Influence of food availability on mate-guarding behaviour of ladybirds

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Abstract

A recent study on ladybird, *Menochilus sexmaculatus* (Fabricius) demonstrates that males perform post-copulatory mate guarding in the form of prolonged mating durations. We investigated whether food resource fluctuation affects pre- and post-copulatory behaviour of *M. sexmaculatus*. It has not been studied before in ladybirds. For this, adults were subjected to prey resource fluctuations sequentially at three levels: post-emergence (Poe; 10 days), pre-mating (Prm; 24 h) and post-mating (Pom; 5 days; only female). The food resource conditions at each level could be any one of scarce, optimal or abundant. Pre-copulatory and post-copulatory behaviour, and reproductive output were assessed. Post-emergence and pre-mating nutrient conditions significantly influenced the pre-copulatory behaviour. Males reared on scarce post-emergence conditions were found to require significantly higher number of mating attempts to establish mating unlike males in the other two food conditions. Under scarce post-emergence and pre-mating conditions, time to commencement of mating and latent period were high but opposite result was obtained for mate-guarding duration. Fecundity and per cent egg viability were more influenced by post-mating conditions, with scarce conditions stopping oviposition regardless of pre-mating and post-emergence conditions. Present results indicate that pre- and post-copulatory behaviour of ladybird is plastic in nature in response to food resource fluctuations.

Keywords: mate-guarding, mating attempts, latent period, time to commencement of mating, prey resource fluctuation

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Introduction

Food quality as well as availability may vary tremendously throughout an environment, both spatially and temporally (Hebets *et al.*, 2008). Being the key determinant of an organism's fitness, food influences life history traits of several insects, at the individual, species and inter-specific levels (Blanckenhorn, 2000). All living organisms continuously attempt to sustain stable population dynamics against ephemeral food resources (Choi *et al.*, 2016). The frequency and magnitude of food resources also varies with time and season

resulting in alternations of low- and high-resource availability (Ostfeld & Keesing, 2000). Unlike routine fluctuations, sometimes occurs 'ephemeral events of resource superabundance' also known as 'resource pulses', which produce drastic changes in resource utilization (Holt, 2008; Chaudhary *et al.*, 2016).

Animals require a certain amount of energy and nutrients for metabolism, growth and reproduction (Sterner & Elser, 2002; Wilder & Rypstra, 2007). Nutritional conditions of both mating partners play an important role in their mating behaviour (Arnqvist & Rowe, 2005; Fisher & Rosenthal, 2006). Mating behaviour includes all the pre- and post-mating events surrounding insemination (Chaudhary *et al.*, 2015, 2016). The pre-mating mechanisms involve mate location, mate recognition, mate reception, time taken to commencement of mating (TCM) and latent period (LP). The post-mating mechanisms may be displayed as mate guarding (Chaudhary

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et al., 2015), sperm competition (Simmons, 2001), cryptic female choice (Arnqvist, 2014) and sperm precedence (de Jong *et al.*, 1998; Chaudhary *et al.*, 2016). Amongst mating behaviours, post-copulatory mate guarding is the most widely occurring phenomenon in insects (Alcock, 1994). Males of a wide range of species spend considerable time and energy to control the mating activities of females (Alcock, 1994; Chaudhary *et al.*, 2015). Such behaviour is commonly referred to as the mate guarding (Chaudhary *et al.*, 2015).

Some male insects must forage for resources, and their success at food gathering may be significantly linked to their ability to engage in reproductive activities (Yuval *et al.*, 1994; Frey-Roos *et al.*, 1995). The pheromone emission during courtship is also directly correlated with the quality and quantity of food (Landolt & Sivinski, 1992). Males of most of the insects increase their ejaculate size in relation to the food resources to overcome the sperm competition and provide the nutrients to females in the form of seminal fluid or spermatophore phylax that regulates the oviposition pattern of female (Vahed, 1998; Edvardsson, 2007). Ejaculate size is also known to be dependent upon the quality and quantity of food during the rearing of adults (Fox, 1993; Ivy *et al.*, 1999). It has been found that males mate more frequently when fed on protein-rich food than those that are protein deprived, and females who copulate with the former are less likely to copulate again than females who mate with the latter (Blay & Yuval, 1997; Yuval *et al.*, 1998). Not only this, but females also show decreased mating frequency in poor diet conditions (Clutton-Brock & Parker, 1995). Both the quality and quantity of food diversify with the changing environment have important effects on the fitness of individuals (Sterner & Elser, 2002).

