

## Avoidance of ladybird trails by an aphid parasitoid *Aphidius ervi*: active period and effects of prior oviposition experience

Yoshitaka Nakashima<sup>1</sup> & Nozomu Senoo

Laboratory of Entomology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Hokkaido, 080-8555, Japan

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### Introduction

Aphids are attacked by a large guild of natural enemies (Hagen & van den Bosch, 1968; Wheeler, 1977; Dixon, 1998). Intraguild interactions are widespread in aphid natural enemy communities (Brodeur & Rosenheim, 2000). For instance, intraguild predation (IGP), defined as trophic interactions among organisms sharing the same resource, has recently been well documented (Polis et al., 1989; Polis & Holt, 1992; Rosenheim et al., 1995). Several authors have reported that IGP changes the extent to which top-down forces by predator guilds affect herbivore populations. The effects of IGP on herbivore population dynamics can be variable, and within aphid-natural enemy systems, there are examples of both negative (Ferguson & Stiling, 1996; Snyder & Ives, 2001) and positive (Colfer & Rosenheim, 1995) effects. Brodeur & Rosenheim (2000) conclude that intraguild interactions are the primary factor driving fluctuations in parasitoid populations. In parasitoid-predator-herbivore systems, parasitoids are usually the intraguild prey because parasitized hosts are potentially consumed by predators.

Although the factors determining the intensity of IGP events are controversial, resource abundance and avoidance behaviour by at-risk guild members may be crucial. Low densities of shared herbivore prey tend to induce greater rates of IGP (Lucas et al., 1998; Obrycki et al., 1998). Avoidance behaviour would reduce the likelihood of IGP, and this has been suggested in predator-predator (Pallini et al., 1998;

Schellhorn & Andow, 1999;) and parasitoid-predator (Taylor et al., 1998; Raymond et al., 2000) interactions. These studies indicate that the inferior species (intraguild prey) tends to avoid patches or microhabitats where the superior member of the same guild (intraguild predator) is already present. Taylor et al. (1998) demonstrated that the aphid parasitoid *Aphidius ervi* Haliday (Hymenoptera: Aphididae) avoids places where the intraguild predator *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) is present or was present recently. They suggest that chemical trails left by the predator induce the avoidance responses of parasitoids. No studies, however, have determined the specific characteristics of the avoidance behaviours exhibited during intraguild predator/parasitoid interactions. For example, it is not known for how long the parasitoid avoidance behaviour persists after the predator has left a patch or how oviposition experiences affect the behavioural responses of the parasitoids to ladybird trails. These factors are important for understanding the functions of such avoidance behaviour by parasitoids in the field. *Aphidius ervi* is a dominant parasitoid attacking the pea aphid *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae) in Hokkaido, Japan (Senoo et al., 2002), where the seasonal distribution of aphids parasitized by *A. ervi* and foraging *C. septempunctata* ladybirds overlap on alfalfa (Y. Nakashima unpubl.).

The effects of ladybird chemical trails on parasitoid foraging behaviour and the flexibility of parasitoid avoidance responses, as influenced by oviposition experience, were investigated in laboratory experiments with *A. ervi*. The following questions were addressed: does prior oviposition experience affect intraguild predator avoidance by parasitoids? For how long is the ladybird trail active? Based on the results, we discuss the function and potential effects of intraguild predator avoidance by *A. ervi* on aphid population dynamics in the field.

\*Correspondence: Yoshitaka Nakashima, Laboratory of Entomology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Hokkaido 080-8555, Japan, E-mail: nksm@obihiro.ac.jp  
Fax: +81 155 49 5494, <sup>1</sup>Present address: Yoshitaka Nakashima, Rothamsted Research, Harpenden, Herts. AL5 2JQ UK  
E-mail: yoshitaka.nakashima@bbsrc.ac.uk Fax: +44 1582760981

## Materials and methods

### Insects

To initiate laboratory colonies, *A. pisum*, mummies of *A. ervi*, and adult *C. septempunctata* were collected from alfalfa fields at Obihiro University of Agriculture and Veterinary Medicine, Hokkaido, Japan (42°92'N, 143°22'E) in spring 2000. *Acyrtosiphon pisum* were reared on potted broad bean *Vicia fabae* L. (Fabaceae) seedlings. *Aphidius ervi* and *C. septempunctata* were reared on broad bean seedlings infested by *A. pisum* and kept in plastic boxes (13.6 l). All insect colonies were maintained at 22 °C and a L16 : D8 h photoperiod.

