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Intraguild interactions and aphid predators: biological efficiency of *Harmonia axyridis* and *Episyrphus balteatus*

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Abstract

Introductions of the harlequin ladybird *Harmonia axyridis* into Belgium for aphid biological control have been followed by declines in native aphid natural enemies. We first examined, in laboratory and field conditions, the impact of larval mobility of either *H. axyridis* or *Episyrphus balteatus*, the most abundant native hoverfly in central Europe, on aphid suppression. The hoverfly larvae consumed more aphids (*Megoura vicia*e) in a short term, whereas the ladybird ones were more efficient in a long term. We second investigated the intraguild interactions between *H. axyridis* and *E. balteatus* larvae and adults. In larva pairings between the two species in laboratory microcosms containing aphid (*M. vicia*e) infested broad bean (*Vicia faba*) plants, *H. axyridis* had an intraguild predation (IGP) advantage over the hoverfly. When conspecific larvae were paired together on aphid-infested plants, no cannibalism between them was detected. The presence of either *H. axyridis* or *E. balteatus* larvae on aphid-infested plants negatively influenced the ovipositional behaviour of *H. axyridis* and *E. balteatus* females; lower numbers of laid eggs were recorded compared to control treatment. Moreover, eggs laid by *E. balteatus* females were also dropped as victims of predation mainly by *H. axyridis* larvae. Our results suggest that while the exotic ladybird was more efficient in aphid biological control, larvae and eggs of the native hoverfly species face increased IGP by *H. axyridis*, which would contribute, as a consequence, to the decline in *E. balteatus* population following invasion.

Introduction

The increase in the introduction of exotic species throughout the world, and the potential of these species to become invasive, is a subject of much concern (Mack et al. 2000). The invasive exotic species often do significant ecological and economic damage (Williamson 1996). Recently, the potential risks of exotic natural enemy releases received great attention outside the biological control world (van Lenteren et al. 2003). Negative impacts of introduced exotic species include competitive suppression or displacement of native natural enemies and suppression or extinction of non-target prey species, some of which being potential beneficial (Elliott et al. 1996; Majerus et al. 2006; Roy et al. 2006; Snyder and Evans 2006). However, when beneficial species share a pest species as their common prey, intraguild interactions between them may take place. Intraguild predation (IGP) occurs in many insect communities and has been defined as 'the killing and eating of species that use similar resources and thus are potential competitors' (Polis and Holt 1992). IGP may be symmetric or asymmetric. In the latter, one dominant species is always the predator of the other, while symmetric IGP occurs when there is mutual predation between both species (Lucas 2005).

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Several studies focused on the understanding of the ecological impact of IGP between the harlequin ladybird, *Harmonia axyridis* Pallas, originating from the Far East (Iablokoff-Khnzorian 1982), and other indigenous species either from West Palearctic such as *Adalia bipunctata* L. (Burgio et al. 2005) or from Nearctic regions such as *Hippodamia convergens* Guerin-Meneville (Snyder et al. 2004). *Harmonia axyridis* beetles feed not only on aphids, but also on a wide range of non-aphid prey including other predators (Evans 1991; Osawa 1993; Hodek and Honěk 1996; Cottrell and Yeargan 1998a; Obrycki et al. 1998; Kajita et al. 2000; Gardiner and Landis 2007; Pell et al. 2008; Ware and Majerus 2008). Because of its efficient searching capacity and high predation activity, *H. axyridis* was considered as an effective biological control agent against aphid pests. *Harmonia axyridis* was permanently established in several European countries (Brown et al. 2008) such as France (Ferran et al. 1996), Germany (Bathon 2003), Switzerland (Klausnitzer 2004), the UK (Majerus and Roy 2005) and Belgium (Adriaens et al. 2008). In South America, *H. axyridis* was also released to control aphids in peach orchards in Argentina (Garcia et al. 1999) and recorded in Brazil (De Almeida and Da Silva 2002). In the US and Canada, *H. axyridis* is established and considered invasive (Hahn and Kovach 2004; Cottrell 2005; Lucas et al. 2007). However, the very functional traits that have made *H. axyridis* an effective biological control agent, also implicate it as an intraguild predator that poses significant risk to the diversity of other natural enemies and their ecosystem services.

