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Predatory hoverflies select their oviposition site according to aphid host plant and aphid species

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Abstract

The hoverfly Episyrphus balteatus De Geer (Diptera: Syrphidae) is an abundant and efficient aphidspecific predator. Several aphidophagous parasitoids and predators are known to respond positively to aphid-infested plants. Semiochemicals from the latter association usually mediate predator/parasitoid foraging behavior toward sites appropriate for offspring fitness. In this study, we investigated the effect of aphid host plant and aphid species on foraging and oviposition behavior of *E. balteatus*. Behavioral observations were conducted using the Noldus Observer v. 5.0, which allows observed insect behavior to be subdivided into different stages. Additionally, the influence of aphid species and aphid host plant on offspring fitness was tested in a second set of experiments. Acyrthosiphon pisum Harris and Megoura viciae Buckton were equally attractive for E. balteatus whereas Aphis fabae Scopoli (all Homoptera: Aphididae) were less attractive. These results were correlated with (i) the number of eggs laid, which was significantly higher for the two first aphid species, and (ii) the fitness of hoverfly larvae, pupae, and adults. Two solanaceous plant species, Solanum nigrum L. and Solanum tuberosum L. (Solanaceae), which were infested with Myzus persicae Sulzer (Homoptera: Aphididae), were also compared using the same approach. Discrimination between these two M. persicae host plants was observed, with S. tuberosum being preferred as an oviposition site by the predatory hoverfly. Larval and adult fitness was correlated with the behavioral observations. Our results demonstrated the importance of the prey-host plant association on the choice of the oviposition site by an aphid predator, which is here shown to be related to offspring fitness.

Introduction

Natural enemies of herbivorous insects play an important role in the population dynamics of their prey (Price, 1987; Schoenly, 1990). In particular, the hoverfly, *Episyrphus balteatus* De Geer (Diptera: Syrphidae), is the most abundant in central Europe (Tenhumberg & Poehling, 1991; Colignon et al., 2001) and one of the most efficient aphid-specific predators in natural agroecosystems, particularly with respect to cereal aphids (Entwistle & Dixon, 1989; Tenhumberg & Poehling, 1995). Because syrphid larvae have limited dispersal abilities (Chandler, 1969), the choice of the oviposition site has an important impact on offspring performance.

Host-finding behavior of stenophagous aphid predators and parasitoids has been investigated intensively (Godfray,

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1994; van Alphen & Jervis, 1996). However, many of the recent studies were focused on coccinellids (Ferran & Dixon, 1993; Sengonça & Liu, 1994), while neglecting syrphids. Several factors were shown to impact the choice of the oviposition site for aphidophagous hoverflies: (i) the aphid species and their associated chemicals (Budenberg & Powell, 1992; Bargen et al., 1998; Sadeghi & Gilbert, 2000a,b); (ii) the host plant's physical and chemical characteristics associated with the aphid species (Dixon, 1958; Chandler, 1968a; Sanders, 1983; Vanhaelen et al., 2001); (iii) the aphid colony size and density (Kan, 1988; Scholz & Poehling, 2000; Sutherland et al., 2001); and (iv) the age of the female (Sadeghi & Gilbert, 2000c). Many semiochemicals, emitted either by prey or by their association with host plants, are presumed to play an important role in habitat selection by reducing the time needed for searching as well as increasing attack rates on prey (Dicke & Sabelis, 1988; Vet & Dicke, 1992).

Most insect species, including predators (Hodek, 1993), show specific food resource preferences (Schoonhoven et al., 1998). Therefore, the correlation between adult preference for particular oviposition sites and subsequent larval performance has been extensively studied in phytophagous species (Harris et al., 2001; Forister, 2004). However, only a small proportion of these studies established a link between oviposition preference and larval performance (Thompson, 1988; Mayhew, 2001). Takeuchi et al. (2005) found that the phytophagous ladybird *Epilachna admirabilis* Crotch showed no preference between *Trichosanthes cucumeroides* Maxim and *Gynostemma pentaphyllum* Makino, even though the larvae performed better on the first plant species.