The amount of food consumed by males and females affect different parameters of reproductive behaviour, including ornament size (Andersson, 1994), mate choice (Cotton *et al.*, 2006), sexual courtship display rate (Kotiaho *et al.*, 1998) fecundity and egg viability (Wilder & Rypstra, 2007). While most studies of the effects of feeding on reproduction have examined the effect of food quantity, some recent studies have also provided evidence that food quality or nutritional status of animals may also be important for reproductive activities (Wilder & Rypstra, 2007). For example, male crickets with low concentrations of nutrients or those provided with low-quality food court females less intensely and are less attractive as mates (Wilder & Rypstra, 2007). However, not much is known about how the mating behaviour of predatory species responds to food quality and if there are interactive effects of male and female food quality on mating activities and egg production.

Previous studies have established that ladybird beetles are polyandrous (Omkar & Mishra, 2014; Colares *et al.*, 2015) and display mate choice (Mishra & Omkar, 2014). They store sperms in spermatheca for extended periods (Hodek, 1973) that increases the chance for sperm competition. In *Menochilus sexmaculatus*, prolonged mating durations beyond a limit that does not increase the reproductive output has been termed as mate guarding (Chaudhary *et al.*, 2015). Recent studies have indicated that this increased mating duration plays an important role in reducing last male sperm precedence (Chaudhary *et al.*, 2016) and is plastic in nature in response to the presence of competitor (Chaudhary *et al.*, 2017).

In light of the above facts, we performed an experiment evaluating the effect of varying food resource conditions (bean aphid, *Aphis craccivora* Koch; Hemiptera: Aphididae)

on the mating behaviour and reproductive output. For this study, we abruptly change the ladybirds from their post-emergence condition (scarce, optimal or abundant prey biomass) to three different pre-mating conditions (scarce, optimal or abundant prey biomass); post-mating the females were again placed in three post-mating conditions (scarce, optimal or abundant) to record pre- and post-copulatory behaviours, in addition to fecundity and per cent egg viability. We hypothesized that the consequences of nutritional variation are not restricted to the pre-mating behaviour only, and that even post-mating behaviour would exhibit plasticity when faced with varying food resources. We also predict that the varying food resources would not only modulate immediate behaviours but would also influence reproductive output. This has been not studied before in ladybirds in reference to their copulatory and reproductive behaviour.

Materials and methods

Stock maintenance

Adult males and females of *M. sexmaculatus* were collected from the agricultural fields of Lucknow, India (26°50′N, 80°54′E) and paired randomly in plastic Petri dishes (9.0 cm × 1.5 cm). They were reared under constant abiotic conditions (27 ± 2°C; 65 ± 5% relative humidity; 14:10 light:dark) in Environmental Test Chambers (Yorco B.O.D. Super Deluxe, York Scientific Industries Pvt. Limited) on a daily replenished supply of *A. craccivora* Koch reared on bean (*Dolichos lablab* L.; Fabaceae) in a polyhouse maintained at 22 ± 1°C; 65 ± 5% R.H. and 14L:10D photoperiod. The eggs laid were collected every 24 h and observed for hatching. The neonates obtained were reared individually in the conditions outlined above to produce a stock population.

Experimental design

Our experiments were divided into two parts. The first and second part of the experiment was performed to evaluate the pre-copulatory time (TCM, LP), and post-copulatory parameters [mate-guarding duration (MGD), fecundity and per cent egg viability], under fluctuating food conditions.

The three food resource conditions selected were scarce, optimal and abundant by providing 2, 10 and 15 mg of aphids per adult per day, respectively.

