

## Oviposition preference of two hoverfly species in response to risk of intraguild predation

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### Abstract

Two experiments were performed in the laboratory to understand the relationships between oviposition preference and larval performance of the two predatory hoverfly species, *Episyrphus balteatus* de Geer and *Metasyrphus corollae* Fabricius. We first conducted laboratory experiments to understand the nature and relative strengths of intraguild predation between the larvae of three ladybird species, *Harmonia axyridis* Pallas, *Propylea japonica* Thunberg, and *Scymnus posticalis* Sicard, and two predatory hoverfly species. The interactions between larvae of the three ladybird and two hoverfly species differed depending on the species and developmental stages involved: the relationships between *H. axyridis* or *S. posticalis* and the two hoverfly larvae tended to be asymmetric with *H. axyridis* being a superior species and *S. posticalis* an inferior species, although the reverse was true for each of these two species when small larvae were paired with large larvae of the hoverflies. The ladybird, *P. japonica*, had both asymmetric and symmetric relationships depending on the hoverfly species with which it interacted. Secondly, we tested the preference and performance hypothesis for hoverflies, by determining whether hoverfly oviposition preference was related to the risk of intraguild predation posed by the presence of a ladybird larva in an aphid colony. Oviposition preference in relation to larval performance of the two hoverflies differed between the species: *E. balteatus* females tended to adjust their rate of eggs laying in response to the presence of ladybird larvae, while similar responses of *M. corollae* females were weak. The relationship between oviposition preference and larval performance in hoverflies is discussed.

**Key words:** Hoverfly; ladybird larvae; larval performance; oviposition response; risk of intraguild predation

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### INTRODUCTION

Understanding the relationships between oviposition preference and larval performance is one of most important issues in insect ecology since these relationships strongly influence individual fitness, population dynamics, and community structure (e.g., Blaustein et al., 2004; Craig and Ohgushi, 2002). In general, natural selection will favor females that lay eggs at a most appropriate site for offspring. To enhance their fitness, for instance, females of insects tend to choose an oviposition site that provides suitable food as well as reduced risk of predation, as achieved by avoiding patches containing potential predators (e.g., Sadeghi and Gilbert, 2000a, b; Blaustein et al., 2004). These

relationships have been studied mainly in several taxonomic groups of phytophagous insects (e.g., Yamaga and Ohgushi, 1999; Mira and Bernays, 2002; Singer et al., 2004), and predatory insects as well (e.g., Doumbia et al., 1998; Nakashima et al., 2006).

It is well known that intraguild predators critically affect the larval fate of intraguild prey species among predatory insects (e.g., Lucas et al., 1998; Phoofolo and Obrycki, 1998; Hindayana et al., 2000). This in turn may influence oviposition site selection by these predators (e.g., Taylor et al., 1998; Takizawa et al., 2000). For example, a parasitoid wasp tends to avoid ovipositing in an aphid colony containing an intraguild predator (Takizawa et al., 2000), suggesting that intraguild prey species

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might avoid laying eggs in patches having potential intraguild predators. However, there are few studies to understand how an intraguild prey species chooses oviposition sites in relation to its intraguild predators.

Ladybirds and predatory hoverflies are common aphidophagous insects that often coexist with each other on the same plants, where the larvae of these species interact strongly each other as they face low food availability (e.g., Agarwala and Yasuda, 2001). Negative impacts of ladybird larvae on larval performances of aphidophagous insects have been reported for various taxonomic groups (e.g., Ferguson and Stiling, 1996; Lucas et al., 1998; Felix and Soares, 2004). In particular, ladybird larvae often reduce survivorship of related species in acting as intraguild predators (Yasuda and Ohnuma, 1999; Hindayana et al., 2000; Meyhofer and Hindayana, 2000). Hoverfly larvae are vulnerable to intraguild predation since the larvae have low mobility (e.g., Hindayana et al., 2000). This suggests that predatory hoverflies might prefer to lay eggs at sites with few predators in addition to many prey. Hoverfly females can recognize a suitable aphid colony at which they lay eggs (Kan and Sasakawa, 1986; Kan, 1988a, b), and they might have similarly strong oviposition preferences for sites in relation to intraguild predators. However, there are no studies to support this hypothesis (Gilbert, 2005).

