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Mating behavior of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant)

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Abstract The mating behavior of *Propylea dissecta* (Mulsant) was investigated in detail. Protandry was evident, as males mature earlier than females. Predicted age of sexual maturation of male and female ladybirds was 7.12 and 9.33 days, respectively. Males performed courtship in six steps, *viz*. approach, watch, examine, embrace, mount and attempt. Embrace is possibly an appeasement act, while examine serves to recognize mate. Chemical signals initiate male attraction toward females. Visual and tactile cues appear to secondarily help in mate recognition. Mating lasted longest (275.40 ± 12.23 min) when it occurred between unmated individuals. It was much shorter (176.60 ± 5.60 min) when prior mated individuals copulated. There was a significant decrease in mating durations when adults were subjected to five successive matings. Fecundity and percent egg viability increased significantly with increase in the number of matings.

Key words *Propylea dissecta*, Coccinellidae, reproduction, mating, behavior
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Introduction

The intensive research on prey-predator interactions of ladybirds, owing to their practical relevance in biocontrol, means there has been lesser attention on their mating behaviors (Hodek & Ceryngier, 2000). Most of the studies pertaining to sexual activities have been modeled on the two-spotted ladybird, *Adalia bipunctata* (Linnaeus) with much emphasis on mate choice (Muggleton, 1979; Majerus *et al.*, 1982; Kearns *et al.*, 1992; Tomlinson, 1996). A few have emphasized the mate-recognition cues and the importance of critical age for mating (Hemptinne *et al.*, 1998, 2001). It appears that both behavioral and chemical cues are involved in mate recognition (Hemptinne *et al.*, 1998). The role of chemical cues using dead models was inconclusively discussed in regard to other ladybirds (Obata, 1987; Omkar & Srivastava, 2002).

Ethological studies on mating revealed that the males' energies are largely consumed in their search for potential mates, and on encountering, they perform pre-mating displays and thereafter copulate (Obata, 1987; Omkar & Srivastava, 2002; Omkar, 2004). Mating affects the reproductive performance, with promiscuity enhancing fecundity (Majerus, 1994a).

Though *A. bipunctata* has been largely used as a model for studies pertaining to sexual activities, other economically important ladybirds have been rarely studied. *Propylea dissecta* (Mulsant) is an aphidophagous ladybird beetle native to India having well-marked sexual dimorphism (Omkar & Pervez, 2000, 2004). *Propylea dissecta* preferentially prey on aphid, *Aphis gossypii* Glover, over other aphid species and can easily adapt themselves against stressful condition of prey deprivation (Omkar & Pervez, 2003; Pervez & Omkar, 2004). The influence of its age on reproductive performance has recently been investigated (Pervez *et al.*, 2004). However, no information is available on its mating behavior. Thus, the present study was designed to investigate age-specific mating incidences to evaluate critical ages for sexual maturation, mating behavior, cues involved in mate recognition, and effects of previous and multiple matings on reproductive performance.

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Materials and methods

Stock maintenance

Adults of *P. dissecta* were collected from the agricultural fields of Lucknow, India and brought to the laboratory. Stock culture was maintained in the laboratory (at 25 ± 1 ℃ and 65% ± 5% relative humidity) in glass jars (14.0 cm height and 10.0 cm diameter), providing sufficient quantity of *A. gossypii*, its suitable prey, infested on leaves of *Lagenaria vulgaris* Seringe.

