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Intraguild interactions between the predatory hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) and the Asian ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae): Effect of larval tracks

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Abstract. The effects of the larval tracks of *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) on the egg laying behavior of females of the predatory hoverfly *E. balteatus* were investigated in two-choice experiments. The oviposition response of *H. axyridis* to larval tracks of *E. balteatus* was also tested in one-choice experiments. Gravid *E. balteatus* females laid significantly fewer eggs on leaf discs with aphids and contaminated with tracks of conspecific or heterospecific larvae than on control leaf discs. *H. axyridis* females laid similar numbers of eggs in Petri dishes with aphids and contaminated with the tracks of *E. balteatus* larvae as in control Petri dishes. This indicates that *E. balteatus* females lay fewer eggs at sites where there are conspecific and heterospecific larval tracks, whereas the tracks of the syrphid larvae did not deter *H. axyridis* females from laying eggs.

INTRODUCTION

Aphidophagous hoverflies and ladybirds are known to exploit temporary aphid colonies as food resources and significantly suppress aphid abundance (Chambers & Adams, 1986; Dixon, 1985; Dixon et al., 1997; Lee & Kang, 2004). It has been also demonstrated that the survival of the larvae of these aphid predators and their efficiency in reducing aphid populations mainly depends on the quality and the quantity of the patches of aphid prey (Kan, 1988; Hemptinne et al., 1993; Kindlmann & Dixon, 1993; Almohamad et al., 2007, 2008). The selection of oviposition sites by gravid females should therefore reflect a preference for patches of prey of high nutritional value and/or where the risks of predation and competition are low, especially in insect species where neonate offspring have limited mobility and are therefore relatively sessile (e.g. syrphid larvae, Chandler, 1969).

Several authors have shown that ovipositing insect predators respond to chemical cues (i.e. oviposition-deterrents) indicating that a prey patch is already being exploited by conspecific larvae (Růžička, 1994, 1996, 1997; Doumbia et al., 1998; Růžička & Havelka, 1998; Yasuda et al., 2000; Oliver et al., 2006; Michaud & Jyoti, 2007). Most of these studies have focused on coccinellids and chrysopids, while studies on syrphids are very recent and scarce (e.g. Scholz & Poehling, 2000; Pineda et al., 2007; Almohamad et al., 2008; Putra et al., 2009).

Larvae of predatory hoverflies and ladybirds occur on the same aphid infested plants and strongly interact with each other when their aphid prey becomes scarce (e.g., Agarwala & Yasuda, 2001). The multicoloured Asian ladybird, *H. axyridis* is native to South-East Asia (e.g. Dobzhansky, 1933; Kuznetsov, 1997). It was introduced as biological control agent in Belgium in 1997 and by 2006 was recorded in all regions of Belgium (for an earlier survey see Adriaens et al., 2003). The hoverfly *E. balteatus* is usually the most abundant syrphid aphid predator in Europe, where it naturally occurs in high numbers in numerous crops (Tenhumberg & Poehling, 1991; Gilbert, 1993; Colignon et al., 2001; Miñarro et al., 2005). These two aphid predators are known to be important biocontrol agents of aphid populations (Chambers & Adams, 1986; Chambers, 1988; Koch, 2003; Roy et al., 2006; Pineda & Marcos-García, 2008).

Pell et al. (2008) have reported that *H. axyridis* remains in equilibrium with its co-evolved native guild of predators through niche complementarity, but outside Asia the native guild of predators have co-evolved without *H. axyridis.* Recent observations also suggest that this species is now invading (semi-)natural ecosystems in Belgium and is a potential threat to native ladybird species and other aphid predators (Adriaens et al., 2003). Field observations have shown that *H. axyridis* and *E. balteatus* often coexist in aphid colonies in different habitats in Belgium-Gembloux (Alhmedi et al., 2007). The objective of this study was to obtain a better understanding of the mechanisms that shape guilds of aphidophagous predators and their potential use in biocontrol. In particular, the effect of the larval tracks of *E. balteatus* and *H. axyridis* on oviposition-site selection by *E. balteatus* females was determined. The oviposition response of *H. axyridis* females to tracks left by *E. balteatus* larvae was also investigated.

