

Effect of presence and semiochemicals of conspecific stages on oviposition by ladybirds (Coleoptera: Coccinellidae)

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Abstract. Reduced oviposition by ladybirds in the presence of tracks of fourth instar larvae owing to the presence of oviposition deterring pheromones is well established across many genera. However, deterrence, if any, by other life stages has not been well investigated, in particular the effect of conspecific presence. The present study investigates the effects of conspecific presence and semiochemicals of conspecific life stages (eggs, fourth instar larvae, pupae, adult males and females) on oviposition by five ladybird (Coleoptera: Coccinellidae) species, viz. *Coccinella septempunctata*, *Coccinella transversalis*, *Cheilomenes sexmaculata*, *Propylea dissecta* and *Aneleis cardoni*. Results reveal that the presence of life stages inhibits oviposition and the inhibition is density-dependent, although the degree of inhibition is species-specific. Surface semiochemicals of eggs and larval and adult tracks also show density-dependent inhibitory effects. Moreover, the semiochemicals in tracks (oviposition deterring pheromones) and egg surface semiochemicals are not similar, indicating semiochemical parsimony. Of all species tested, *C. transversalis* and *C. septempunctata* were the most and the least responsive to both conspecific presence and semiochemicals, respectively.

INTRODUCTION

Oviposition site selection is a critical determinant of female fitness. A suitable oviposition site is postulated to have: (a) an optimum microclimate for embryonic development, (b) availability of food in proximity for offspring, and (c) low probability of parasitism, predation or pathogenic infection (Pasteels et al., 1986; Dixon, 2000; Seagraves, 2009). During the selection of suitable oviposition sites, coccinellid females may evaluate: (a) patch quality and quantity of food (Hemptinne et al., 2000a; Fréchette et al., 2006; Oliver et al., 2006), (b) the cost of inter-patch movement (in energy and time), and (c) mortality risks (Hilker & Meiners, 2002; Seagraves, 2009).

The process of oviposition site selection and its consequences have led to the application of optimal foraging theory to aphidophagous ladybirds (Kindlmann & Dixon, 1993; Dixon, 1997), and the postulation of an “oviposition window” in the exponential growth phase of the aphid population. Oviposition in this window is hypothesized to optimize offspring development and survival and thus female fitness (Dixon, 2000). The opening of this window is determined by the minimum density of aphids required for complete development of larvae (Dixon, 1959; Evans & Dixon, 1986). Honeydew (Wiedemann et al., 2004; Kazana et al., 2007), aphid alarm pheromones (Pettersson et al., 1995, 2008; Quiroz et al., 1997), plant volatiles released in response to infestations (Zhu et al., 1999; Birkett et al., 2000; Zhu & Park, 2005; Alhmedi et al., 2010) and species-specific plant substances (Schaller & Nentwig, 2000; Pettersson et al., 2005) may all serve to

orient ladybirds towards aphid patches (Hatano et al., 2008; Petterson et al., 2008).

The closing of the window is determined by the maturation of aphid colony (Kan, 1988a, b), as indicated by the presence of alate aphids (Kan & Sasakawa, 1986) and larval tracks (Růžička, 2001a, 2003; Magro et al., 2007, 2010). The inhibitory effect of the presence of conspecific larvae on oviposition was first reported in *Adalia bipunctata* (Linnaeus) (Hemptinne & Dixon, 1991). Thereafter, the oviposition deterring effects of larval tracks have been identified in a number of ladybirds (Růžička, 1997, 2001a, b, 2002, 2003, 2006; Yasuda et al., 2000) and that of adult tracks in *Propylea dissecta* (Mulsant) (Mishra & Omkar, 2006). The effect of oviposition deterring pheromone (ODP) has been most intensively studied in coccinellids but in such arenas that allowed contact with conspecific females, a situation that has been shown to affect oviposition behavior in aphid parasitoids (Michaud & Mackauer, 1995) and coccinellids (Hemptinne et al., 1993; Mishra & Omkar, 2006), with an increased incident of superparasitism being observed in the former. To account for the possibly important influences of prey, host plant and conspecific interference, Yasuda et al. (2000) and Michaud & Jyoti (2007) studied oviposition responses by solitary females to larval tracks in *Harmonia axyridis* (Pallas) and *Coccinella septempunctata* Linnaeus, and *Hippodamia convergens* Guerin respectively, in the presence of host plants and aphids. It is also now known that the secretion of ODP takes place from the anal disk on the 10th abdominal segment of larvae (Laubertie et al., 2006). Hemptinne et al. (2001) attributed ODP effect to a mixture of discovered alkanes

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TABLE 1. Two way ANOVA showing the effects of egg density, clustering pattern and their interactions on oviposition.

