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Reproductive behaviour of a generalist aphidophagous ladybird beetle *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae)

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Abstract. The reproductive behaviour of a generalist aphidophagous ladybird beetle *Cheilomenes sexmaculata* (Fabricius) was studied in detail. The males first mated at an age of about 2 days, while females mated at 1 day after their emergence. Mate recognition was displayed in five steps, viz. approach, watch, examine, mount and copulatory attempt. Being provided with four dummy models, the male appeared to recognize the female through visual and other possible cues, maybe chemical. The duration of mating was maximum (mean ± SE; 133.0 ± 2.8 min) when an unmated male copulated with a virgin female and minimum (95.0 ± 4.2 min) when a mated male copulated with a mated female. Mating duration seems to be influenced more by the change in male sexual status, thus revealing it to be male dominated. The maximum oviposition period (46.0 ± 1.2 days), fecundity (861.0 ± 2.2) and hatching percentage (64.0 ± 0.6) in *C. sexmaculata* were noticed after multiple matings, while these parameters were minimum (15.0 ± 1.0, 70.0 ± 2.8 and 37.0 ± 1.0, respectively) after single mating. Thus, multiple matings enhanced the total egg output and percentage of hatchability.

Key words: coccinellids, ladybird beetle, *Cheilomenes sexmaculata*, reproductive behaviour, courtship and mating, mate recognition, mating duration, oviposition, fecundity, fertility

Introduction

Reproduction forms one of the most important aspects of an organism's life. The efforts involved and the resources spent in progeny production are directly related to the fate of an organism in long-term processes of evolution and extinction. Despite this, reproductive biology of ladybird beetles, some of which are important biological control agents, has been largely ignored (Hodek and Ceryngier, 2000). Applied aspects, such as predation and effect of abiotic and biotic parameters, on the life attributes have received much attention, because of their direct relevance to the success of biological control. Despite the relevance of mass multiplication of biological control agents, various aspects of reproduction have been ignored.

There is, thus, a need to unravel intricacies of reproductive biology of ladybird beetles, particularly the parameters pertaining to reproductive behaviour, which include mate recognition,

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courtship, mating and termination displays, and ovipositional preference and pattern.

Cheilomenes sexmaculata (Fabricius) (Coleoptera: Coccinellidae), a common oriental ladybird beetle found abundantly in the agroecosystems adjoining Lucknow, India, was selected as the experimental model. It is a potent predator of aphids and other soft-bodied insect pests (Agarwala and Yasuda, 2000; Omkar and Pervez, 2002). Certain aspects of its reproductive behaviour including mating and sperm transfer have previously been studied (Obata and Johki, 1991), however not in much detail. Recent reproductive studies on *C. sexmaculata* have discussed the deteriorative role of ageing on reproduction (Dixon and Agarwala, 2002).

In the present study, experiments were designed to investigate certain basic aspects of reproductive behaviour and biology of this ladybird beetle, viz. sexual maturity, pre-mating, mating and post-mating behaviour, mate recognition (cues involved), effect of sexual status on mating duration and effect of multiple matings on certain reproductive attributes.

Materials and methods

Stock cultures

Different life stages of *C. sexmaculata* were collected from local agricultural fields and reared on *ad libitum* supply of its preferred aphid species, *Aphis craccivora* Koch (Homoptera: Aphididae) on the aphid's host plant *Dolichos lablab* L. (Fabaceae) at 25 ± 2 °C, 65 ± 5% RH and a photoperiod of 14L:10D. The adults were paired in Petri dishes (9.0 × 2.5 cm) and subsequently laid eggs were observed for hatching. Immature stages were reared in muslin-covered glass beakers with abundant supply of prey. Abiotic conditions for experiments were same as that for the stock culture.

Sexual maturity

An experiment was conducted to evaluate the sexual maturity of male and female *C. sexmaculata*. First successful mating was considered as sexual maturity for a male, while the period from emergence to first oviposition (i.e. pre-oviposition period) was considered as an indicator of sexual maturity for a female. For this purpose, newly emerged (NE) adults of both the sexes were paired in glass Petri dishes with *ad libitum* supply of *A. craccivora* under laboratory conditions (25 ± 2 °C, 65 ± 5% RH, 14L:10D). The adults were paired daily at 1000 h and separated at 1800 h. The same procedure was carried out with the 1-, 2-, 3- and 4-day-old male and female beetles. In the event of mating, the sexes were separated immediately after the termination of mating and females were observed throughout the oviposition. All observations were made in 10 replicates.

