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Oviposition preference of aphidophagous hoverflies toward oviposition site quality: The presence of intra- and interspecific competitor, glucosinolate content, and prey species

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ABSTRACT

The selection of oviposition sites by aphidophagous insects is complex because of tritrophic interactions among host plant, aphid, and natural enemies. Several factors are known to affect the choice of oviposition site by aphidophagous hoverflies. The decisions of ovipositing females about where to lay their eggs are even more important in insects whose newly hatched offspring have limited dispersal ability, such as most aphidophages. In this study, we focused on the oviposition responses of two generalist aphidophagous syrphids (*Eupeodes luniger* and *Episyrphus balteatus*) toward host plant–aphid combinations differing in sinigrin content and the presence of intra- and interspecific competitors. The oviposition preference of *Eupeodes luniger* was significantly influenced in a reverse manner by the presence of intraguild competitors and also by the sinigrin content of host plants ($P < 0.0001$ for both factors). Likewise, the overall proportion of eggs laid by female *Episyrphus balteatus* was greater on aphids with relatively low levels of sinigrin. Our findings help in understanding the factors governing the oviposition responses of aphidophagous predators.

Introduction

Insect oviposition behaviour is a vital component of many aspects of their biology: population dynamics, life history evolution, host specificity, and their abilities in the biological control of pests (Sadeghi and Gilbert, 2000a; Almohamad et al., 2009). One crucial aspect of oviposition behaviour is host choice, especially in those insects whose newly hatched offspring have limited dispersal ability. For these insects, the choices made by the mother cannot subsequently be corrected. When searching in the habitat for hosts, the adult female must make a decision whether to oviposit on any particular host discovered, or to search for another more suitable one. Several factors are known to affect this decision: habitat (Bell, 1990), host plant (Cortesero et al., 2000; Sadeghi and Gilbert, 2000a; Almohamad et al., 2007), prey type (Hodek, 1993; Sadeghi and Gilbert, 2000b; Sadeghi et al., 2014), prey availability (Dixon, 1959; Chandler, 1968; Sutherland et al., 2001; Almohamad et al., 2006; Amiri-Jami and Sadeghi-Namaghi, 2014), semiochemicals (Dicke, 1999; Ninkovic et al., 2001; Francis et al., 2004; Harmel et al., 2007; Verheggen et al., 2008; Almohamad et al., 2010), the presence of intra- and interspecific competitors (Hindayana et al., 2001; Almohamad et al., 2010), female age (Sadeghi and Gilbert, 2000b; Frechette et al., 2004), egg load and host deprivation (Sadeghi and Gilbert, 2000c).

In the case of insect natural enemies, host plant characteristics could affect oviposition behaviour in various ways. Plant chemistry (allelochemicals or secondary metabolites) can affect foraging females not only by providing cues for discovering their prey (Hopkins et al., 2009), but also via chemically mediated effects, such as altering prey suitability (Francis et al., 2001; Ode, 2006; Gols and Harvey, 2009; Kos et al., 2011). The suitability of prey types is an intrinsic factor which follows a rank-order hierarchy of preference among prey or among prey–hostplant combinations (Courtney et al., 1989; Sadeghi and Gilbert, 2000b, 2000c). Unsuitable prey can include toxic species where the toxicity is obtained via the host plant (Hodek, 1993; Nishida, 2002; Optiz and Muller, 2009; Chaplin-Kramer et al., 2011; Kos et al., 2011), so the degree of host or prey suitability to a large extent depends on secondary chemistry of the food plants of the prey or host. Aphidophagous predators do not exist in isolation and are part of a larger community within the aphidophage guild (Gilbert, 2005), so adult females must select oviposition sites that not only provide their offspring with sufficient resources to complete development but also

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minimise the negative effects of competition suffered by their offspring (Doumbia et al., 1998; Almohamad et al., 2010).