Ladybird species	Factors	F-value	P-value	DF
<i>C. septempunctata</i>	Egg density	12.09	0.001	4, 99
	Clustering pattern	402.88	0.001	1, 99
	Egg density \times Clustering pattern	0.53	0.312	4, 99
<i>C. transversalis</i>	Egg density	15.72	0.001	4, 99
	Clustering pattern	0.83	0.365	1, 99
	Egg density \times Clustering pattern	0.14	0.968	4, 99
<i>C. sexmaculata</i>	Egg density	12.02	0.001	4, 99
	Clustering pattern	0.98	0.325	1, 99
	Egg density \times Clustering pattern	0.38	0.822	4, 99
<i>P. dissecta</i>	Egg density	5.46	0.001	4, 99
	Clustering pattern	15.72	0.001	1, 99
	Egg density \times Clustering pattern	1.12	0.354	4, 99
<i>A. cardoni</i>	Egg density	12.02	0.001	4, 99
	Clustering pattern	4.54	0.036	1, 99
	Egg density \times Clustering pattern	1.90	0.673	4, 99

with the major component n-pentacosane. In a recent study, (z)-Pentacos-12-ene, was found to be solely an ODP of *Cheilomenes sexmaculata* (Fabricius) (Klewer et al., 2007). The predominantly alkane constituents of ODP have been attributed as the reason for the long lasting signal (Hemptinne et al., 2001). Studies on *A. bipunctata* (Doubbia et al., 1998) and *P. dissecta* (Mishra & Omkar, 2006), indicate the effects of ODP to be density-dependent and not age or sex-specific. Further, the response of *A. bipunctata* to ODP has been found to be modified by age and experience of the ovipositing female (Fréchette et al., 2004).

The oviposition deterrence of larval tracks also extends to heterospecifics (Růžicka, 2001a; 2003; Magro et al., 2007, 2010). The ODP primarily signals the presence and density of larvae in a patch, thereby allowing assessment of predation and cannibalism risk to eggs that may be laid (Martini et al., 2009; Moser et al., 2010; Meisner et al., 2011). Studies indicate that the deterrence induced by ODP is more prominent amongst conspecifics than heterospecifics owing to qualitative similarity; the closer the phylogenetic relations, the more the deterrence (Michaud & Jyoti 2007; Magro et al., 2007, 2010).

Most of the studies on oviposition deterrence in ladybirds have concentrated on larval presence (primarily semiochemical presence, but a few with actual presence) and have ignored the possible role of other life stages in the process. Only a few studies discuss the role of egg (Hemptinne & Dixon, 1991; Hemptinne et al., 1993), pupal (Hemptinne & Dixon, 1991) or adult presence (Hemptinne et al., 1992, 1993; Mishra & Omkar, 2006) and/or their semiochemicals in influencing oviposition (Doubbia et al., 1998; Mishra & Omkar, 2006). Previous studies have found no influence of egg and pupal presence on oviposition (Hemptinne & Dixon, 1991; Hemptinne et al., 1993). Adult ladybirds known to leave tracks include *Epilachna vigintioctomaculata*, *Epilachna vigintioctopunctata* (Fabricius) and *C. septempunctata* (Kosaki & Yamaoka, 1996; Nakashima et al., 2004).

These were found to cause no oviposition deterrence in *A. bipunctata* (Doubbia et al., 1998), whereas the opposite was observed in *P. dissecta* (Mishra & Omkar, 2006).

In view of the ambiguity on oviposition deterrence by the presence of adults or their semiochemical residues, and the lack of information on deterrence by most life stages in five locally abundant ladybird species, viz. *Aneleis cardoni* (Weise) (Ac), *C. sexmaculata* (Cs), *C. septempunctata* (C7), *Coccinella transversalis* Fabricius (Ct) and *P. dissecta* (Pd), the present study was undertaken. We studied here the role of varying densities of actual and semiochemical presence of conspecific life stages (egg, fourth instar larvae, pupae, adult males and females) on oviposition deterrence. We hypothesized that the presence and/or semiochemicals of motile stages (i.e., larvae and adults) will deter oviposition, whereas that of the eggs and pupae would not, as they do not pose any danger of cannibalism to eggs.

MATERIAL AND METHODS

Stock maintenance

Approximate 50 adults each of Ac, Cs, C7, Ct and Pd were collected from agricultural fields surrounding Lucknow, India (26°50'N, 80°54'E). They were paired for mating in transparent plastic Petri dishes (9.0 \times 2.0 cm) containing pea aphid, *Acyrtosiphon pisum* (Harris) (on the host plant *Vigna unguiculata* taken from glasshouse cultures 21 \pm 1°C; 65 \pm 5% R.H.) under laboratory conditions (27 \pm 1°C; 65 \pm 5% R.H.; 14L : 10D). Males were removed after mating. Food was replaced and the eggs laid were collected every 24 h and incubated under the above abiotic conditions until hatching. The larvae were reared until adult emergence in plastic beakers (14.5 \times 10.5 cm; 5 larvae per beaker). The requisite stages were taken from the stock culture for experiments.