Evaluation of pre- and post-copulatory behaviour

Randomly selected similar sized (8.92 ± 1.05 mg) newly emerged ladybird adults from the stock culture were placed individually in Petri dishes (size as above) under scarce ($n = 180$; 90 males and 90 females), optimal ($n = 180$; 90 males and 90 females) and abundant ($n = 180$; 90 males and 90 females) prey resource conditions for 10 days (abiotic conditions similar to that of stock). These conditions were considered as post-emergence conditions (Poe). During this period, six adults of *M. sexmaculatus* from the scarce prey resource condition died within 10 days of emergence; more ladybird species were added to the experimental setup from the stock culture to equalize the sample size.

The adults from each prey supply were divided into three equal groups and shifted for the next 24 h onto any one of three pre-mating conditions (Prm): scarce (30 males and 30 females), optimal (30 males and 30 females) or

abundant (30 males and 30 females) prey conditions. After 24 h, different mating pairs were formed based on the pre-mating regimes, *viz.* scarce × scarce, optimal × optimal and abundant × abundant.

For each mating treatment, TCM, LP and MGD were recorded. Each treatment was replicated 30 times (*n* = 30).

TCM is defined as the time in minutes taken by the male to first mount the female after its introduction to the arena; LP is defined as the duration between mounting and the first stroke after the insertion of the aedagus (recorded in seconds). MGD is calculated as the complete mating duration minus 30 min (recorded in minutes, based on Chaudhary *et al.*, 2015).

Evaluation of reproductive output

For further evaluation of post-copulatory behaviour, the mated females from the above treatments were isolated and placed individually in Petri dishes and provided with any one of three different post-mating conditions (Pom; scarce, optimal or abundant) of prey resource under above abiotic conditions. These abiotic and biotic conditions were maintained for the next 5 days and daily oviposition and consequent per cent egg viability were recorded. All treatments were conducted in ten replicates.

Statistical analysis

The data were checked for normality using the Kolmogorov–Smirnoff test. Means were separated using Tukey's test when data were normally distributed and variances were homogeneous (Bartlett's test for equal variances). TCM, LP, MGD, fecundity (total oviposition over 5 days per replicate) and per cent egg viability (number of viable eggs × fecundity/100) as dependent variables were subjected to multivariate analysis of variance (MANOVA) followed by Tukey's *post hoc* comparison of means, with: (i) post-emergence, (ii) pre-mating and (iii) post-mating conditions as independent factors. All statistical analyses were performed using MINITAB 16 (Minitab Inc., State College, PA, USA).

Results

Pre- and post-copulatory behaviour

General MANOVA revealed a significant effect of food regimes (scarce, optimal and abundant) at post-emergence (F_{Poe} = 08.04; P = 0.003; df = 1, 89) and at pre-mating conditions (F_{Prm} = 10.84; P = 0.041; df = 1, 89) and their interaction also significantly influenced the number of mating attempts ($F_{Poe \times Prm}$ = 7.87; P = 0.008; df = 1, 89). Scarce post-emergence condition was shown to increase the number of mating attempts prior to successful mating; conversely no such detrimental effect was observed on mating pairs reared on optimal and abundant post-emergence conditions (table 1). Scarce pre-mating conditions also seemed to have a slight additive effect on the number of mating attempts, though optimal and abundant conditions had an ameliorative effect.

Similar effect of post-emergence (F_{Poe} = 12.76; P = 0.038; df = 1, 89) and pre-mating conditions (F_{Prm} = 5.83; P = 0.008; df = 1, 89), and their interactions ($F_{Poe \times Prm}$ = 6.09; P = 0.002; df = 1, 89) were evident on TCM. TCM was found to be influenced more by post-emergence condition than by pre-mating conditions. Improved prey resource under pre-mating conditions seemed to reduce the stress of post-emergence conditions.

TCM was similar under optimal and abundant pre-mating conditions irrespective of post-emergence conditions. Maximum TCM was found when females and males of scarce post-emergence conditions were provided with scarce pre-mating conditions (table 1).