In view of the fact that gravid females are likely to encounter diverse prey types when foraging for an oviposition site, each prey must either be rejected or accepted during each encounter. According to the hierarchy-threshold model of host choice (Courtney et al., 1989), this decision depends on both the intrinsic suitability of the prey type (rank order) and the current acceptance threshold of the female (which can vary with physiological factors such as female age or ecological factors such as competition). In insects with sedentary larvae, such as aphidophagous syrphids, oviposition should reflect a preference for minimising potential sources of offspring mortality, such as prey toxicity (Chaplin-Kramer et al., 2011) and competition (Almohamad et al., 2010). Some literature (e.g., Chaplin-Kramer et al., 2011; Kos et al., 2011) have shown the toxicity effect of glucosinolate compounds on larval performance of aphidophagous syrphids and there are also some evidence of intraguild predation among them (e.g., Hindayana et al., 2001). As a result, oviposition responses of gravid females have a crucial role in relation to their offspring fate.

There are some papers about the oviposition responses of various aphidophages toward the presence of intra- and interspecific competitors such as chrysopids (e.g., Ruzicka, 1994, 1996), coccinellids (e.g., Agarwala et al., 2003; Michaud and Jyoti, 2007), and *Aphidoletes aphidimyza* (Rondani) (Diptera:Cecidomyiidae: Ruzicka and Havelka, 1998), but little information is available for syrphids (Almohamad et al., 2010). Many studies show host plant chemistry effects on the suitability of prey for overall performance and subsequent fecundity of aphidophages (e.g., Francis et al., 2001; Kos et al., 2011), but again, few are on syrphids (e.g., Vanhaelen et al., 2001; Verheggen et al., 2008; Chaplin-Kramer et al., 2011). Aphidophagous syrphids are well-known natural enemies that can have a significant impact on the suppression of aphid populations (Chambers, 1988).

It is interesting to look at the oviposition responses of aphidophagous syrphids to different host plants infested with the same aphid (Vanhaelen et al., 2001; Almohamad et al., 2007). Inter- and intraspecific competition may be an additional important factor in the performance of aphidophagous syrphids because their larvae share the same aphid prey and often engage in intraguild predation (Benestad Hågvar, 1972; Branquart et al., 1997; Hindayana et al., 2001; Frechette et al., 2007). Females should have evolved discriminating capacities that enable them to detect the presence of inter- and intraspecific competitors. However, the degree to which competition shapes the oviposition decisions of syrphids is not well understood.

Glucosinolates are well-known secondary metabolites of the Brassicaceae, with profound biological effects on phytophagous and entomophagous insects (Francis et al., 2001; Gols and Harvey, 2009; Hopkins et al., 2009). More than 120 different glucosinolates are known, four common ones of which are sinigrin, sinalbin, glucobrassicanapin ,and glucobrassicin (Fahey et al., 2001).

The objective of the present study was to investigate the oviposition responses of two common generalist aphidophagous hoverflies (*Eupeodes* [*Metasyrphus*] *luniger* Meigen and *Episyrphus balteatus* De Geer) toward two very important factors related to mortality, i.e., prey toxicity and resource competition. Prey toxicity in our chosen system arises from toxin concentration in the host plant, and its effect could be different among aphid prey (Francis et al., 2001; Kos et al., 2011). Therefore, in our first experiment using the responses of female *Eupeodes luniger* to a single aphid species (*Myzus persicae* Sulzer), our experimental design consisted of two *Brassica* species differing in levels of the toxin sinigrin (Black mustard *Brassica nigra*, a wild species with high levels of sinigrin, and Canola *Brassica napus*, a cultivated species without any sinigrin) with or without an intraguild competitor (*Episyrphus balteatus* eggs or larvae). A second experiment using *Episyrphus balteatus* studied responses to two different aphid species (*Myzus persicae* and *Brevicoryne brassicae* Linneaus) associated with the toxic Black mustard.