Experimental design

Presence of conspecific eggs

A single 10-day-old conspecific once-mated female (referred to hereafter as focal female) was weighed (Sartorius CP225-D; 0.01mg precision) and placed in a Petri dish (14.5 \times 1.5 cm) containing 5 freshly laid conspecific eggs (< 12 h old) in cluster

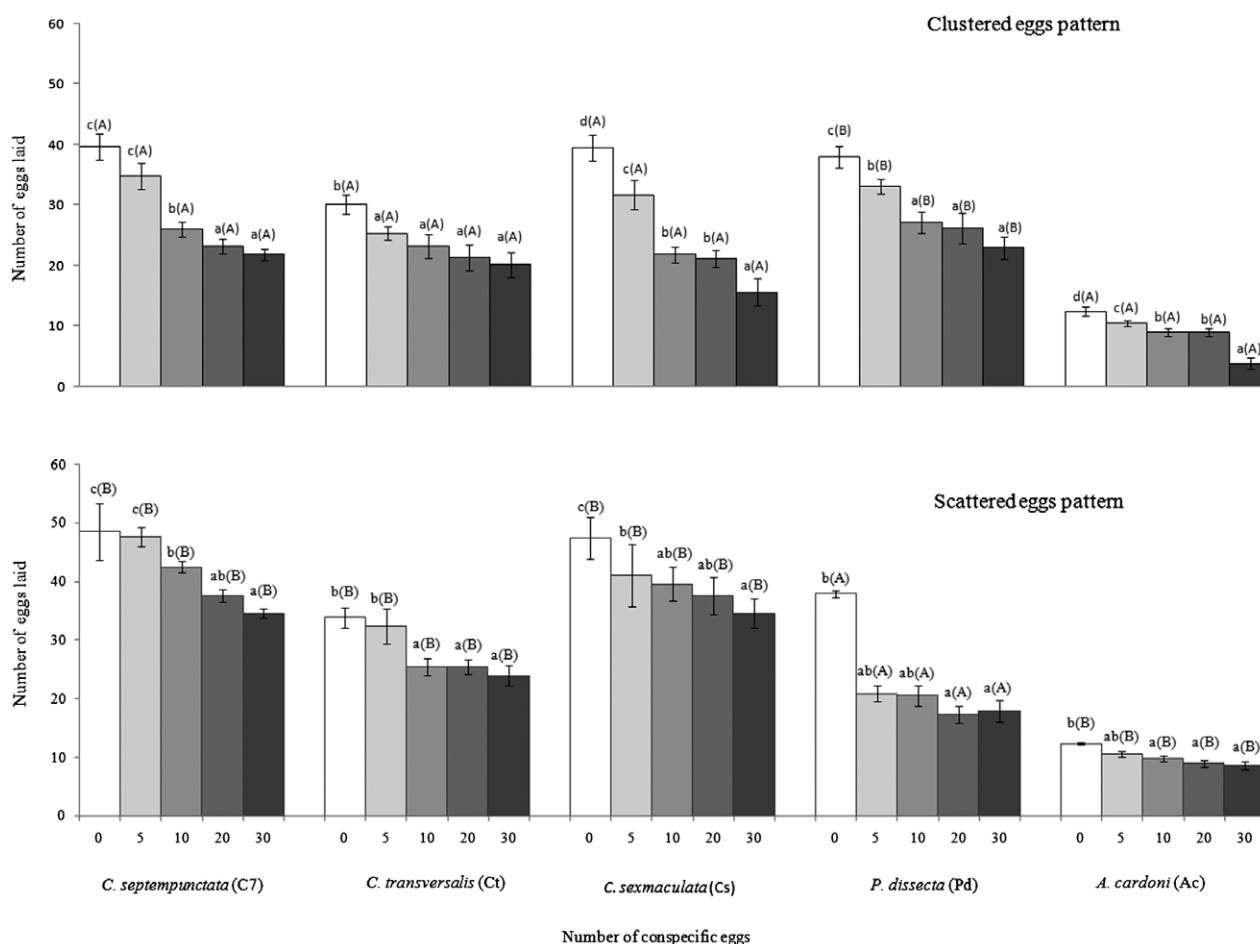


Fig. 1. Mean (\pm SE) numbers of eggs laid in 24 h by 10 d-old female coccinellids ($n = 10$) of five species in 14.5×1.5 cm Petri dishes in the presence of aphids and different numbers of conspecific eggs arranged in clustered and scattered pattern. Values are Mean \pm SE. For each ladybird species, small and large alphabets (placed in parentheses) represent comparison of means between different egg density levels within and between egg patterns, respectively. Similar alphabets indicate lack of significant differences amongst means of a species.

in the centre of the dish. Eggs were removed and placed with the help of wet fine camel hair brush. Aphids (50 mg freshly weighted, without plant material) were provided along with the eggs. After 24 h the number of eggs laid, amount of aphids consumed, and weight of the females were recorded. The same treatment was repeated with an equal number of eggs dispersed (scattered) in the Petri dish, to assess the effects of clustering pattern on oviposition, if any. The placement of eggs was recorded with a marker pen.