We conducted a couple of laboratory experiments to understand larval interactions between the larvae of three ladybird species, *Harmonia axyridis* Pallas, *Propylea japonica* Thunberg, and *Scymnus posticalis* Sicard, and two predatory hoverfly species, *Episyrphus balteatus* de Geer and *Metasyrphus corollae* Fabricius. As these insects provided differ in size, foraging behavior, and food habit, these differences are likely important for larval interactions involving intraguild predation between the ladybirds and hoverflies (Lucas et al., 1998).

We examined first the nature and relative strengths of intraguild predation between different development stages of the three ladybird and two hoverfly larvae. We predicted that hoverfly larvae would most often serve as the prey due to their low mobility, although the outcome of interactions would also vary with larval stages as depend on their body size, aggressiveness and mobility. Sec-

ondly, we tested the preference and performance hypothesis that the potential for intraguild predation by ladybird larvae on hoverfly larvae would affect oviposition preference of hoverfly females.

## MATERIALS AND METHODS

**Insect rearing.** Adults of the two hoverfly species, *E. balteatus* and *M. corollae*, and three ladybird species, *H. axyridis*, *P. japonica* and *S. posticalis*, were collected from the Yamagata University farm and the Akagawa riverbank, Tsuruoka, Yamagata, Japan. Similar numbers of females and males of each hoverfly species were reared separately in two muslin cages (60×60×70 cm) with 20–30 adults of each species in total. Food for these adults was provided by putting crushed-pollen in a Petri dish (5 cm in diameter and 1 cm in height). Water and honey were provided for adults by inserting an aluminum stick (40 cm in length and 2 mm in diameter), with thin layer of honey on the upper part and towel paper wrapped on the lower part, through a small hole on the cap of a 500 ml plastic bottle filled with water. Females and males were allowed to pair, and a couple of bean plant (*Vicia faba*) cuttings with *Aphis craccivora* Koch colonies were introduced into the cage as oviposition sites. Eggs were collected daily, and then were placed into a Petri dish until hatching. Hoverfly larvae were reared by providing ample numbers of *A. craccivora* as prey. A pair of adult ladybirds was kept in a Petri dish (5 cm in diameter and 1 cm in height) and fed with *Acyrtosiphon pisum* (Harris) for *H. axyridis* and *P. japonica*, and *A. craccivora* for *S. posticalis*. Eggs were collected and the larvae hatching from these eggs were reared in similar fashion to the adults. All insects were maintained in a controlled room at 23°C, 75% relative humidity, and under a photoperiod of 16L8D.

**Larval interaction between the two individuals of ladybirds and hoverflies.** Of the three ladybird species, *H. axyridis* is the largest and most aggressive species that consumes not only aphids, but also other arthropods such as ladybird larvae, lepidopteran larvae, and spiders, in serving as a top predator in an aphidophagous guild (Yasuda and Shinya, 1997; Yasuda and Ohnuma, 1999; Sato et al., 2003). *S. posticalis* is the smallest and least mobile and *P. japonica* is intermediate in body size

and mobility. The hoverflies, *E. balteatus* and *M. corollae*, are different in body size (Putra and Yasuda, 2006), but both are polyphagous species (Owen and Gilbert, 1989; Gilbert and Owen, 1990), although *E. balteatus* seems to have wider range of prey species.

To intensify the interactions between two individuals, larval interactions between the three ladybird and the two hoverfly species at different developmental stages were examined in the absence of extraguild prey. In order to understand these interactions, we used a small Petri dish (5 cm in diameter and 1 cm in height) as an experimental arena. We tested combinations of ladybirds and hoverflies based on (1) larval developmental stages (early and late instars), and (2) species that differ in size, mobility, and aggressiveness, with 24 combinations in total and 15–20 replications for each combination.

Hoverfly and ladybird larvae were reared on plenty of aphids in a small Petri dish (5 cm in diameter and 1 cm in height) as described above. The first instar larvae of the predatory insects were tested less than 12 h after they hatched, while the third instar larvae of the hoverfly and the fourth instar of ladybird larvae were tested within 24 h after molting. These predators were starved for 6 h prior to the experiment in order to increase hunger level, and the experiments were conducted in a controlled room as mentioned before for insect rearing.

A hoverfly larva was released in the Petri dish before releasing a ladybird larva in the same dish. The two larvae were allowed to interact for the next 24 h. The outcome of the interactions was expressed as the percent of pairing in which intraguild predation occurred, since predation was observed in all combinations. Chi-square tests (Sokal and Rohlf, 1995) were performed to determine whether these interactions were symmetrical or not (i.e., whether ladybird and hoverfly larvae preyed on each other with equal frequency).