Material and methods

Insects and plants

Canola *B. napus* var. Hyola 308 (supplied from Torogh Agricultural Research Center, Razavi Khorasan Province, Iran), and black mustard *B. nigra* (supplied from Pakan-Bazr Co. Isfahan Province, Iran) were grown in a greenhouse at 25 ± 2 °C, 60 ± 10% RH and 16 L: 8D photoperiod. The seeds were sown in April 2014 in plastic pots (10 cm diameter, 15 cm height filled with a 2:2:1 mixture of soil, sand and leaf compost, respectively). Aphids supplied from laboratory cultures of *B. brassicae* on *B. nigra* and *M. persicae* on *B. nigra* and *B. napus*, respectively, which were established for several generations on the given host-plants. Stock cultures of *Episyrphus balteatus* and *Eupeodes luniger* were established using gravid females captured at the campus of Ferdowsi University of Mashhad, NE Iran, in May 2014. The stock cultures were maintained in a constant environment of 22–23 °C under a 15 L: 9D photoperiod. The insects were provided with cut flowers of candy tuft (*Iberis sempervirens*) as a pollen source, diluted bee honey (10%), solid crystalline sugar, and water from a soaked pad of cotton wool in a conical flask, all placed on the floor of a net-covered cage (100 × 70 × 70 cm). To obtain a group of larvae of the same age, gravid females were induced to lay eggs on cut sections of broad bean plants (*Vicia faba* L.) infested with black bean aphids (*Aphis fabae* Scopoli). For experimental purposes, eggs laid over a period of 12 h were selected and placed in a large Petri dish in an incubator (20 ± 1 °C, 60–70% RH and 16 L: 8D photoperiod) to hatch. These hoverfly larvae were fed every other day ad libitum with *A. fabae* as standard diet and after emergence of adults, they were used for preference tests.

Chemical analysis

Fifty apterous aphids in their penultimate instar were selected from colonies reared on each plant–aphid combination for several generations (from at least five different plants in each treatment) and preserved in 5 ml methanol 90% for HPLC analysis. Approximately 1 g of fresh leaf matter from fully expanded leaves of six different plants in each treatment was collected and immediately frozen in liquid nitrogen and preserved at −80 °C until HPLC analysis. The extraction method of sinigrin from plant and aphid samples was made according to the EEC Regulation N1864/90. The chromatographic analyses were carried out on an HPLC system (Knauer Corporation, Scientific Instruments, Germany) equipped with a manager 5000, pump 1000 and UV detector 2600. Sinigrin and desulfo-sinigrin were separated on a Eurospher (C 18) 100 A column (250 × 4.6 mm, 5 μm), at 30 °C. The data were processed with the software EZ Chrom Elite (Shimadzu). The sinigrin in both plants and aphids were identified and quantified in relation to a previously purified standard (sinigrin hydrate: Sigma Ltd., Cat. No. 85,440).

Oviposition response of Eupeodes luniger

Oviposition responses were determined in the laboratory using females of known age. One culture of males and females of *Eupeodes luniger* obtained from a cohort of same-aged larvae (supplied from laboratory stock culture) were established initially. At the beginning of the oviposition experiment, females were about 2 weeks old (when the majority of females contained some mature eggs and were ready to lay). Oviposition responses were assessed toward factorial combinations of two factors: host–plant (*B.nigra*, *B.napus*) and competitor (control, presence of 5-day-old *Eupeodes luniger* larva, presence of a 5-day-old *Episyrphus balteatus* larva, presence of two *Episyrphus balteatus* eggs). Also because the age of tested females was increasing during the experiment, we considered the effect of time as block factor, because this factor is known to affect selectivity of females (Sadeghi and Gilbert, 1999, 2000a; Amiri-Jami et al., 2016). In all treatments, an equal number of *M. persicae* (100 aphids of various instars) were used as prey on the same-aged potted host-plants. Plants infestation with aphids were done at least one week before introducing them to the female syrphids. Syrphid larvae were left on infested plants at least 12 h prior to introduce them to gravid females. Based on our previous studies (Sadeghi and Gilbert, 1999, 2000a; Amiri-Jami and Sadeghi-Namaghi, 2014), one gravid female *Eupeodes luniger* per treatment combination (i.e. 8) was selected from the stock culture, deprived of oviposition opportunities for 12 h prior to the experiment, and then individually introduced into a preference-test cage (30 × 40 × 40 cm) and allowed to lay eggs for 90 min. Then the tested female was removed from the cage and the number of eggs recorded. Fifteen replicates of each treatment were performed.

Oviposition response of Episyrphus balteatus

One culture of male and female *Episyrphus balteatus* was established initially. After 3–4 days, mating occurred and the ovaries began to enlarge about 7–10 days after emergence. Usually, 12 days after emergence, the majority of females were ready to lay eggs, but to be certain that all females were ready, oviposition preference tests began 15 days after eclosion with 11 females of known age. Females were initially naive, having had no previous exposure to the test aphids. Individual host-plants (*B. nigra*) were infested with either of the two tested aphid species (*M. persicae* or *B. brassicae*) and then introduced to singly-caged females. Great care was taken to provide equal densities of aphids, by making sure that all potted plants were approximately the same age and size (15–20 cm tall with 4–5 fully expanded leaves) and infesting each with 40 aphids of various instars.