LP was also significantly influenced by the post-emergence (F_{Poe} = 10.06; P = 0.078; df = 1, 89) and pre-mating food conditions (F_{Prm} = 3.54; P = 0.438; df = 1, 89) and their interactions ($F_{Poe \times Prm}$ = 6.93; P = 0.018; df = 1, 89). LP varied from 40.20 ± 1.80 to 62.40 ± 0.24 s, 1.20 ± 0.18 to 0.96 ± 0.30 s and 1.50 ± 0.06 to 2.28 ± 0.01 s under scarce, optimal and abundant post-emergence conditions, respectively. LP was also maximum when the mates experienced scarce pre-mating food conditions preceded by scarce post-emergence food conditions. Unlike TCM, post-emergence and pre-mating food conditions had a strong additive effect on LP (table 1).

In case of MGD, it varied significantly with post-emergence (F_{Poe} = 7.83; P < 0.001; df = 1, 89), pre-mating (F_{Prm} = 13.40; P < 0.001; df = 1, 89) conditions and their interactions ($F_{Poe \times Prm}$ = 8.56; P = 0.0001; df = 1, 89). It varied from 5.00 ± 0.84 to 20.06 ± 1.34 min, 52.66 ± 4.06 to 72.30 ± 3.05 min and 9.00 ± 0.51 to 78.0 ± 3.02 min under scarce, optimal and abundant post-emergence conditions, respectively. Maximum MGD was 78.00 ± 3.02 min when mating occurred between females and males from abundant post-emergence condition and were further kept on abundant pre-mating condition. Interestingly, MGD was highest when post-emergence and pre-mating conditions matched except for under matching of scarce conditions (table 1).

Reproductive output

General MANOVA further revealed a significant effect of post-emergence, pre-mating and post-mating conditions on fecundity and per cent egg viability. Interaction between post-emergence and pre-mating conditions, post-emergence and post-mating conditions, and pre-mating and post-mating conditions, post-emergence, pre-mating and post-mating conditions also showed significant effect on fecundity and per cent egg viability of *M. sexmaculatus* (table 2). There was no egg laying under scarce post-mating conditions, regardless of the post-emergence and pre-mating conditions that the adults had been previously subjected to (fig. 1). Maximum per cent egg viability was found on optimal and abundant post-mating conditions of both optimal and abundant post-emergence conditions in comparison to scarce post-emergence condition (fig. 2).

Discussion

Adults reared under optimal and abundant prey resource after post-emergence conditions established mating in a single attempt, while those on scarce food condition took multiple attempts to successfully mate, probably owing to their poor fitness. This reluctance could be a result of poor fitness of males, in terms of poor cuticular hydrocarbon profile (Chapman *et al.*, 1995; Ferveur, 2005), reduced ejaculate size or less spermatophore phylax of males. Under more suitable conditions, males have been found to transfer larger ejaculates, potentially achieved by an increased rate of ejaculate transfer in comparison to low nutritional status of males (Perry & Rowe, 2010). In cases where females show low receptivity owing to poor fitness of males, increased number of mating attempts by such

Table 1. Effect of prey resource fluctuation on pre- (TCM and LP) and post-mating (MGD) behaviour of *Menochilus sexmaculatus*.

S.N.	Post-emergence condition (10 days)		Pre-mating conditions (24 h)		After 24 h (♀ × ♂)			
	♀	♂	♀	♂	Mating attempts	TCM (min)	LP (s)	MGD (min)
1	Scarce$_{90}$	Scarce$_{90}$	S$_{30}$	S$_{30}$	0.80 ± 0.10^{cC}	13.20 ± 0.24^{cC}	62.40 ± 0.24^{aC}	05.00 ± 0.84^{aA}
5			O$_{30}$	O$_{30}$	0.00 ± 0.00^{aA}	6.20 ± 0.21^{bB}	40.20 ± 0.18^{cC}	12.75 ± 3.02^{bA}
9			A$_{30}$	A$_{30}$	0.40 ± 0.00^{b}	3.20 ± 0.02^{aB}	55.80 ± 0.24^{bC}	20.06 ± 1.34^{cA}
10	Optimal$_{90}$	Optimal$_{90}$	S$_{30}$	S$_{30}$	0.20 ± 0.00^{bB}	4.21 ± 0.01^{bA}	15.60 ± 0.30^{bB}	54.40 ± 4.31^{aC}
14			O$_{30}$	O$_{30}$	0.00 ± 0.00^{aA}	6.60 ± 0.00^{cC}	0.96 ± 0.10^{aA}	72.30 ± 3.05^{bC}
18			A$_{30}$	A$_{30}$	0.00 ± 0.00^{aA}	3.70 ± 0.23^{aC}	13.20 ± 0.18^{bB}	52.66 ± 4.01^{aB}
19	Abundant$_{90}$	Abundant$_{90}$	S$_{30}$	S$_{30}$	0.00 ± 0.00^{aA}	5.00 ± 0.19^{bB}	1.56 ± 0.30^{aA}	09.00 ± 0.51^{aB}
23			O$_{30}$	O$_{30}$	0.00 ± 0.00^{aA}	5.40 ± 0.18^{bA}	1.50 ± 0.06^{aB}	42.04 ± 3.01^{bB}
27			A$_{30}$	A$_{30}$	0.00 ± 0.00^{aA}	3.00 ± 0.11^{aA}	2.28 ± 0.40^{bA}	78.0 ± 3.02^{cC}