To obtain adult parasitoids for experiments, mummies were removed from the laboratory colony and kept individually in gelatin capsules until emergence. One day after emergence, females were divided into two groups: females with and without oviposition experience. The former were provided with 50 *A. pisum* and cotton soaked in 15% honey solution and confined in a Petri dish (7 cm diameter) for 24 h to allow oviposition and feeding. The latter was kept in Petri dishes without aphids but with cotton soaked in honey solution. Two-day-old females were used in all experiments. Adults and 4th instar larvae of *C. septempunctata* were removed directly from the colony for use in experiments.

### Effect of prior oviposition experience on avoidance behaviour

The aim of the experiment was to determine the effect of prior oviposition experience on a female parasitoids' avoidance behaviour. Parasitoid females that were provided with 50 aphids 24 h before the experiment and aphid-deprived females were used (see above). The experiment was conducted in plastic arenas (4 cm in height, 6 cm in diameter at the bottom and 8 cm in diameter at the top). A single fourth instar larva or adult of *C. septempunctata* was introduced into each treatment arena and confined for 24 h by means of a plastic lid, after which it was removed. Fifty aphids (mixed age) were then released into each treated arena and into control arenas that had not contained ladybirds. A glass tube (5 mm in diameter and 15 mm in length) containing a parasitoid female was placed in the centre of each arena. After the parasitoid exited the tube and moved onto the container surface, its residence time in the container was measured until it left the inside of the arena by flying or walking. For each treatment, 40 replicates were tested.

### Persistence of the predator trail

To determine how long the effects of predator trails on parasitoid responses persisted, the residence times of parasitoids on broad bean leaves with or without trails

were measured. Treated broad bean leaves, on broad bean seedlings at the 4-leaf stage, were exposed to fourth instar larvae of *C. septempunctata*, by confining the leaf in a plastic container (160 ml) with a mesh cover containing a larva. A slit in the container allowed the leaf to remain attached to the plant. This procedure ensured that the larva was allowed to walk upon the leaf. Twenty-four hours after introduction, the larva and container were removed from the plant. These plants were used in experiments at intervals of 0 h, 6 h, 12 h, 18 h, or 24 h after predator removal. The same procedures were used for control leaves but no predators were placed in the containers. To measure parasitoid responses, single *A. ervi* females were released into Petri dishes (5 cm diameter), each containing a treated and a control leaf placed 1 cm apart. The time spent foraging on each leaf was measured during a 15-min period. Twenty-four parasitoid females were tested for each of the treatment intervals.

### Statistical analysis

The female parasitoid residence times in the test arenas were analysed using a two-way ANOVA with oviposition experience and ladybird presence as the main effects. Comparisons of residence times in each treatment were analysed using a Fisher Protected Least Significant Difference test. The foraging times of parasitoids on treated and control leaves in the persistence experiment were analysed using paired t-tests. All data were log transformed before the analyses to stabilize the variance. All tests were done with a 5% level of significance.

### Results and Discussion

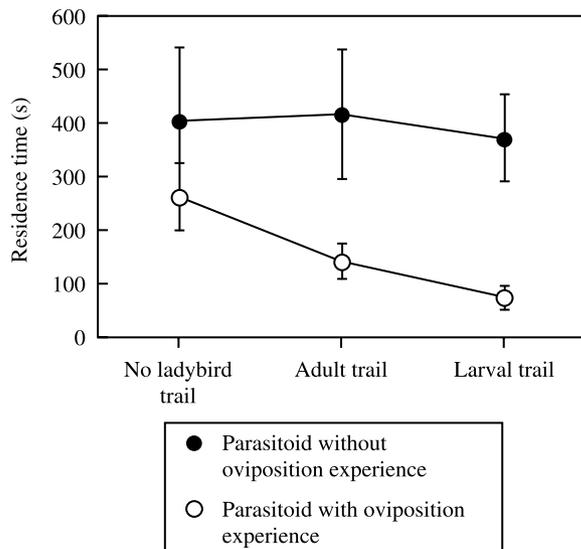
This study confirmed that parasitoids use trails left by intraguild predators on plant surfaces to avoid areas containing or already searched by predators. Furthermore parasitoids without oviposition experience were not sensitive to the trails of intraguild predators, whereas parasitoids with oviposition experience avoided areas where predators had recently been present (Figure 1), demonstrating for the first time that prior oviposition experience affects intraguild predator avoidance by parasitoids. A two-way ANOVA of residence times indicated that the effect of oviposition experience was highly significant (Table 1). Although there was no significant difference in mean time spent in treated and control arenas for females without oviposition experience, significant differences were found for females with oviposition experience. Thus, in the analysis, the interaction between oviposition experience and predator existence was significant (Table 1). These results indicate that the response of parasitoids to the predator chemical trail differed depending on oviposition experience, suggesting