The above treatments were repeated with 10, 20 and 30 eggs in all five ladybird species ($n = 10$ per treatment). For the control, females were placed in Petri dishes containing equal amount of aphids but no eggs and the same observations were recorded.

Presence of conspecific larvae, pupae, adult males and females

A single 10-day-old focal female was weighed and placed in a Petri dish (14.5×1.5 cm) containing 2 conspecific well fed fourth instar larvae along with 50 mg of aphids per insect. After 24 h, number of eggs laid, amount of aphids consumed and body weight of females were recorded. The treatment was repeated with 4 and 6 fourth instar larvae in each of the five ladybird species (food @ 50 mg of aphids per insect). For the control, female was placed in the Petri dish with no fourth instar larvae but with an equal amount of aphids. Voracity of focal female

was taken as an average of total aphid consumption within 24 h. All treatments were repeated 10 times.

The influence of presence of varying densities of conspecific pupae, adult males and females were assessed, following the above mentioned protocol, replacing larvae with the requisite stages. Pupae employed in the experiment were used within 12 h of their formation. Conspecific pupae were removed from their formation site with the help of fine mounted needle and brush prior to their shifting to experimental arena. Care was taken not to damage them and they were reattached with the help of odourless diluted glue. Adult males and females used as interfering individuals in the experiment were 10-day-old virgins. Interfering conspecific females did not lay eggs as they were not mated.

Hexane extract of conspecific eggs

To obtain semiochemicals from the surface of eggs, the requisite numbers (viz. 5, 10, 20 and 30) used in experiment (A) were transferred to a corked tube containing 2 ml of n-hexane 95% LR (Company-SDFCL, Product and Pack code 38487 L25) for 2 min (Chan, 1995), with the help of a fine wet camel hair brush. Only undamaged eggs were used for the experiment. Thereafter, the entire 2 ml of hexane extract of eggs was painted at the centre of Petri dishes (14.5×1.5 cm). 50 mg aphids were introduced along with a weighed 10-day-old conspecific once-mated female. After 24 h, number of eggs laid, amount of

TABLE 2. Oviposition by ladybird females in presence of varying densities of different life stages. Two way ANOVA showing the effects of stage (larvae, pupae, adult males and females), density and their interactions on oviposition.

Interfering stage	Density	<i>C. septempunctata</i> (C7)	<i>C. transversalis</i> (Ct)	<i>C. sexmaculata</i> (Cs)	<i>P. dissecta</i> (Pd)	<i>A. cardoni</i> (Ac)
4 th instar	0	46.80 ± 1.99 ^a (A)	32.00 ± 1.43 ^b (D)	43.00 ± 2.35 ^a (C)	38.00 ± 1.88 ^a (C)	11.20 ± 0.71 ^a (C)
	2	44.90 ± 2.50 ^a (A)	24.70 ± 3.04 ^b (C)	35.90 ± 1.87 ^a (B)	33.10 ± 3.69 ^a (B)	7.60 ± 1.29 ^a (B)
	4	36.70 ± 2.80 ^a (A)	15.30 ± 2.74 ^b (B)	34.40 ± 3.03 ^a (AB)	30.10 ± 2.67 ^a (B)	4.30 ± 1.04 ^a (AB)
	6	39.50 ± 3.65 ^a (A)	9.20 ± 1.89 ^a (A)	32.70 ± 2.48 ^{ab} (A)	22.60 ± 2.22 ^a (A)	3.70 ± 0.96 ^a (A)
Pupa	0	47.20 ± 3.45 ^b (A)	31.00 ± 1.59 ^b (A)	44.30 ± 1.22 ^b (A)	35.40 ± 1.78 ^a (C)	10.10 ± 0.84 ^a (A)
	2	44.20 ± 3.21 ^a (A)	29.10 ± 1.94 ^c (A)	43.60 ± 3.16 ^b (A)	34.00 ± 2.24 ^a (B)	9.70 ± 0.84 ^b (A)
	4	45.30 ± 1.62 ^b (A)	28.40 ± 1.84 ^d (A)	43.60 ± 1.64 ^b (A)	31.00 ± 3.08 ^a (AB)	8.90 ± 0.91 ^b (A)
	6	47.00 ± 2.48 ^b (A)	27.90 ± 1.70 ^c (A)	42.10 ± 3.39 ^b (A)	26.10 ± 2.28 ^a (A)	8.10 ± 0.87 ^b (A)
Adult male	0	48.30 ± 3.75 ^b (A)	28.00 ± 1.59 ^a (C)	47.20 ± 2.65 ^b (C)	37.25 ± 1.65 ^a (C)	10.50 ± 0.89 ^a (C)
	2	47.60 ± 2.20 ^a (A)	17.10 ± 2.83 ^a (B)	45.50 ± 2.24 ^b (C)	33.00 ± 3.92 ^a (B)	7.00 ± 0.47 ^a (B)
	4	43.50 ± 3.33 ^b (A)	9.00 ± 2.72 ^a (A)	41.60 ± 3.16 ^b (B)	29.70 ± 2.51 ^a (B)	3.50 ± 0.87 ^a (A)
	6	42.90 ± 3.68 ^a (A)	8.70 ± 2.41 ^a (A)	26.80 ± 2.44 ^a (A)	17.90 ± 1.96 ^a (A)	2.70 ± 0.86 ^a (A)
Adult female	0	48.40 ± 3.81 ^b (A)	30.00 ± 1.59 ^b (C)	46.50 ± 2.82 ^b (B)	36.37 ± 1.29 ^a (B)	10.90 ± 0.99 ^a (C)
	2	49.80 ± 3.83 ^a (A)	26.80 ± 3.15 ^c (B)	46.10 ± 3.65 ^b (B)	32.80 ± 5.65 ^a (A)	7.90 ± 1.07 ^a (BC)
	4	44.20 ± 2.84 ^b (A)	18.10 ± 3.04 ^c (A)	42.30 ± 2.80 ^b (A)	30.10 ± 2.34 ^a (A)	6.20 ± 0.96 ^a (B)
	6	43.90 ± 3.51 ^a (A)	16.80 ± 3.50 ^b (A)	41.90 ± 3.51 ^b (A)	29.10 ± 2.56 ^a (A)	4.40 ± 0.83 ^a (A)
F _{Stage} (P-value); df		3.00 (< 0.0001); 3, 159	5.53 (< 0.0001); 3, 159	6.47 (< 0.0001); 3, 159	2.49 (0.063); 3, 159	2.07 (0.107); 3, 159
F _{Density} (P-value); df		2.38 (0.073); 3, 159	28.84 (< 0.0001); 3, 159	5.15 (0.002); 3, 159	16.67 (< 0.0001); 3, 159	14.67 (< 0.0001); 3, 159
F _{Stage × Density} (P-value); df		1.08 (0.384); 9, 159	1.64 (0.109); 9, 159	1.78 (0.076); 9, 159	1.18 (0.313); 9, 159	0.83 (0.588); 9, 159

