*Bulletin of Entomological Research* (2006) **96**, 407–412 DOI: 10.1079/BER2006444

# Conspecific interference by adults in an aphidophagous ladybird *Propylea dissecta* (Coleoptera: Coccinellidae): effect on reproduction

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**Abstract**

The effects of conspecific adult interference on the reproductive output of an aphidophagous ladybird, *Propylea dissecta* (Mulsant) were investigated. Ovipositing females were subjected to physical interference with conspecific adults (0 to 4 males or females) in Petri dishes and the effects on egg cannibalism, oviposition and egg viability were recorded. The absence of interference was related to the lowest egg cannibalism (0.00%) and higher fecundity ($336.30 \pm 32.16$ eggs) and egg viability ($95.83 \pm 1.60\%$). Fecundity decreased with increasing physical interference from either sex. Egg viability declined with increasing male density, but was not influenced by conspecific females. In a second experiment, evaluating the role of conspecific adult chemical tracks on fecundity and egg viability, it was observed that adult chemical track density (fresh and ten-day-old) was negatively correlated. Egg viability was not affected by the presence of adult chemical tracks. The decrease in fecundity was not affected by the sex of the adults making the tracks, thus revealing that the chemical constitution of these deterrent compounds was not sex-specific. Conspecific interference in a Petri dish reduces reproductive output, as a result of physical interference and response to what seem to be oviposition-deterring pheromones present in adult tracks.

**Keywords:** coccinellid, physical interference, chemical interference, reproduction, *Propylea dissecta*, oviposition-deterring pheromones, semiochemicals

## Introduction

Intraguild predators are likely to have a negative impact on each other through interference and/or active predation (Lucas *et al*., 1998). Such interference among guild members may affect both the foraging ability, and the reproductive output of individual species (Wise, 1975; Evans, 1976; Růžička, 1996, 1997a). This interference can be both physical and chemical in nature.

The influence of physical interference on predation has been incorporated in predation models as a constant value (Hassell & Varley, 1969; Omkar & Pervez, 2004). However, little is known about the actual impact of physical interference in most biological systems. For example, the influence of adult physical interference on ladybird reproduction is largely ignored (Hemptinne & Dixon, 1991; Hemptinne *et al*., 1992, 2001; Lemaitre, 1992; Doumbia *et al*., 1998). The few studies exploring the influence of adult presence in insects other than ladybirds show a deterrent role of physical presence on reproductive output (e.g. Leather, 1990; Giga & Smith, 1991; Giga & Canhao, 1997).

Unlike physical interference, chemical interference and its effects on reproduction in ladybirds have been more extensively studied. The deterrent effect of pheromones and allomones present in larval tracks (i.e. hydrocarbon footprints left while walking on plants in search of prey, which probably prevent slipping off) on oviposition is well established in certain aphidophagous species, including

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ladybirds (e.g. Hemptinne *et al*., 1992, 1993, 2001; Růžička, 1994, 1996, 1997a,b; Takizawa *et al*., 2000; Yasuda *et al*., 2000; Fréchette *et al*., 2003). However, the influence of adult tracks on oviposition deterrence has been largely ignored except for one study that found no oviposition deterrence (Doumbia *et al*., 1998). For *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), it was observed that adults made fewer visits to areas previously searched by others (Mondor & Warren, 2000) thus suggesting the presence of detectable chemicals in adult tracks.

Egg cannibalism is a major cause of mortality in ladybirds as demonstrated through numerous field and theoretical examinations (e.g. Osawa, 1989, 1993). Larval tracks act to indicate that larvae are already present within a patch such that there is danger of cannibalism of eggs laid in the vicinity; it is thus advantageous for females to avoid laying eggs in the presence of such larval tracks (e.g. Takizawa *et al*., 2000; Yasuda *et al*., 2000; Fréchette *et al*., 2003). However, whether or not the adults also lay such chemical tracks and the eventual response of a conspecific adult to that track is not known. In the larvae, the chemicals are secreted predominantly from the pygopodium and thus have a probable role in adherence to substrata (Hemptinne & Dixon, 2000). Since the pygopodium is absent in the adults, we hypothesized that it is unlikely that adults will lay chemical tracks. In the present study, we check for the existence of chemical tracks through observations on oviposition in response to surfaces on which adults have walked. Following initial results suggesting that chemical avoidance cues were indeed deposited by adult beetles, we next hypothesized that these tracks would not have a deterrent effect on oviposition because any existing conspecific eggs encountered could simply be eaten by the female.

