Discrimination of parasitized aphids by an hoverfly predator: Effect on larval performance, foraging and oviposition behavior

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Running head: Oviposition site discrimination by hoverfly predator.
Abstract – The choice of the oviposition site by female aphidophagous predators is crucial for offspring performance, especially in hoverflies whose newly hatched larvae are unable to move on large distance. Predators and parasitoids interactions within the aphidophagous guild are likely to be very important in influencing the choices made by predatory hoverfly females. In the present study, the foraging and oviposition behavior of the aphidophagous hoverfly *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) was investigated according to parasitized states of aphid prey, *Acyrthosiphon pisum* Harris (Homoptera: Aphididae), parasitized by *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae). In similar experiments, the number of eggs laid by hoverfly females was counted when subjected to parasitized aphids. The influence of feeding with parasitized aphid as food on hoverfly larval performance was also studied in the present work. Hoverfly females did not exhibit any preference for plants infested with unparasitized or aphids parasitized for 7 days. On the other hand, plants infested with mummies or exuvia were less attractive for *E. balteatus*. These results were also correlated with (1) the number of eggs laid by *E. balteatus* females and with (2) larval performance. Thus, our results demonstrate that *E. balteatus* behavior is affected with parasitoid presence through their exploitation of aphid colonies. Indeed, hoverfly predators select their prey according to the development state of the parasitoid larvae that is potentially present.

Aphid communities are subjected to predation by a broad range of specialist and generalist arthropod predators and parasitoids that number and variety vary according to host plant species and phenology, season and weather conditions. Aphid natural enemies such as hoverflies (Gilbert, 1986), coccinellids (Hodek & Honek, 1996), lacewings (Principi & Canard, 1984), midges (Nijveldt, 1988), spiders (Sunderland et al., 1986) and parasitoids (Stary, 1970), are major components of the predatory guild associated with aphid colonies. Among these natural enemies, intraguild predation tends to be asymmetrical with the larger individuals acting as ‘superpredators’ and the smaller individuals being the intraguild prey (Lucas et al., 1998). The effects of such interactions may lead to a stabilization of prey-predators populations (Hanski, 1981; Godfray & Pacala, 1992) or adversely affect the foraging and oviposition performance of individual predators (Polis et al., 1989; Hemptinne et al., 1992; Rosenheim et al., 1995; Ruzicka, 1996). These intraguild interactions are probably influencing the choices made by aphidophagous female hoverflies (Gilbert, 2005).

The influence of parasitism on prey discrimination by the predatory hoverfly *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) was studied in the present work. The larvae of this species show a predation behavior on more than 100 species of aphids worldwide (Sadeghi & Gilbert, 2000b). Although many aphidophagous hoverflies are generalist, previous studies indicate that they are selective in their prey choice (Sadeghi & Gilbert, 2000a,b; Almohamad et al., 2007) and that they can forage in an optimal way (Hemptinne et al., 1993; Almohamad et al., 2007). For polyphagous syrphid, such as *Episyrphus balteatus*, the choice of the oviposition site has an important effect on the offspring performance, as syrphid larvae have rather limited dispersal abilities (Chandler, 1969).

In the current study, *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae) was used as parasitoid and the pea aphid *Acyrthosiphon pisum* Harris (Homoptera: Aphididae) as the
prey/host. This parasitoid has a great potential for successful aphid control because of its short
development time, high fecundity and high dispersal capacity (Rabasse & van Steenis, 1999). Previous laboratory and field studies suggested that spatial population dynamics, foraging
behavior and oviposition decisions of aphid parasitoids and predators are determined by the
density, distribution and quality of aphid colonies (Cappuccino, 1988; Morris, 1992; Mackauer & Völkl, 1993; Müller et al., 1999a,b). Thus, most natural enemies compete for the
same prey/host (Polis et al., 1989) and tend to aggregate in aphid patches (Frazer, 1988),
thereby creating favourable situations for intra- and interspecific encounters. In several
documented cases exploring predators-parasitoids interactions, generalist predators attacked
parasitized hosts, consuming both the host and the immature parasitoid developing inside the
host (Ruberson & Kring, 1991; Hoelmer et al., 1994, Meyhöfer & Hindayana, 2000). Additionally, interspecies prey discrimination (i.e., between parasitized and unparasitized
prey) could also enable foraging predators to evaluate prey and patch quality. According to
Rosenheim et al. (1995), few studies have described this discrimination behavior in predators
and none has discussed its functional significance. In the present study, we investigated the
foraging and oviposition behavior of predatory hoverfly *E. balteatus* in relation to the
presence of interspecific encounters (parasitized aphids) in patch aphids. The effects of
parasitized aphids as food on the performance of *E. balteatus* larvae in relation to
development of parasitoid larvae were also investigated.
Materials and methods