Values are Mean ± SE.

For each ladybird species, small alphabets represent comparison of means between interfering stages within each density level, and large alphabets in parentheses represent comparison of means between different density levels within each interfering stage.

Similar alphabets indicate lack of significant differences amongst means of a species at P < 0.05.

aphids consumed, and weight of the females were recorded. For the control treatment, females (n = 10 per treatment) were placed in Petri dishes containing no hexane egg extract but equal amount of aphids and the above mentioned observations were recorded.

Tracks of conspecific larvae, adult males and females

Varying densities (2, 4 and 6) of 12-h starved fourth instar larvae were placed in Petri dishes for a period of 2 h to form tracks. Thereafter they were removed and a pre-weighed 10-day-old conspecific once-mated female was placed in the Petri dish containing these tracks along with 50 mg aphids. After 24 h the number of eggs laid, amount of aphids consumed, and weight of the female were recorded. For control, a female was placed in a Petri dish with no tracks but an equal amount of aphids. All treatments were repeated 10 times. The same protocol was followed for adult males and females.

Statistical analysis

Data obtained in experiments A (Presence of eggs and their distribution patterns) was subjected to two way ANOVA with density (5, 10, 20, 30) and clustering pattern (clustered and scattered) as independent factors and oviposition as dependent factor followed by Tukey's post hoc comparison of means. To assess the effects of presence interference (Experiment B) on oviposition (dependent factor), two way ANOVA was conducted for each ladybird species with stage (larvae, pupae, adult female, adult male) and density (0, 2, 4, 6) as independent factors followed by Tukey's post hoc comparison of means.

For semiochemical interference, data obtained from Experiment C was subjected to one way ANOVA with varying densities of egg surface semiochemicals as independent factor and oviposition as dependent factor. Data from Experiment D (semiochemical presence of life stages) was subjected to two way ANOVA with stage (larvae, adult female, adult male) and density (0, 2, 4, 6) as independent factors and oviposition as dependent factor for each ladybird species followed by Tukey's post hoc comparison of means. All statistical analyses were performed using MINITAB 16.0.

RESULTS

Presence of conspecific eggs

Results obtained from two way ANOVA revealed that oviposition by focal females of all the species (C7, Ct, Cs, Pd and Ac) varied significantly with the density of conspecific eggs. Egg clustering had a significant oviposition deterrent effect in all except Ct and Cs. The interactions between egg density and clustering pattern were insignificant in all five ladybirds (Table 1).