**Effect of a ladybird larva on the oviposition preference of the two hoverfly species.** The effect of a ladybird larva on the oviposition preference of a hoverfly female was examined by a non-choice test using 30 different gravid females for each species with the same age, i.e. 25–30 d after eclosion. A non-choice test was chosen since it enables the insect to perceive only one treatment, as shown in previous studies (Sadeghi and Gilbert, 2000b). A cutting of a bean plant (20 cm in height) which had

been infested with 20–25 individuals of apterous *A. craccivora* at the apical portion was put into a bottle (5 cm in height, and filled with water) to serve as an oviposition site. The cutting was covered with a cylindrical plastic cage (8 cm in diameter and 42 cm in height). One gravid female was released into one replicate cage of each treatment as mentioned below for an hour. Since we applied seven treatments, each female was tested with the seven different types of oviposition sites, which were presented to the female in random order. The number of eggs laid on the bean plant in each treatment was counted. The seven treatments were arranged as follows, (1) an aphid colony without any ladybird larva as control, and (2) an aphid colony with a fresh-frozen ladybird larva that was (i) a first instar larva or (ii) a fourth instar larva of *H. axyridis*, (iii) a first instar larva or (iv) a fourth instar larva of *P. japonica*, and (v) a first instar larva or (vi) a fourth instar larva of *S. posticalis*. One-way ANOVA was performed on the number of eggs laid by a female among treatments, and means were compared by post-hoc Fisher LSD (Sokal and Rohlf, 1995).

## RESULTS

### Larval interactions between the two individuals of ladybirds and hoverflies

Among the three species of ladybirds, *H. axyridis* larvae most reduced survival of *E. balteatus* larvae (Fig. 1). For an equivalent larval stage, *H. axyridis* larvae were superior against the hoverfly larvae. Moreover, the first instar of hoverfly larvae was more vulnerable than the third instar larvae when confronted with *H. axyridis* larvae, and the first instar was always the victim in significantly asymmetric interactions with the ladybird larvae. The hoverfly larvae were superior only as third instars facing the first instar of *H. axyridis* larva. Interactions between *E. balteatus* and *P. japonica* larvae tended to result in asymmetric interactions, where first and third instar larvae of *E. balteatus* were prey and predator respectively when faced against the fourth and first instars of *P. japonica*. The other two interactions (L-1 vs L-1 and L-3 hoverfly vs L-4 ladybird) led to symmetric outcomes. Consequences of larval interactions between *E. balteatus* and *S. posticalis* were asymmetrical, with *E. balteatus* larvae significantly superior

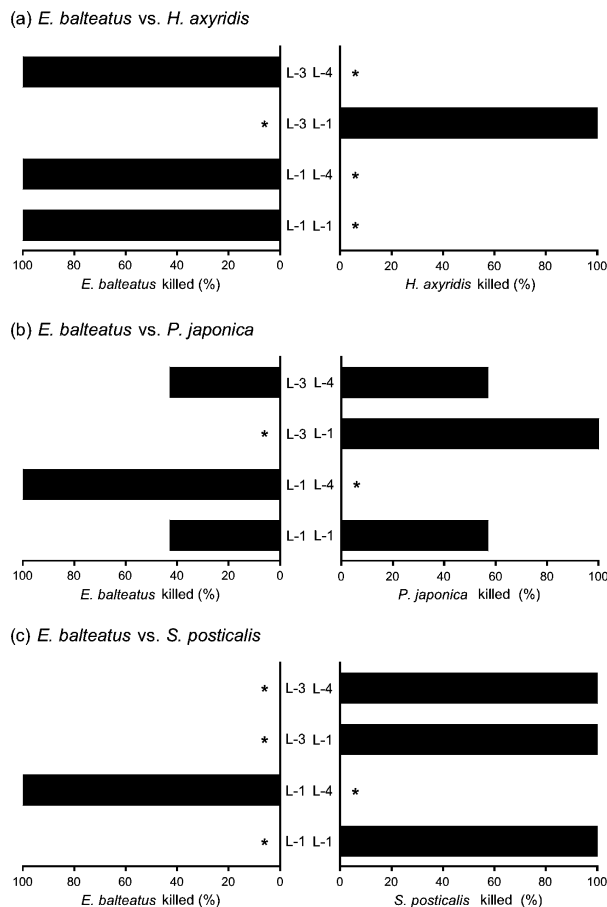


Fig. 1. Intraguild predation between the hoverfly, *E. balteatus* and three species of ladybirds, (a) *H. axyridis*, (b) *P. japonica*, and (c) *S. posticalis* at different developmental stages. Bars represent the percentage killed by each predator larva. Significant difference in the percentage is indicated with an asterisk ( $p < 0.05$  for  $\chi^2$  test). L-1, L-3, and L-4 are first, third, and fourth instar larva, respectively.

in three out of four combinations, but inferior when the first instar larva was paired with the fourth instar of *S. posticalis* larva.