Plants and insects rearing – Broad beans (*Vicia faba* L.) were grown in 30 x 20 x 5 cm plastic trays filled with a mix of perlite and vermiculite (1/1) and maintained in controlled environment growth rooms (16L:8D and 20 ± 1°C). The two aphid species, namely *Megoura viciae* Buckton and *Acyrthosiphon pisum* Harris, were taken from stock rearing on *V. faba*, in separated air-conditioned rooms set at the same conditions as above. Adult *E. balteatus* were reared in 75 x 60 x 90 cm net cages and were provided with bee-collected pollen, sugar and water. Broad beans infested with *M. viciae* were introduced into the cages for 3 hours every two days to allow oviposition. Hoverfly larvae were mass-reared in aerated plastic boxes (110 x 140 x 40 mm) and were daily fed *ad libitum* with *M. viciae* as standard diet. *A. pisum* was used as *E. balteatus* prey or *Aphidius ervi* host. In order to obtain parasitized aphids and mummies, 150 aphids were introduced into a 9 cm of diameter Petri dish. Three previously mated parasitoid females were released in the petri dish and kept with the aphid colony for 4 hours. This method allowed us to obtain 91±2% of parasitized aphids (mean ± SE). Parasitized aphids were subsequently placed on broad beans for 7 days, and will be referred to as parasitized aphids. Mummies were obtained after 10-12 days after the parasitoid infestation. The parasitized aphids used in our experiments contained a 3-day-old parasitoid larvae and the mummies contained pupae.

Oviposition preference

Influence of parasitized aphids on hoverfly behavior – In no-choice experiments, a single *E. balteatus* female was placed in a net cage (30 X 30 X 60 cm) with a 20cm-tall *V. faba* plant infested with parasitized *A. pisum* at different development stades of parasitoid larvae. Four developmental stades of parasitoid larvae were tested: (i) healthy *A. pisum* (control), (ii)
parasitized *A. pisum* after seven days, (iii) mummified *A. pisum* and (iiii) exuvia of mummies. The female foraging behavior was recorded for 10 minutes using the Observer® (Noldus information Technology, version 5.0, Wageningen - The Netherlands). Descriptions of the four observed behavioral subdivisions are presented in Table 1. Behavioral observations were conducted in an air-conditioned room at 20 ± 1°C. Tested *E. balteatus* females were approximately 20-30 days old and no induction of oviposition had been realized for 24h prior to the experiment. This experiment was replicated ten times for each treatment.

*Influence of parasitized aphids on hoverfly oviposition rate* – In similar no-choice experiments, a single *E. balteatus* female was presented in a net cage and was allowed to lay eggs. The number of eggs (oviposition rate) was counted after 3 hours. Experimentations were conducted in an air-conditioned room at 20 ± 1°C. *Episyrphus balteatus* females were approximately 20-30 days old and no induction of oviposition had been realized for 24h prior to the experiment. These experiments were repeated ten times for each stage of parasitism.

Larval performance

To assess the effect of parasitized aphids as food on *E. balteatus* larval performance, 20 second instar larvae were weighted and individually placed in plastic petri dish (9 cm in diameter). Each day, the larvae were fed in excess of either unparasitized *A. pisum* or parasitized *A. pisum* (aphids parasitized for 7 days according to the same method as presented above). Among the 20 previously tested larvae, six larvae from each treatment (unparasitized and parasitized *A. pisum*) were observed daily to estimate their food consumption, defined as the difference between the weight of the food supplied and the weight of the food consumed. The weight gained by these second instar larvae was also measured as the difference between the weight of second instar larvae at the beginning of the experiment and weight on the day following pupation.
Additionally, mummified *A. pisum* were used as food and the impact on larval performance was tested. Ten second and seven third instar larvae fed in excess with mummified *A. pisum* were observed daily in plastic Petri dish (9 cm in diameter). Observations were made daily until the larvae died or developed into adults. Hoverfly larvae were kept in an incubator at 20 ± 1°C and 16:8 (L/D) photoperiod. The duration of their development, survival rates, food consumption and weight gained were determined. The pupae and the adults were also weighted (using a Sartorius micro balance scale model Mc5).