**Table 1** Two-way ANOVA for effect of oviposition experience and predator existence on residence time

Factor	d.f.	SS	F	P
Predator existence	2	12.5	2.8	0.065
Oviposition experience	1	22.8	10.1	0.0017
Interaction	2	16.4	3.6	0.028
Error	234	527.7		

that aphid density could affect the intraguild avoidance behaviour of *A. ervi*, because oviposition experience is influenced by host density.

Some insects make foraging decisions when under predation risk (Kohler & McPeck, 1989; Cartar, 1991). In our system, immature stages of parasitoids suffer the risk of predation from intraguild predators and this could affect an adult parasitoid's decision whether or not to oviposit in a host patch. Our results suggest that adult parasitoids make patch leaving decisions according to the relative requirements of oviposition and avoidance of intraguild predation. This decision may be adjusted by oviposition experience, egg load or their combined effects, but our present study could not separate these factors. It can be hypothesised, however, that host density in patches that adult females have previously visited affects the individual's response to the chemical trails of intraguild predators. Recent theoretical and empirical studies conclude

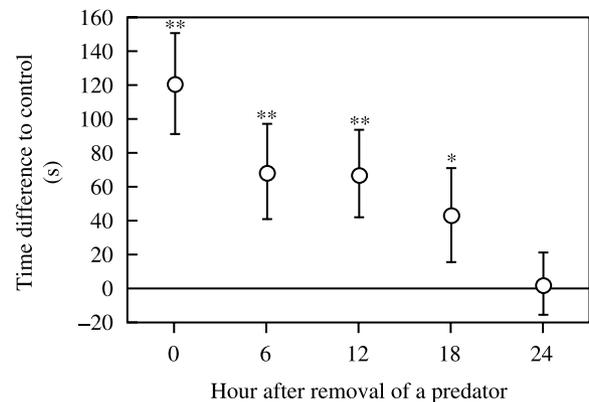


**Figure 1** Patch residence time of parasitoids with (open circle) and without (solid circle) oviposition experience in response to trails of *Coccinella septempunctata*. Two-way ANOVA showed that effects of ladybird trails differently affected the patch residence time according with oviposition experiences.

that lower egg loads in foraging insects lead to more selective oviposition behaviour (Minkenberget al., 1992) and thus, as egg load decreases, foragers become more selective by ovipositing in patches where fitness returns may be higher. The prediction may be consistent with our results in that parasitoids with recent oviposition experience, and therefore a lower egg load than naive females, tended to avoid patches where intraguild predators were potentially present (i.e., patches giving lower fitness returns).

The total residence times of parasitoids on control leaves were significantly longer than those on leaves with ladybird trails when treatments were applied 18 h or less before parasitoid release in the persistence experiments (Figure 2). This result indicates that the trails have a relatively short active period (between 18 h and 24 h). Because of their limited active period, the trails deposited by predators are a reliable indicator of areas in which intraguild predators potentially are still present. Thus, the active period may serve to decrease the frequency of intraguild predation. The chemical composition of the trails of *C. septempunctata* has been determined (Kosaki & Yamaoka, 1996), but the specific chemical compounds involved in the parasitoid avoidance behaviour remain to be identified.

Intraguild predation and the avoidance behaviour may occur in the same patches. It is difficult to separate these two effects in the suppression of herbivore populations, because both factors apparently reduce the number of parasitized aphids. However, these two types of intraguild interactions may lead to opposite impacts on herbivore populations. IGP removes parasitized aphids from the aphid population, reducing the subsequent adult parasitoid population. On the other hand, predator avoidance helps to increase parasitized aphid populations in other



**Figure 2** Differences in total residence time on leaflets with and without ladybird trails. Bars with plots indicate 1 SE. Asterisks show significant differences by paired t-tests (\* $P < 0.5$ , \*\* $P < 0.01$ ).

patches without intraguild predators. So far, no study has separated these effects. The relative effects of IGP and intraguild predator avoidance should be determined in future studies. However, it can be concluded that intraguild predator avoidance should be a factor affecting parasitoid population dynamics and thus may affect aphid population suppression.

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