S.N., serial number; TCM, time to commencement of mating; LP, latent period; MGD, mate-guarding duration; S, scarce; O, optimal; A, abundant.
Values are mean ± SE.
Small and large alphabets compare mating attempts, TCM, LP and MGD in different pre-mating conditions per post-emergence condition, based on Tukey's *post hoc* comparison of means.

Table 2. Results of multivariate analysis of variance (MANOVA) showing the effects of post-emergence condition (Poe), pre-mating condition (Prm) and post-mating condition (Pom) on time to commencement of mating and latent period of *Menochilus sexmaculatus* (*F*-values are significant at $P < 0.05$).

| S.N.	Independent factors	Dependent factors	
		Fecundity	% egg viability
1	Post-emergence condition (Poe)	$F = 15.33$; $P = 0.021$; df = 1, 89;	$F = 6.03$; $P = 0.038$; df = 1, 89;
2	Pre-mating condition (Prm)	$F = 7.03$; $P < 0.0001$; df = 1, 89;	$F = 3.83$; $P = 0.008$; df = 1,89;
3	Post-mating condition (Pom)	$F = 28.33$; $P = 0.035$; df = 1, 89;	$F = 21.33$; $P < 0.0001$; df = 1, 89;
4	Post-emergence condition × pre-mating condition (Poe × Prm)	$F = 9.03$; $P < 0.0001$; df = 1, 89;	$F = 41.93$; $P < 0.0001$; df = 1, 89;
5	Post-emergence condition × post-mating condition (Poe × Pom)	$F = 5.33$; $P < 0.0001$; df = 1, 89;	$F = 10.33$; $P = 0.034$; df = 1, 89;
6	Pre-mating condition × post-mating condition (Prm × Pom)	$F = 4.93$; $P < 0.0001$; df = 1,89;	$F = 18.03$; $P < 0.0001$; df = 1, 89;
7	Post-emergence condition × pre-mating condition × post-mating condition (Poe × Prm × Pom)	$F = 6.99$; $P = 0.041$; df = 1, 89;	$F = 31.33$; $P = 0.039$; df = 1, 89;

S.N., serial number.
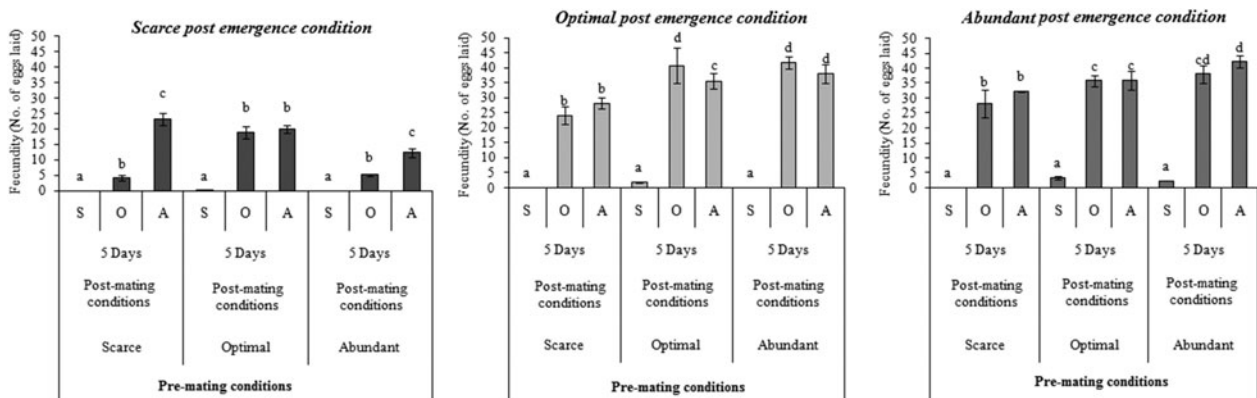
Fig. 1. Effect of food resource fluctuation on fecundity of *Menochilus sexmaculatus* (S, scarce; O, optimal; A, abundant; small letters compare the fecundity of different experimental conditions, based on Tukey's *post hoc* comparison of means; similar letters indicates lack of significant difference).

