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 aphid-specific 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. Acyrthosiphonpisum 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, 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 admiraloris* 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* (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 × 20 × 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 ± 1°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. viciei*, *A. pisum*, and *A. fabae*, were taken from stock cultures grown on *V. faba*. Adult *E. balteatus* were reared in 75 × 60 × 90 cm cages and were fed with bee-collected pollen, sugar, and water. Broad beans infested with *M. viciei* were introduced into the cages for 3 h every 2 days to allow oviposition. Hoverfly larvae were mass reared in aerated plastic boxes (110 × 140 × 40 mm) and were daily fed ad libitum with *M. viciei* as a standard diet.

**Oviposition preference**

**Aphid host plant preference.** In two-choice experiments, females were placed individually in net cages (30 × 30 × 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>
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<tr>
<th>Observed behavior</th>
<th>Description of behavior</th>
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<tbody>
<tr>
<td>Immobility/cage</td>
<td>Predator immobilized on the cage</td>
</tr>
<tr>
<td>Searching</td>
<td>Fly/cage</td>
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<td>Fly/plant</td>
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<td>Acceptance of host plant</td>
<td>Immobile/plant</td>
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<td>Walking/plant</td>
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<td></td>
<td>Immobile proboscis/plant</td>
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<tr>
<td></td>
<td>Walking proboscis/plant</td>
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<tr>
<td>Oviposition</td>
<td>Immobile abdomen/plant</td>
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<td></td>
<td>Walking abdomen/plant</td>
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<td>Egg laying</td>
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<td>Oviposition</td>
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V. faba plants (with six leaves and 20 cm high), which were infested with different aphid species. Three combinations of aphid 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 ± 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 × 30 × 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: \( r = \frac{\text{Ln}(m \cdot V)}{D} \), 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 ± 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 × 30 × 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 \( \chi^2 \) tests. Percentage of mortality and egg viability were transformed using the angular transformation before ANOVA (arcsine \( \sqrt{x} \); 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.
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 (χ² = 0.00, d.f. = 2, P = 1.00 and χ² = 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 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
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 A. pisum or M. viciae than on V. faba infested with A. fabae (F$_{2,13} = 4.69$, P = 0.029).

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

<table>
<thead>
<tr>
<th>Biological parameters</th>
<th>Myzus persicae/host plants</th>
<th>Test statistic</th>
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<tbody>
<tr>
<td></td>
<td>Solanum tuberosum Chang</td>
<td>Solanum nigrum Chang</td>
</tr>
<tr>
<td>Larval development (day)</td>
<td>7.75 ± 0.79</td>
<td>8.81 ± 0.93</td>
</tr>
<tr>
<td>Percentage of larval survival</td>
<td>66.66</td>
<td>66.66</td>
</tr>
<tr>
<td>Percentage of survival (to adult emergence)</td>
<td>63.33</td>
<td>66.66</td>
</tr>
<tr>
<td>Pupal weight (mg)</td>
<td>35.16 ± 4.41</td>
<td>31.06 ± 0.93</td>
</tr>
<tr>
<td>Pupal development (day)</td>
<td>7.53 ± 0.51</td>
<td>8.35 ± 0.67</td>
</tr>
<tr>
<td>Adult weight (mg)</td>
<td>22.01 ± 2.78</td>
<td>20.46 ± 2.53</td>
</tr>
<tr>
<td>Egg-to-adult development (day)</td>
<td>18.74 ± 1.66</td>
<td>20.20 ± 0.77</td>
</tr>
<tr>
<td>Preoviposition duration</td>
<td>9.66 ± 2.81</td>
<td>9.20 ± 1.79</td>
</tr>
<tr>
<td>Fecundity (eggs per female per day)</td>
<td>30.83 ± 31.25</td>
<td>25.25 ± 27.35</td>
</tr>
<tr>
<td>Percentage of total egg viability</td>
<td>81.29 ± 7.91</td>
<td>80.93 ± 5.24</td>
</tr>
<tr>
<td>Fitness (r)</td>
<td>0.78 ± 0.08</td>
<td>0.65 ± 0.09</td>
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### 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.
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 axyridis* 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 \textit{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, \textit{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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