**Statistical analysis**

Mean frequencies and durations were compared using ANOVA (General Linear Model) and Dunnett’s test, conducted with Minitab® software (12.2 version, Minitab Inc, State College, PA, USA). In cases of heterogeneity of variables demonstrated by Bartlett’s test, data were log-transformed before parametric tests. Percentages of survival rate of hoverfly larvae were compared using Chi-square test.
Results

Oviposition preference

Influence of parasitized aphids on hoverfly behavior – The mean frequencies and mean durations observed for each *E. balteatus* behavior according to the developmental stage of the parasitoid larvae are presented in Figure 1a and Figure 1b, respectively. The hoverfly oviposition behavior was significantly affected by the parasitic state of its aphid prey, either in terms of frequencies (ANOVA, $F_{3,39} = 16.61$, $P < 0.001$) or durations (ANOVA, $F_{3,39} = 20.27$, $P < 0.001$). Similar results were obtained when observing the acceptance behavior; the means frequencies (ANOVA, $F_{3,39} = 12.61$, $P < 0.001$) and durations (ANOVA; $F_{3,39} = 6.28$, $P = 0.002$) of this behavioral stage were significantly affected by the presence and development stage of a parasitoid larvae inside the prey.

The presence of a 7-day old parasitoid larvae inside the aphid prey did not affect the foraging behavior of the predator *E. balteatus*. Indeed, the hoverfly predator showed similar acceptance for a plant infested by healthy aphids or by a 7-day parasitic aphids, either in terms of frequencies (Dunnett, $T = 2.336$, $P=0.069$) or durations (Dunnett, $T = 0.247$, $P=0.989$) of the corresponding observed behavior.

In presence of a plant infested with healthy prey, the *E. balteatus* female showed short period of immobility, that remained unchanged with 7-day parasitic aphids (Dunnett, $T = 0.225$, $P=0.992$). However, when presenting a *V. faba* infested with mummies, the hoverfly predators stayed immobile for longer period (Dunnett, $T = 4.039$, $P=0.001$). Similar observation can be made with exuvia of mummies as “prey” (Dunnett, $T = 4.145$, $P<0.001$).

Influence of parasitized aphids on hoverfly oviposition rate – The number of eggs laid by *E. balteatus* females was significantly affected by the presence of a parasitoid pupae inside the aphid prey (Figure 2). Indeed, whereas hoverfly predators did not distinguish healthy and 7-
day parasitized aphids in terms of number of laid eggs (Dunnett, $T = -1.335$, $P=0.414$), the oviposition rate was reduced when presenting mummified aphids (Dunnett, $T = -4.684$, $P<0.001$), and even more reduced when presenting exuvia (Dunnett, $T = -8.096$, $P<0.001$) to an hoverfly female.

Larval performance

Several parameters concerning the development, growth, and survival of second instar larvae, pupae and adult of *E. balteatus* have been compared for hoverflies fed with aphids at three levels of parasitism (i.e., healthy aphids, aphid infested with a 7-day larvae and mummies). Results concerning mummified aphids are not listed in Table 2 as they were not consumed by the hoverfly larvae. *Episyrphus balteatus* larvae developed successfully to maturity with unparasitized or parasitized *A. pisum*. No difference in survival of *E. balteatus* second instar larvae fed on unparasitized or parasitized pea aphid was observed ($\chi^2 = 0.06; P = 0.801$). Most of these larvae pupated and most of the resulting pupae developed into adults. There was no significant difference of development time between larvae fed on healthy and parasitized *A. pisum* (ANOVA, $F_{1,33} = 0.03$, $P = 0.873$). Additionally, no difference in pupae weight was highlighted (ANOVA, $F_{1,33} = 2.37; P = 0.134$). However, the adults resulting from larvae fed with unparasitized *A. pisum* were significantly heavier (ANOVA, $F_{1,28} = 9.57; P = 0.005$). Although weight gain in second instar larvae did not differ significantly when fed on unparasitized and parasitized aphids (ANOVA, $F_{1,33} = 2.92$, $P = 0.097$), hoverfly larvae consumed a smaller amount of parasitized aphid compared to unparasitized aphids (ANOVA, $F_{1,11}=9.35$, $P = 0.012$).

We also found that second instar hoverfly larvae fed with mummified aphids did not develop to pupae because they did not consume the mummified aphids. Similarly, we found that hoverfly third instar larvae pupated rapidly and did not exploit the mummified aphids as
food either. The weight of hoverfly third instar larvae did not differ significantly at the day following pupation when compared to the weight of thirty instar larvae at the beginning of experiment (ANOVA, $F_{1,13} = 2.00; P = 0.183$).
In natural environment, most aphidophagous hoverflies feed on a wide range of prey species (Rojo et al., 2003), that are not of equivalent nutritional value (Sadeghi & Gilbert, 2000b, Almohamad et al., 2007). As predicted by optimal foraging models, predators searching for prey should select the most profitable prey individuals and reject unprofitable ones (Crawley & Krebs, 1992). Such decision minimize loss of opportunity time and maximize energy return (Stephens & Krebs, 1986). Therefore, if parasitism alters prey suitability and profitability, the detection and recognition of chemical marks left by a parasitoid female, or of morphological and physiological changes provoked by the developing immature parasitoid, would have strong advantages for predators.