According to Gilbert (2005), there are few studies concerning the oviposition preference of female aphidophagous syrphids and larval performance towards different host plants or different aphid species. In this study, the oviposition behavior of E. balteatus was investigated for two host plants [Solanum tuberosum L. and Solanum nigrum L. (Solanaceae)] infested by one aphid species, Myzus persicae Sulzer (Homoptera: Aphididae), in a dual-choice experiment. Hoverfly fitness calculations for different aphid host plants were based on larval and adult performance (development and reproduction parameters) and were related to oviposition behavior. Additionally, similar experiments were conducted with three aphid species, Acyrthosiphon pisum Harris, Aphis fabae Scolpi, and Megoura viciae Bucton (all Homoptera: Aphididae), that infested Vicia faba L. (Leguminosae). Lastly, we investigated oviposition behavior and larval and adult performances.

Materials and methods

Plant and insect rearing

Broad beans (V. faba L.) and the two Solanaceae plants (S. tuberosum L. and S. nigrum L.) were grown in $30 \times 20 \times 5$ cm plastic trays filled with a mix of compost, perlite, and

vermiculite (1:1:1) and maintained in controlled environment growth rooms (L16:D8 and $20\pm1\,^{\circ}\text{C}$). Six-leaf solanaceous plants were used in the following experiments. *Myzus persicae* was reared on *V. faba*, *S. tuberosum*, and *S. nigrum* in separate controlled temperature rooms set at the same conditions as described above. The other aphid species, *M. viciae*, *A. pisum*, and *A. fabae*, were taken from stock cultures grown on *V. faba*. Adult *E. balteatus* were reared in $75\times60\times90$ cm cages and were fed with bee-collected pollen, sugar, and water. Broad beans infested with *M. viciae* were introduced into the cages for 3 h every 2 days to allow oviposition. Hoverfly larvae were mass reared in aerated plastic boxes $(110\times140\times40\,\text{mm})$ and were daily fed ad libitum with *M. viciae* as a standard diet.

Oviposition preference

Aphid host plant preference. In two-choice experiments, females were placed individually in net cages $(30 \times 30 \times$ 60 cm) with two host plants infested with 400 M. persicae (M. persicae/S. tuberosum vs. M. persicae/S. nigrum). Their foraging behavior was then recorded for 10 min using the Observer® software (Noldus information Technology, version 5.0, Wageningen, The Netherlands). Descriptions of the four observed behavioral subdivisions are presented in Table 1. In similar two-choice experiments (M. persicae) S. tuberosum vs. M. persicae/S. nigrum), a single E. balteatus female was allowed to lay eggs for 3 h and the number of eggs laid on each aphid host plant was counted. The experiments were conducted in a controlled temperature room at 20 ± 1 °C. Episyrphus balteatus females were approximately 20-30 days old and no induction of oviposition had been realized for 24 h prior to the experimentation. There were 10 replicates for each of the aforementioned experiments.

Aphid species preference. In similar two-choice experiments, a single *E. balteatus* female was placed in a cage with two

Table 1 Description of the behavioral events recorded for aphidophagous hoverfly *Episyrphus balteatus* exposed to different host plants of prey aphid

Observed behavior Description of behavior		Description of behavior	
Immobility/cage	Predator immobilized on the cage		
Searching	Fly/cage Fly/plant	Predator fly in the cage Predator fly near the plant	
Acceptance of host plant	Immobile/plant Walking/plant Immobile proboscis/plant Walking proboscis/plant	Predator landing on the plant Predator moving on the plant Predator extends its proboscis and identifies the stimulatory substrate to accept the host	
Oviposition	Immobile abdomen/plant Walking abdomen/plant Egg laying	Predator exhibits an abdominal protraction or oviposition Oviposition	

V. faba plants (with six leaves and 20 cm high), which were infested with different aphid species. Three combinations of aphids species were used (A. pisum vs. M. viciae, A. pisum vs. A. fabae, and M. viciae vs. A. fabae). By using the Observer® recorder, the behavioral subdivisions of the female hoverfly were recorded for 10 min and were observed to be identical to earlier tests (Table 1). In similar two-choice experiments (A. pisum vs. M. viciae, A. pisum vs. A. fabae, and M. viciae vs. A. fabae), a single E. balteatus female was allowed to lay eggs for 3 h and the number of eggs laid (oviposition rate) on each infested plant was counted. Experiments were conducted in a controlled temperature room at 20 ± 1 °C. Episyrphus balteatus females were approximately 20-30 days old and no induction of oviposition had been realized for 24 h prior to the experiment. Eight replicates for each pair of aphid species were performed.

