on lifetime fitness in the ladybird beetle (*Harmonia axyridis).* Journal of Evolutionary Biology 20: 1298–1310. doi:10.1111/j.1420-9101.2007.01349.x.

Dubey A., Omkar and Mishra G. (2016) Adult body size drives sexual selection mutually in the ladybird, *Menochilus sexmaculatus* (Coleoptera: Coccinellidae). Acta Entomol Sinica 59: 209–218.

Ernande B., Boudry P., Clobert J. and Haure J. (2004) Plasticity in resource allocation based life history traits in the Pacific oyster *Crassostrea gigas*. I. Spatial variation in food abundance. Journal of Evolutionary Biology 17: 342–356. doi:10.1046/j.1420-9101.2003.00674.x

Evans E.W. (2003) Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera:

Coccinellidae): a review. European Journal of Entomology 100: 1–10. doi: 10.14411/eje.2003.001.

Fiedler L. and Nedvìd O. (2019) Fifty shades of the harlequin ladybird and a sexually transmitted fungus. Journal of Insect Science 19: 10. doi.10.1093/jisesa/iez107.

Fox C.W. and Moya-larano J. (2009) Diet affects female mating behaviour in a seed feeding beetle. Physiological Entomology 34: 370–378. doi:10.1111/j.1365-3032.2009.00700.x.

French S.S., Johnston G.I.H. and Moore M.C. (2007) Immune activity suppresses reproduction in food limited female tree lizards *Urosaurus ornatus.* Functional Ecology 21: 1115–1122. doi:10.1111/j.1365-2435.2007.01311.x.

Holwell G.I., Allen P.J.D., Goudie F., Duckett P.E. and Painting C.J. (2016) Male density influences mate searching speed and copulation duration in millipedes (Polydesmida: *Gigantowales chisholmi*). Behavioral Ecology and Sociobiology 70: 1381–1388. doi:10.1007/s00265-016-2145-8.

Karl I., Lorenz M.W. and Fischer K. (2007) Energetics of reproduction: consequences of divergent selection on egg size food limitation and female age for egg composition and reproductive effort in a butterfly. Biological Journal of Linneaus Society 91: 403–418. doi:10.1111/j.1095-8312.2007.00806.x.

Khan M.K. (2020) Female prereproductive coloration reduces mating harassment in damselflies. Evolution 74: 2293–2303. doi:10.1111/evo.14048.

Kindlmann P. and Dixon A.F.G. (1993) Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. European Journal of Entomology 90: 443–450.

Li Y., Wang S., Liu Y., Lu Y., Zhou M., Wang S. and Wang S. (2020) The effect of different dietary sugars on the development and fecundity of *Harmonia axyridis.* Frontiers in Physiology 11: 574851. doi:10.3389/fphys. 2020.574851.

Lupold S., Manier M.K., Ala-Honkola O., Belote J.M. and Pitnick S. (2011) Male *Drosophila melanogaster* adjust ejaculate size based on female mating status fecundity and age. Behavioral Ecology 22: 184–191. doi:10.1093/beheco/arq193.

Maurice N., Pervez A., Kumar A. and Ramteke P.W. (2011) Duration of development and survival of larvae of *Coccinella transversalis* fed on essential and alternative foods. European Journal of Environmental Sciences 1: 24–27. doi:10.14712/23361964.2015.61.

Michaud J.P., Bista M., Mishra G. and Omkar (2013) Sexual activity diminishes male virility in two Coccinella species: consequences for female fertility and progeny development. Bulletin of Entomological Research 103: 570–577. doi:10.1017/S0007485313000199.

Mirhosseini M.A., Michaud J.P., Jalali M.A. and Ziaaddini M. (2014) Paternal effects correlate with female reproductive stimulation in the polyandrous ladybird *Cheilomenes sexmaculata.* Bulletin of Entomological Research 104: 480–485. doi:10.1017/S0007485314000194.

Monalisa, Pervez A. and Jahan M. (2020) Mating behaviour of the predaceous ladybird *Harmonia dimidiata.* European Journal of Environmental Sciences 10: 5–8. doi:10.14712/23361964.2020.

Moore P.J. and Attisano A. (2011) Oosorption in response to poor food: complexity in the trade off between reproduction and survival. Ecology and Evolution 1: 37–45. doi: 10.1002/ece3.4.

Muller M.N., Kahlenberg S.M., Thompson M.E. and Wrangham R.W. (2007) Male coercion and the costs of promiscuous mating for female chimpanzees. Proceedings of Royal Society B: Biological Sciences 274: 1009–1014. doi:10.1098/rspb.2006.0206.

Obata S. (1988) Mating refusal and its significance in females of the ladybird beetle *Harmonia axyridis.* Physiological Entomology 13: 193–199. doi:10.1111/j.1365-3032.1988.tb00923.x.

Omkar and James B.E. (2004) Influence of prey species on immature survival development predation and reproduction of *Coccinella transversalis* Fabricius (Coleoptera, Coccinellidae). Journal of Applied Entomology 128: 150–157. doi:10.1111/j.1439-0418.2004.00826.x.

Osawa N. (2005) The effect of prey availability on ovarian development and oosorption in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). European Journal of Entomology 102: 503. doi:10.14411/eje.2005.072.

Partridge L. and Farquhar M. (1983) Lifetime mating success of male fruitflies (*Drosophila melanogaster*) is related to their size. Animal Behaviour 31: 871–877. doi:10.1016/S0003-3472(83)80242-5.

Peretti A.V. and Aisenberg A. (2011) Communication under sexual selection hypotheses: challenging prospects for future studies under extreme sexual conflict. Acta Ethologica 14: 109–116. doi:10.1007/s10211-011-0099-4.