In our experiments, behavioural observations showed that E. balteatus females are unable to distinguish healthy from newly parasitize d aphids and did not exhibit any preference for either prey. On the other hand, plants infested with mummified aphids and exuvia of mummies were less attractive and fewer eggs were laid close to them by hoverfly females.

A key component of prey discrimination is the perception of patch quality and the adjustment of patch residence time to exploit the patch according to its relative quality. Theoretical models, principally elaborated for parasitoids, propose that a female parasitoid should allocate more time for the exploitation of patch perceived as being of good quality (Waage, 1979; McNair, 1982). Similarly, it can be expected that a predator with discrimination ability will invest in searching and exploitation time according to patch profitability. Flexible residence time and giving up time would determine the payoff of different patch qualities (van Alphen & Galis, 1983). In the present study, we found that E. balteatus females spent more time on plants infested with healthy or parasitized aphids in terms of acceptance and oviposition behaviors, compared with similar plants infested with
mummified aphids or exuvia of mummies. A reason for this might be the discrimination
ability, which could allow a generalist predator such as hoverfly *E. balteatus* to select an
ovioposition site with high quality and to exploit the encounters patches according to their
relative value. It was previously found that coccinellid *Coleomegilla maculata lengi* Timb
larvae spent less time in patches containing solely *Trichoplusia ni* old eggs parasitized by
*Trichogramma evanescens* Westwood, and their level of exploitation was greatly reduced,
compared with similar patches containing unparasitized *Trichoplusia ni* young eggs (Roger et
al., 2001). The reasons behind the preference of *E. balteatus* for plants infested with
parasitized aphids compared to those infested with mummified aphids or exuvia of mummies
remain uncertain. When predators attempt to locate a prey habitat, they use odors associated
with prey presence, such as those from the herbivorous prey itself (Witman, 1988), or from
prey by-products, such as feces or honeydew (Budenberg & Powell, 1992). It has been shown
that parasitized aphids *A. pisum* produce more honeydew, a carbohydrate-rich excretion, and
are more likely to attract aphid predators and parasitoids that use honeydew as a kairomone
(Carter & Dixon, 1984; Budenberg, 1990). Honeydew was shown to induce higher behavioral
preference in the predatory hoverfly *E. balteatus* (Sutherland et al., 2001), which may also
explain the preference of *E. balteatus* females for plants infested with parasitized aphids over
plants infested by mummified aphids. In a previous study, Almohamad et al. (2007) showed
that *E. balteatus* females prefere *Solanum tuberosum* L. as host plant than *Solanum nigrum* L.,
because apart from the aphid-released (E)-β-farnesene, *S. tuberosum* releases important
amounts of the aphid alarm pheromone (Agelopoulos et al., 2000) whereas *S. nigrum* does not
release this sesquiterpene (Schmidt et al., 2004), which is known to attract predators such as
*E. balteatus* (Francis et al., 2005). In present study, although Parasitized aphids release less
alarm pheromone than healthy ones (Verheggen, unpublished data), *E. balteatus* females did
not exhibit significant preference for plants infested by healthy aphids *A. pisum*. 

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According to Chandler (1968b), 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. Some individual females of *E. balteatus* differed from others in their preferences, and at the individual level, there appeared to be life-history trade-offs in performance with these preferences (Sadeghi & Gilbert, 1999). Additionally, the performance of predatory hoverflies larvae is often affected by the aphid species (Sadeghi & Gilbert, 2000b). The quality of prey is also important for survival, development and reproduction in aphidophagous hoverflies (Almohamad et al., 2007). Our findings here clearly show a good quality of healthy and parasitized pea aphids as food for the development and survival of second instar larvae of hoverfly *E. Balteatus*, 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 more true for insects that are unable to migrate easily from habitats poor in food, such as syrphid larvae. However, the hoverfly second instar larvae are more reluctant to feed on mummified pea aphid, but do not make a difference between parasitized and unparasitized aphids. This last statement agrees with the results of Brodeur (1994) who demonstrated in the laboratory that the incidence of predation by aphidophagous predators (Coccinellid, syrphid and predatory midge) was similar for parasitized and unparasitized potato aphids. Additionally, predatory midge and syrphid larvae, that are aphid specific predators, may feed on recently parasitized aphids but ignore mummified aphids (Harizanova & Ekborn, 1997; Kindlmann & Ruzicka, 1992). It was also found that mummified aphids produce also negative effects on the growth of predatory ladybirds (Takizawa et al., 2000).