Thus in the present study we have assessed the reproductive response of ladybird, *Propylea dissecta* (Mulsant) (Coleoptera: Coccinellidae) females to interference, both physical and chemical, with conspecific adults.

## Materials and methods

### *Stock culture*

Adults of *P. dissecta* were collected from agricultural fields in the suburbs of Lucknow (India) and brought to the laboratory for establishment of a stock culture. The beetles were paired in Petri dishes ($9.0 \times 2.0$ cm), and provided a daily excess of locally abundant aphids on the leaves and twig of their host plants (*Rhopalosiphum maidis* (Fitch) from *Sorghum bicolor*, *Aphis gossypii* Glover from *Lagenaria vulgaris*, *Aphis craccivora* Koch from *Dolichos lablab* and *Lipaphis erysimi* (Kaltenbach) from *Brassica campestris*). Ladybird eggs were collected every 24 h and observed for hatching. The newly hatched neonates were transferred to muslin covered beakers ($11.0 \times 6.5$ cm). Five neonates were reared per beaker with an excess of aphids until adult emergence.

A subculture was maintained apart from the stock culture on an exclusive diet of *A. craccivora* on *D. lablab* until adult emergence. It has been established that *A. craccivora* is the most suitable of the seven prey species tested for *P. dissecta* (Omkar & Mishra, 2005). The subculture was started from neonates and the same rearing practices were followed as in the main stock. Non-sibling adults obtained from the subculture were used for the following experiments.

### *Experimental setups*

#### *Physical interference*

To assess the effects of physical interference on reproduction, seven experimental treatments were compared. All adults used in these treatments were 5 days old at the beginning of the experiment. The treatments were: (i) a once mated single female (control; no interference); (ii) a once mated female paired with one virgin female (level 1 of interference); (iii) one virgin female paired with an unmated male (level 1 of interference); (iv) a once mated female paired with two virgin females (level 2 of interference); (v) a virgin female paired with two unmated males (level 2 of interference); (vi) a once mated female paired with four virgin females (level 4 of interference); and (vii) one virgin female paired with four unmated males (level 4 of interference). The ovipositing female is referred to as the focal individual. For treatments providing female interference (treatments ii, iv and vi), unmated females were used as sources of interference in order to avoid errors in recording the number of eggs laid by the focal female. Observations of unmated adult stock reveal that unmated females usually do not oviposit prior to 25–30 days of age (G. Mishra, personal observation).

All the experiments were performed in Petri dishes ($9.0 \times 2.0$ cm placed in growth chambers set at $25 \pm 2^{\circ}$C; $65 \pm 5\%$ R.H.; 12L:12D). The ladybirds were supplied with an *ad libitum* supply of *A. craccivora* on *D. lablab* twigs refreshed every 12 h. The experiment lasted for 10 days, which was considered sufficient for evaluating oviposition trends. The total number of eggs laid in 10 days was recorded and the number of eggs cannibalized was determined daily under a stereoscopic binocular microscope by counting damaged eggs (disruption in the normal oval outline of the egg) and egg traces. Through this method all eggs cannibalized could be recorded. The remaining eggs were observed to determine the number of eggs that hatched. Ten replicates were performed for each experimental treatment. All the experiments were conducted using non-sibling individuals drawn from ten parental lines.

