

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

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4 Raki Almohamad<sup>1</sup>, François J. Verheggen<sup>1\*</sup>, Frédéric Francis<sup>1</sup>, Thierry Hance<sup>2</sup>, Eric  
5 Haubruge<sup>1</sup>

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7 <sup>1</sup>Department of Functional and Evolutionary Entomology, Gembloux Agricultural University,  
8 Passage des Déportés 2, B-5030 Gembloux (Belgium).

9 <sup>2</sup>Department of Ecology and Biogeography, Louvain Catholic University, Croix du Sud, 5, B-  
10 1348 Louvain-la-Neuve, (Belgium)

11 \*Correspondence: François J. Verheggen, Department of Functional & Evolutionary  
12 Entomology, Gembloux Agricultural University, Passage des Déportés 2, B-5030 Gembloux  
13 Belgium. E-mail : [entomologie@fsagx.ac.be](mailto:entomologie@fsagx.ac.be)

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15 Running head: Oviposition site discrimination by hoverfly predator.

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

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45 Keywords: Intraguild competition, *Episyrphus balteatus*, Diptera, Syrphidae, Parasitoid,  
46 *Aphidius ervi*, Hymenoptera, Aphidiidae, Pea aphid, *Acyrtosiphon pisum*, Homoptera,  
47 Aphididae

48 Introduction

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

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

71 In the current study, *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae) was used as  
72 parasitoid and the pea aphid *Acyrtosiphon pisum* Harris (Homoptera: Aphididae) as the

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

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94 Materials and methods

95

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

113

114 Oviposition preference

115 *Influence of parasitized aphids on hoverfly behavior* – In no-choice experiments, a single *E.*  
116 *balteatus* female was placed in a net cage (30 X 30 X 60 cm) with a 20cm-tall *V. faba* plant  
117 infested with parasitized *A. pisum* at different development stades of parasitoid larvae. Four  
118 developmental stades of parasitoid larvae were tested : (i) healthy *A. pisum* (control), (ii)

119 parasitized *A. pisum* after seven days, (iii) mummified *A. pisum* and (iiii) exuvia of mummies.  
120 The female foraging behavior was recorded for 10 minutes using the Observer® (Noldus  
121 information Technology, version 5.0, Wageningen - The Netherlands). Descriptions of the  
122 four observed behavioral subdivisions are presented in Table 1. Behavioral observations were  
123 conducted in an air-conditioned room at  $20 \pm 1^\circ\text{C}$ . Tested *E. balteatus* females were  
124 approximately 20-30 days old and no induction of oviposition had been realized for 24h prior  
125 to the experiment. This experiment was replicated ten times for each treatment.

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

### 132 Larval performance

133 To assess the effect of parasitized aphids as food on *E. balteatus* larval performance,  
134 20 second instar larvae were weighted and individually placed in plastic petri dish (9 cm in  
135 diameter). Each day, the larvae were fed in excess of either unparasitized *A. pisum* or  
136 parasitized *A. pisum* (aphids parasitized for 7 days according to the same method as presented  
137 above). Among the 20 previously tested larvae, six larvae from each treatment (unparasitized  
138 and parasitized *A. pisum*) were observed daily to estimate their food consumption, defined as  
139 the difference between the weight of the food supplied and the weight of the food consumed.  
140 The weight gained by these second instar larvae was also measured as the difference between  
141 the weight of second instar larvae at the beginning of the experiment and weight on the day  
142 following pupation.

143           Additionally, mummified *A. pisum* were used as food and the impact on larval  
144 performance was tested. Ten second and seven third instar larvae fed in excess with  
145 mummified *A. pisum* were observed daily in plastic Petri dish (9 cm in diameter).  
146 Observations were made daily until the larvae died or developed into adults. Hoverfly larvae  
147 were kept in an incubator at  $20 \pm 1^\circ\text{C}$  and 16:8 (L/D) photoperiod. The duration of their  
148 development, survival rates, food consumption and weight gained were determined. The  
149 pupae and the adults were also weighted (using a Sartorius micro balance scale model Mc5).