Larval performance

Effect of aphid host plant. To assess the effect of aphid host plants on the fitness of E. balteatus, 30 newly emerged first instars were weighed and individually placed in plastic Petri dishes (9 cm in diameter). Each day, the larvae were fed an excess of M. persicae, which was taken from either of the host plants (S. tuberosum or S. nigrum). Hoverfly larvae were kept in an incubator at 20 \pm 1 °C and L16:D8, and the developmental time and survival rates were determined. The pupae and the adults were also weighed (using a Sartorius microbalance scale model Mc5) and placed, in male/female pairs, in $60 \times 30 \times 30$ cm net cages. Fecundity and egg viability of female hoverflies were recorded daily during 3 weeks. Individual fitness (r) was calculated as a performance measure (McGraw & Caswell, 1996) by integrating developmental time (D), survival (m = 1 or 0), and potential fecundity using the equation: $r = [Ln(m \cdot V)]/D$, where Ln is the natural logarithm.

Effect of aphid species. To assess the effect of the consumed aphid species on E. balteatus fitness, 30 newly emerged first instars were weighed and individually placed in plastic Petri dishes (9 cm in diameter). Each larva was fed an excess of each aphid species daily. This experiment was conducted with the three following aphid species: A. pisum, M. viciae, or A. fabae. The Petri dishes were kept in a controlled temperature room at 20 \pm 1 °C and L16:D8, and the developmental time and survival rates were determined. The pupae male/female the adults were also weighed and placed in male and female pairs in $60 \times 30 \times 30$ cm net cages. Fecundity and viability of eggs were recorded daily during 3 weeks. Individual fitness (r) was calculated as presented above (McGraw & Caswell, 1996).

Statistical analysis

Means were compared using one-way analysis of variance (ANOVA) and Student's t-test or Tukey's test, conducted with Minitab® software (version 12.2, Minitab Inc, State College, PA, USA). Observed frequencies related to the adult emergence rates were compared to the corresponding frequencies from the control using χ^2 tests. Percentage of mortality and egg viability were transformed using the angular transformation before ANOVA (arcsine Dagnelie, 1973).

Results

Oviposition preference

Aphid host plant preference. In the dual-choice experiment, a significant preference of female hoverflies for the M. persicae-infested S. tuberosum was observed (Figure 1). Solanum tuberosum induced higher frequencies of acceptance (landing, walking, and proboscis extension) (Student's t-test: t = 5.17, P = 0.001) and oviposition (Student's t-test: t = -3.71, P = 0.005) by the hoverfly.

In addition, the number of eggs laid by E. balteatus females was significantly affected by the aphid host plant species with S. tuberosum being significantly preferred as an oviposition site (Student's t-test: t = -3.54, P = 0.004) (Figure 2).

Aphid species preference. Whereas no significant difference in terms of hoverfly acceptance behavior observed between A. pisum- and M. viciae-infested broad beans plants (Student's t-test: t = 1.33, P = 0.226), female hoverflies prefer and lay eggs on one of the two aforementioned aphid colonies rather than on A. fabae-infested plants

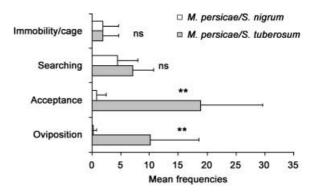


Figure 1 Behavioral observations (mean frequencies + SD) on the oviposition pattern of *Episyrphus balteatus* females in relation to aphid host plants in two-choice experiment; ns and ** indicate no significant and significant differences at P < 0.01 (n = 10).

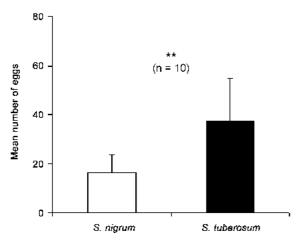


Figure 2 Effects of aphid host plants on oviposition rates (mean number of eggs + SD) of *Episyrphus balteatus* in two-choice experiments after 3-h exposure with *Myzus persicae* as prey and *Solanum nigrum* and *Solanum tuberosum* as host plants. ** indicates significant differences at P<0.01.

(Figure 3). Female *E. balteatus* significantly preferred landing and laying eggs on *A. pisum*-infested broad beans rather than on the same host plant infested with *A. fabae* (Student's t-test: t = 2.64, P = 0.033). *Megoura viciae*-infested broad beans were also significantly preferred to *A. fabae*-infested broad beans in terms of host-plant acceptance and oviposition site (Student's t-test: t = 3.62, P = 0.014).