MATERIAL AND METHODS

Plant and insect rearing

Broad-bean plants (*Vicia faba* L.) were grown in 30 cm × 20 cm × 5 cm plastic trays filled with a mixture of perlite and vermiculite (1/1) and maintained in controlled-environment growth rooms (16L : 8D; 20 ± 1°C). Two aphid species (*Myzus persicae* Sulzer and *Megoura viciae* Buckton) were reared on broad-bean plants in separate rooms. Adult *E. balteatus* were reared in 75 × 60 × 90 cm cages provided with bee-collected pollen, sugar and water. Broad-bean plants infested with *M. viciae* were introduced into the cages for 3 h every two days for the adults to lay their eggs on. Hoverfly larvae were mass-reared in aerated plastic boxes (110 × 140 × 40 mm) and fed daily *ad libitum* with *M. viciae*.

H. axyridis adults were obtained from Montreal Canada (Eric Lucas laboratory, Université du Québec à Montréal). Adults and larvae were then mass-reared in aerated plastic boxes (up to 25 individuals per container) and fed daily ad libitum with *M. viciae*. Bee-collected pollen, sugar and water were also provided. Boxes were placed in controlled-environment incubators (25 ± 2°C; 70% RH and photoperiod 16L: 8D). Mated and fertile females used in the experiment were isolated individually in separate boxes; no oviposition occurred in the 24 h prior to experimentation.

EXP 1. Effect of conspecific and heterospecific larval tracks on syrphid oviposition

This experiment was conducted using aphids on leaf discs (Almohamad et al., 2006). A 2.5 cm-diameter circular piece of *V. faba* leaf was cut and placed in a Petri dish containing agar solution (7 ml agar, 1% water solution w : w), which increased the humidity and prevented the leaf disc from drying out. Prior to use, either two third-instar larvae of *E. balteatus*, or two fourth-instar larvae of *H. axyridis* were confined with an excess of *M. persicae* (125 individuals) on each leaf-disc by parafilm paper (Parafilm®, Pechiney Plastic Packaging, Chicago, USA) and kept in the controlled incubator (16L: 8D; 20 ± 1°C) for 24 h. After 24 h the larvae and all aphid material were carefully removed. Then, each leaf disc with the tracks left by syrphid or coccinellid larvae was infested with an excess of recently collected *M. persicae* (125 individuals). The control consisted of a leaf disc infested with the same numbers of aphids but lacking larval tracks. In a two-choice experiment, both treated and control leaf-discs (i.e. with and without larval tracks) were positioned on two Plexiglass holders 20-cm high, separated by 15 cm, in a net cage (30 × 30 × 60 cm). This arrangement was previously used to evaluate the oviposition response of *E. balteatus* to aphid-infested plants (Almohamad et al., 2006). A single female was then introduced into the cage and allowed to lay eggs for 3 h. The number of eggs laid on each leaf disc was then counted. These experiments were conducted in an air-conditioned room at 21 ± 1°C. *Episyrphus balteatus* females were approximately 20–30 days old, and had not oviposited during the previous 24 h. There were ten replicates of each treatment (one assessing the control leaf discs vs. those with larval tracks of *E. balteatus*, and the other control leaf discs vs. those with larval tracks of *H. axyridis*).

EXP 2. Effect of tracks of syrphid larvae on *H. axyridis* oviposition

Ten third-instar hoverfly larvae were supplied with an excess of a mixture of different instars of *M. viciae* aphids (150 individuals) in a 9 cm-diameter glass Petri dish, the base of which was covered with filter paper. After 24 h the larvae and all aphid material were carefully removed. In a no-choice experiment, a single mated *H. axyridis* female was then placed in each dish with an excess of aphids (150 individuals) and the number of eggs laid during the next 24 h was recorded. The control consisted of 10 females kept individually in clean glass Petri dishes that contained a similar number of aphids. The experiment was repeated 10 times for each treatment.