Age-specific mating incidence

Newly emerged (NE) adults of *P. dissecta* were sexed on the basis of certain patches on their heads and pronotum (Omkar & Pervez, 2000) and the individuals of two sexes were isolated in Petri dishes (11.0 cm diameter, 2.0 cm height) containing *A. gossypii* on tender twigs of *L. vulgaris* for 1, 2, 3, 4, 5, 10, 20 and 30 days. A NE (8-hour-old) unmated male was paired with a NE (8-hour-old) virgin female in a Petri dish at 1000 hours. They were observed continuously for the next 30 min and thereafter every half-hour until 1800 hours. Timing of the observation was suitable as mating lasts for 3-6 hours (Pervez, 2002). The experiment was repeated ten times (n=10). Similarly, NE males were placed with virgin females, which were 1, 2, 3, 4, 5, 10, 20 and 30-days-old. The experiment was repeated, using 1, 2, 3, 4, 5, 10, 20 and 30-day-old unmated males. The mating incidence in relation to different ages was observed using each ladybird only once. The proportion of mating incidences at different ages of adults were analyzed by chi-square tests. Mating proportion was correlated with the age of ladybirds and the predicted age of sexual maturation of male and female was determined by an eye fit curve to a point where 50% of mating occurred, following Hemptinne *et al.* (2001). This experiment helped us to evaluate critical ages of the two sexes of *P. dissecta* to design further experiments.

Mating behavior

A nine-day-old sexually mature unmated male was kept along with a ten-day-old sexually mature virgin female (space and prey as above). Pre-mating behavior of the male ladybird was studied under a WILD stereoscopic binocular at 6.4 ×, 16 × and 40 × magnifications. The entire mating and its termination were carefully observed in ten replicates (n=10).

Behavior of male ladybird with dead models

Six dead models of male counterparts were used to study the cues responsible for mate recognition by male ladybirds. The models were: (i) freshly dead female; (ii) 1-day-long dead female; (iii) 7-day-long dead female; (iv) 1-month-long dead female; (v) freshly dead male; and (vi) freshly dead *Cheilomenes sexmaculata* (Fabr.) female (heterospecific). Dead models were prepared by freezing 10-day-old mature females and males (used as model no. v) to death at −10℃. They were refrigerated to prevent them from microbial attack and to protect their bodies from mutilation. A sexually mature (20-day-old) unmated male was introduced in each Petri dish (as above) containing the dead model (one model per Petri dish), placed in the centre and his behavior was observed for 1 hour (n=10). If the male mated with the dead model, the mating duration was recorded.

Effect of previous and consecutive matings on mating duration

To study the effect of previous matings, four sets of mating pairs were arranged in accordance with the adult sexual status. These were: (i) 10-day-old unmated male with 10-day-old virgin female; (ii) 15-day-old mated male with 10-day-old virgin female; (iii) 10-day-old unmated male with 15-day-old mated female; and (iv) 15-day-old mated male with 15-day-old mated female (Mated individuals used had mated five time previously). Two sexes were kept with prey in the usual space and allowed to mate. Mating duration in each set was recorded (n=10) and subjected to one-way ANOVA following a statistical package MINITAB using a PC. A comparison of *F*-values of ANOVA was made to evaluate the role of sexual status of male and female on the mating durations. To study the effect of consecutive matings, 10-day-old unmated adults were paired (space and prey as usual). They were subjected to consecutive matings, *viz.* 1, 2, 3, 4 and 5 on different days. Mating duration was recorded after each mating and subjected to one-way ANOVA (n=10). Differences between means of activity were calculated using Tukey' s honest significant test at 5% level.

Effect of mating(s) on oviposition, fecundity and egg viability

Four sets of 10-day-old unmated adults were paired (space as usual). From these, the males were removed after one, two, three and multiple matings, respectively. Thereafter, the females in each set were observed for their lifetime to record the oviposition period, fecundity and percent egg viability (prey as usual). The experiment was replicated ten times and data were analyzed by one-way

ANOVA using MINITAB. Differences between means of performances were calculated using Tukey' s honest significant test at 5% level.