Interactions between the other hoverfly, *M. corollae*, and the two ladybirds, *H. axyridis* and *P. japonica* larvae, were asymmetric, favoring the ladybird larvae (Fig. 2). The first instar of hoverfly larva was always vulnerable when faced with either the first and fourth instar of *H. axyridis* and *P. japonica*. *M. corollae* larvae were only superior when the third instar larva was paired with the first instar larva of the two ladybird species. When the hoverfly larva interacted with the *S. posticalis* larva, the hoverfly killed all the individuals of the ladybird larva in three out of four combinations. The ladybird larva always killed the hoverfly larva

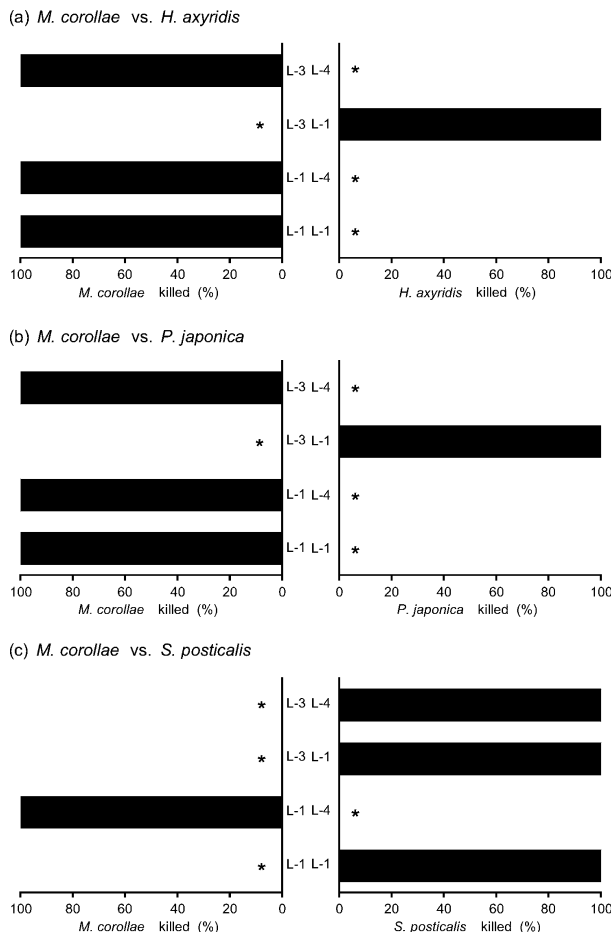


Fig. 2. Intraguild predation between the hoverfly, *M. corollae* and three species of ladybirds, (a) *H. axyridis*, (b) *P. japonica*, and (c) *S. posticalis* at different developmental stages. Bars represent the percentage killed by each predator larva. Significant difference in the percentage is indicated with an asterisk ( $p < 0.05$  for  $\chi^2$  test). L-1, L-3, and L-4 are first, third, and fourth instar larva, respectively.

when the fourth instar was paired with the first instar of hoverfly larva.

### Impact of a ladybird larva on the oviposition preference of the two hoverfly species

The oviposition response of *E. balteatus* females on aphid colonies that also included a first or fourth instar of three ladybird species varied significantly among treatments (Fig. 3a;  $F_{(6,203)} = 3.55$ ,  $p < 0.05$ ). *E. balteatus* females tended to lay fewer eggs in aphid colonies with a ladybird larva than without the larva. Furthermore, it seems that the presence of the fourth instar ladybird affected oviposition by the female hoverfly more negatively than did the presence of a first instar ladybird, al-