males may be the only way to convince females of their vigour and thereby procure a mating (Rowe, 1992).

Similar trends to those observed in mating attempts were also in TCM and LP. Maximum TCM and LP were observed in pairs reared under scarce post-emergence conditions, particularly if the female and male were exposed to scarce pre-mating conditions. These findings clearly indicate that the rearing conditions are more important than the experimental
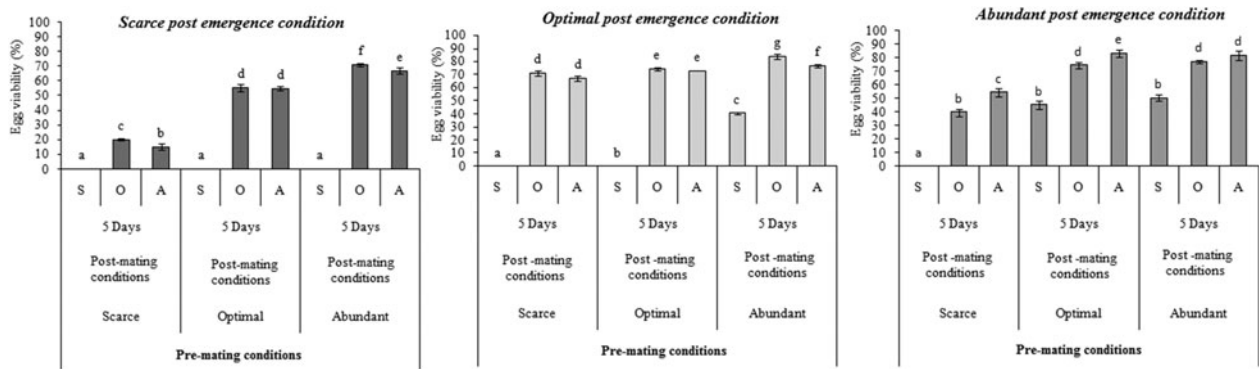
Fig. 2. Effect of food resource fluctuation on per cent egg viability of *Menochilus sexmaculatus* (S, scarce; O, optimal; A, abundant; small letters compare the per cent egg viability of different experimental conditions, based on Tukey's *post hoc* comparison of means; similar letters indicates lack of significant difference).

condition for the mating behaviour of ladybirds. The delay in the onset of mating between the partners of scarce post-emergence condition and scarce pre-mating condition may be a form of avoidance by both partners to enter into the mating which may be costly to them in terms of increased energy expenditure under poor nutritional state (Omkar & Mishra, 2005). It has been previously suggested that variation in both mate quality and mate choice costs will influence TCM and LP (Parker, 1983). The negative correlation between TCM and duration of copulation observed in this study finds support in a previous study on *Drosophila* (Singh & Singh, 2014).