In Europe, *Episyrphus balteatus* DeGeer is the most common hoverfly and is a voracious aphid predator found in different crops. Particularly in cereals, it is known as an effective aphid biocontrol agent (Ankersmith et al. 1986; Chambers and Adams 1986; Poehling 1988; Tenhumberg and Poehling 1995). However, this biocontrol efficacy has showed considerable variability that could not explained simply by abiotic conditions (Poehling et al. 1991; Tenhumberg and Poehling 1995). As the relationship between eggs laid and the number of resulting young larvae was the most variable factor influencing the population size of *E. balteatus*, it was hypothesized that biotic interactions with other predators might impact the survival of these highly vulnerable life stages. Cannibalism, defined as the act of feeding on conspecifics, occurs in various insect species (Fox 1975; New 1991) mainly when food resources are scarce (Agarwala and Dixon 1992; Branquart et al. 1997), although some reports show that cannibalism can also be observed even when food is abundant (Hassan 1975; Chapman et al. 1999). Cannibalistic tendencies have been reported for *E. balteatus* (Branquart et al. 1997; Hindayana 2001) and coccinellids such as, *A. bipunctata* and *Coccinella septempunctata* L. (Agarwala and Dixon 1992). Different studies performed by Chandler (1968a,b) and then by Scholz and Poehling (2000) showed that cannibalism in *E. balteatus* in the field is an uncommon phenomenon.

Along with beneficial impacts as a biological control agent, *H. axyridis* may threaten beneficial organisms. For example, densities of native predators seem to have decreased as the abundance of *H. axyridis* increased (Colunga-Garcia and Gage 1998; Alyokhin and Sewell 2004), which may be partly due to IGP (Cottrell and Yeargan 1998a; Cottrell 2004; Yasuda et al. 2004). In addition, *H. axyridis* can be a pest of fruit production (Koch et al. 2004), particularly as a contaminant during wine production (Pickering et al. 2004; Galvan et al. 2006). The objectives of this study were to investigate: (i) the impact of larval mobility of *H. axyridis* and *E. balteatus* on aphid consumption rate and (ii) intraguild interactions between *H. axyridis* and *E. balteatus* adults and larvae.

Materials and Methods

Insect rearing and host plant culture

Rearing and experimental conditions were 22 ± 2°C and 16 : 8 (L : D) photoperiod. Broad bean, *Vicia faba* plants grown in plastic pots (12 cm diameter × 10 cm height) in a climate-controlled room were used in all experiments. The growing medium was a mixture 1 : 1 of vermiculite and perlite. *Megoura viciae* Buckton (Sternorrhyncha: Aphididae) were mass-reared on broad bean plants in the laboratory and used as prey for both predators.

Adults and larvae of *H. axyridis* were fed with *M. viciae* aphids in aerated plastic boxes (10 × 30 × 10 cm) with mesh screen on the sides. In addition to aphids as food, *H. axyridis* adults were provided with pollen, sugar and water. Egg clusters were regularly collected on pieces of paper placed in these boxes.

The hoverfly *E. balteatus* adults were reared in net cages (60 × 100 × 100 cm) and were provided with pollen, sugar and water. Pollen and water were changed every other day. Adult females were stimulated to oviposit by presenting *M. viciae* infested broad bean plant. Emerged larvae were fed on *M. viciae* reared on broad bean.

Larval mobility and aphid consumption

The experiments were conducted in the laboratory and the field using net cages. Broad bean plants were grown in pots (12 cm diameter × 10 cm height), five plants per pot. One hundred *M. viciae* aphid individuals (mixed of 2nd and 3rd larval stages) were placed on each broad bean plant; then, after 1 day, either *H. axyridis* or *E. balteatus* 2nd instar larvae were released as follows.

In laboratory conditions

Each pot containing five aphid-infested plants was placed into a net cage (25 × 25 × 35 cm), then five 2nd instar larvae of either *H. axyridis* or *E. balteatus* were placed on the central plant. Ten replicates were simultaneously conducted for *H. axyridis* and 10 more for *E. balteatus*.

In field conditions

Five pots, each containing five aphid-infested plants, were placed into a net cage (100 × 100 × 120 cm), then ten 2nd instar larvae of either *H. axyridis* or *E. balteatus* were placed on the central plant in each pot. Ten replicates were simultaneously conducted for *H. axyridis* and ten other for *E. balteatus*. The distribution of predatory larvae (both their number and their location) on aphid-infested plants and the number of living aphids were recorded daily until predators pupated.