#### 150 Statistical analysis

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

156

157 Results

158 Oviposition preference

159 *Influence of parasitized aphids on hoverfly behavior* – The mean frequencies and mean  
160 durations observed for each *E. balteatus* behavior according to the developmental stage of the  
161 parasitoid larvae are presented in Figure 1a and Figure 1b, respectively. The hoverfly  
162 oviposition behavior was significantly affected by the parasitic state of its aphid prey, either  
163 in terms of frequencies (ANOVA,  $F_{3,39} = 16.61$ ,  $P < 0.001$ ) or durations (ANOVA,  $F_{3,39} =$   
164  $20.27$ ,  $P < 0.001$ ). Similar results were obtained when observing the acceptance behavior ; the  
165 means frequencies (ANOVA,  $F_{3,39} = 12.61$ ,  $P < 0.001$ ) and durations (ANOVA;  $F_{3,39} = 6.28$ ,  
166  $P = 0.002$ ) of this behavioral stage were significantly affected by the presence and  
167 development stage of a parasitoid larvae inside the prey.

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

173 In presence of a plant infested with healthy prey, the *E. balteatus* female showed short  
174 period of immobility, that remained unchanged with 7-day parasitic aphids (Dunnett,  $T =$   
175  $0.225$ ,  $P=0.992$ ). However, when presenting a *V. faba* infested with mummies, the hoverfly  
176 predators stayed immobile for longer period (Dunnett,  $T = 4.039$ ,  $P=0.001$ ). Similar  
177 observation can be made with exuvia of mummies as “prey” (Dunnett,  $T = 4.145$ ,  $P<0.001$ ).

178

179 *Influence of parasitized aphids on hoverfly oviposition rate* – The number of eggs laid by *E.*  
180 *balteatus* females was significantly affected by the presence of a parasitoid pupae inside the  
181 aphid prey (Figure 2). Indeed, whereas hoverfly predators did not distinguish healthy and 7-



182 day parasitized aphids in terms of number of laid eggs (Dunnett,  $T = -1.335$ ,  $P=0.414$ ), the  
183 oviposition rate was reduced when presenting mummified aphids (Dunnett,  $T = -4.684$ ,  
184  $P<0.001$ ), and even more reduced when presenting exuvia (Dunnett,  $T = -8.096$ ,  $P<0.001$ ) to  
185 an hoverfly female.

#### 186 Larval performance

187 Several parameters concerning the development, growth, and survival of second instar  
188 larvae, pupae and adult of *E. balteatus* have been compared for hoverflies fed with aphids at  
189 three levels of parasitism (i.e., healthy aphids, aphid infested with a 7-day larvae and  
190 mummies). Results concerning mummified aphids are not listed in Table 2 as they were not  
191 consumed by the hoverfly larvae. *Episyrphus balteatus* larvae developed successfully to  
192 maturity with unparasitized or parasitized *A. pisum*. No difference in survival of *E. balteatus*  
193 second instar larvae fed on unparasitized or parasitized pea aphid was observed ( $\chi^2_1 = 0.06$ ;  $P$   
194  $= 0.801$ ). Most of these larvae pupated and most of the resulting pupae developed into adults.  
195 There was no significant difference of development time between larvae fed on healthy and  
196 parasitized *A. pisum* (ANOVA,  $F_{1,33} = 0.03$ ,  $P = 0.873$ ). Additionally, no difference in pupae  
197 weight was highlighted (ANOVA,  $F_{1,33} = 2.37$ ;  $P = 0.134$ ). However, the adults resulting from  
198 larvae fed with unparasitized *A. pisum* were significantly heavier (ANOVA,  $F_{1,28} = 9.57$ ;  $P =$   
199  $0.005$ ). Although weight gain in second instar larvae did not differ significantly when fed on  
200 unparasitized and parasitized aphids (ANOVA,  $F_{1,33} = 2.92$ ,  $P = 0.097$ ), hoverfly larvae  
201 consumed a smaller amount of parasitized aphid compared to unparasitized aphids (ANOVA,  
202  $F_{1,11}=9.35$ ,  $P = 0.012$ ).

203 We also found that second instar hoverfly larvae fed with mummified aphids did not  
204 develop to pupae because they did not consume the mummified aphids. Similarly, we found  
205 that hoverfly third instar larvae pupated rapidly and did not exploit the mummified aphids as

206 food either. The weight of hoverfly third instar larvae did not differ significantly at the day  
207 following pupation when compared to the weight of thirty instar larvae at the beginning of  
208 experiment (ANOVA,  $F_{1,13} = 2.00$ ;  $P = 0.183$ ).

