

Effects of conspecific and heterospecific competitors on feeding and oviposition of a predatory ladybird: a laboratory study

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Abstract

There are several examples of intraguild interactions among insect predators of aphids, but little is known regarding the effects of interactions on feeding and oviposition of individual competitors in a guild. In the laboratory, we determined the feeding and oviposition responses of a ladybird predator to its conspecific and heterospecific competitors in an aphidophagous guild. Gravid females of *Menochilus sexmaculatus* (Fabricius) (Coleoptera, Coccinellidae) reduced oviposition, but not feeding, when exposed to immobilised conspecific or *Coccinella transversalis* (Fabricius) (Coleoptera, Coccinellidae) individuals in the short-term (3 h) and long-term (24 h). Feeding and oviposition responses were not affected when *M. sexmaculatus* females were exposed to larvae or adults of *Scymnus pyrocheilus* Mulsant (Coleoptera, Coccinellidae) beetles or larvae of the syrphid fly *Ischiodon scutellaris* (Fabricius) (Diptera: Syrphidae). The ratio of eggs laid to numbers of aphids consumed by *M. sexmaculatus* females was also affected by the presence of conspecific or *C. transversalis* larvae. The results suggest that fecundity of this predator may be affected by both conspecific and heterospecific competitors in a patchy resource.

Introduction

Communities in which several consumers converge or specialise on the same resource are characterised by competition among consumers (Muller & Godfray, 1999; Amarasekare, 2000). This is particularly true if the food resource is patchy and short-lived (Dixon, 1997). Plant-sap feeding insects like aphids are typical examples of such a resource for predators (Dixon, 2000). Interactions between coexisting species of predators that share the same aphid prey resource in a patchy habitat often result in intraguild predation (Polis et al., 1989; Rosenheim et al., 1995). For example, coccinellid predators that feed on the same aphid resource engage in conspecific and heterospecific predation of eggs and larvae (Agarwala & Dixon, 1992; Hironori & Katsuhiko, 1997; Agarwala et al., 1998; Obrycki et al., 1998a,b; Yasuda & Ohnuma, 1999; Yasuda et al., 2001). Similar interactions involving heterospecific predators have also been reported for a range of species (Ninomiya, 1968; Lucas et al., 1998;

Phoofolo & Obrycki, 1998; Taylor et al., 1998; Takizawa et al., 2000; Yasuda & Kimura, 2001). The effects of such interactions in a guild may either lead to stabilizing of prey–predator populations (Hanski, 1981; Godfray & Pacala, 1992) or adversely affect the foraging and oviposition performance of individual predators (Polis et al., 1989; Hemptinne et al., 1992; Rosenheim et al., 1995; Ruzicka, 1996).

Aphidophagous predators of a guild often differ in size and mobility of their larvae and adults (Agarwala & Yasuda, 2001b), and the intraguild predation in them tends to be asymmetrical with the larger individuals being the intraguild predators and the smaller individuals being the intraguild prey (Lucas et al., 1998). Most field and cage studies indicate that the total mortality inflicted by an aphidophagous guild on a prey population is nonadditive, i.e., it is less than the sum of the individual mortalities (Dixon, 2000). However, very few studies have recorded the exact relation of competition between different predators of a guild based on their natural occurrence (Phoofolo & Obrycki, 1998). This was examined for *Menochilus sexmaculatus*, a native predator of aphids in Oriental and

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Palearctic regions (Tao & Chiu, 1971; Agarwala & Ghosh, 1988; Hussaein, 1991). This coccinellid is a predator of 57 species of aphid prey in agricultural, horticultural, and forest habitat (Agarwala & Yasuda, 2001a), and was introduced in North America for the biological control of greenbug, *Schizaphis graminum* (Cartwright et al., 1977). In Asia and the Middle-East, the cowpea aphid, *Aphis craccivora* on bean plants, is considered to be its most suitable prey (Hussaein, 1991; Sugiura & Takada, 1998). Field studies on *M. sexmaculatus* suggest that adults become active at low aphid density per plant and closely synchronise their aggregation and reproduction with natural populations of the most preferred prey (Agarwala & Bardhanroy, 1999). The eggs and new-born larvae of this coccinellid are vulnerable to attack from other predators of the guild, which consists of large-sized species, *Coccinella transversalis*, and small-sized species, *Scymnus (Pullus) pyrocheilus* and the syrphid *Ischiodon scutellaris* (Agarwala & Bardhanroy, 1997; Agarwala et al., 1998).