#### *Chemical interference*

To determine whether chemical tracks laid by *P. dissecta* adults deter conspecific females from laying eggs, individual 5-day-old mated females (focal females) were randomly assigned to any one of seven treatments. All the treatments consisted of adult tracks, which had been formed by allowing 12-h starved 5-day-old unmated adults to walk in a Petri dish ($9.0 \times 2.0$ cm) for a period of 4 h, after which the adults were removed. The treatments were: (i) a Petri dish containing no adult tracks; (ii) a Petri dish containing tracks from a single female; (iii) a Petri dish containing tracks from a single male; (iv) a Petri dish containing tracks from two females; (v) a Petri dish containing tracks from two males; (vi) a Petri dish containing tracks from four females; and (vii) a Petri dish containing tracks from four males.

Mated (focal) females were placed in the Petri dishes with an *ad libitum* supply of only *A. craccivora* (without the host plant) within 10 min, after completion of track formation. Ladybirds were thereafter allowed to oviposit for a period of 24 h at $25 \pm 2^{\circ}$C and $65 \pm 5\%$ R.H. Oviposition and egg viability were recorded. Ten replicates were performed for each experimental treatment.

The persistence of adult chemical tracks was also determined. For this, mated 5-day-old females were placed in Petri dishes in the presence of 10-day-old adult tracks (experimental treatments as above). Petri dishes were kept at ambient temperature for a period of 10 days prior to experimentation in order to simulate natural conditions. Ten replicates were performed for each experimental treatment.

### *Statistical analysis*

To address the first question of whether the physical or chemical presence of a conspecific adult affects the numbers of eggs laid and percentage egg viability of the focal individual and also the number of eggs cannibalized, data of the control individuals (no interference) was compared with the pooled data of other treatments using Student's t-test. To address the second question, i.e. whether degree of disruption changes as the level of interference or the sex of the interfering individual changes, a two factor ANOVA was conducted, with the control treatment omitted. In this analysis, sex of interfering individuals was the first factor (2 levels), while level of interference acting was the second factor (3 levels, namely 1, 2 or 4 interfering conspecifics). All statistical analyses were executed on MINITAB (2003) software.

## Results

### *Physical interference*

The number of eggs laid by focal females in the control treatment (i.e. zero interference) was significantly higher ($336.30 \pm 32.16$ eggs) than those laid in the six treatments including some degree of interference ($t = 9.83$; $P < 0.001$) (fig. 1). Among the treatments with interference, fecundity was strongly influenced by the level of interference ($F = 430.36$; $P < 0.001$), but not by the sex of the interfering individuals ($F = 1.81$; $P > 0.05$). There was no significant interaction between the level of conspecific interference and the sex of interfering conspecifics ($F = 2.39$; $P > 0.05$).

The lowest percentage ($0.00 \pm 0.00\%$) of eggs cannibalized was observed in the control treatment, while the highest ($77.40 \pm 6.06\%$; fig. 1) was observed in the treatment with four unmated males. The presence of physical interference was found to significantly influence the number of eggs cannibalized compared to the control treatment ($t = 4.64$; $P < 0.001$). The interaction effects between the level of interference and the sex of interfering individuals significantly affected the incidence of cannibalism ($F = 5.29$; $P < 0.001$). The level of interference ($F = 1788.69$; $P < 0.001$) also showed a statistically significant influence on the number of eggs cannibalized. Interfering males cannibalized more eggs than did females, leading to a statistically significant interaction between conspecific sex and density ($F = 10.92$; $P < 0.001$).

Percentage egg viability of controls was also significantly higher than that of the treatments with interference ($t = 56.51$; $P < 0.001$). The interaction effect between the level of interference and sex was significant when the data were subjected to two-way ANOVA ($F = 5.06$; $P < 0.001$). The percentage of viable eggs was significantly influenced by both the level of interference ($F = 9.41$; $P < 0.001$) and the sex of the individuals ($F = 18.46$; $P < 0.001$). Only treatments having male interference showed a significant decrease in percentage egg viability with increasing interference levels (fig. 1).