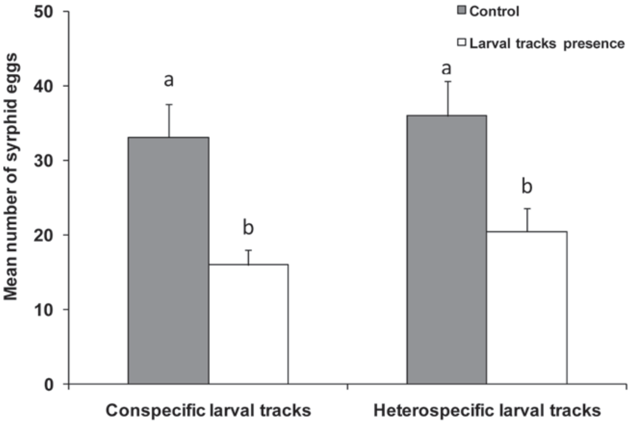

Fig. 1. Mean (± SE) number of eggs laid by *E. balteatus* females on leaf discs contaminated with the tracks of larvae of their own species or that of larvae of the ladybird *H. axyridis* compared with a control in two-choice experiments. Means with different letters are significantly different (paired t-test, $P < 0.01$).

Statistical analysis

A paired t-test was used to compare the mean number of eggs laid by the aphid predators in the two-choice experiments. In the one-choice experiment, the means were compared using a two-sample t-test. All statistical tests were conducted using Minitab® release 15.2.

RESULTS

EXP 1. Effect of conspecific and heterospecific larval tracks on syrphid oviposition

Gravid *E. balteatus* females laid significantly fewer eggs on leaf discs on which there were tracks of either conspecific hoverfly larvae ($\text{mean1}_{16.00} \pm \text{SE}_{1.99}$) (paired t-test, $t = 4.47$, $P = 0.002$) or heterospecific ladybird larvae ($\text{mean2}_{20.50} \pm \text{SE}_{3.10}$) (paired t-test, $t = 3.06$, $P = 0.014$) compared to the controls ($\text{mean1}_{33.10} \pm \text{SE}_{4.29}$; $\text{mean2}_{36.00} \pm \text{SE}_{4.60}$) (Fig. 1). Thus the presence of conspecific and heterospecific larval tracks deterred gravid female *E. balteatus* from ovipositing.

EXP 2. Effect of tracks of syrphid larvae on *H. axyridis* oviposition

Compared to the control ($\text{mean}_{15.50} \pm \text{SE}_{3.10}$), gravid *H. axyridis* females were not deterred from ovipositing by the tracks of *E. balteatus* larvae ($\text{mean}_{15.80} \pm \text{SE}_{3.20}$) (two-sample t-test, $t = –0.07$, $P = 0.947$, *df* = 18) (Fig. 2).

DISCUSSION

Adults of predators, the larvae of which compete for the same trophic resource, can reduce the intensity of interspecific competition between their larvae by avoiding food resources contaminated with heterospecific semiochemicals (e.g. Růžička, 2001a, b). Several studies have reported lower frequencies of inter- vs. intra-specific