Clustered eggs inhibited oviposition by focal females of all ladybird species except Pd more than scattered eggs. Increasing the density of conspecific eggs (in both distribution patterns) increased the inhibitory effect on oviposition in focal females of all species (Fig. 1), with maximum oviposition being observed in the absence of conspecific eggs. The threshold egg density for maximum

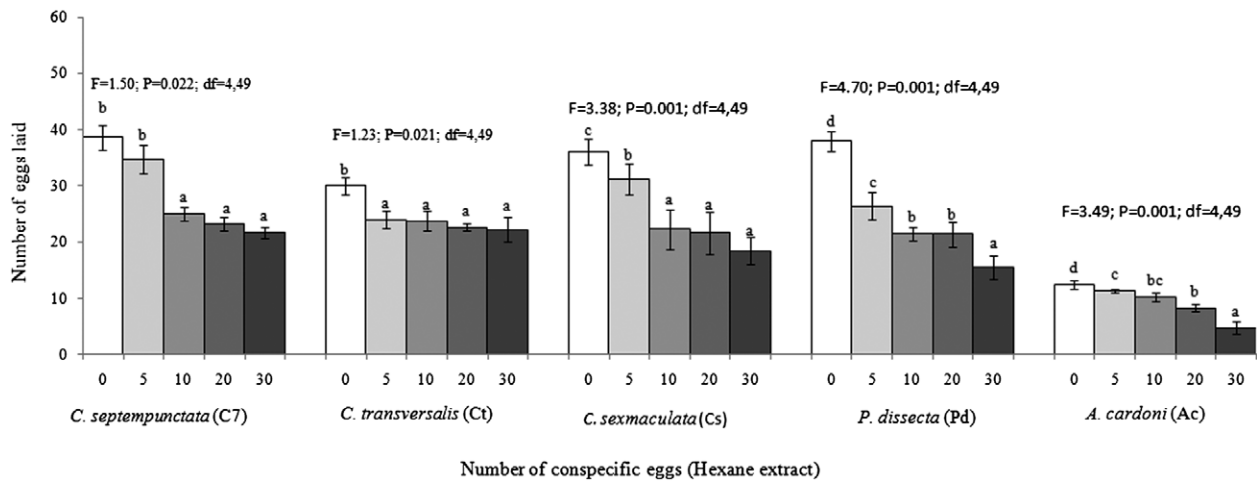


Fig. 2. Mean (\pm SE) numbers of eggs laid in 24 h by 10 d-old female coccinellids ($n = 10$) of five species in 14.5×1.5 cm Petri dishes in the presence of aphids and hexane extracts of varying numbers of conspecific eggs. Values are Mean \pm SE. For each ladybird species, small alphabets represent comparison of means between different egg density levels. Similar alphabets indicate lack of significant differences amongst means of a species.

oviposition inhibition, however, varied from species to species.

Presence of conspecific larvae, pupae, adult males and females

Two way ANOVA revealed that interfering stage had significant influence on oviposition by C7, Ct, Cs females but not on Pd and Ac. Density of stages significantly influenced oviposition by focal females in all ladybirds

except C7. Interactions between stages and densities were not significant in any of the five ladybirds (Table 2).

Focal females of Ct, Cs, Pd and Ac showed reduced oviposition in the presence of increasing densities of fourth instars, adult males and females. However, increasing densities of pupal stage were deterrent only to Pd. Further, the deterrence of focal females was lowest in the presence of pupa compared to other life stages in all species tested (Table 2).

TABLE 3. Oviposition by ladybirds in the presence of varying densities of semiochemicals of different life stages. Two way ANOVA showing the effect of density of tracks, track forming stages and their interaction on oviposition.