Each day, infested plants of each treatment were presented in a randomised sequence to each female (i.e. a no-choice situation, with only one aphid–plant combination available at any time) (cf. Singer, 1986; Courtney et al., 1989; Sadeghi and Gilbert, 2000a, 2000b, 2000c). Each presentation of an aphid–plant combination lasted for 45 min. The number of eggs laid was counted and then the plant was replaced by the other treatment. Each day, both aphid–plant combinations were offered to all test females; presentations continued for 10 successive days encompassing most of the oviposition period of each female.

Statistical analysis

The data from *Eupeodes luniger* were analysed using ANOVA implemented in the statistical software, SAS version 9.2 (SAS Institute, Cary NC, USA). Data were transformed where appropriate to satisfy assumptions of normality and homogeneity of variance for ANOVA. We considered sinigrin content (high, absent) and competition (absent, larvae, eggs) as main factors and female age as block factor. Since no sinigrin content × competition interactions were found, we focused just on the main effects. Duncan's multiple range tests (at $\alpha = 0.05$) were used to suggest where the significant differences lay.

For analysing the data from *Episyrphus balteatus* females, we first tested whether any significant choice (preference) existed between the two prey treatments. For this, a paired t-test was carried out using SAS, with the data being the overall proportion of eggs laid on one prey minus the proportion laid on the other, for each female. To test for differences among individual females, and for an effect of time (factors known to affect selectivity of females: Sadeghi and Gilbert, 1999, 2000a, 2000c), because each egg was laid separately, we treated each egg as an independent event and hence used a binomial GLM using R. The mean selectivity for *M. persicae* at the start of testing was obtained from the 'intercept' via back-transforming the logistic transformation.

Results

Sinigrin was detected in both aphid species reared on *Brassica nigra*, but with obviously larger concentrations in the specialist (*Brevicoryne brassicae*) than the generalist (*Myzus persicae*) (Fig. 1). High amounts of sinigrin were found in leaf samples of *B. nigra* (mean ± SE 10.83 ± 0.337 μmol g^{-1}), but in *Brassica napus*, sinigrin was detected neither in the leaf samples nor from aphids reared on it.

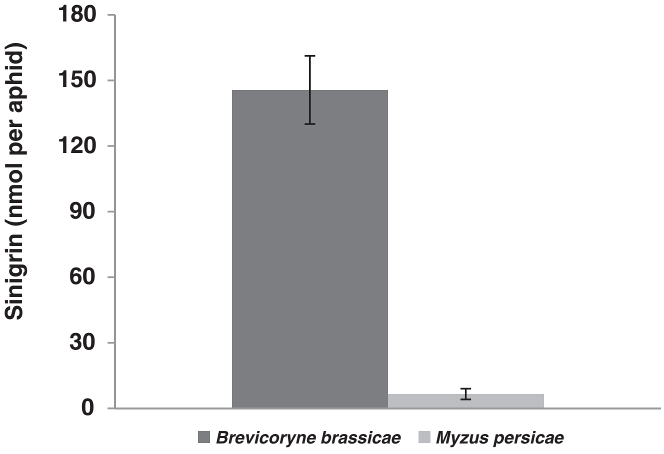

Fig. 1. Sinigrin content (mean ± SE) in samples of *Brevicoryne brassicae*, and *Myzus persicae* reared on *Brassica nigra.*

The oviposition response of *Eupeodes luniger* was influenced significantly by the presence of intraguild competitors and the sinigrin content of host plant but there was no interaction: oviposition preference was also influenced by female age (Table 1). Gravid females laid significantly fewer eggs when sinigrin was present in the host-plant (Fig. 2). They also laid fewer eggs in the presence of a competitor, differentiating between conspecifics and heterospecifics, but not between life stages of the heterospecific competitor (Table 2).