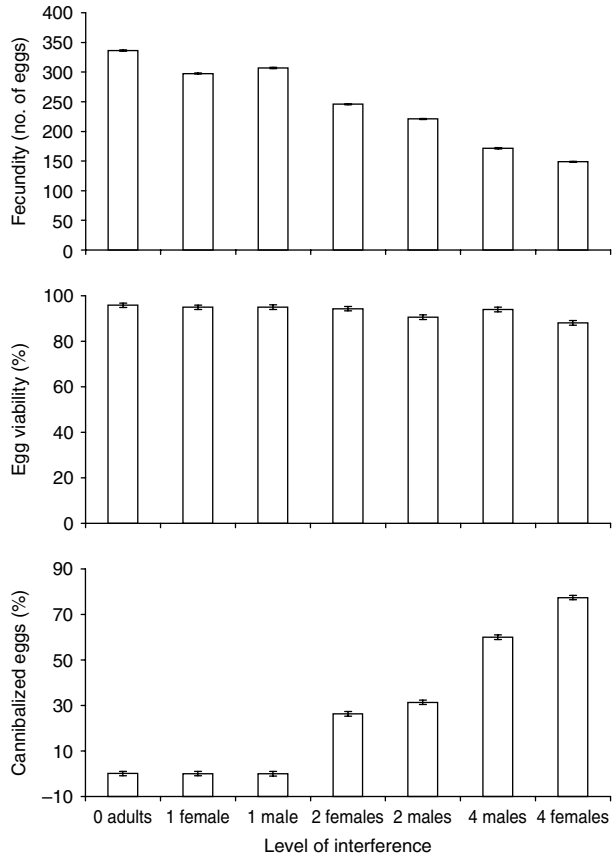


Fig. 1. Effect of physical interference on fecundity, percent egg viability and percent egg cannibalism of *Propylea dissecta*.

### *Chemical interference*

Oviposition by control females, when no tracks were present, was highest ($61.07 \pm 4.62$ eggs; fig. 2). The presence of fresh tracks at varying densities significantly reduced the number of eggs laid by focal females ($t = 11.59$; $P < 0.001$). There was a significant influence of the number of individuals that laid tracks ($F = 65.41$; $P < 0.001$), but not of sex ($F = 1.36$; $P > 0.05$) on the oviposition response of *P. dissecta* females. The interaction effect of the two independent factors was statistically non-significant in the presence of fresh adult chemical tracks ($F = 0.13$; $P > 0.05$).

The fecundity of the focal females in the presence of 10-day-old tracks followed similar statistical trends to those placed with fresh tracks (fig. 3). There was significant difference between the number of eggs laid in the control, and the number of eggs laid in the presence of 10-day-old tracks ($t = 7.54$; $P < 0.001$). The impact of 10-day-old adult chemical tracks was also significantly influenced by the number of individuals that laid tracks ($F = 8.51$; $P < 0.001$), but not by their sex ($F = 1.14$; $P > 0.05$). The interaction between conspecific sex and density was not statistically significant ($F = 0.37$; $P > 0.05$).

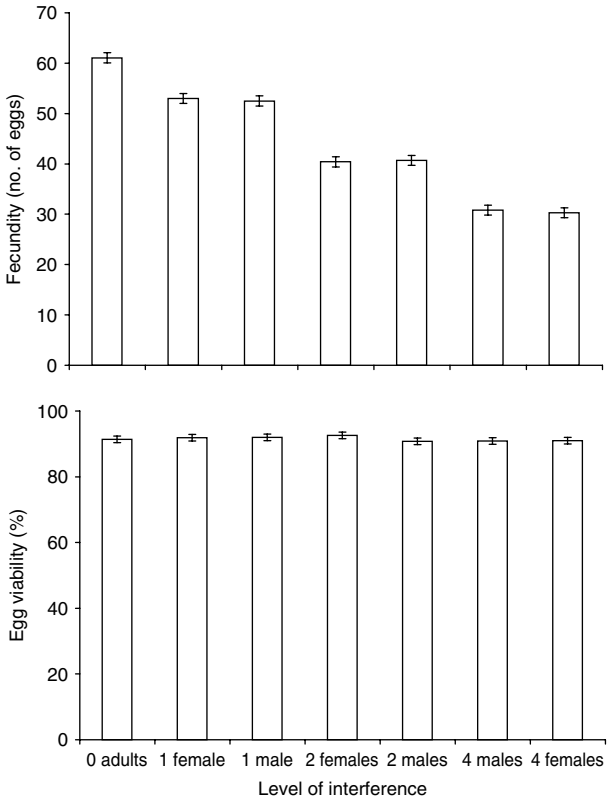


Fig. 2. Effect of chemical interference (0-day-old tracks) on fecundity and percent egg viability of *Propylea dissecta*.