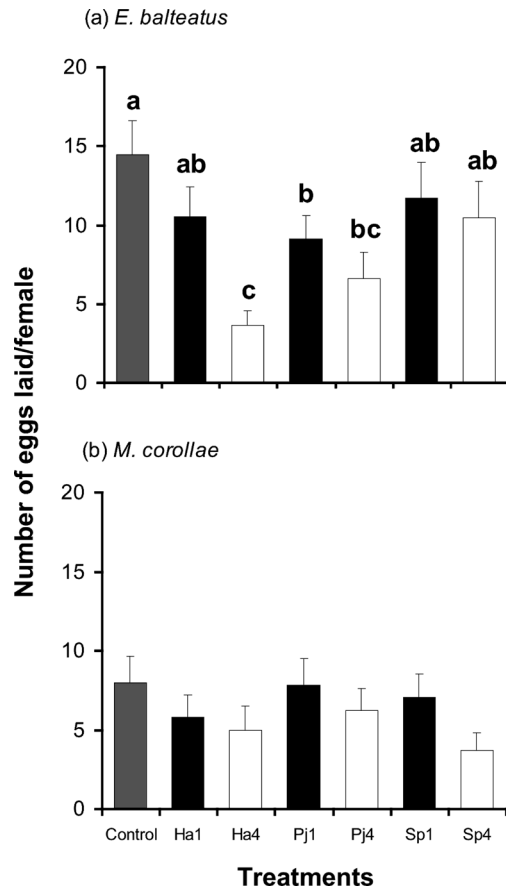


Fig. 3. Number of eggs laid by the two hoverflies, (a) *E. balteatus* and (b) *M. corollae*, as a response to the presence of each ladybird larva, *H. axyridis* (Ha), *P. japonica* (Pj), and *S. posticalis* (Sp). 1, 4, and control show the treatment with first, fourth instar larva, and without a larva, respectively. Different letters indicate significant difference among treatments ( $p < 0.05$  for Fisher LSD test).

though only the differences in the number of eggs laid between the control and the treatment with a fourth instar of *H. axyridis* and *P. japonica* were significant. The negative effect of the fourth instar larva of the ladybirds on the number of eggs laid by the female of *E. balteatus* was as follows: *H. axyridis* > *P. japonica* > *S. posticalis*. The response of the female of *M. corollae* to the treatments with a ladybird was weakly negative (Fig. 3b;  $F_{(6,203)} = 1.08$ ,  $p > 0.05$ ), but again the negative response of the female to fourth instar larva tended to be stronger than to the first instar larva.

## DISCUSSION

The results presented here reveal that the larval

interactions between the three ladybird and two hoverfly larvae differed depending on the species and developmental stages involved. For instance, the relationships between *H. axyridis* or *S. posticalis* and the two hoverfly larvae tended to be asymmetric with *H. axyridis* prevailing over *S. posticalis*, although the opposite was true when the hoverfly was much older and larger than the ladybird. On the other hand, *P. japonica* had both asymmetric and symmetric relationships with hoverflies depending on the hoverfly species with which it interacted.

Intraguild predation is a well known phenomenon among the species that constitute an aphidophagous insect guild (Yasuda and Shinya, 1997; Snyder et al., 2004; Yasuda et al., 2004), and body size, aggressiveness, and voracity determine the outcome of the interaction between predatory arthropods (e.g. Lucas et al., 1998; Hindayana et al., 2000). In the experiments presented here, body size appears especially important, since the superiority in *H. axyridis* is attributable to it being the largest predator, while *S. posticalis* was inferior because it was the smallest predator. The size effect was also apparent in the interactions between *P. japonica* and the two hoverfly species in present study due to the difference in the size between the two hoverfly species (Putra and Yasuda, 2006). The fact that differences in developmental stages of the two individuals paired together resulted in asymmetric interactions also supports the importance of body size in influencing the outcome of interactions, as previously reported for a number of predators (Lucas et al., 1998; Hindayana et al., 2000; Snyder et al., 2004; Yasuda et al., 2004).

In addition to size, mobility is also regarded as an important factor influencing larval interactions, and species with higher mobility tend to have advantage in the interactions (Lucas et al., 1998). However, mobility appears less important than size in our experiments. Previous study revealed that *E. balteatus* larvae were aggressive against the predatory ladybird, *Coccinella septempunctata* larvae, which are similar to *H. axyridis* in size (Yasuda et al., 2004), and that *C. septempunctata* larvae were often preyed upon by the hoverfly larvae (Hindayana et al., 2000). This occurred despite the fact that *C. septempunctata* larvae are more mobile than *E. balteatus* larvae (Yasuda, personal observation). The different outcome of interactions be-



tween *E. balteatus* and *C. septempunctata* and *H. axyridis* larvae seem attributable to differences not in size or mobility per se, but rather in aggressiveness and escape behavior between *H. axyridis* and *C. septempunctata* larvae (Yasuda et al., 2001, 2004).