The oviposition preference of *Episyrphus balteatus* females showed a significantly higher proportion of eggs laid on the generalist rather than

Table 1
Summary of ANOVA results for effects of sinigrin and competition on oviposition preference of *Eupeodes luniger.*

Source of variation	df	F	P
Female age	14	2.4	**0.006**
Sinigrin content	1	34.49	<**.0001**
Competition	3	34.44	<**.0001**
Competition × sinigrin content	3	0.48	0.7

Significant P-values (P < 0.05) are shown in bold-face type.

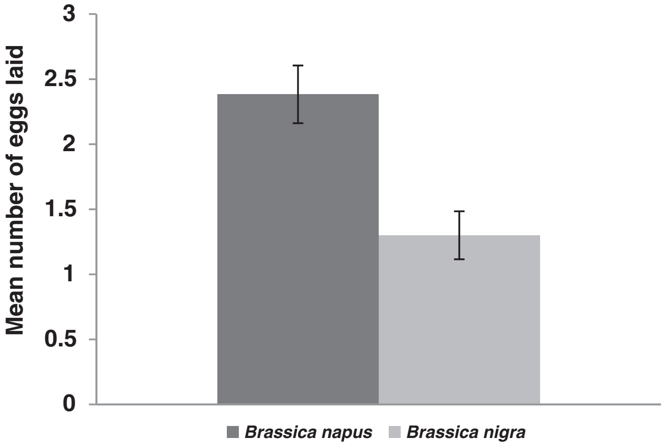

Fig. 2. The mean ± SE number of eggs laid per *Eupeodes luniger* female per replicate toward *Myzus persicae* on the zero-sinigrin *Brassica napus* and the high-sinigrin *Brassica nigra.*

Table 2
Mean (±SE) number of eggs laid by each *Eupeodes luniger* female in each introduction toward the presence of intraguild competitor and control treatment.

Treatments	Mean ± SE		
Control	3.77 ± 0.31	a	(n = 30)
Heterospecific eggs	1.5 ± 0.21	b	(n = 30)
Heterospecific larva	1.3 ± 0.19	b	(n = 30)
Conspecific larva	0.8 ± 0.15	c	(n = 30)

Columns with the same letter were not significantly different based on Duncan's multiple range tests at $\alpha = 0.05$.

the specialist aphid (Figure 3a; $t = 10.14$, df = **, $P < 0.0001$). Preference did not vary significantly among individuals, but females became less choosy with time (Fig. 3b & c).

Discussion

The selection of oviposition sites by syrphids and other aphidophagous insects is complex because of tritrophic interactions: host plant, aphid, and natural enemies (Ode et al., 2004; Gilbert, 2005). Although some literature examines the effect of prey species on choices made by gravid syrphids (e.g., Budenberg and Powell, 1992; Sadeghi and Gilbert, 2000a; Almohamad et al., 2007), relatively less attention has been paid to the effect of defensive responses of aphids (especially chemical defence). In the present study, the overall proportion of eggs laid by *Episyrphus balteatus* toward the generalist aphid (*Myzus persicae*) on a high-sinigrin host was significantly greater than toward a specialist aphid (*Brevicoryne brassicae*) on the same host plant. *B. brassicae* on black mustard sequesters sinigrin in high concentrations (e.g., Francis et al., 2001; Chaplin-Kramer et al., 2011; Kos et al., 2011; Amiri-Jami et al., 2016) and, since it contains its own aphid-specific myrosinase (Hopkins et al., 2009), it is able to hydrolyse the sinigrin in its body upon damage by predators. As a result, the performance of predators when they fed on the brassica specialist aphid *B. brassicae* was lower than when they fed on a non-sequestering generalist aphid (*Myzus persicae*) reared on the same plants. Several studies, such as Kos et al. (2011) and Amiri-Jami et al. (2016) have indicated a decrease in the performance of the generalist aphidophagous *E. balteatus*. If a generalist predator suffers a reduction in fitness when it has a diet of prey containing detrimental plant chemicals, it would be expected that adult females avoid selecting those kinds of prey. Although preference declined with age, the rank order remained fixed because polyphagous prey on high-toxin host plant was always the more preferred prey. This consistency in oviposition preference over time agrees with the prediction of the hierarchy threshold model of Courtney et al. (1989) that says intrinsic suitability of prey is a fixed factor and some other data (Sadeghi and Gilbert, 2000a, 2000b; Vanhaelen et al., 2001).