Pre-mating, mating and post-mating behaviour

To observe the pre-mating, mating and post-mating behaviour, 5-day-old (post-emergence) male and female ladybird beetles were placed in Petri dishes (9.0 × 3.5 cm) with *ad libitum* natural prey, i.e. *A. craccivora*, under a stereoscopic binocular (at 16 and 40 × magnifications). The behaviour of the male before, during and after mating was observed following the protocol developed by Obata (1987).

Mate recognition (cues involved)

This experiment was designed to evaluate the importance of various steps involved in mate recognition and also their possible association with different cues. Four dummy models were provided to a male as substitutes for a live female. A 5-day-old unmated male was introduced into the centre of a Petri dish containing the model that was placed at the periphery. The models were: (i) a dead female after 1 day of natural death and kept in the refrigerator for 24 h after death, (ii) a dead male after 1 day of natural death and kept in the refrigerator for 24 h after death, (iii) a dead female kept refrigerated for 1 month and (iv) a freshly dead female of the pale morph type of the ladybeetle *Propylea dissecta* (Mulsant) (Coleoptera: Coccinellidae), killed by placing a cotton swab dipped in 70% alcohol on its head. *P. dissecta* was used because of its similarity in size with *C. sexmaculata*. A new male was used each time. The time during courtship and number of courtship steps displayed or missed in each set-up were observed and their details were recorded.

Effect of previous matings

The effect of the sexual status of copulating individuals on mating duration was studied. For this purpose, four sets of mating pairs, viz. (i) an unmated male with a virgin female, (ii) an unmated male with a mated female, (iii) a mated male with a virgin female and (iv) a mated male with a mated female, were kept together and allowed to mate for 5 days. The mated males and mated females selected for the experiments had mated at least twice in the previous 24 h.

Effect of multiple matings

The aim of this experiment was to evaluate the effect of one (male separated after one mating), two (male separated after two matings), three (male separated after three matings) and multiple matings (male allowed to mate with female for lifetime) on the oviposition period, fecundity and hatching percentage of eggs. The ladybird beetles were separated daily at 1800 h after a single mating and re-paired the next day at 1000 h for the next mating. This process was continued until the females were subjected to the required number of matings. The mated females were maintained for their entire lifetime on *ad libitum* prey (*A. craccivora*) to conclusively determine the oviposition period and fecundity. All the eggs were observed and the hatching percentage for each female was determined. The data on matings were subjected to ANOVA and comparison of means following Bonferroni's method using Statistix 4.1 (1985, 1994) software.

Results

Sexual maturity

Males and females first mated at an age of about 2 and 1 day after their emergence, respectively. Two or more days old males attempted mating with NE, 1-, 2-, 3- and 4-day-old females (9 out of 10). NE females rejected such advances by either running away from the male or by shaking their abdomen ($n = 9$; NE females with NE to 3-day-old males). Two-day-old males succeeded in mating with 1 or more days old females; however, 1- to 3-day-old mated females did not oviposit but 4-day-old mated females started oviposition (pre-oviposition period, 4 days).

Pre-mating and mating behaviour of the male

Males (5-day-old) displayed pre-mating behaviour and the mate recognition was performed in five steps: approach ($n = 10$), watch ($n = 7$), examine ($n = 9$), mount ($n = 10$) and copulatory attempt ($n = 10$) (Table 1). After genital contact, the mating posture was maintained during mating. The active processes, such as bouts and strokes, were not witnessed. The male beetle rubbed the elytra of the female with its mouthparts and forelegs during mating ($n = 7$). The female ($n = 3$) slowly moved ahead in search of a place where its abdominal end was kept slightly upwards to facilitate the mating. The male possesses slender unjointed accessory copulatory organs, the parameres, having fine hairs (one on either side of the aedeagus). These parameres vibrated continuously on the ventral surface of the female abdomen during mating.