In conclusion, our results demonstrated that the choice of the oviposition site by *E. balteatus* females may be affected with the parasitoid presence through their exploitation of aphid colonies. This suggest that predators and parasitoids interactions represent an
asymmetrical exploitation competition that have to be understood to elucidate the mechanisms which shape guilds of aphidophagous insects. However, as we tested colonies that were homogeneously constituted of either healthy or parasitized aphids, which is likely to never be found in nature, these conclusions should be carefully considered, and one should investigate the ability of hoverfly females to discriminate aphid colonies partly constituted of parasitized aphids.
Acknowledgement

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(Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. European

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Table 1. Description of the behavioral events recorded for aphidophagous hoverfly *Episyrphus balteatus* associated with parasitized *A. pisum* infested broad beans.

<table>
<thead>
<tr>
<th>Observed behaviors</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immobility/ cage</td>
<td>Predator immobilized on the cage</td>
</tr>
<tr>
<td>Searching</td>
<td></td>
</tr>
<tr>
<td>Fly/cage</td>
<td>Predator fly in the cage</td>
</tr>
<tr>
<td>Fly/plant</td>
<td>Predator fly near the plant</td>
</tr>
<tr>
<td>Acceptance of host plant</td>
<td></td>
</tr>
<tr>
<td>Immobile/plant</td>
<td>Predator landing on the plant</td>
</tr>
<tr>
<td>Walking/plant</td>
<td>Predator moving on the plant</td>
</tr>
<tr>
<td>Immobile proboscis/plant</td>
<td>Predator extends its proboscis and identifies the stimulatory substrate to accept the host</td>
</tr>
<tr>
<td>Walking proboscis/plant</td>
<td></td>
</tr>
<tr>
<td>Oviposition behavior</td>
<td></td>
</tr>
<tr>
<td>Immobile abdomen/plant</td>
<td>Predator exhibits an abdominal protraction or oviposition</td>
</tr>
<tr>
<td>Walking abdomen/plant</td>
<td>oviposition</td>
</tr>
<tr>
<td>Egg laying</td>
<td>Oviposition</td>
</tr>
</tbody>
</table>
Table 2. Effects of parasitized aphids *Acyrthosiphon pisum* as food on various performance parameters of the development of *Episyrphus balteatus* (mean ± SE).

<table>
<thead>
<tr>
<th>Biological parameters</th>
<th>Pea aphid <em>Acyrthosiphon pisum</em></th>
<th>Statistical test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Healthy</td>
<td>Parasitized</td>
</tr>
<tr>
<td>2nd instar larvae to adult developmental time (days)</td>
<td>4.44 ± 0.22</td>
<td>4.50 ± 0.27</td>
</tr>
<tr>
<td>% survival (from second instar larvae to adult emergence)</td>
<td>75.00</td>
<td>70.00</td>
</tr>
<tr>
<td>Pupal weight (mg)</td>
<td>39.07 ± 1.32</td>
<td>36.29 ± 1.21</td>
</tr>
<tr>
<td>Pupal development to adult (days)</td>
<td>8.13 ± 0.09</td>
<td>8.21 ± 0.21</td>
</tr>
<tr>
<td>Adult weight (mg)</td>
<td>27.03 ± 0.85</td>
<td>23.36 ± 0.83</td>
</tr>
<tr>
<td>Weight gain of second instar larvae (mg)</td>
<td>32.50 ± 1.27</td>
<td>29.44 ± 1.22</td>
</tr>
<tr>
<td>Food consumption of second instar larvae per day (mg)</td>
<td>105.42 ± 5.60</td>
<td>87.71 ± 1.46</td>
</tr>
</tbody>
</table>
Figures legends

Figure 1. Effects of parasitized *Acyrthosiphon pisum* on the oviposition behavior of female *Episyrphus balteatus* in relation to development of parasitoid larvae. (A) Mean frequencies (± SE) of behavioral observations of hoverfly females. (B) Mean durations (± SE) of behavioral observations of hoverfly females. * indicate to significant difference among the treatments when compared with control (healthy aphids) (ANOVA, Dunnet’s test. P<0.05).

Figure 2. Effects of parasitized aphid *Acyrthosiphon pisum* on oviposition rates of *Episyrphus balteatus* females in relation to development of parasitoid larvae. * indicate to significant difference among mean number of eggs laid (± SE) when compared with the control (healthy aphids) (ANOVA, Dunnet’s test. P<0.05).