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

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25 **Introduction**

Aphids are attacked by a large guild of natural enemies (Hagen and van den Bosch 1968; Wheeler 1977; Dixon 1998). Intraguild interactions are widespread in aphid natural enemy communities (Brodeur and 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 and 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. IGP effects on herbivore population dynamics can be variable, and within aphid-natural enemy systems, there are examples of both negative (Ferguson and Stiling, 1996; Synder & Ives 2001) and positive (Colfer and Rosenheim, 1995) effects. Brodeur and 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 (Schellhorn and Andow 1999; Pallini et al., 1998;) 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 (Aphidiidae) avoids places where the intraguild predator *Coccinella septempunctata* L. is present or was

present recently. They suggest that chemical trails left by the predator induce the avoidance
50 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
55 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* in Hokkaido, Japan (Senoo., et al. 2001), where
the seasonal distribution of aphids parasitized by *A. ervi* and foraging *C. septempunctata*
ladybirds overlap on alfalfa (Nakashima unpublished data).

The effects of ladybird chemical trails on parasitoid foraging behaviour and the flexibility
60 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.

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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
70 Medicine, Hokkaido, Japan (42°92'N, 143°22'E) in spring 2000. *A. pisum* were reared on
potted broad bean *Vicia fabae* L. (Fabaceae) seedlings. *A. 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 LD 16 : 8 h photoperiod.

To obtain adult parasitoids for experiments, mummies were removed from the laboratory
75 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
80 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
85 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 hours by means of a plastic lid,
90 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
95 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.

100 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.

105 These plants were used in experiments at intervals of 0h, 6h, 12h, 18h 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 (5cm diameter), each containing a treated and a control leaf placed 1cm apart. The time spent foraging on each leaf was measured during a 15 min period. Twenty-four

110 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

115 of residence times in each treatment were analysed using a Fisher PLSD test. The foraging times of parasitoids on treated and control leaves in the persistence experiment were analysed using paired t-tests. All data were transformed to logarithms to stabilize the variance before these analyses. All tests were done with a 5% level of significance.

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

135 Some insects make foraging decisions when under predation risk (Kohler and Mcpeek, 1989; Cartar, 1991). In our system, immature stages of parasitoids suffer the risk of predation from intraguild predators and this could affect an adult parasitoids 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 that lower egg loads in foraging insects lead to
145 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 naïve females, tended to
avoid patches where intraguild predators were potentially present (i.e. patches giving lower
150 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
155 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 and Yamaoka, 1996), but the specific chemical
compounds involved in the parasitoid avoidance behaviour remain to be identified.

160 IGP 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,
165 predator avoidance helps to increase parasitized aphid populations in other 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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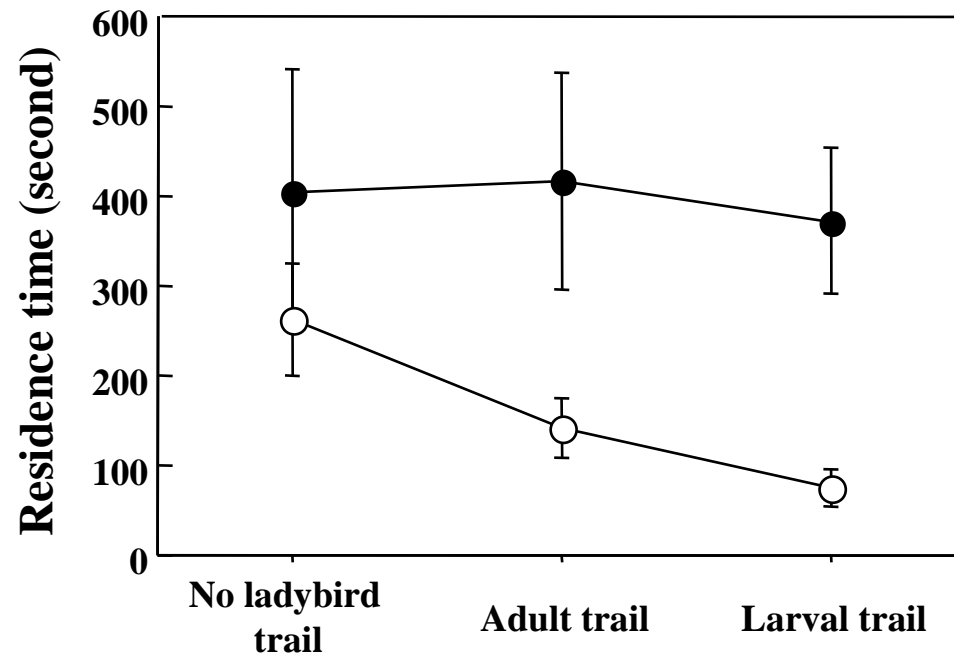
Figure Legends (Nakashima & Senoo)

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 effect of ladybird trails differently affected the patch residence time according with oviposition experiences.

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** (* $P < 0.5$, ** $P < 0.01$).

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

Factor	df	SS	<i>F</i>	<i>P</i>
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		



**Parasitoid without
oviposition experience**

**Parasitoid with
oviposition experience**

Figure 1
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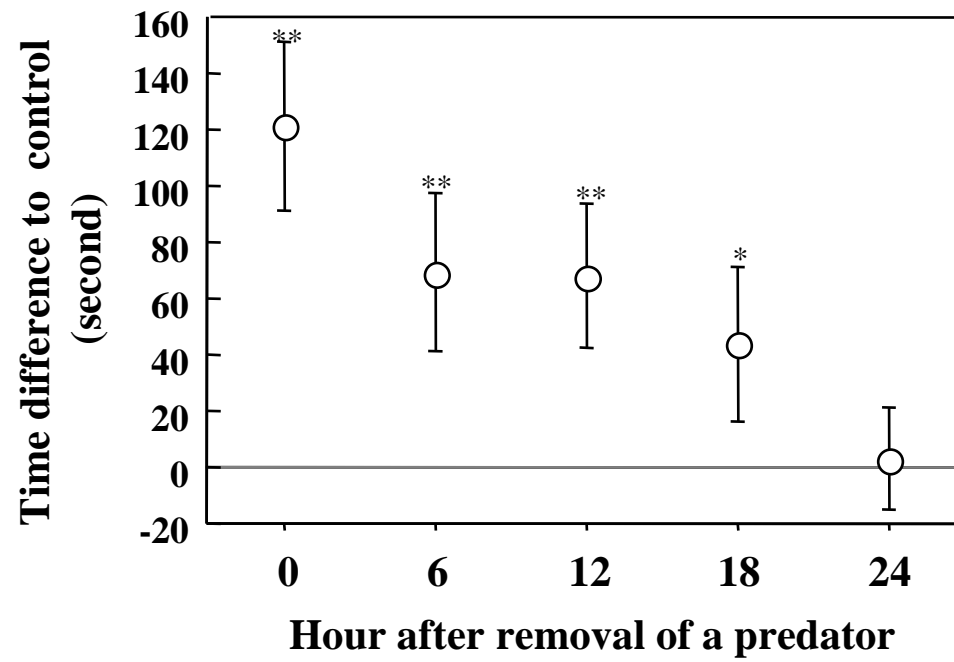


Figure 2
Nakashima & Senoo