The female ($n = 4$) lifted her hind legs during mating, shook gently and returned to the substratum. In cases of prolonged matings, the male shifted towards the abdominal end of female ($n = 4$) and returned to its original posture (for a few seconds). However, mating was not disrupted, even during changes in posture. Five to ten minutes after the commencement of mating, frequent rhythmic protraction and retraction occurred at the terminal end of the abdomen of both sexes, which continued almost throughout the mating. Thereafter, the female ladybird beetle kicked away the male with her hind legs to terminate mating. After depairing, both ladybird beetles rubbed and cleaned their mouthparts and antennae with forelegs. The pulsation was resumed (3–4 times) at the posterior abdominal ends of both the sexes after the termination of mating.

Mate recognition (cues involved)

The pattern of occurrence of various mate recognition steps differed quite prominently with different mating models (Table 1). When a 1-day-dead conspecific female was provided as mating model, the male ladybird beetles mounted and made frequent copulatory attempts. Not as many males were observed mounting (7 out of 10) and attempting copulation (3 out of 10) with a 1-day-dead conspecific female as they did with a live female (10 out of 10). When a dummy 1-month-refrigerated conspecific female, freshly dead dummy heterospecific female (*P. dissecta*) and

Table 1. Mate recognition display (in number) by male *Cheilomenes sexmaculata* when provided with mating partners (live as well as dead models) out of 10 pairs

Mating models	Approach	Watch	Examine	Mount	Copulatory attempt
Live female *C. sexmaculata*	10	7	9	10	10
1-day-dead female *C. sexmaculata*	10	6	10	7	3
1-month-dead female *C. sexmaculata*	8	4	3	NM	NCA
Freshly dead conspecific male *C. sexmaculata*	9	8	4	NM	NCA
Freshly dead heterospecific female *Propylea dissecta*	7	5	2	NM	NCA

NM, nil mount; NCA, nil copulatory attempt.

1-day-dead conspecific male were provided as mating models, the male ladybird beetles approached, watched and examined them, but did not make copulatory attempts. All the males from set-up (ii), (iii) and (iv) limited themselves to watch and examine and not even 1 out of 30 made copulatory attempts with the dummy models provided.

Effect of previous matings

The duration of mating was maximum when an unmated male mated with a virgin female and minimum in matings between a mated male and a mated female (Table 2). The differences in mating durations with change in sexual status of males and females were statistically significant ($F = 767.57$; df = 4; $P < 0.001$) and the decreasing order of mating durations in the copulating pairs was unmated male with virgin female, unmated male with mated female, mated male with virgin female and mated male with mated female. Though change in sexual status of both adults had a prominent effect on the mating durations, change in male status had a more prominent effect on the mating durations of the ladybird beetles ($F = 633.06$; df = 4; $P < 0.001$) than those of female ($F = 141.86$; df = 4; $P < 0.001$).

The females were observed rejecting male advances at times when they had mated recently (52–105 min after mating) or when oviposition was due (after 5–45 min).

Effect of multiple matings

The oviposition period of female beetle increased with an increase in number of matings (Table 3). The same trend was observed for fecundity and hatching percentage. The differences in oviposition period ($F = 505.76$; df = 9; $P < 0.001$), fecundity ($F = 179.63$; df = 9; $P < 0.001$) and hatching percentage ($F = 300.70$; df = 9; $P < 0.001$) were found to be statistically significant.

Table 2. Sexual status on the copulation period of *Cheilomenes sexmaculata* ($n = 10$)

Mating combinations	Mating duration (min)
Unmated male × virgin female	133.0 ± 2.8^{a}
Unmated male × mated female	122.0 ± 2.7^{b}
Mated male × virgin female	111.0 ± 2.2^{c}
Mated male × mated female	95.0 ± 4.2^{d}
F-value	767.6*

Values are mean ± SE.
*Value significant at $P < 0.001$.
Different letters in the column denote statistically significant data.