These behavioral preferences were correlated with the number of observed eggs on the host plant of the aphid species (Figure 4). Similarly to the previously presented results, no significant preference was observed between M. viciae and A. pisum (Student's t-test: t = -0.47, P = 0.648). These two aphid species corresponded with the more suitable species to induce egg oviposition by female hoverflies. Indeed, these females laid fewer eggs on A. fabae-infested broad beans than on M. viciae (Student's t-test: t = 3.90, P = 0.001) or A. pisum-infested plants (Student's t-test: t = 6.22, P < 0.001).

Larval performance

Effect of aphid host plant. Several parameters concerning the larval, pupal, and adult development of *E. balteatus* have been compared for hoverflies fed with the same aphid species (*M. persicae*) but reared on two different host plants (*S. tuberosum* and *S. nigrum*) (Table 2). No difference in survival of larvae and adults was observed ($\chi^2 = 0.00$, d.f. = 2, P = 1.00 and $\chi^2 = 0.073$, d.f. = 2, P = 0.964, respectively). However, larvae fed on *M. persicae* infesting *S. tuberosum* needed less time to reach the pupal stage (t = -3.95, P<0.001). The resulting pupae were significantly heavier (t = 2.66, P = 0.012), the time required to reach the

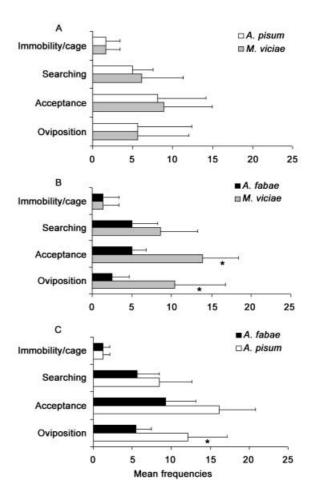


Figure 3 Behavioral observations (mean frequencies + SD) on the oviposition pattern of *Episyrphus balteatus* adults in relation with aphid species in two-choice experiment; an * indicates significant differences at P<0.05 (n = 10).

adult stage was significantly shorter (t = -4.32, P<0.001), and no difference in adult weight was observed (t = 1.82, P = 0.077). Although hoverfly fecundity (eggs/female/day) and egg viability did not differ significantly according to solanaceous host plant (t = 1.22, P = 0.223 and t = 0.29, P = 0.775, respectively), hoverfly fitness (r) was significantly higher on *M. persicae/S. tuberosum* rather than on *M. persicae/S. nigrum* (t = 2.45, P = 0.040).

Effect of aphid species. Differences in E. balteatus developmental parameters by aphid species (M. viciae, A. pisum, and A. fabae) were observed (Table 3) and E. balteatus larvae developed to maturity with each of the aphid species tested. Additionally, there was no significant difference in larval survival rates, which ranged from 73.33% for A. fabae to 80.00% for A. pisum. However, the aphid species significantly influenced the time needed for the larvae to

	Myzus persicae/host pla			
Biological parameters	Solanum tuberosum	Solanum nigrum	Test statistic	
Larval development (day)	7.75 ± 0.79	8.81 ± 0.93	t = -3.95	P<0.001
Percentage of larval survival	66.66	66.66	$\chi^2 = 0.00$, d.f. = 2	P = 1.000
Percentage of survival (to adult emergence)	63.33	66.66	$\chi^2 = 0.07$, d.f. = 2	P = 0.964
Pupal weight (mg)	35.16 ± 4.41	31.06 ± 0.93	t = 2.66	P = 0.012
Pupal development (day)	7.53 ± 0.51	8.35 ± 0.67	t = -4.32	P<0.001
Adult weight (mg)	22.01 ± 2.78	20.46 ± 2.53	t = 1.82	P = 0.077
Egg-to-adult development (day)	18.74 ± 1.66	20.20 ± 0.77	t = -3.50	P = 0.002
Preoviposition duration	9.66 ± 2.81	9.20 ± 1.79	t = 0.33	P = 0.747
Fecundity (egg per female per day)	30.83 ± 31.25	25.25 ± 27.35	t = 1.22	P = 0.223
Percentage of total egg viability	81.29 ± 7.91	80.93 ± 5.24	t = 0.29	P = 0.775
Fitness (r)	0.78 ± 0.08	0.65 ± 0.09	t = 2.45	P = 0.040

Table 2 Effect of aphid host plant on development and reproductive performance of predatory hoverfly *Episyrphus balteatus* (mean \pm SD). Significant, grand significant differences, and high significant differences are at P<0.05, P<0.01, and P<0.001, respectively

reach pupal stage, where days required ranged from 8.85 (*A. pisum*) to 9.86 (*A. fabae*) ($F_{2,65} = 19.88$, P < 0.001). The pupae on a diet of *A. fabae* were significantly lighter ($F_{2,65} = 8.55$, P = 0.001) and needed more time to reach the adult stage ($F_{2,65} = 4.84$, P = 0.011). In terms of the egg-to-adult development time, the time required on *A. fabae* was significantly greater, reaching 17.81 days whereas only 15.5 days were needed for the individuals reared on *A. pisum*.