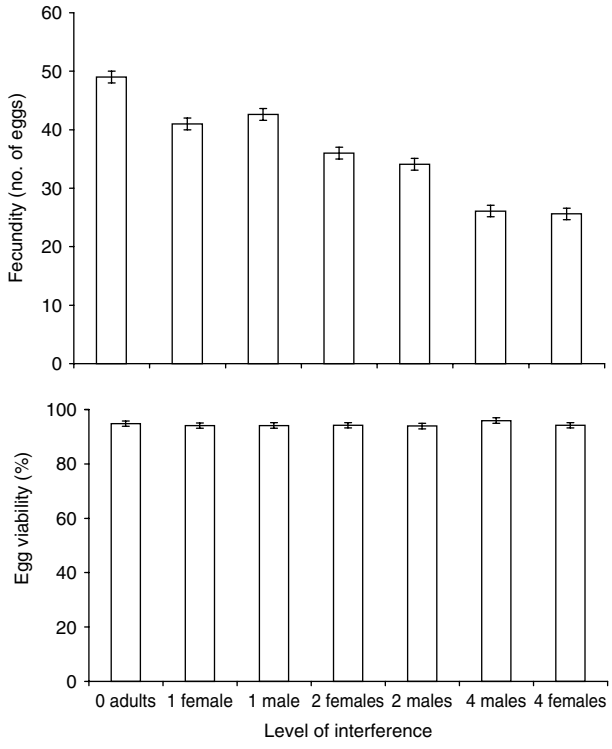


Fig. 3. Effect of chemical interference (10-day-old tracks) on fecundity and percent egg viability of *Propylea dissecta*.

The viability of eggs in the control treatment versus in the pooled experimental treatments was not affected by the presence of chemical tracks, either fresh ($t = 0.13$; $P > 0.05$) or 10-day-old ($t = 0.49$; $P > 0.05$). Egg viability in the presence of fresh tracks was not affected by the number of individuals that laid tracks ($F = 0.40$; $P > 0.05$), their sex ($F = 0.43$; $P > 0.05$), or the interaction between these two independent variables ($F = 0.26$; $P > 0.05$). Similar results were seen in the presence of 10-day-old tracks, i.e. the viability was not influenced by the degree of interference ($F = 0.36$; $P > 0.05$), sex of interfering individuals ($F = 0.45$; $P > 0.05$) or the interaction between these two factors ($F = 0.27$; $P > 0.05$).

## Discussion

This study reveals that: (i) both physical and chemical interference negatively impact the reproductive performance of *P. dissecta* females; (ii) the fecundity decreases with increasing physical interference, regardless of the sex of the interfering individuals; (iii) the egg viability decreases in the presence of males; and (iv) fresh and 10-day-old adult chemical tracks have an oviposition-deterring effect, which does not influence egg viability.

Physical interference had a negative impact on both fecundity and egg viability. The fecundity of focal females decreased with increasing numbers of surrounding individuals, regardless of the sex of those conspecifics. This decrease could be the result of females sensing increased risk of egg predation. Also, crowding can lead to decreased per capita consumption of aphids due to physical interference among multiple foragers (Hassell & Varley, 1969; Omkar & Srivastava, 2003; Pervez & Omkar, 2003; Omkar & Pervez, 2004) and may be responsible for the decrease in the number of eggs laid (Veeravel & Baskaran, 1997; Omkar & Pervez, 2004).