Differences in size and mobility among diverse predatory species in a guild can influence the outcome of interactions between the competitors (Polis et al., 1989; Rosenheim et al., 1995; Lucas et al., 1998). To understand how these differences among the predators in the guild of *A. craccivora* might influence the feeding and oviposition responses of *M. sexmaculatus*, a study was made to determine the effects of conspecific and heterospecific competitors on feeding, egg laying, and ratio of prey consumed to eggs laid by *M. sexmaculatus* females. The results that were obtained demonstrate that: (1) oviposition is suppressed in the presence of some, but not all, of the predators; (2) predator size and foraging speed of a predator may influence its likelihood of acting as an intraguild predator, and (3) this may explain the differences observed in responses by *M. sexmaculatus* females to different predators. On the whole, this work provides another example of how predator oviposition behaviour may respond to the perception of varying risk of intraguild predation.

Materials and methods

Insect

Males and ovipositing females of *M. sexmaculatus* were collected from bean plants, *Vigna catjang*, in the fields of the University campus at Suryamaninagar, Tripura in north-east India. Groups of 20 adult beetles were kept in ventilated plastic containers (16 cm × 9 cm × 12 cm) in a sex ratio of 1 : 1 and provided with corrugated papers, moistened filter papers and cut twigs of bean plants to facilitate egg laying. They were fed daily on an *ad libitum* supply of the cowpea aphids, *A. craccivora*, until females oviposited. Four such containers were maintained in this

study. Eggs from these females were kept in 9 cm paired Petri dishes, one cluster of 10–16 eggs in each, lined with a filter paper in the bottom that was slightly dampened every 12 h. New-born larvae were supplied with an excess of cowpea aphids until the second moult when the larvae were transferred, one per Petri dish, to new 9 cm Petri dishes and kept until pupation. Aphids were collected from bean plants in a culture maintained on bean plants in a greenhouse. The cultures were kept clean by replacing food and other contents every 24 h.

Following this method, separate cultures of larvae and adults of *C. transversalis*, *S. pyrocheilus*, and *I. scutellaris* were also maintained in the laboratory. In the case of *I. scutellaris*, however, adult flies were released in cylindrical glass jars (30 cm height, 10 cm diameter) provided with 12–15 cm long flower-bearing twigs of the bean, *Vigna catjang*, and the mustard, *Brassica juncea* cv M27, and a wad of cotton slightly dampened in diluted honey as source of food. These adults became gravid within 7–8 days and laid eggs in aphid colonies.

Experimental protocol

Menochilus sexmaculatus females used in the experiments were controlled for their size at eclosion from pupae ($n = 120$, ANOVA: $F_{15,104} = 1.94$, $P = 0.09$) to eliminate size-related differences in prey consumption and oviposition of female beetles (Rhamlingam, 1986; Dixon & Guo, 1993; Hodek & Honek, 1996). After eclosion, each *M. sexmaculatus* female used in the experiment was kept on a daily food supply of 40 cowpea aphids. A previous functional response study has shown that young beetles of this species were satiated at this feeding rate (Agarwala et al., 2001). These beetles were allowed to mate by confining a female with a male for 3 h in a Petri dish. This was done every 48 h at the time of food change to maintain the reproductive vigour of beetles. Ten-day-old *M. sexmaculatus* females were starved for 16 h in order to induce the same level of hunger and were kept individually in 9 cm Petri dishes in an incubator at 20 ± 1 °C and a L16:D8 photoperiod, and provided with 20 adult aphids in the 3 h experiment or 40 in the 24 h experiment (mean aphid weight \pm SE = 0.808 ± 0.045 mg, $n = 70$). The following treatments were used: (1) no other individual predator, (2) a 1-day-old fourth instar *M. sexmaculatus* larva, (3) a 10-day-old *M. sexmaculatus* female, (4) a 1-day-old fourth instar *C. transversalis* larva, (5) a 10-day-old *C. transversalis* female, (6) a 1-day-old fourth instar *S. pyrocheilus* larva, (7) a 10-day-old *S. pyrocheilus* female, and (8) a 5-day-old maggot of *I. scutellaris*. Larvae and adults of *C. transversalis*, *M. sexmaculatus*, *S. pyrocheilus*, and maggots of *I. scutellaris* used in the treatments were anaesthetised with CO₂ and kept in a refrigerator at ≤ 2 °C for 6 h. This process