209

210 Discussion

211 In natural environment, most aphidophagous hoverflies feed on a wide range of prey  
212 species (Rojo et al., 2003), that are not of equivalent nutritional value (Sadeghi & Gilbert,  
213 2000b, Almohamad et al., 2007). As predicted by optimal foraging models, predators  
214 searching for prey should select the most profitable prey individuals and reject unprofitable  
215 ones (Crawley & Krebs, 1992). Such decision minimize loss of opportunity time and  
216 maximize energy return (Stephens & Krebs, 1986). Therefore, if parasitism alters prey  
217 suitability and profitability, the detection and recognition of chemical marks left by a  
218 parasitoid female, or of morphological and physiological changes provoked by the developing  
219 immature parasitoid, would have strong advantages for predators.

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

225 A key component of prey discrimination is the perception of patch quality and the  
226 adjustment of patch residence time to exploit the patch according to its relative quality.  
227 Theoretical models, principally elaborated for parasitoids, propose that a female parasitoid  
228 should allocate more time for the exploitation of patch perceived as being of good quality  
229 (Waage, 1979; McNair, 1982). Similarly, it can be expected that a predator with  
230 discrimination ability will invest in searching and exploitation time according to patch  
231 profitability. Flexible residence time and giving up time would determine the payoff of  
232 different patch qualities (van Alphen & Galis, 1983). In the present study, we found that *E.*  
233 *balteatus* females spent more time on plants infested with healthy or parasitized aphids in  
234 terms of acceptance and oviposition behaviors, compared with similar plants infested with

235 mummified aphids or exuvia of mummies. A reason for this might be the discrimination  
236 ability, which could allow a generalist predator such as hoverfly *E. balteatus* to select an  
237 oviposition site with high quality and to exploit the encounters patches according to their  
238 relative value. It was previously found that coccinellid *Coleomegilla maculata lengi* Timb  
239 larvae spent less time in patches containing solely *Trichoplusia ni* old eggs parasitized by  
240 *Trichogramma evanescens* Westwood, and their level of exploitation was greatly reduced,  
241 compared with similar patches containing unparasitized *Trichoplusia ni* young eggs (Roger et  
242 al., 2001). The reasons behind the preference of *E. balteatus* for plants infested with  
243 parasitized aphids compared to those infested with mummified aphids or exuvia of mummies  
244 remain uncertain. When predators attempt to locate a prey habitat, they use odors associated  
245 with prey presence, such as those from the herbivorous prey itself (Witman, 1988), or from  
246 prey by-products, such as feces or honeydew (Budenberg & Powell, 1992). It has been shown  
247 that parasitized aphids *A. pisum* produce more honeydew, a carbohydrate-rich excretion, and  
248 are more likely to attract aphid predators and parasitoids that use honeydew as a kairomone  
249 (Carter & Dixon, 1984; Budenberg, 1990). Honeydew was shown to induce higher behavioral  
250 preference in the predatory hoverfly *E. balteatus* (Sutherland et al., 2001), which may also  
251 explain the preference of *E. balteatus* females for plants infested with parasitized aphids over  
252 plants infested by mummified aphids. In a previous study, Almohamad et al. (2007) showed  
253 that *E. balteatus* females prefer *Solanum tuberosum* L. as host plant than *Solanum nigrum* L.,  
254 because apart from the aphid-released (*E*)- $\beta$ -farnesene, *S. tuberosum* releases important  
255 amounts of the aphid alarm pheromone (Agelopoulos et al., 2000) whereas *S. nigrum* does not  
256 release this sesquiterpene (Schmidt et al., 2004), which is known to attract predators such as  
257 *E. balteatus* (Francis et al., 2005). In present study, although Parasitized aphids release less  
258 alarm pheromone than healthy ones (Verheggen, unpublished data), *E. balteatus* females did  
259 not exhibit significant preference for plants infested by healthy aphids *A. pisum*.