A decrease in the number of viable eggs was seen in treatments with male interference. Reduced egg viability caused by male physical interference could be the result of mating interruptions and probable subsequent incomplete sperm transfer. Ladybirds usually transfer sperms either continuously, i.e. directly (Omkar, 2004; Omkar & Pervez, 2005) or through indirect means, using sperm packets known as spermatophores (Fisher, 1959; Obata, 1987; Omkar, 2004; Omkar & Srivastava, 2002). Longer matings are likely to result in higher fertility in the case of *P. dissecta*, which probably transfers sperm directly and continuously (Omkar & Pervez, 2005). Longer matings in ladybirds have been found to result in higher fertility probably owing to receipt of an increased number of sperm (Omkar *et al.*, 2006). Such physical interference effects have also been observed in parasitoids (Jackson, 1966; Viktorov, 1968; Holmes, 1972). The influence of female presence on egg viability was, however, insignificant since ovipositing females had been subjected to a single complete uninterrupted mating.

Egg cannibalism in ladybeetles is a well-known phenomenon (Shands *et al.*, 1970; Agarwala & Dixon, 1991; Osawa, 1989, 1993; Omkar *et al.*, 2002). In the present study, a negligible number of eggs were cannibalized in arenas

with zero interference or with one interfering conspecific, regardless of sex. However, an increase in the number of conspecific adults (up to four males or females) resulted in increased egg cannibalism. The number of eggs cannibalized was not influenced by the sex of the interfering individuals, except for the sudden increase seen in the treatment with four males. Previous studies state that some ladybird females are reluctant to eat their own eggs, though this reluctance has not been observed in males (Agarwala & Dixon, 1993; Hemptinne *et al*., 2000a,b). Based on this prior finding, we suspect that the egg cannibalism observed in treatments with conspecific females is likely to be by the co-occurring unrelated virgin females rather than the ovipositing focal female.

*Propylea dissecta* fecundity was reduced in the presence of adult tracks, indicating the presence of deterrent chemicals in these tracks thereby rejecting our first hypothesis. Fecundity was observed to be negatively correlated with the density of individuals from which chemical tracks were produced. The sex of the adults involved in track formation had no effect on *P. dissecta* oviposition behaviour. The oviposition-deterrent effect of ladybird larval tracks is well documented (Hemptinne *et al*., 1992, 1993, 2001; Růžička, 1994, 1996, 1997b; Dixon, 1997; Doumbia *et al*., 1998; Yasuda *et al*. 2000; Fréchette *et al*. 2003). However, studies on adult tracks were lacking. Agarwala *et al*. (2003) have described the oviposition-deterring effects of adult faeces, but since they were controlled in the present study the same was not possible here. To our knowledge, the only other study conducted to determine the effect of adult tracks on ladybird oviposition behaviour has not found such a deterrent effect (Doumbia *et al*., 1998).

Why do females refrain from ovipositing in the presence of adult tracks? The presence of adult tracks might signal that the patch has already been extensively searched and that the presence of prey is unlikely. Higher track density is likely to indicate an increased number of prior searches, thus suggesting a lack of prey and therefore an unsuitable patch. Under such conditions in the field, *P. dissecta* females are likely to fly away after being in contact with these tracks. However, in the laboratory, females were unable to leave the Petri dish and thus probably responded to the adult tracks by withholding or decreasing oviposition.

The fact that adult tracks have no effect on egg viability indicates that the decrease in egg viability observed in the physical interference experiment is probably the result of disturbance and mating interruptions, as has been discussed above. Ten-day-old adult tracks were found to deter oviposition, which is similar to what has been reported for larval tracks (Hemptinne *et al*., 1992, 2001; Růžička, 1997b; Doumbia *et al*., 1998).

## Acknowledgements

The authors are thankful to Dr Bruno Frechette, University of Québec, Montréal, Dr Robert Koch, Department of Entomology, University of Minnesota, and two anonymous reviewers for scrutinizing earlier drafts of the manuscript and providing valuable suggestions. GM is thankful to the Council of Science and Industrial Research, New Delhi for the award of a fellowship.

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(Accepted 4 May 2006)