Interfering stage	Density	<i>C. septempunctata</i> (Cs)	<i>C. transversalis</i> (Ct)	<i>C. sexmaculata</i> (Cs)	<i>P. dissecta</i> (Pd)	<i>A. cardoni</i> (Ac)
4 th instar	0	40.00 \pm 1.84 ^a (A)	29.70 \pm 2.51 ^b (B)	38.20 \pm 1.98 ^b (A)	34.70 \pm 1.59 ^a (C)	11.20 \pm 0.71 ^a (C)
	2	37.30 \pm 3.36 ^a (A)	20.90 \pm 1.39 ^a (A)	35.30 \pm 3.36 ^a (A)	28.40 \pm 1.61 ^a (C)	10.10 \pm 1.06 ^a (C)
	4	30.10 \pm 3.10 ^a (A)	20.60 \pm 1.77 ^b (A)	28.10 \pm 3.10 ^a (A)	26.20 \pm 1.91 ^a (B)	9.80 \pm 0.41 ^c (B)
	6	31.80 \pm 3.49 ^a (A)	20.50 \pm 1.88 ^a (A)	28.80 \pm 3.89 ^a (A)	24.80 \pm 0.89 ^a (A)	8.10 \pm 0.60 ^a (A)
Adult male	0	35.50 \pm 4.30 ^a (A)	29.70 \pm 2.51 ^b (B)	39.80 \pm 1.89 ^b (A)	38.00 \pm 1.59 ^b (C)	11.20 \pm 0.71 ^a (B)
	2	36.70 \pm 3.13 ^a (A)	28.60 \pm 3.47 ^c (B)	38.20 \pm 1.98 ^b (A)	28.00 \pm 1.69 ^a (B)	11.00 \pm 0.42 ^a (B)
	4	35.20 \pm 3.88 ^b (A)	23.60 \pm 1.53 ^c (A)	35.80 \pm 3.16 ^b (A)	25.40 \pm 1.35 ^a (A)	8.90 \pm 0.56 ^a (A)
	6	35.50 \pm 4.30 ^b (A)	21.40 \pm 1.70 ^a (A)	33.20 \pm 3.88 ^b (A)	24.50 \pm 1.90 ^a (A)	8.60 \pm 0.89 ^a (A)
Adult female	0	40.80 \pm 1.89 ^b (A)	25.70 \pm 1.70 ^a (C)	35.50 \pm 4.30 ^a (A)	35.00 \pm 1.55 ^a (C)	10.00 \pm 2.68 ^a (BC)
	2	40.20 \pm 1.98 ^b (A)	24.00 \pm 1.63 ^b (C)	35.80 \pm 3.16 ^a (A)	31.60 \pm 1.54 ^b (B)	10.40 \pm 0.45 ^a (C)
	4	38.00 \pm 3.17 ^c (A)	17.70 \pm 1.80 ^a (A)	33.20 \pm 3.88 ^b (A)	26.50 \pm 1.91 ^a (A)	9.40 \pm 0.40 ^b (B)
	6	35.20 \pm 3.88 ^b (A)	21.70 \pm 1.70 ^a (A)	33.50 \pm 4.30 ^b (A)	26.80 \pm 1.55 ^a (A)	8.50 \pm 0.52 ^a (A)
F Density of tracks (P-value); df		1.50 (0.220); 3,119	2.71 (0.002); 3,119	1.28 (0.284); 3,119	20.20 (<0.0001); 3,119	7.11 (0.001); 3,119
F Track forming stage (P-value); df		0.16 (0.001); 2,119	5.90 (0.004); 2,119	8.90 (0.002); 2,119	3.88 (0.024); 2,119	13.25 (<0.0001); 2,119
F Stage \times Density (P-value); df		2.04 (0.067); 6,119	2.14 (0.054); 6,119	1.50 (0.186); 6,119	11.04 (0.002); 6,119	0.48 (0.820); 6,119

Values are Mean \pm SE.

For each ladybird species, small alphabets represent comparison of means between interfering stages within each density level, and large alphabets in parentheses represent comparison of means between different density levels within each interfering stage.

Similar alphabets indicate lack of significant differences amongst means of a species $P < 0.05$.

Semiochemicals of conspecific eggs

Increasing concentrations of surface semiochemicals of conspecific eggs increased their inhibitory effects on oviposition by focal females of all species, with females ovipositing maximally in their absence (Fig. 2).

Tracks of conspecific larvae, adult males and females

Track forming stages and track densities influenced the oviposition of Ct, Pd and Ac females. However, the oviposition of C7 and Cs was influenced by the track forming stages and not track densities. Insignificant interactions were observed between track forming stages and their densities in all species except Pd. Oviposition by females of Ct, Pd and Ac diminished with increasing track densities of fourth instar larvae, adult males and females (Table 3).

DISCUSSION

Results reveal that oviposition was influenced by the presence of eggs, fourth instars, pupae (only in Pd), adult males and females, though the degree of inhibition was species-specific. The deterrence was largely density-dependent with species-specific variations. The pattern of egg distribution had a significant effect with clustered eggs inhibiting oviposition more than scattered ones in all ladybirds except Pd. Increasing concentrations of egg surface semiochemicals were also effective in deterring oviposition.

The observed increased oviposition inhibition in the presence of clustered eggs may be attributed to (a) aposematic look of the clusters (Agarwala & Dixon, 1991, 1993) and/or (b) the species-specific semiochemical odours present on the surface of eggs. Each ladybird species is known to produce species-specific alkanes that constitute semiochemical signatures used for defense (Pasteels et al., 1973; Marples et al., 1989; Dixon, 2000; Hemptinne & Dixon 2000; Hemptinne et al., 2000b, c; Magro et al., 2007). Adults and neonates are known to use olfactory cues to detect conspecifics (Al Abassi et al., 1998; Schaller & Nentwig, 2000; Omkar et al., 2004). The results obtained with n-hexane chemical extracts of eggs surface reveal that all species show decreased oviposition responses to these extracts and that the deterrence is density dependent. Thus, it seems that both the actual presence of eggs and their semiochemicals influence oviposition.