Chemical and physical substances are well known to provide protection against attacks by predators (Völkl and Vohland, 1996). For example, hoverfly larvae produce sticky slime as physical defense (Gilbert, 1993). In our experiments, older larvae of *E. balteatus* may have benefited more from this substance than younger larvae because the older larvae produce larger amounts of the substance. Such may have been beneficial especially when these larvae were paired with weaker opponents such as *P. japonica* and *S. posticalis* larvae. However, when hoverflies were paired with fourth instars of *H. axyridis*, this slime did not protect hoverfly larvae from attacks. The substance produced by *M. corollae* may not work effectively as a defense because the small larvae of this species produce too little of sticky slime (Putra and Yasuda, 2006). *S. posticalis* larvae are covered with a waxy substance that functions as defense against ant attacks (Völkl and Vohland, 1996). However, in this study the waxy substance appeared ineffective as a defense against hoverflies, as the ladybird larvae were often preyed upon by the hoverfly larvae.

Oviposition preference in relation to larval performance of the two hoverflies differed between the species: *E. balteatus* females tended to reduce egg laying in response to the presence of ladybird larvae, while the response of *M. corollae* was weak. Oviposition preference of hoverfly species is well known to vary in response to development of an aphid colony (Kan and Sasakawa, 1986; Kan, 1988a, b) as well as to aphid quality (Sadeghi and Gilbert, 2000a, b). Thus, prey quantity and quality appear to strongly influence the oviposition behavior of hoverfly species.

In the present experiment, the hoverfly females also seemed to consider the potential risk of predation in patches such as a leaf and/or a plant. In general, arthropods tend to act to reduce the risks of being attacked or preyed by selecting an enemy free site for an oviposition site (Kanno and Harris, 2002; Mira and Bernays, 2002; Kiflawi et al., 2003). As shown in this study, *E. balteatus* females seem to consider both the species and developmen-

tal stages of the ladybird larvae present at a potential oviposition site. As a result, *E. balteatus* laid fewest eggs at the aphid colonies which also had a *H. axyridis* larva, the strongest predator of the hoverfly larva. In addition, the number of eggs laid by an *E. balteatus* female was negatively related to the risk of predation. Interestingly, although the pattern of relative egg laying activity among treatments was similar for *M. corollae* as for *E. balteatus* females, but *M. corollae* females discriminated weakly among treatments such that insignificantly different numbers of eggs were laid among patches of different treatments. The difference in oviposition response between two hoverfly species was also apparent in relation to prey quality; however, the mechanism is still unclear (Sadeghi and Gilbert, 2000a, b). Therefore, the reason why the two species differed in oviposition response as shown in the present study should be addressed in future studies.

The mechanism of finding an oviposition site often appears to involve visible and chemical cues as important factors (Kan, 1988a, b; Blaustein et al., 2004). Hoverfly females recognized the developmental phase of aphids and the presence of the winged morph (Kan, 1988a, b), suggesting that *E. balteatus* females might detect the ladybird larva in an aphid colony by visible cues rather than by chemical cues.

Variation in the response of arthropods to predation risk for offspring is common. For example, some herbivorous insects choose low quality rather than high quality plant species in terms of larval performance, because the low quality plant provide opportunity for chemical defense against predators (Gross and Price, 1988; Denno et al., 1990; Mira and Bernays, 2002). That oviposition site selection may be important not only for phytophagous insects but also predatory insects is suggested by previous studies (Nomikou et al., 2003; Blaustein et al., 2004). Blaustein et al. (2004) reported that the oviposition response of two dipteran species to a hemipteran predator differed between the two species due to their vulnerabilities against the predator. Interestingly, the present study showed that *M. corollae* had a relatively weak oviposition response to the presence of intraguild predators, even though the vulnerability of *M. corollae* larvae to intraguild predation was higher than the vulnerability of *E. balteatus* larvae. Given the expectation that natural

selection would favor strong oviposition responses when the threat of intraguild predation is high (Sadeghi and Gilbert, 2000a, b), *M. corollae* might not have a long history of coexistence with the ladybirds. This suggests that understanding the relationship of preference and performance requires consideration of the degree of coevolution between the related species.

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