The fecundity (eggs/female/day) and egg viability were not significantly influenced by the aphid species M. viciae, A. pisum, and A. fabae ($F_{2,221} = 0.87$, P = 0.419; $F_{2,157} = 2.03$, P = 0.135, respectively). However, E. balteatus female fitness (r) was significantly higher on broad beans infested with E0. E1 with E2 with E3 infested with E3. E4 E5 with E6 E7 infested with E8. E9 infested with E

Discussion

In this study, the effect of the aphid host plant variety on the choice of oviposition site by *E. balteatus* was clearly demonstrated. Sadeghi & Gilbert (2000a,b) highlighted the ability of hoverflies to discriminate their potential oviposition sites, which consisted of aphid species and their associated host plant. However, these authors could not conclude whether the attraction and oviposition induction was due to the aphid species, the host plant, or the interaction of host plant and prey. Using the same aphid species (*M. persicae*), reared on both *S. tuberosum* and *S. nigrum*, we were able to compare the effect of the host plant on the oviposition site preference and hoverfly fitness. Indeed, *S. tuberosum* induced higher frequencies of acceptance and received more eggs from hoverfly females

Table 3 Influence of aphid species on various performance parameters of development of *Episyrphus balteatus* (mean \pm SD). Significant, grand significant differences, and high significant differences are at P<0.05, P<0.01, and P<0.001, respectively

	Aphid prey species				
Biological parameters	Megoura viciae	Acyrthosiphon pisum	Aphis fabae	Test statistic	
Larval development (day)	9.17 ± 0.39	8.58 ± 0.65	9.86 ± 0.91	$F_{2,65} = 19.88$	P<0.001
Percentage of survival of larvae	76.66	80.00	73.33	$\chi^2 = 0.37$	P = 0.830
Percentage of survival (to adult emergence)	73.33	73.33	66.67	$\chi^2 = 0.43$	P = 0.805
Pupal weight (mg)	31.82 ± 3.55	34.49 ± 4.10	29.69 ± 4.03	$F_{2,65} = 8.55$	P = 0.001
Pupal development (day)	7.09 ± 0.41	6.88 ± 0.45	7.29 ± 0.46	$F_{2,65} = 4.84$	P = 0.011
Adult weight (mg)	19.85 ± 2.51	22.45 ± 3.55	18.66 ± 3.67	$F_{2,61} = 7.45$	P = 0.001
Egg-to-adult develoment (day)	16.35 ± 1.81	15.50 ± 0.72	17.81 ± 1.81	$F_{2,65} = 18.14$	P<0.001
Preoviposition duration	10.33 ± 0.52	9.20 ± 1.30	10.40 ± 0.55	$F_{2.13} = 3.25$	P = 0.072
Fecundity (egg per female per day)	32.11 ± 32.75	34.43 ± 32.77	27.06 ± 36.02	$F_{2,221} = 0.87$	P = 0.419
Percentage of total egg viability	77.46 ± 11.54	72.79 ± 10.60	74.53 ± 16.16	$F_{2,157} = 2.03$	P = 0.135
Fitness (r)	0.66 ± 0.06	0.70 ± 0.06	0.58 ± 0.08	$F_{2,13} = 4.69$	P = 0.029

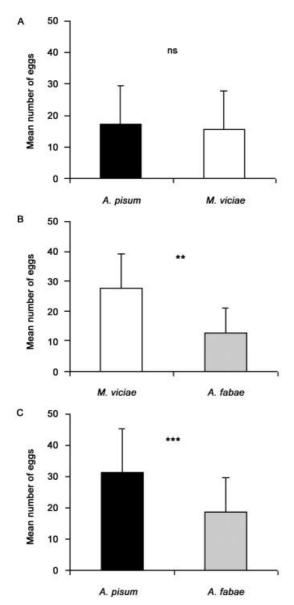


Figure 4 Effects of aphid species on oviposition rates (mean number of eggs + SD) of *Episyrphus balteatus* in two-choice experiment after 3-h exposure; ns, **, and *** indicate no significant and significant differences at P<0.01 and P<0.001, respectively. (A) Comparison between *Acyrthosiphon pisum* and *Megoura viciae*; (B) Comparison between *M. viciae* and *Aphis fabae*; and (C) Comparison between *A. pisum* and *A. fabae* (n = 8).