A recent study in *M. sexmaculatus* demonstrates that males perform post-copulatory mate guarding in the form of prolonged mating durations (Chaudhary *et al.*, 2015), which significantly influences paternity share via last male sperm precedence as indicated by the phenotype of the offspring (Chaudhary *et al.*, 2016). Mate-guarding behaviour has been shown to vary considerably according to food resource (Burdfield-Steel & Shuker, 2014). Our study, which investigates the effects of fluctuating prey resource on pre- and post-copulatory behaviour, also found similar effects on MGD, fecundity and per cent egg viability in *M. sexmaculatus*. With scarce rearing conditions, MGD decreased in comparison to optimal and abundant rearing conditions. The decreased mate-guarding modulation under low nutrient condition might be attributed to (a) rapid ejaculation (Perry & Rowe, 2010), and/or (b) lower energy levels due to initial multiple unsuccessful mating attempts. Adults reared on abundant food under post-emergence achieved higher MGD than their counterparts. While resource stress during development is known to lead to lower lifetime fitness via its detrimental effects on body size and energy reserves, which are independent of the adult nutrient availability (Dmitriew & Rowe, 2011). Our study indicates that adult nutrient availability also influences mating behaviour.

The increased mating success incurred by adults reared on abundant food supply under post-emergence condition may reflect the condition-dependent response (Perry & Rowe, 2010). Previous studies have shown that well-fed individuals are at profit in several respects when compared with individuals from food-limited condition. Organisms reared on abundant food have higher probability of being selected as mates, receive higher number of matings and have longer mating durations and higher reproductive output (Hebets *et al.*,

2008; Eraly *et al.*, 2009). A few studies have also shown that males reared on abundant food transfer larger ejaculates with more accessory gland proteins and thus are preferred over low condition males (Gwynne & Simmons, 1990; Perry *et al.*, 2009).

Fecundity proved a much better predictor of reproductive success following different food resource condition than egg viability. Minimum oviposition was observed by females reared on a scarce post-mating food irrespective of the fact that they were reared on different post- and pre-mating conditions. The reduction in fecundity of offspring of low-food parents observed in our study is in accordance with the finding of Townsend *et al.* (2012) on *Chironomus tepper*. Previous study has shown that intake and optimal allocation of nutrients to the gonads can subsequently reinforce the individual fecundity (Zhao *et al.*, 2014). Males may ejaculate more sperm into well-fed females either because it pays them to 'spend' more reproductive resources on matings that provide greater reproductive potential, or because heavier (longer lived and more attractive) females mate more frequently and have larger spermathecal size (Gage, 1998). This is in accordance with the previous studies reporting that clutch size and oviposition rate to be influenced by the food available to females at the time of oviposition (Dixon, 2000). However, the strength of correlation between body size and reproductive success is also known to be modified by factors, *viz.* food (Dixon, 2007), and presence of predators (Blanckenhorn, 1998), climate (Gotthard *et al.*, 2007) and age (Amin *et al.*, 2012). In the absence of sufficient quantity of prey, a reduction in the number of progeny produced was reported (Omkar & Pervez, 2003).

Food stress in early life stages produces individuals that perform better under food-limited resource conditions than in energy-abundant resource conditions, as has been observed in humans and other mammals (Ozanne & Hales, 2005). However, growth and reproductive performance are adversely affected. Studies have shown that adult stages of beetles are capable of surviving prolonged food stress (Omkar & Pervez, 2003) but their reproductive success is hampered in comparison to beetles provided with *ad libitum* aphids (Koch, 2003; Dmitriew & Rowe, 2007).

To summarize, prey resource conditions experienced during post-emergence may result in developing adaptations for future food fluctuating condition. However, plasticity of food resource is not limited to particular stages only as the adult females are also under constant selection pressure during

ovipositional periods. Thus, our study reveals that (i) food resource is of paramount importance and any change imposes immediate effects on ladybirds: (ii) adults reared on scarce prey post-emergence had reduced mating and reproductive success despite the fact that their pre-mating and post-mating stages were reared on *ad libitum* food; (iii) post-emergence and pre-mating conditions showed significant influence on TCM, LP and MGD; (iv) highest MGD was found when post-emergence and pre-mating conditions were abundant; (v) despite the post-emergence and pre-mating conditions, post-mating condition also showed significant effect on fecundity and per cent egg viability; (vii) post-emergence conditions play a more important effect on pre- and post-copulatory behaviour than their pre- and post-mating conditions; (viii) pre- and post-copulatory behaviour of *M. sexmaculatus* showed plasticity in fluctuating food condition.

Acknowledgements

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