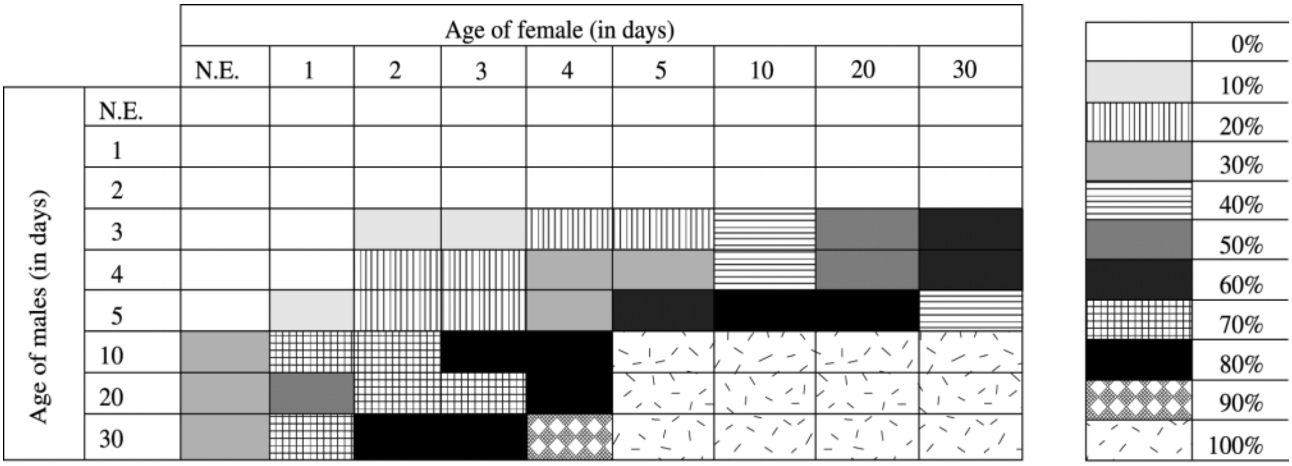
Results

Age-specific mating incidence

Three-day-old males of *P. dissecta* started mating and the mating incidence increased from 10% to 60% with increase in female age from 2 to 30 days, respectively (Fig. 1). Mating in 3- to 5-day-old males commenced earlier (within 5 minutes to 3 hours) when paired with 10- to 30-day-old females than those of the same age (2−5 hours). Ten- to 30-day-old males responded quickly to 5- to 30-day-old females (mating started within 0.1−5.0 min after pairing), which culminated in 100% mating incidence.

Mating incidences in younger males (3-to 5-day-old) with females of increasing age were statistically significant ($P < 0.001$, n=10) (Table 1), while those of older males (10- to 30-day-old) were not. Mating incidences in younger females (2- to 4-day-old) were statistically significant ($P < 0.05$, n=10), while those of older females (10- to 30-day-old) were not significant, with males of increasing age (Table 1).

Best fit lines drawn in Fig. 2 followed a curvilinear pathway when the proportion of individuals mated at a particular age was correlated with the adult age. The predicted age of sexual maturation in male and female ladybirds was 7.12 and 9.33 days, respectively, which revealed protandry.



N.E.=Newly Emerged (8-hour-old)

Fig. 1 The percent mating incidence amongst male and female of different ages of *P. dissecta*.

Table 1 The number of male and female *P. dissecta* that mated with their counterparts of varying ages (n=10).

Male age(day)	Female age (day)									χ^2 test
	NE	1	2	3	4	5	10	20	30	
NE	−	−	−	0	0	0	0	0	0	−
1	−	−	−	0	0	0	0	0	0	−
2	−	−	−	0	0	0	0	0	0	−
3	−	−	−	1	2	2	4	5	6	23.90**
4	−	−	−	2	3	3	4	5	6	23.90**
5	0	1	2	2	3	6	8	8	4	17.30**
10	3	7	7	8	8	10	10	10	10	0.80
20	3	5	7	7	8	10	10	10	10	0.93
30	3	7	8	8	9	10	10	10	10	0.50
χ^2 test	6.37	12.40*	8.60*	8.60*	5.80	1.60	0.40	0.40	3.60	

NE, newly emerged (8-hour-old); $^*P < 0.05$, $^{**}P < 0.001$.