immobilised them for at least 12 h. Two of these treated individuals of larvae or adults of *M. sexmaculatus*, *C. transversalis*, *S. pyrocheilus*, or *I. scutellaris* were used every 24 h for each *M. sexmaculatus* female that was tested for feeding and oviposition responses. This was done to avoid direct competition between MS females and other predators for the limited number of prey individuals used in the treatments.

Feeding and oviposition by individual *M. sexmaculatus* female beetles in each of the treatments were recorded at 3 h and 24 h intervals to account for any differences in immediate and delayed responses (Agarwala & Dixon, 1992, 1993).

Size and speed of searching of predators

The predatory guild of *A. craccivora* consisted of diverse species, therefore differences in their size and speed of searching were recorded for their possible effect on intraguild interaction. Ten individuals each of 1-day-old fourth instar and 1-day-old female *M. sexmaculatus*, *C. transversalis*, and *S. pyrocheilus* and *I. scutellaris* (only larvae) were measured for their length, fresh weight, and speed of searching. Body length of individual larva or adult was measured by placing it on a fixed point of graph paper (mm) and holding it in that position near its posterior tip until its body was normally extended. This procedure allowed recording of the length from the anterior tip to the posterior tip of a larva or an adult. Fresh weight of a larva or an adult was measured by a microbalance after the insect was anaesthetised with CO₂. Speed of searching by a larva or an adult was determined by releasing an individual insect, starving for the previous 12 h, at the base of a 50 cm long plastic rod (8 mm diameter) having a slightly rough surface. The rod was gently turned upside down if the insect neared the top of it in order to maintain geonegative searching. The height of the rod, in cm, travelled by individual larva or adult in 60 s was recorded.

Feeding and oviposition responses by *M. sexmaculatus* females after 3 h

Each gravid *M. sexmaculatus* female was presented 20 aphids and engaged in interaction with one larva, one adult, or no individual. Numbers of aphids eaten and eggs laid were recorded after 3 h. Ten *M. sexmaculatus* females of similar age were used in each of the eight treatments. Thus the total number *M. sexmaculatus* females used in the experiment was 80.

Feeding and oviposition responses by *M. sexmaculatus* females after 24 h

Here each gravid *M. sexmaculatus* female was presented 40 aphids and engaged in interaction with one larva or adult

or none at each treatment. Five *M. sexmaculatus* females of similar age were used in the control and in each of the seven treatments. Number of aphids eaten and eggs laid by each female beetle were noted at 24 h intervals for 4 consecutive days in treatments with *C. transversalis* larvae, 3 consecutive days in other treatments, and 5 consecutive days in the control. Different durations of studies in different treatments were inevitable due to the practical difficulty of obtaining the sufficient number of properly anaesthetised animals used.

To remove the effect of differences in water content of aphids eaten and eggs oviposited by *M. sexmaculatus* females in the experiments, fresh (FW) to dry weight (DW) conversions of aphids and eggs were determined by drying at 40 °C for 10 days [DW of eggs (mg) = 0.036 × FW of eggs, n = 80; DW of aphids (mg) = 0.183 × FW of aphids, n = 77]. Differences in oviposition responses in the two experiments were measured with respect to: (1) dry mass of aphids eaten, (2) dry mass of eggs produced, (3) proportion of eggs laid in a cluster or single after 3 h and 24 h, and (4) ratio of eggs produced to aphids consumed after 24 h. All the weights in this study were recorded in a microbalance sensitive to 0.1 µg.