Perry J.C. (2011) Mating stimulates female feeding: testing the implications for the evolution of nuptial gifts. Journal of Evolutionary Biology 24: 1727–1736. doi:10.1111/j.1420-9101.2011.02299.x.

Perry J.C. and Rowe L. (2015) The evolution of sexually antagonistic phenotypes. Cold Spring Harbor perspectives in Biology 7: a017558. doi: 10.1101/cshperspect.a017558.

Perry J.C. and Rowe L. (2008) Ingested spermatophores accelerate reproduction and increase mating resistance but are not a source of sexual conflict. Animal Behaviour 76: 993–1000. doi:10.1016/j.anbehav.2008.05.017.

Perry J.C., Sharpe D.M. and Rowe L. (2009) Condition-dependent female remating resistance generates sexual selection on male size in a ladybird beetle. Animal Behaviour 77: 743–748. doi:10.1016/j.anbehav.2008.12.013.

Pervez A., Jahan M. and Monalisa (2022) Courtship behaviour and mating refusals in an aphidophagous ladybird *Coccinella transversalis*. International Journal of Tropical Insect Science 42: 227–233. doi:10.1007/s42690-021-00536-1.

Pervez A. and Singh S. (2013) Mating patterns in the aphidophagous ladybird *Hippodamia variegata* depend on body size. European Journal of Environmental Sciences 3(2): 109–112 doi:10.14712/23361964.2015.13.

Pervez A., Omkar and Richmond A.S. (2004) The influence of age on reproductive performance of the predatory ladybird beetle *Propylea dissecta.* Journal of Insect Science 4: 22. doi:10.1093/jis/4.1.22.

Pervez A. and Sharma R. (2021) Influence of intraspecific competition for food on the bodyweight of the adult aphidophagous ladybird, *Coccinella transversalis* European Journal of Environmental Sciences 11: 5–11. doi:10.14712/23361964.2021.1.

Pervez A., Omkar and Harsur M.M. (2020) Coccinellids on crops: Nature's gift for farmers. In: Innovative Pest Management Approaches for the 21st Century. Springer Singapore. pp429–460. doi:10.1007/978-981-15-0794-6_21.

Pilastro A., Benetton S. and Bisazza A. (2003) Female aggregation and male competition reduce costs of sexual harassment in the mosquitofish *Gambusia holbrooki.* Animal Behaviour 65: 1161–1167. doi:10.1006/anbe.2003.2118.

Richardson J. and Smiseth P.T. (2019) Nutrition during sexual maturation and at the time of mating affects mating behaviour in both sexes of a burying beetle. Animal Behaviour 151: 77–85. doi:10.1016/j.anbehav.2019.03.013.

Ronn J., Katvala M. and Arnqvist G. (2007) Coevolution between harmful male genitalia and female resistance in seed beetles. Proceedings of National Academy of Sciences 104: 10921–10925. doi: 10.1073/pnas.0701170104.

Rowe M., Veerus L., Trosvik P., Buckling A. and Pizzari T. (2020) The reproductive microbiome: an emerging driver of sexual selection sexual conflict mating systems and reproductive isolation. Trends in Ecology and Evolution 35: 220–234. doi.:10.1016/j.tree.2019.11.004.

Ryan M., McKnab R. and Schlupp I. (2001) Sexual harassment as a cost for molly females: bigger males cost less. Behaviour 138: 277–286.

SAS 9.0 (2002) SAS/Stat Version 9 SAS Institute Inc. Cary North Carolina, USA.

Shandilya A., Singh P., Mishra G. and Omkar (2021) Cost of mating in male *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae). Ethology 127: 59–67. doi: 10.1111/eth.13099.

Singh S., Mishra G. and Omkar (2016) Perceived prey quantity modulates oviposition in the ladybird *Menochilus sexmaculatus.* Journal of Ethology 34: 59–64. doi:10.1007/s10164-015-0446-4.

Singh S., Mishra G. and Omkar (2021) Maternal body size and age govern reproduction and offspring phenotype in the zig-zag ladybird beetle (*Menochilus sexmaculatus*). Canadian Journal of Zoology 99: 97–105. doi:10.1139/cjz-2020-0152.

Sipos J., Kvastegård E., Baffoe K.O., Sharmin K., Glinwood R. and Kindlmann P. (2012) Differences in the predatory behaviour of male and female ladybird beetles (Coccinellidae). European Journal of Environmental Science 2: 51–55. doi:10.14712/23361964.2015.38.

Vargas G., Michaud J.P. and Nechols J.R. (2012) Maternal effects shape dynamic trajectories of reproductive allocation in the ladybird *Coleomegilla maculata.* Bulletin of Entomological Research 102: 558–565. doi:10.1017/S000748531200020X.

Wallen M.M., Patterson E.M., Krzyszczyk E. and Mann

J. (2016) The ecological costs to females in a system with allied sexual coercion. Animal Behaviour 115: 227–236. doi:10.1016/j.anbehav.2016.02.018.

Watters J.V. (2005) Can the alternative male tactics 'fighter' and 'sneaker' be considered 'coercer' and 'cooperator' in coho salmon? Animal Behaviour 70: 1055–1062. doi: 10.1016/j.anbehav.2005.01.025.

Yuan M.L., Zhang L.J., Zhang Q.L., Zhang L., Li M., Wang X.T., Feng R.Q., Tang P.A. (2020) Mitogenome evolution in ladybirds: Potential association with dietary adaptation. Ecology and Evolution 10: 1042–1053. doi:10.1002/ece3.5971.

(Received October 27, 2023; revised ms accepted January 03, 2024; published March 31, 2024)