Intraguild interactions

These experiments were conducted in laboratory conditions using plastic cages (9 cm diameter × 25 cm height) covered with mesh screen cloth. A single five to six leaf bean plant grown in pot (12 cm diameter × 10 cm height) was infested with 100 *M. viciae* aphids of mixed larval stages (2nd and 3rd).

Intraguild interactions between larvae

One day after aphid infestation, con- or heterospecific larval pairs were placed on each aphid-infested plant. Our experiments consisted of 15 sets of larval pairs as follows: (a) conspecific larva pairings: (i) two 2nd instar *H. axyridis*, (ii) one 2nd and one 3rd instar *H. axyridis*, (iii) one 2nd and one 4th instar *H. axyridis*, (iv) two 3rd instar *H. axyridis*, (v) one 3rd and one 4th instar *H. axyridis*, (vi) two 4th instar *H. axyridis*, (vii) two 2nd instar *E. balteatus*, (viii) one 2nd and one 3rd instar *E. balteatus*, (ix) two 3rd instar *E. balteatus* and (b) heterospecific larva pairings: (i) one 2nd instar *H. axyridis* and one 2nd instar *E. balteatus*, (ii) one 2nd instar *H. axyridis* and one 3rd instar *E. balteatus*, (iii) one 3rd instar *H. axyridis* and one 2nd instar *E. balteatus*, (iv) one 3rd instar *H. axyridis* and one 3rd instar *E. balteatus*, (v) one 4th instar *H. axyridis* and one 2nd instar *E. balteatus*, (vi) one 4th instar *H. axyridis* and one 3rd instar *E. balteatus*.

After 3 days, the number of aphids alive and all consumed predatory larvae were counted in each replicate. Each larval combination was simultaneously replicated 10 times.

Impact of larval presence on oviposition

One day after aphid infestation, three 2nd instar larvae of either *H. axyridis* or *E. balteatus* were placed on aphid-infested plant for a 24-h period. Aphid numbers were then adjusted to 100 individuals par plant prior to introduction of *H. axyridis* or *E. balteatus* females into experimental cages. A single gravid ladybird or hoverfly female was carefully introduced into each cage containing one aphid-infested plant and three con- or heterospecific 2nd instar larvae. The lab-trials included six treatments: (a) conspecific interactions: (i) one *H. axyridis* female was introduced into a cage containing an aphid-infested plant and three 2nd instar *H. axyridis* larvae, (ii) one *E. balteatus* female was introduced into a cage containing an aphid-infested plant and three 2nd instar *E. balteatus* larvae; (b) heterospecific interactions: (i) one *H. axyridis* female was introduced into a cage containing an aphid-infested plant and three 2nd instar *E. balteatus* larvae, (ii) one *E. balteatus* female was introduced into a cage containing an aphid-infested plant and three 2nd instar *H. axyridis* larvae and (c) control treatments: either one *H. axyridis* or one *E. balteatus* female was introduced into a cage containing an aphid-infested plant without any predatory larvae present.

The numbers of eggs laid by females and eaten by predatory larvae were recorded in each treatment after 2 and 24 h. Each treatment was simultaneously replicated 10 times.

Statistical analyses

SAS (1998) and Minitab 15 were used for statistical analyses. A data $\log_{10}$ (n + 1) transformation was applied as needed to stabilize the variance. ANOVA was performed to determine the effects of larval mobility of both *H. axyridis* and *E. balteatus* on predation efficiency. General linear model and Student–Newman–Keuls test were used to compare the eggs laid by females in relation to the presence of predatory larvae. IGP frequencies on either predatory larvae or eggs laid by females were compared using chi-squared test. The differences in aphid consumption rates between IGP treatments were compared using a two-sample *t*-test.

Results

Larval mobility and aphid consumption

Larvae of both species dispersed similarly over aphid-infested plants. In laboratory conditions, *E. balteatus* 2nd instar larvae consumed significantly more aphids, after 24 h, than *H. axyridis* 2nd instar larvae ($F_{1,98} = 22.98$ and $P < 0.001$; fig. 1). Over the longer term, *H. axyridis* larvae consumed significantly more aphids than *E. balteatus* ($F_{1,98} = 72.71$ and $P < 001$). Ladybird larvae had consumed all available aphids by the time they formed a puparium, whereas an average of 9.2 ± 1.08 aphids (per plant) were left when *E. balteatus* larvae pupated (fig. 1).