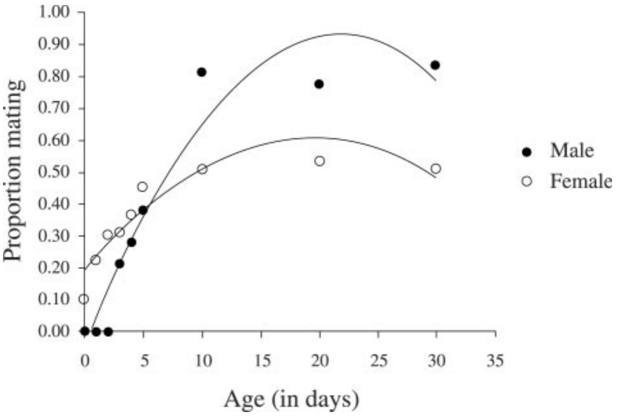


Fig. 2 Proportion of matings amongst male and female *P. dissecta* of different ages.

Mating behavior

A virgin male ladybird when placed with a virgin female, located and came close to her (*Approach*). He paused for a few second(s) (ranging 1–5 sec) and watched her (*Watch*) from 1.0–1.5 cm. The male examined her with antennae (*Examine*) and leaned on the postero-lateral aspect of the female's body for a few minutes (2–13 min). The leaning of the male appeared like an embrace and so may be referred to as such. Thereafter, he mounted from the posterior end of her body (*Mount*). During mounting, the receptive females (n=8), remained motionless. However, on two occasions, she refused to mate by moving away and the male displayed counter-courtship by encircling around the female, perhaps to calm or appease or prevent the female from escaping. Thereafter, he mounted over her body, bent the tip of his abdomen downwards and inserted his aedaegus into the female genitalia and made copulatory attempts (*Attempt*), culminating to genital contact.

Vigorous bouts and strokes, as reported in other ladybirds, were not observed. However, there was a mild rhythmic pulsation in the lower abdomen of the male after the commencement of mating, owing to discontinuous protraction and retraction of aedeagus. The male ladybird occasionally drummed the female elytra with his forelegs. During mating, the female occasionally: (i) moved carrying the male on her back to find a suitable substratum; and (ii) preyed on *A. gossypii*.

Mating terminated as the female kicked the male. She also moved randomly to terminate mating and dislodge the male. After de-pairing, the female moved quickly and randomly away from the male (n=9); however, one female cleaned her mouthparts and antennae with her forelegs, while, the male rubbed and cleaned his mouthparts and antennae with his forelegs (n=10).

Behavior of male ladybird with different dead models

Pre-mating steps of the male beetle to dead models are listed in Table 2. Males mated with the freshly dead, 1-day and 7-day-old dead females. Mating duration increased with increase in age of the dead female (Table 2). Male beetles did not go further after examination of freshly dead heterospecific females and conspecific males. They approached, watched and moved away when a one-month dead female was provided.

Effect of previous and consecutive matings on mating duration

Sexual status significantly affected mating duration ($F = 23.16$, $P < 0.001$). Mating lasted longest (275.40 ± 12.23 min) when unmated individuals copulated and shortest (176.60 ± 5.60 min) when prior mated individuals copulated (Table 3). The difference in mating duration between unmated individuals when compared to that

Table 2 Courtship and mating displays of male ladybeetles when provided with dead mates (n=10).

Dead models	Events of courtship[†]							Mating duration (mins)
	A	W	E	Eb	M	At	Mt	
Freshly dead female	10	4	2	2	9	9	6	222.50 ± 19.00
1-day dead female	10	5	3	2	5	5	4	284.50 ± 22.50
7-day dead female	5	5	5	3	4	4	3	373.67 ± 9.53
1-month dead female	5	3	0	0	0	0	0	–
Freshly dead heterospecific female	9	9	4	0	0	0	0	–
Freshly dead male	5	5	3	0	0	0	0	–

A=Approach, W=Watch, E=Examine, Eb=Embrace, M=Mount, At=Attempt, Mt=Mated.