than *S. nigrum*. In addition, the global hoverfly fitness was higher with *M. persicae* fed on *S. tuberosum*, confirming the hypothesis that ovipositing insects can select sites that improve the growth and survival of their offspring (Peckarsky et al., 2000). This should be even more true for insects that are unable to migrate easily from habitats poor

in food, such as syrphid larvae. The reason behind the preference of E. balteatus for one plant rather than the other remains uncertain. When predators attempt to locate the prey habitat, they often use odors associated with prey presence, such as those from the herbivorous prey itself (Whitman, 1988), or from prey by-products, such as feces or honeydew (Budenberg & Powell, 1992; Scholz & Poehling, 2000; Francis et al., 2004). Moreover, predators can use volatiles that are produced by plants in response to herbivore damage, such as 'green' alcohols and aldehydes (Al Abassi et al., 2000; Francis et al., 2001). For example, Obata (1986, 1997) suggested that the Asian ladybird Harmonia axiridis Pallas was more strongly attracted to the odor of aphid-infested plants than to those of uninfested plants, and the volatile profiles of the two host plants are indeed different. Apart from the aphid-released (E)-β-farnesene, S. tuberosum release important amounts of the aphid alarm pheromone (Agelopoulos et al., 2000) whereas S. nigrum does not release this sesquiterpene (Schmidt et al., 2004). The (E)- β -farnesene was shown to attract predators such as E. balteatus (Francis et al., 2005a), which may explain the preference of female hoverflies for S. tuberosum. Plant color is one of the many stimuli used by herbivorous insects to recognize their host plant (Kelber, 2001). Sutherland et al. (1999) also demonstrated that aphid host plant color influenced the foraging behavior of the predatory hoverfly E. balteatus. However, this parameter could not explain the differences we obtained, as both plants (S. tuberosum and S. nigrum) were of similar color.

Our results also confirm the statement that hoverflies choose their oviposition site according to the infesting aphid species. Indeed, we demonstrated that A. fabae was not as attractive for *E. balteatus* as for *A. pisum* and *M. viciae*. Our data are also in accordance with those of Sadeghi & Gilbert (2000a), who showed the pea aphid to be preferred among eight aphid species. However, M. viciae and A. fabae were not tested. The size of the aphid species tested might be a factor of importance in host selection. Indeed, similar numbers of aphids were tested, but whereas A. pisum and M. viciae are large aphids, A. fabae is slightly smaller and therefore represented less food for hoverfly offspring. The three tested aphid species release (E)- β farnesene (Francis et al., 2005b) but might not release similar quantities, which could be specific or size dependent. The oviposition stimulus can also come from the aphid honeydew (Bargen et al., 1998; Scholz & Poehling, 2000), which varies qualitatively and quantitatively from one species to another and during the season (Fischer & Shingleton, 2001; Wool et al., 2006). Data vary from one predator to another. For example, even when reared on the same host plant (V. faba), the pea aphid (A. pisum) is considered suitable and the black bean aphid (A. fabae) is moderately suitable for larval development of the two-spotted ladybird *Adalia bipunctata* L. (Rana et al., 2002; Fréchett et al., 2006). However, the vetch aphid was found to be highly toxic for the same species (Fréchett et al., 2006).

The concordance between oviposition site selection and offspring performance is complex (Janz et al., 1994). Observed relationships between adult preference and some components of larval performance range from good concordance (Rausher, 1982; Singer, 1983) to poor concordance (Courtney, 1981). In some cases, poor concordance between preference and performance may result from oviposition onto introduced host plants (Chew, 1977; Legg et al., 1986) or relative rarity of the preferred host (Williams, 1983). Chandler (1968b) showed that the selection of an adequate oviposition site by syrphid females that lay eggs close to aphid colonies is essential to ensure the survival and fast development of their offspring. In our work, E. balteatus females demonstrated variations in their oviposition preference among the three tested aphids or among the two host plants and these differences had important consequences for the performance of their offspring.

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