Data were subjected to one factor analysis of variance both for the measurements of size and speed of searching in the predators and also for interactions between the effects (feeding and oviposition responses) and the treatments. In both cases, mean values of measurements and treatments were compared by the Scheffé multiple range test. Wherever multiple observations were conducted with a single female, these were averaged to produce a single datum per experimental female per treatment. Data of proportions and ratios were arcsine square root transformed before statistical tests. As the proportions of egg mass that were retained after drying did not vary across treatments, data have been reported in graphs simply as number of eggs laid. Feeding and oviposition by *M. sexmaculatus* in treatments after 3 h and 24 h are compared in graphs.

Results

Size and speed of searching of predators

Length and fresh weight of larvae and adults of *M. sexmaculatus*, *C. transversalis*, *S. pyrocheilus*, and *I. scutellaris* and their speed of searching are provided in Table 1. In fresh weight, both larvae and adults of *M. sexmaculatus* were about half the size of the *C. transversalis*, and about 10 times the size of the *S. pyrocheilus* beetles (ANOVA: larvae $F_{3,36} = 216.28$, $P < 0.0001$; adults $F_{2,27} = 183.71$, $P < 0.0001$). In length, both larvae and adults of *M. sexmaculatus* were significantly smaller than that of

Predators	Mean (\pm SE) of		
	Length (mm)	Weight (mg)	Speed of searching (cm 60 s ⁻¹)
Larvae			
<i>M. sexmaculatus</i>	7.77 \pm 0.19a	16.85 \pm 0.15a	62.20 \pm 1.05a
<i>C. transversalis</i>	10.21 \pm 0.23b	32.29 \pm 0.41b	83.10 \pm 0.75b
<i>S. pyrocheilus</i>	3.57 \pm 0.19c	1.69 \pm 0.18c	31.96 \pm 0.08c
<i>I. scutellaris</i>	11.57 \pm 0.19b	3.36 \pm 0.15d	36.80 \pm 0.46d
Adults			
<i>M. sexmaculatus</i>	5.57 \pm 0.14a	14.91 \pm 0.22a	61.20 \pm 1.01a
<i>C. transversalis</i>	6.91 \pm 0.13b	29.84 \pm 0.17b	126.20 \pm 0.42b
<i>S. pyrocheilus</i>	3.28 \pm 0.13c	1.52 \pm 0.12c	43.80 \pm 6.41c

Table 1 Measurements of length, fresh weight, and speed of searching in 1-day-old larvae and 1-day-old adult females of *M. sexmaculatus*, *C. transversalis*, *S. pyrocheilus*, and *I. scutellaris* predators. Means were separated by Scheffé multiple range test. Different letters following mean values in a column indicate significant difference at $P < 0.001$

C. transversalis but longer than that of *S. pyrocheilus* beetles. The larvae of *I. scutellaris*, however, were the longest among the larval predators (ANOVA: larvae $F_{3,36} = 106.18$, $P < 0.0001$; adults $F_{2,27} = 154.22$, $P < 0.0001$).

Starving adults and larvae of *M. sexmaculatus* had slower searching speeds than that of *C. transversalis*. However, both predators showed higher speeds of searching in comparison to larvae and adults of *S. pyrocheilus* beetles and maggots of *I. scutellaris* (ANOVA: larvae $F_{3,36} = 139.64$, $P < 0.0001$; adults $F_{2,27} = 117.32$, $P < 0.0001$).

Feeding and oviposition responses by *M. sexmaculatus* females after 3 h

Menochilus sexmaculatus females laid significantly fewer eggs in 3 h when they were kept with a larva or an adult female of conspecifics or *C. transversalis* in comparison to *M. sexmaculatus* females in the control or kept with a larva or an adult female of *S. pyrocheilus* beetles or a maggot of *I. scutellaris* (no. of eggs: $F_{7,72} = 16.80$, $P < 0.0001$; dry mass of eggs: $F_{7,72} = 17.66$, $P < 0.0001$; Figure 1A). During the same period, aphids eaten by *M. sexmaculatus* females in all the treatments were not significantly different (no. of aphids: $F_{7,72} = 1.60$, $P = 0.15$; dry mass of aphids: $F_{7,72} = 1.60$, $P = 0.15$; Figure 1B).