Our findings indicate that specialist prey could promote specialization at higher trophic levels (i.e. predators). In fact, it arises from mutual interactions among host plant, specialist aphid and the natural enemy. *B. brassicae* obviously sequestered more sinigrin than *M. persicae* when both were reared on Black mustard. Our results are consistent with some other studies (e.g., Francis et al., 2001; Chaplin-Kramer et al., 2011; Kos et al., 2011). A high concentration of sinigrin and its hydrolytic products (such as isothiocyanates & nitriles: Francis et al., 2001) in *B.brassicae* could act as a deterrent for gravid females, creating oviposition avoidance relative to a generalist aphid. Vanhaelen et al. (2001) observed that *Episyrphus balteatus* females preferred to oviposit on White mustard plants (*Sinapis alba* L., containing high glucosinolate levels) rather than on Oilseed rape plants (*Brassica napus* L., containing low levels) when both were infested with the same aphid (*Myzus*

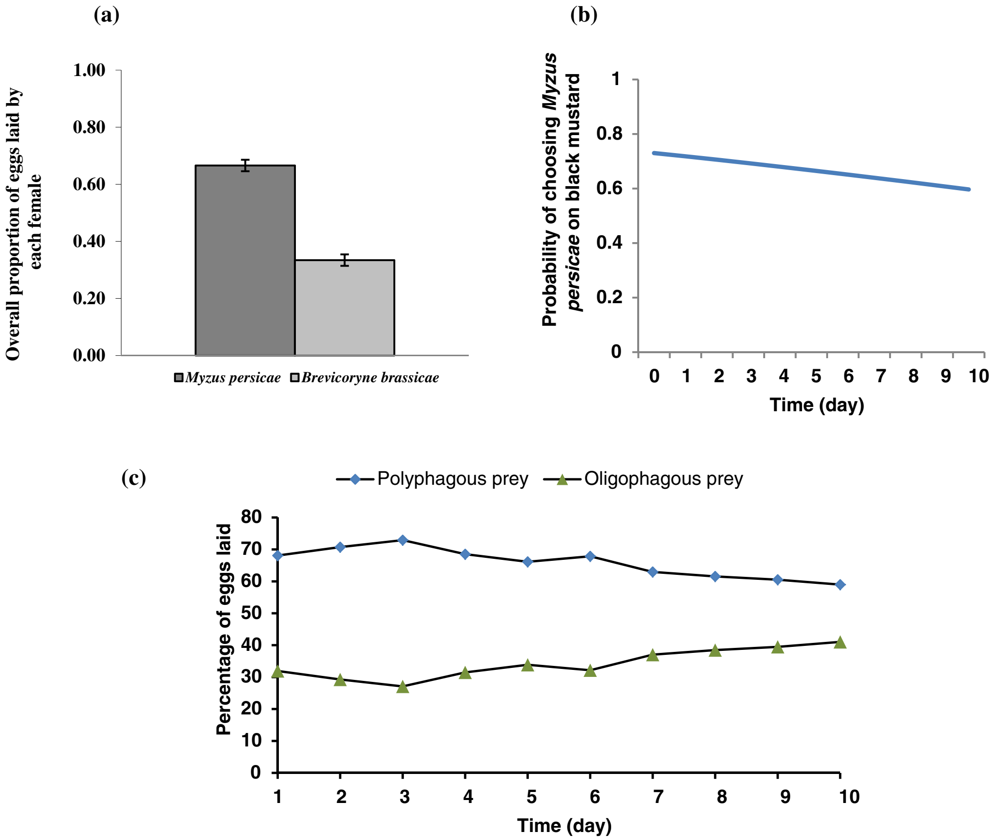

Fig. 3. (**a**) Mean (±SE) proportion of eggs laid on each prey per *Episyrphus balteatus* female over 10 successive days; (**b**) fitted regression line for selectivity for the generalist prey (*Myzus persicae*) over time; (**c**) actual percentage laid on each prey type over time.

persicae). In a field experiment, Chaplin-Kramer et al. (2011) demonstrated that aphidophagous syrphids were found at far lower densities in *Brassica nigra* patches than in nearby crop plants (*Brassica oleracea*). This discrepancy could be due to an oviposition preference toward a generalist aphid on different host plants (as in the Vanhaelen et al., 2001) study, or the same toward specialist as opposed to generalist aphids on a high-toxin plant.