[†] The values in this table indicate the number of males out of ten replicates performing the particular courtship or mating acts.

Table 3 Effect of sexual status on the mating duration of *P. dissecta.*

Mating status	Mating duration (mins)
Unmated male and virgin female	275.40 ± 12.23 a
Unmated male and mated female	259.30 ± 10.18 b
Mated male and virgin female	210.40 ± 8.36 c
Mated male and mated female	176.60 ± 5.60 d
F-value	23.16*

*$P < 0.001$, Different letters denote that data are statistically significant(Tukey’ s Test; range = 3.81; df = 39).

Table 4 A comparison of analysis of variance (One way) of the mating durations when the unmated individuals of *P. dissecta* copulated with their mated counterparts.

Comparison			*F*-value
Virgin female & unmated male	v/s	Mated female & unmated male	$F = 1.02$ (N.S.)
Virgin female & unmated male	v/s	Virgin female & mated male	$F = 19.26$ $P < 0.001$

(Tukey’ s Test; range = 2.97; df = 19)

between unmated males and mated females, was not significant. However, the difference in mating durations was significant ($F = 19.26$, $P < 0.001$) when compared between unmated individuals with mated males × virgin females (Table 4). Mating duration decreased significantly ($F = 16.10$, $P < 0.001$) with increase in successive matings (Fig. 3).

Effect of number of matings on female reproductive attributes

The differences in oviposition periods were not significant when individuals mated once, twice, thrice or multiple times. However, oviposition period increased with increase in number of matings (Table 5). Fecundity ($F = 43.62$, $P < 0.001$) and percentage egg viability ($F = 13.18$, $P < 0.001$) increased significantly with increase in number of matings.

Discussion

Males of *P. dissecta* started mating when 3 days old, which revealed the incapability of NE to 2-day-old males to mate, perhaps owing to the lack of elytral hardness and probable immature gonads. The incapability of males to mate in *Coccinella septempunctata* L. was also attributed to the delay in elytral hardening (Omkar & Srivastava, 2002). Younger males were more responsive towards older females as indicated by the earlier initiation of mating. The initial attraction of the former towards the latter may probably be a result of increased release of pheromones by older and mature females. A similar pattern of mating incidences was observed in *A. bipunctata* (Hemptinne *et al.*, 2001) and in the green capsid bug, *Lygocoris pabulinus* (L.) (Groot *et al.*, 1998). The older males (20 to 30 days old) were efficient mating models, owing to their willingness to mate. They utilized relatively lesser time to recognize their potential mate with very brief or almost no courtship compared to younger males.

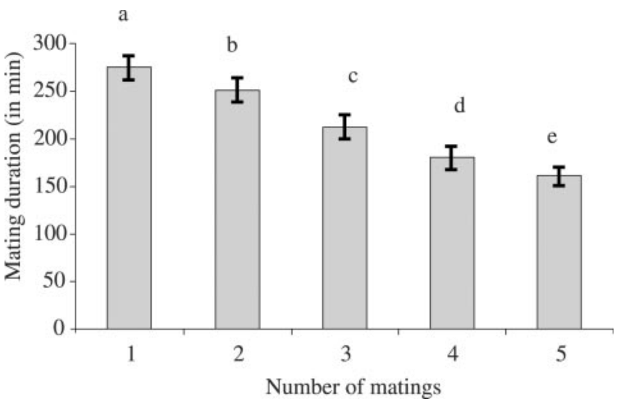


Fig. 3 Effect of consecutive matings on mating duration (n=10); bars with different letters are significantly different ($P < 0.001$).