In the control, all the *M. sexmaculatus* females laid eggs. In comparison, a higher proportion of *M. sexmaculatus* females that were kept with conspecific larvae or *C. transversalis* larvae did not lay eggs than those females that were kept in other treatments (ANOVA: $F_{7,72} = 2.204$, $P = 0.04$).

Feeding and oviposition responses by *M. sexmaculatus* females after 24 h

Numbers of eggs produced by *M. sexmaculatus* females after 24 h was significantly different among the treatments (no. of eggs: $F_{7,31} = 4.382$, $P = 0.002$; dry mass of eggs: $F_{7,31} = 4.376$, $P = 0.002$; Figure 2A). *Menochilus sexmaculatus* females produced significantly fewer eggs in the presence

of larvae of conspecifics or *C. transversalis*, but there was no difference in the number or dry mass of eggs produced by *M. sexmaculatus* females in interactions with other treatments. During the same period, however, *M. sexmaculatus* females had eaten the same amount of aphids in all the treatments and the control (no. of aphids: $F_{7,31} = 1.79$, $P = 0.124$; dry mass of aphids: $F_{7,31} = 1.795$, $P = 0.124$; Figure 2B). After 24 h, the proportion of *M. sexmaculatus* females laying eggs, whether in the control or in treatments, did not differ (ANOVA: $F_{7,31} = 1.325$, $P = 0.272$).

Ratio of aphids consumed to eggs laid by *M. sexmaculatus* females

After 24 h *M. sexmaculatus* females that were kept with conspecific larvae or *C. transversalis* larvae converted, on average, significantly less mass of aphids into eggs, by dry mass, in comparison to *M. sexmaculatus* females that were kept on their own or with conspecific adults, *C. transversalis* adults, larvae or adults of *S. pyrocheilus*, or maggots of *I. scutellaris* (ANOVA: $F_{7,31} = 5.019$, $P < 0.001$).

Discussion

The results of this study suggest that the predators differed in their size and speed of searching. *Menochilus sexmaculatus* females responded to the presence of conspecific as well as heterospecific predatory adults, larvae of conspecific or *C. transversalis* in particular, by reducing egg laying but not competing for aphid prey.

In a competitive environment of patchy resources, encounters with both prey and predators are expected. Chances of encountering conspecifics within a patch are not less than that of heterospecific predators (Sengonca & Fringes, 1985; Evans, 1991; Agarwala & Dixon, 1993) and are dependent, at least partly, on the aggregation of predators and parasites that are attracted to aphid colonies (Sih et al., 1998). Risks of competition largely come from