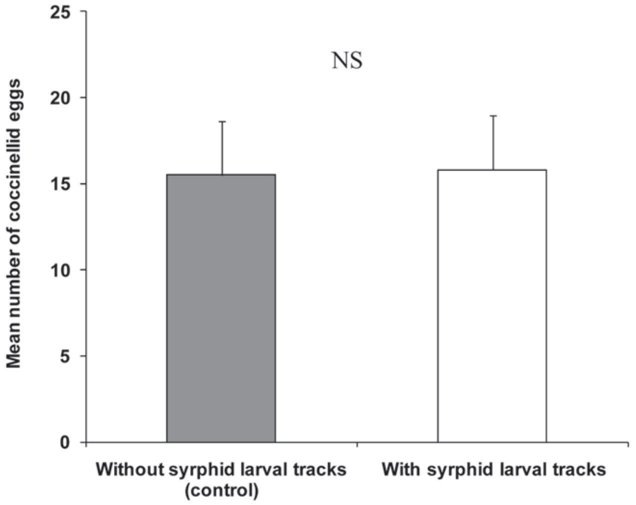

Fig. 2. Mean (± SE) number of eggs laid by *H. axyridis* in Petri dishes containing aphids and contaminated with the tracks left by *E. balteatus* larvae compared with the average number laid in the control (clean Petri dishes containing only aphids). NS indicates no significant difference between treatments (two-sample t-test, $P > 0.05$).

interactions in phytophagous insects (Birch et al., 1980; Byers et al., 1984; Thiéry et al., 1992) and parasitoids (Janssen et al., 1995). In insect predators, interspecific interactions occur between chrysopids (Růžička, 1996, 1998) and coccinellids (Růžička, 2001a, b). This study records for the first time interspecific interactions between hoverflies and coccinellids.

In our experiments, *E. balteatus* females laid fewer eggs when ovipositing in aphid colonies contaminated with the tracks of both conspecific larvae and heterospecific coccinellid larvae. A similar response is also shown by female *Coccinella septempunctata* L. to tracks left by larvae of both *C. septempunctata* and *Chrysopa oculata* Say (Růžička, 1997). Putra et al. (2009) also report that hoverflies tend to reduce their rate of laying eggs when ladybird larvae are present. The mechanism underlying the reduction in oviposition by *E. balteatus* females in the presence of the tracks or larvae of both conspecific and heterospecific predators is unknown. This response is likely to be adaptive as laboratory studies have demonstrated that *H. axyridis* larvae will eat *E. balteatus* eggs (Alhmedi et al., unpubl. data) and syrphid larvae (Putra et al., 2009).

H. axyridis females are deterred from ovipositing on broad-bean plants contaminated with conspecific larval tracks but not those of *C. septempunctata* larvae (Yasuda et al., 2000). The no-choice tests used here indicate that *H. axyridis* females exhibit a weak response to the presence of oviposition-deterring substances in the tracks of *E. balteatus* larvae (10 replicates only). It is interesting to speculate why adult ladybirds respond only to conspecific cues. It is likely that each species of ladybird is associated mainly with one particular habitat (Honěk, 1985), where it is more likely to meet individuals of its own species than of other species.

It is well established that females of insects occupying the third trophic level (i.e. parasitoids and predators) avoid ovipositing where competitors threaten the survival of their offspring by responding to the semiochemicals released by conspecific competitors. For example parasitoids are sensitive to volatiles signaling the previous or actual presence of conspecifics and to chemical trails deposited by their enemies (Price, 1970; Janssen et al., 1995; Nakashima et al., 2004). Several aphidophagous and coccidophagous predators respond to oviposition-deterring semiochemicals in the tracks left by conspecific larvae (Merlin et al., 1996; Růžička, 1997, 2002, 2006; Doumbia et al., 1998; Hemptinne et al., 2001). In our experiments, *E. balteatus* females laid fewer eggs on leaf discs contaminated with the tracks of conspecific and heterospecific larvae, possibly by responding to a chemical(s) in the tracks (i.e. oviposition – deterrents). Such responses enable females to quickly assess the quality of patches of prey and enhance their probability of discovering suitable oviposition sites.

E. balteatus and *H. axyridis* have been used to control aphids in greenhouses (Snyder et al., 2004; Pineda & Marcos-García, 2008). The present study provides new information on semiochemical spacing of these aphidophagous predators over prey patches of different quality. This knowledge could be employed to improve the effectiveness of these aphid predators when used in biological control programs.

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