260 According to Chandler (1968b), the selection of an adequate oviposition site by  
261 syrphid females, that lay eggs close to aphid colonies, is essential to ensure the survival and  
262 fast development of their offspring. Some individual females of *E. balteatus* differed from  
263 others in their preferences, and at the individual level, there appeared to be life-history trade-  
264 offs in performance with these preferences (Sadeghi & Gilbert, 1999). Additionally, the  
265 performance of predatory hoverflies larvae is often affected by the aphid species (Sadeghi &  
266 Gilbert, 2000b). The quality of prey is also important for survival, development and  
267 reproduction in aphidophagous hoverflies (Almohamad et al., 2007). Our findings here clearly  
268 show a good quality of healthy and parasitized pea aphids as food for the development and  
269 survival of second instar larvae of hoverfly *E. Balteatus*, confirming the hypothesis that  
270 ovipositing insects can select sites that improve the growth and survival of their offspring  
271 (Peckarsky *et al.*, 2000). This should be more true for insects that are unable to migrate easily  
272 from habitats poor in food, such as syrphid larvae. However, the hoverfly second instar larvae  
273 are more reluctant to feed on mummified pea aphid, **but do not make a difference between**  
274 **parasitized and unparasitized aphids**. This last statement agrees with the results of Brodeur  
275 (1994) who demonstrated in the laboratory that the incidence of predation by aphidophagous  
276 predators (Coccinellid, syrphid and predatory midge) was similar for parasitized and  
277 unparasitized potato aphids. Additionally, predatory midge and syrphid larvae, that are aphid  
278 specific predators, may feed on recently parasitized aphids but ignore mummified aphids  
279 (Harizanova & Ekbom, 1997; Kindlmann & Ruzicka, 1992). It was also found that  
280 mummified aphids produce also negative effects on the growth of predatory ladybirds  
281 (Takizawa *et al.*, 2000).

282 In conclusion, our results demonstrated that the choice of the oviposition site by *E.*  
283 *balteatus* females may be affected with the parasitoid presence through their exploitation of  
284 aphid colonies. This suggest that predators and parasitoids interactions represent an

285 asymmetrical exploitation competition that have to be understood to elucidate the  
286 mechanisms which shape guilds of aphidophagous insects. However, as we tested colonies  
287 that were homogeneously constituted of either healthy or parasitized aphids, which is likely to  
288 never be found in nature, these conclusions should be carefully considered, and one should  
289 investigate the ability of hoverfly females to discriminate aphid colonies partly constituted of  
290 parasitized aphids.

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292

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

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

420 Table 2. Effects of parasitized aphids *Acyrtosiphon pisum* as food on various performance  
 421 parameters of the development of *Episyrphus balteatus* (mean  $\pm$  SE).

Biological parameters	Pea aphid <i>Acyrtosiphon pisum</i>		Statistical test	
	Healthy	Parasitized		
2 <sup>nd</sup> instar larvae to adult developmental time (days)	4.44 $\pm$ 0.22	4.50 $\pm$ 0.27	F <sub>1,33</sub> = 0.03	P = 0.873
% survival (from second instar larvae to adult emergence)	75.00	70.00	X <sup>2</sup> <sub>1</sub> = 0.02	P = 0.888
Pupal weight (mg)	39.07 $\pm$ 1.32	36.29 $\pm$ 1.21	F <sub>1,33</sub> = 2.37	P = 0.134
Pupal development to adult (days)	8.13 $\pm$ 0.09	8.21 $\pm$ 0.21	F <sub>1,28</sub> = 0.13	P = 0.724
Adult weight (mg)	27.03 $\pm$ 0.85	23.36 $\pm$ 0.83	F <sub>1,28</sub> = 9.57	P = 0.005
Weight gain of second instar larvae (mg)	32.50 $\pm$ 1.27	29.44 $\pm$ 1.22	F <sub>1,33</sub> = 2.92	P = 0.097
Food consumption of second instar larvae per day (mg)	105.42 $\pm$ 5.60	87.71 $\pm$ 1.46	F <sub>1,11</sub> = 9.35	P = 0.012

423 Figures legends

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

429 Figure 2. Effects of parasitized aphid *Acyrtosiphon pisum* on oviposition rates of *Episyrphus*  
430 *balteatus* females in relation to development of parasitoid larvae. \* indicate to significant  
431 difference among mean number of eggs laid ( $\pm$  SE) when compared with the control (healthy  
432 aphids) (ANOVA, Dunnet's test.  $P < 0.05$ ).

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