The deterrence in oviposition in the vicinity of the fourth instars or their tracks, as observed in the present study, supports findings of earlier researchers, indicating fourth instars to be the most active inhibitors of oviposition (Růžicka, 1997, 2001a, b, 2002, 2003, 2006; Yasuda et al., 2000). This was not the case for *C. septempunctata*, though previous studies have shown that this species actively responds to presence of oviposition deterring allomone (Růžicka, 1997, 2001a, b; Doumbia et al., 1998). However, Magro et al. (2007) have also found a relatively weaker response of *C. septempunctata* to its own larval tracks in comparison to that shown by *A. bipunctata* and *Adalia decempunctata*.

That the larval presence signals danger of egg cannibalism (Banks, 1956; Mills, 1982; Majerus, 1994; Dixon, 2000; Cottrell, 2004) is well established and may cause females to reduce or withhold oviposition at sites with larvae (Agarwala et al., 2003). Restlessness or the tendency to fly away from the area in females may also be a reason for the reduction in egg laying under field conditions (Hemptinne et al., 1992) but not in the laboratory. Presence of pupae did not deter oviposition in ladybird species except for *P. dissecta*, where slight inhibitions are observed with increase in density. This lack of oviposition deterrence is possibly due to the fact that pupae do not seemingly pose any danger to eggs. The results are in agreement with Hemptinne & Dixon (1991). The pupae used in this study are early ones and whether the late age pupae also have the similar effects will require further experimentation.

Presence of adult males and females had density dependent inhibitory effects on oviposition in all the ladybird species. This may be attributable to one or more of the following: (a) crowding (reported in *Sasajiscymnus tsugae* (Sasaji & McClure) and *H. axyridis* by Flowers et al., 2005 and in *P. dissecta* by Mishra & Omkar, 2006) (b) harassment of focal females by males, or (c) disturbance during oviposition. Female expenditure of time and/or energy on avoiding competition or harassment is likely to result in reduced oviposition, as reported in *H. axyridis* and *Propylea japonica* (Thunberg) by Agarwala et al. (2003) and *A. bipunctata* by Kajita et al. (2006). A previous study on *P. dissecta* by Mishra & Omkar (2006) also reports similar results, finding reduction in egg viability in the presence of conspecific males. Soares & Serpa (2006) have observed no oviposition in *Coccinella undecimpunctata* L. in the presence of adult *H. axyridis*, but the reverse in case of conspecific adults. Females of *C. sexmaculata* are known to lay fewer eggs in the presence of an immobilized conspecific adult female (Agarwala et al., 2003), whereas *C. septempunctata* does not oviposit in the presence of conspecific adult females (Hemptinne et al., 1993). Mishra & Omkar (2006) have also shown inhibitory effects of female conspecific presence and semiochemicals in *P. dissecta*. The time frame of the above experiments differed, which may also play a role in modifying the extent of the inhibition displayed by the ovipositing females.

Encounters with conspecific adults are known to deter oviposition by gravid females of ladybird species (Seagraves, 2009) and similar interference effects have also been reported in parasitoids (Jackson, 1966; Viktorov, 1968; Holmes, 1972). The deterrence of oviposition by adult males and females in the present study is contradictory to the findings of Doumbia et al. (1998) where no inhibitory effects of adult presence was reported on oviposition by *A. bipunctata*. Our present findings are in agreement to that of Mishra & Omkar (2006).

The oviposition inhibitory effects of increased density of semiochemicals present either in egg surface or tracks indicate that the effect of these ODPs is density dependent. The effect of the track forming stage was observed

only in Ct, Pd and Ac and not in Cs and C7. In the three former ladybirds ODPs may be stage specific which is contrary to the previous findings of Mishra & Omkar (2006) and also to the concept of semiochemical parsimony suggested by Hemptinne & Dixon, 2000). It is more likely that there may be quantitative differences in the amount secreted by different stages (Seagraves, 2009) with larvae leaving more tracks as they use their anal discs to adhere to surfaces. It has been suggested that larval tracks may be more deterrent than those of adults as larvae are more frequent consumers of ladybird eggs than adults (Cottrell & Yeargan 1998a, b; Seagraves, 2009). The difference in responses to actual presence versus semiochemical presence could also reflect a difference in the chemistry of tracks versus the larval body surface. Also, the increased deterrence in the case of actual presence vis a vis semiochemical presence probably a combined effect of harassment and chemical tracks, as one can't be present without the other.

The present study establishes that the presence and semiochemicals of different life stages (except pupae) have an inhibitory effect on oviposition by conspecific females in these ladybird species. The degree of inhibition is often species-specific. Of all the experimental species, *C. septempunctata* was least responsive to both actual conspecific presence and semiochemicals. Our results further provide support to our hypothesis that active stages are likely to be more oviposition deterrent than passive ones. However, the oviposition deterrence appeared to be more density-dependent it is more so in presence interference than in semiochemicals.

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