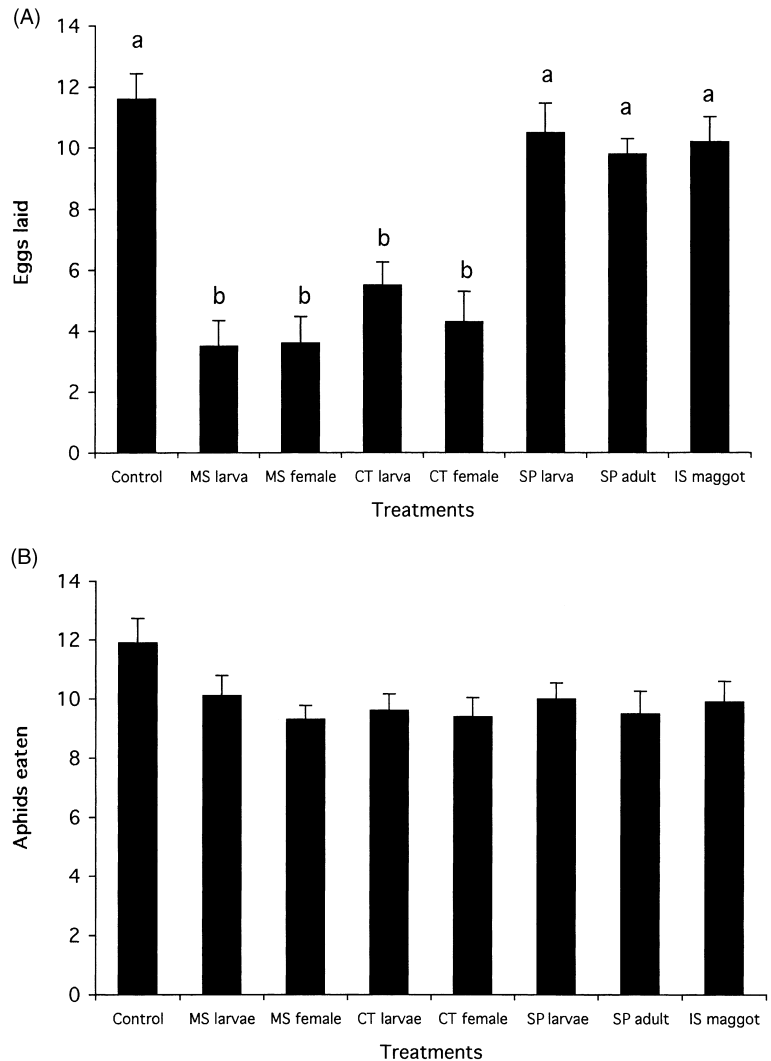


Figure 1 Mean number of eggs laid (A) and aphids eaten (B), after 3 h, by *M. sexmaculatus* females in interaction with larvae or adults of conspecific or heterospecific predators. Bars indicate standard errors of means. Same letters above bars indicate no difference between the treatments (Scheffé multiple range test, $P > 0.05$).

growing larvae that have poor powers of dispersal and are likely to attack prey and predators alike (Dixon, 1997, 2000; Lucas et al., 1998), whereas adults are able to leave the patch and search for another (Kindlmann & Dixon, 1999). Immobile eggs and new-born larvae are particularly vulnerable to cannibalism and predation when prey is scarce (Agarwala & Dixon, 1992; Agarwala & Bardhanroy, 1997; Hironori & Katsuhiko, 1997).

In this study, *M. sexmaculatus* females reduced oviposition in the presence of immobilised larvae of conspecifics or *C. transversalis* after 3 h and 24 h, but only after 3 h in the presence of adults of conspecific and *C. transversalis*. In contrast, feeding and oviposition by *M. sexmaculatus* females were not affected in the presence of *S. pyrocheilus* beetles or *I. scutellaris* maggots. This pattern of response could possibly be shaped by relative risks of competition among predators of a common prey. Factors such as

difference in size, age, and speed of searching between the predators, among others, can influence the outcome of competition between predators (Stevens, 1992; Polis & Holt, 1992; Rosenheim et al., 1995; Obrycki et al., 1998a). Both *S. pyrocheilus* beetles and *I. scutellaris* maggots are small sized predators at low prey abundance on hibiscus trees (Agarwala & Yasuda, 2001b), and usually avoid predation of eggs and larvae of large coccinellids (Ninomiya, 1968). Also, both predators showed slower speeds of searching in comparison to *M. sexmaculatus* and *C. transversalis* beetles. Moreover, syrphid maggots are usually active at night whereas ladybirds are usually diurnal (Majerus, 1994), and their feeding rates are less than half of *M. sexmaculatus* females (Tao & Chiu, 1971; Kawauchi, 1990). It may, however, be added that the lack of response by *M. sexmaculatus* females to *S. pyrocheilus* and *I. scutellaris*, in this study, may partly be attributed