Table 3. Influence of number of matings on oviposition period, fecundity and percentage of hatchability in *Cheilomenes sexmaculata*

No. of matings	Oviposition period (days)	Fecundity (eggs)	Hatching percentage
One	15.0 ± 1.0^{a}	70.0 ± 2.8^{a}	37.0 ± 1.0^{a}
Two	26.0 ± 1.8^{b}	123.0 ± 5.0^{b}	42.0 ± 0.6^{b}
Three	31.0 ± 1.3^{c}	196.0 ± 3.1^{c}	47.0 ± 1.3^{c}
Multiple	46.0 ± 1.^{d}	861.0 ± 2.2^{d}	64.0 ± 0.6^{d}
F-value	505.8*	179.6*	300.7*

Values are mean ± SE.
*Values significant at $P < 0.001$.
Different letters in the columns denote statistically significant data.

Discussion

The male *C. sexmaculata* succeeded in mating after 2 days of their emergence but pre-oviposition period of females was 4 days. This indicates that males become sexually mature after 2 days, while females only after 4 days of emergence indicating that this ladybird beetle species is protandrous. Protandry is also recorded in other ladybird beetles, viz. *Coccinella septempunctata* Linnaeus and *P. dissecta* (Srivastava and Omkar, 2004; Omkar and Pervez, 2005) but *Adalia bipunctata* (Linnaeus) is protogynous (Hemptinne *et al.*, 2001). In *P. dissecta*, the minimum age at which males mated was recorded 3 days after emergence (Pervez *et al.*, 2004). A pronounced delay in the commencement of mating was observed despite the males being sexually mature at the time of their emergence (Hodek and Honek, 1996). The delay in mating can be attributed to (i) the rejections due to the probable immature state of the female gonads (Obata, 1988) and (ii) the time taken in elytral hardening (Omkar and Srivastava, 2002). The presence of a pre-mating period is corroborated in *C. septempunctata* (Obata and Johki, 1991; Omkar and Srivastava, 2002), *Harmonia axyridis* Pallas (Obata and Hidaka, 1987; Obata and Johki, 1991) and *A. bipunctata* (Hemptinne *et al.*, 2001). The delay in mating may be an adaptation to lessen the risk of consanguineous mating (Antolin and Strand, 1992; Hemptinne *et al.*, 2001) and inbreeding depression (Morjan *et al.*, 1991). This is especially helpful as ladybird beetles are capable of dispersing from an area in a few hours after emergence (Hodek and Honek, 1996).

Mating in *C. sexmaculata* is devoid of active processes, viz. bouts and strokes, noticed in *C. septempunctata* (Omkar and Srivastava, 2002) and *Coccinella transversalis* Fabricius (Omkar, 2004; Omkar and James, 2005). Such quiescent matings are also witnessed in *P. dissecta* (Omkar and Pervez, 2005). The male is definitely stimulated by the other cues, including chemical releases of the female ladybird beetle and exhibited the five steps of mate recognition (Obata, 1987) towards 1-day-dead females, though less prominent than those displayed for live conspecific females. The presence of olfactory receptors on the antennae of male ladybird beetles almost certainly aids in perceiving chemical signals released by the females, which acts as key stimuli in triggering the male response (Wang *et al.*, 1991). This view is further strengthened by the observation that the male touches the antennae of the female with its own antennae during the process of mate recognition. Other than the chemicals released by the female, the male almost certainly recognizes the species-specific alkanes present on the cuticular surface of the female ladybird beetle (Hemptinne *et al.*, 1998), possibly via antennal contact. These alkanes might also be sex specific. Presence of such chemical cues is known to affect the oviposition in aphidophagous ladybirds (Mishra and Omkar, 2006).

The male approached, watched and examined a 1-month-refrigerated dead conspecific female, dead conspecific male and freshly dead heterospecific dummy female but did not show any copulatory attempt. The performance of these steps may be attributed to similarity in shape and size of the dummies. The reluctance of a male to attempt copulation with a conspecific freshly dead male, freshly dead heterospecific female and 1-month-old refrigerated female is perhaps due to the absence of pheromones and surface alkanes, and the consequent non-stimulation. Perhaps, visual cues also have a role to play in the reluctance displayed by male *C. sexmaculata* with a *P. dissecta* dummy. The absence of copulatory attempts for 1-month-refrigerated dead females of *C. sexmaculata* may be attributed to the absence of probable chemical cue and disfigurement due to freezing. The visual cues most likely play a lesser role than chemical or other signals as can be suggested by the observation that the male consistently ignored even the freshly dead male *C. sexmaculata* though it is similar in appearance to the female of the species.