Mating occurrence in NE females (having unhardened elytra and incomplete pigmentation) is a feature in *P. dissecta,* as 30% mating occurred when paired with 10- to 30-day-old males. The finding disagrees with earlier reports, regarding unresponsiveness of males towards NE females, owing to the lack of pigmentation and unhardened elytra (Obata, 1988; Majerus, 1994b; Hodek & Honek, 1996). Obata (1988) in particular discussed that newly emerged females of *Harmonia axyridis* (Pallas) remained unattractive for 2 days. In a ladybird, *Leptothea galbula* (Mulsant), males were strongly attracted towards female pupae, perhaps due to the release of chemicals by the latter (Richards, 1980). Thereafter, when the female emerged, the male mounted over her, but mating occurred only after hardening of the female’s elytra, (*i.e.*, 1 h after eclosion) (Richards, 1980).

Though NE and young females exhibited mating refusals, they were forced to mate by the over-persuasion of excited older males. Similar refusals have been reported earlier in *H. axyridis* (Obata, 1987), *C. sexmaculata* (Bind, 1998), *Coccinella transversalis* Fabr. (James, 2001) and *C. septempunctata* (Omkar & Srivastava, 2002). This overpowering of young females reveals the dominance of males in mating. Omkar and Srivastava (2002)

Table 5 Effect of one, two, three and multiple matings on the reproductive attributes of *P. dissecta.*

Mating (s)	Oviposition period (in days)	Fecundity	Egg viability (% in eggs)
One	46.60 ± 5.41 a	278.30 ± 35.65 a	65.03 ± 5.39 a
Two	52.20 ± 3.74 ab	349.80 ± 23.00 b	72.42 ± 2.97 ab
Three	55.70 ± 3.32 bc	472.70 ± 29.09 c	77.79 ± 2.06 b
Multiple	61.00 ± 2.67 c	710.20 ± 25.42 d	93.01 ± 0.66 c
F-value	2.38	43.62*	13.18*

*Significant at $P < 0.001$. Different letters denote that data are statistically significant (Tukey' s Test; range = 3.81; df = 39).

reported the physiological status of males to be a crucial aspect in the sexual activity in ladybirds, which was corroborated by 1% to 10% mating in 1-to 2-day-old immature females of *A. bipunctata* when paired with older males (Hemptinne *et al.*, 2001). The gradual acceptance towards mating increased with female age.

Protandry in *P. dissecta* agrees with earlier reports on *H. axyridis* (Obata, 1987), *C. sexmaculata* (Bind, 1998), *C. transversalis* (James, 2001) and *C. septempunctata* (Omkar & Srivastava, 2002). The difference in sexual maturity in the two sexes based on post-emergence refractory period reduces the risk of sibling mating (Antolin & Strand, 1992) and incidence of inbreeding depressions (Morjan *et al.*, 1999). The early mating in immature females may be advantageous in a bid to store the sperm for a short period in the spermathecae to facilitate fertilization of ova on becoming sexually mature (Hemptinne *et al.*, 2001).

Pre-mating behavior of the male *P. dissecta* was almost similar to that reported in *H. axyridis* (Obata, 1987), *C. septempunctata* (Omkar & Srivastava, 2002), *C. sexmaculata* and *C. transversalis* (Omkar, 2004). But in addition to five positions described by Obata (1987) in *H. axyridis*, a very peculiar *Embrace* position has been recorded in *P. dissecta*, which is possibly an act of appeasement of females by the males as also reported in other insects and spiders (Omkar *et al.*, 2000, 2001). Occasional drumming of female elytra by the male may also be a part of appeasement. Maisin *et al.* (1997) observed that the male *C. sexmaculata* "licks" the dorsal elytral surface of the female by his maxillary palps. Such behavior was also noticed by Rodriguez (1995) in Tenebrionidae and is considered a part of the copulatory courtship. It is known that copulatory courtship in insects induced the female to remain still during copulation and post-copulation (Maisin *et al.*, 1997).