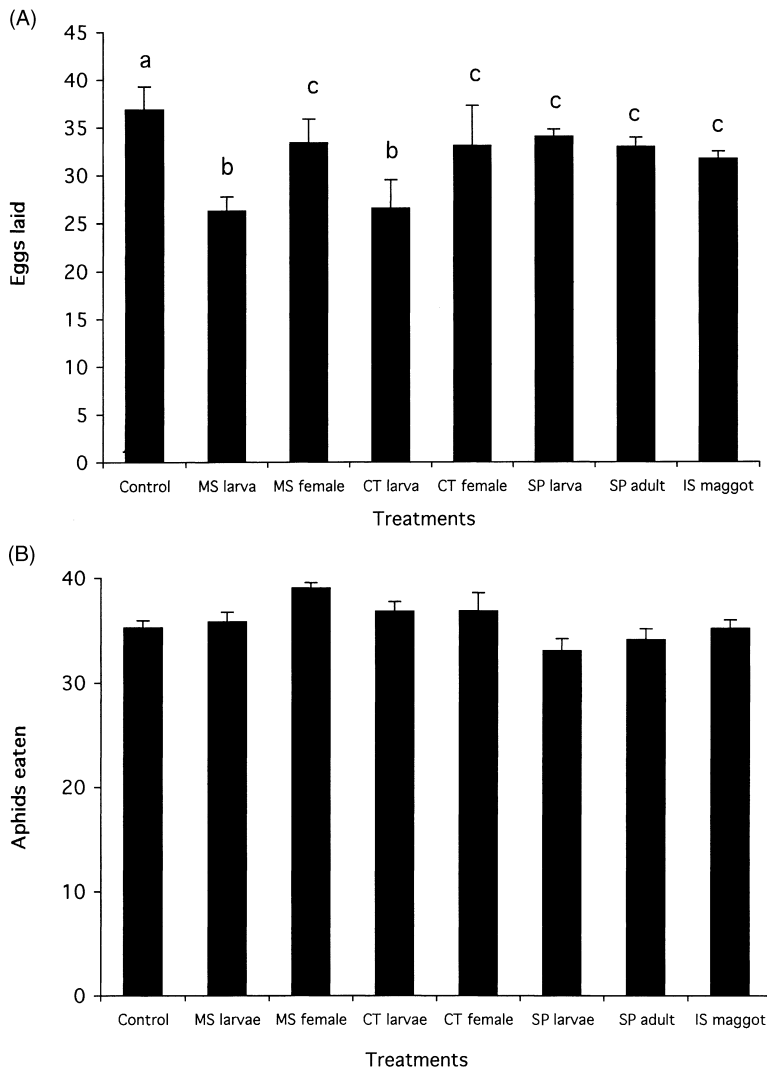


Figure 2 Mean number of eggs laid (A) and aphids eaten (B), after 24 h, by *Menochilus sexmaculatus* females in interaction with larvae or adults of conspecific or heterospecific predators. Bars indicate standard errors of means. Same letters above bars indicate no difference between the treatments (Scheffé multiple range test, $P > 0.05$).

to the procedure of immobilisation of their larvae and adults that might have eliminated cues by which *Menochilus* females might recognise other predators present in their environment.

Menochilus sexmaculatus and *C. transversalis* lay their eggs in batches whereas *S. pyrocheilus* beetles and *I. scutellaris* lay eggs singly. Clustering of eggs in ladybird predators is found to be an advantageous trait for these insects because alkaloid defense on their egg surface protects them from interspecific predation (Agarwala & Dixon, 1993). For example, eggs of *M. sexmaculatus* beetles are defended from *C. transversalis* adults in interspecific interactions (Agarwala et al., 1998), but significantly less so from *C. transversalis* larvae (Bardhanroy, 2000). The observed reduction in number of eggs laid by *M. sexmaculatus* females in response to *C. transversalis* larvae, in this study,

could be related to the risk of predation between the two predators. Results from other studies on aphidophagous ladybird have reported that an increase in predation risk among larvae (Ives, 1989) or decrease in food supply (Dixon & Guo, 1993) could lead to a decrease in the optimal clutch size of eggs per ladybird female per patch.

Arthropods are known to display an array of morphological, chemical, or behavioural defensive means of avoiding the risks of predation and parasitism (Endler, 1986, 1991; Lima, 1998). The type of defensive strategy varies according to the need of an organism and components of its environment (Lucas et al., 1997). Aphid-aphidophaga dynamics, usually dominated by one predatory species in a guild (Hodek & Honek, 1996; Dixon, 2000), may be partly explained by the effects of interactions as observed in this study.

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