These observations lead to the conclusion that the male *C. sexmaculata* recognizes a potential mate with the help of visual or other cues including chemical. Similar observations were also reported in *H. axyridis* (Obata, 1987), *C. septempunctata* (Omkar and Srivastava, 2002), *C. transversalis* (Omkar, 2004; Omkar and James, 2005) and *P. dissecta* (Omkar and Pervez, 2005).

Mating display in the present study exhibited the occurrence of mild pulsation on the ventral surface of abdomen of female, during the course of mating, which commenced soon after genital contact. The pulsation almost certainly facilitates the sperm transfer. *Propylea dissecta* also exhibits a similar pattern of pulsation soon after genital contact (Omkar and Pervez, 2005). The generation of pulsation has led to the inference that sperm transfer in *C. sexmaculata* starts soon after intromission.

Initialization of termination of mating by the female kicking away the male with her hind legs suggests that the female almost certainly determines the duration of mating, which is definitely governed by female satiation and/or completion of sperm transfer. This has been opined by Wang *et al.* (1990). The observations suggest that the female exhibits rejection display at the times when it is not sexually mature, has recently mated or is about to oviposit. Similar observations in ladybird beetles have also been reported earlier (Majerus and Kearns, 1989; Omkar and Srivastava, 2002; Omkar, 2004; Omkar and James, 2005).

The mating duration was maximum when an unmated male copulated with a virgin female, followed by matings between unmated male and mated female, mated male and virgin female and mated male and mated female. This indicates that the unmated male and virgin female ladybird beetles were perhaps more vigorous in comparison with mated male and mated female ladybird beetles and hence the duration of mating was maximum. The present results are in conformity with the findings in other ladybirds (Obata, 1987; Omkar and Srivastava, 2002; Omkar, 2004; Omkar and James, 2005; Omkar and Pervez, 2005). The more prominent effect of male sexual status on the mating durations reveals mating duration to be male dominated, but the observed kicking behaviour of the female for the termination of mating suggests that under certain conditions the female also plays an important role in determining the mating duration. Mating duration to be male dominated is further supported by previous findings by Obata (1987) and Omkar and Pervez (2005).

Maximum fecundity, oviposition period and percentage of hatchability were recorded after multiple matings as compared with one, two and three matings. Multiple matings increased the oviposition period and enhanced the total egg output and percentage of hatchability, most likely by enhanced fertilization owing to increased and frequent supply of sperm. The findings are in conformity with those reported earlier in other ladybird species (Obata, 1987; Obata and Johki, 1991; Omkar and Srivastava, 2002; Omkar, 2004; Omkar and James, 2005; Omkar and Pervez, 2005). The subsequent and frequent matings are certainly needed for maximum egg outputs during the life span of ladybird beetle species like *Harmonia quadripunctata* (Pontoppidan) (Majerus, 1994) and *Cryptolaemus montrouzieri* Mulsant (Kaufmann, 1996). However, multiple matings have certain costs, especially in terms of decreased longevity with increased number of matings, but they increase the fecundity and fertility of ladybirds (Omkar and Mishra, 2005). Similarly, multiple matings and promiscuity are reported to enhance the fecundity and fertility in ladybirds (Srivastava and Omkar, 2005; Omkar and Mishra, 2005). Optimal number of matings in the ladybirds *C. sexmaculata* and *P. dissecta* have also been worked out for better reproductive output (Omkar *et al.*, 2006).

Conclusions

This study revealed that: (i) *C. sexmaculata* shows protandry as males mate at the age of 2 days and females start oviposition after 4 days, (ii) the visual cues seem to be of more importance for the initial orientation towards the mate, (iii) chemical or other cues might be responsible for courtship displays and mating, (iv) mating seems to be male dominated, at least in a Petri dish environment as 2-day-old males succeeded in mating with immature females, (v) mating duration is affected by the sexual status of both the sexes but more pronounced by the status of male, (vi) in certain conditions (e.g. satiation), females also determine the duration of mating by kicking away the male with their hind legs and (vii) multiple matings are responsible for increased oviposition period, fecundity and hatching percentage.

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