Mostly, when courted by males, the females remained motionless, which indicates the readiness of females to mate, as is also reported by Hemptinne *et al.* (1998). There was pulsation in the lower abdomen of the male as soon as genital contact was established, which probably facilitated sperm transfer, as is also reported in *C. sexmaculata* (Obata & Johki, 1991). This occurrence of pulsation led to the inference that sperm transfer possibly starts soon after the genital contact. The mechanism of sperm transfer is delayed in the cases of *H. axyridis* (Obata & Johki, 1991), *C. septempunctata* (Obata & Johki, 1991; Omkar & Srivastava, 2002) and *C. transversalis* (James, 2001; Omkar, 2004); the time taken in sperm transfer following a genital contact is referred to as the latent period.

Lesser pre-mating displays by males with freshly dead models rather than 1- and 7-day dead models suggests that chemical factors that initiate the male copulatory behavior, may be still present on these models, as in some cases males seemed to recognize their potential mates without any contact. More examination of 7-day dead models could be due to probable fading of chemical signals, which troubled the males in recognizing mates. This is strengthened by the fact that only half the number of males who approached these models and examined them. One-month dead models were almost universally neglected by males, which indicates the probable removing of chemical signals by that time.

The shape and size of the female' s body appeared to have played a secondary role in mate recognition, which is evident by the behavior of the male towards the freshly dead heterospecific female. Almost half the number of males examined these models and moved away after recognizing them as heterospecifics. The reasons for the male approaching the freshly dead female are unclear; however, it can be said that a probable release of certain pheromones by the males may also have some effect.

Mating with dead females is a surprising feature in the present study. It is not a natural occurrence in the field, as it may be difficult for the males to find the mate in the absence of chemical signals, which are largely considered to play a major role in mate-recognition (Hemptinne *et al.*, 1998). In addition, the dead bodies of females easily get disintegrated and decay in the field. However, in laboratory conditions, mating with a dead female might be due to the confined experimental arena, the high sexual urge of unmated males, non-disintegrated female bodies, and no other mate option for the sexually aroused male ladybirds. Mating with dead females up to a certain period suggests that possibly the chemical signals were still present on their bodies, which stimulated the males and stiffening of genital pouch has not taken place. It decreased with the passage of time, possibly on account of stiffening of the body in general, and the genitalia in particular. Prior to this observation, mating with dead bodies has not been recorded in Coccinellidae.

Mating duration is largely dependent on the sexual status of ladybirds, as it was longest in unmated adults. It was more dependent on male sexual status, which may also be attributed to the degree of mate deprivation (Pervez *et al.*, 2004). The oviposition period was not significantly dependent on multiple matings, though it increased with increase in number of matings. It appears that on providing mating, females can lay eggs for a considerable duration with essential prey, as a prerequisite. In some species, single mating is sufficient for lifetime fertility (Hodek & Honek, 1996). Fecundity increased significantly with the number of matings, as the sizes of egg clusters were reduced when the female mated once, while the reverse was the case with females that mated multiple times. Semyanov (1970) found that the oviposition rate in *A. bipunctata* constantly decreased after the first mating but increased again when provided with a new mating stimulus. Egg viability was also significantly affected, as egg clusters laid in the later phase of the oviposition period failed to hatch in the event of single mating. This may be attributed to the limited amount of sperm that is stored in the spermathecae, resulting in single mating not being sufficient for lifetime fertility. Thus, repeated matings are required to maximize fecundity and egg viability and the latter appears to be a male-dependent function.

Thus, it can be concluded: (i) there is protandry in *P. dissecta*; (ii) six pre-mating steps, *viz*. approach, watch, examine, embrace, mount and attempt, were recorded; (iii) *Embrace* is an additional step, not reported earlier in mating behavior of ladybird-appeasement act as performed by males; (iv) *Examine* serves to recognize the potential mate; (v) chemical signal appears to initiate the attraction of males towards females, thereafter, visual and tactile cues secondarily help in mate recognition; (vi) mating with the dead females in Coccinellidae has been recorded for the first time; (vii) mating duration is male sexual status-dependent: unmated males copulated longer than mated ones; and (viii) egg viability is male-dependent.

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