Gravid females not only respond to oviposition-site quality in relation to the suitability of prey types, but they should also consider ecological factors such as the likelihood of intra- or interspecific competition (Branquart et al., 1997; Hindayana et al., 2001; Frechette et al., 2007). In the present study, *Eupeodes luniger* females preferred to oviposit on aphid-infested plants that carried no conspecific larvae. Similar results have been reported by other studies. For example, Scholz and Poehling (2000) on *Episyrphus balteatus* demonstrated that ovipositing females avoid aphid colonies in which conspecific eggs are already present, and the oviposition-deterring stimuli were still active when the eggs were removed. Similar oviposition avoidance was shown by *E. balteatus* females to the presence of conspecific larvae (Volk, 1964). Studies by Almohamad et al. (2010) revealed that detection of intraspecific competitors involves chemical cues derived from eggs, larvae, or larval tracks. Amorós-Jiménez et al. (2015) found that odours from conspecific immature stages had a repellent effect on oviposition choices of *Sphaerophoria rueppellii*.

Ovipositing *Eupeodes luniger* tended to avoid laying eggs on aphid-infested host-plants with a heterospecific competitor. Such avoidance has been reported by other studies (e.g., Almohamad et al., 2008, 2009, 2010; Hindayana et al., 2001; Putra et al., 2009). In Almohamad et al.'s (2008) study, the foraging and oviposition behaviour of *Episyrphus balteatus* females were affected by the presence of parasitoids: females laid significantly fewer eggs in colonies with mummified aphids than in unparasitised colonies, or in parasitised colonies without mummies. There was also oviposition avoidance to the presence of *Harmonia axyridis* larvae. In contrast, the oviposition choices of *Sphaerophoria rueppellii* were not affected by volatiles from immature stages of the heterospecific competitor, *Adalia bipunctata* (Amorós-Jiménez et al., 2015). The cause underlying for lower intensity of the avoidance response by females in the presence of heterospecific competitor than conspecific one, is likely lower frequencies of inter- vs. intraspecific interactions among aphidophagous hoverflies. Several studies have demonstrated this situation in relation to phytophagous insects (Birch et al., 1980; Byers et al., 1984), parasitoids (Janssen et al., 1995), and coccinellids (Honek, 1985). It is interesting also to explore for niche overlap in relation to aphidophagous syrphids. However, as aphidophagous hoverflies generally are part of larger community within aphidophagous guild, these predators may interact strongly with each other, which leads to intraguild predation (Hindayana et al., 2001; Frechette et al., 2007). Syrphid species that coexist and share the same aphid prey resource often engage in conspecific and heterospecific predation of eggs and larvae (Benestad Hågvar, 1972; Hindayana et al., 2001; Frechette et al., 2007). Additionally several studies have shown that syrphid eggs and larvae are vulnerable to cannibalism (e.g., Branquart et al., 1997). Therefore oviposition decision by *E. luniger* females at the present study would benefit their offspring by developing an avoidance of inter- and intraspecific competitor present in the same colonies.

In conclusion, our findings support and complement findings on larval performance in other study (Kos et al., 2011) and show that specialist prey can induce specialization in a syrphid. As in several other aphidophagous hoverflies, oviposition responses have evolved behavioural mechanisms in response to semiochemicals emitted either from aphids or from their association with host'plants, as well as from the presence of intra- or interspecific competitors. The identity and specificity of semiochemicals involved in shaping these decisions needs further investigation, which will help to obtain a fuller understanding of the ability to detect and avoid intraguild predation. Cannibalism or intraguild predation between two predatory hoverflies *E. luniger* and *E. balteatus* may explicate oviposition avoidance of aphid colonies with the inrtraguild competitor. Oviposition behaviour in aphidophagous hoverflies is a complex process that involves several cues (visual, auditory, olfactory, and gustatory). Olfactory and gustatory cues due to aphid honeydew of both specialist or generalist species infested plants with or low content of sinirgin may explicate these oviposition response. To confirm this idea, it is utile to test host plants with aphid tracks (honeydew).

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