Under field conditions, *E. balteatus* 2nd instar larvae consumed significantly more aphids than *H. axyridis* 2nd instar larvae after one day ($F_{1,98} = 22.01$ and $P < 0.001$, fig. 1). Whereas live aphids remained after larvae of both species pupated, significantly more living aphids ($F_{1,98} = 7.10$ and $P = 0.009$) remained on plants with *E. balteatus* (6.4 ± 1.45) than *H. axyridis* (2.2 ± 0.61).

Intraguild interactions

Intraguild interactions between larvae

In conspecific larval pairs, no cannibalism between larvae was observed for either *H. axyridis* or *E. balteatus*. Aphid consumption was, therefore, a simple function of larval age; older larvae consumed significantly more aphids than younger ones (table 1).

Table 1 Mean number (±SE) of aphids eaten by different conspecific larva pairings of either *Harmonia axyridis* or *Episyrphus balteatus*

	Larva pairings	Mean number of eaten aphids (±SE)	d.f.	F	P-value
H. axyridis	L2 × L2	40.4 ± 1.6d	5,54	171.63	<0.001
	L3 × L2	43.1 ± 1.4d			
	L3 × L3	61.1 ± 1.9c			
	L4 × L2	71.0 ± 2.4b			
	L4 × L3	95.2 ± 2.1a			
	L4 × L4	99.7 ± 0.2a			
E. balteatus	L2 × L2	70.6 ± 2.8b	2,27	57.01	<0.001
	L3 × L2	91.0 ± 1.5a			
	L3 × L3	99.6 ± 0.3a			

L2, L3 and L4 are the larval stages used for *H. axyridis*; L2 and L3 are the larval stages used for *E. balteatus*. For each predator, different letters after the means indicate a significant difference between the means (SNK test, P < 0.05).

In heterospecific larval pairs, the exotic *H. axyridis* had an IGP advantage over the native species *E. balteatus* only when either 4th or 3rd instar ladybird larvae were paired with 2nd instar hoverfly larvae (fig. 2), where IGP occurred respectively in 90% and 70% of replicates. No significant difference in the total number of eaten 2nd instar *E. balteatus* larvae was found between 4th and 3rd instar *H. axyridis* larvae ($\chi^2 = 1.250$; d.f. = 1; $P = 0.264$, fig. 2).

Aphid consumption was not influenced by IGP when *H. axyridis* 4th instar larvae were IG predators of *E. balteatus* 2nd instar larvae as all available aphids were consumed whether IGP occurred or not. In contrast, aphid consumption was negatively influenced by IGP in cages where *H. axyridis* 3rd instar larvae were IG predators of *E. balteatus* 2nd instar larvae ($t = 8.50$; d.f. = 6; $P < 0.001$, fig. 3).

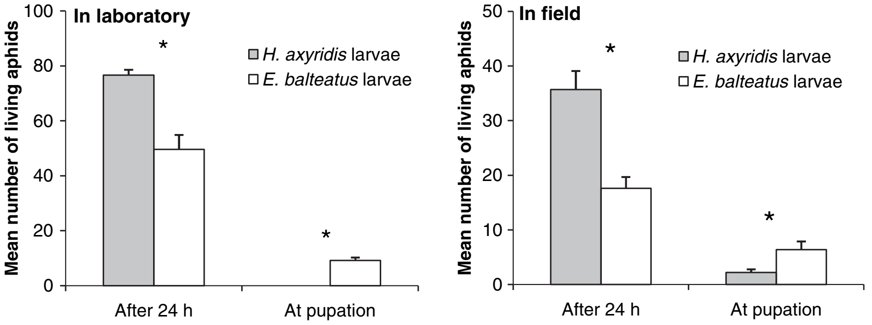

Fig. 1 Mean number (±SE) of aphids eaten after 24 h and by the time of predator pupation by *Harmonia axyridis* and *Episyrphus balteatus* larvae under laboratory and field conditions.

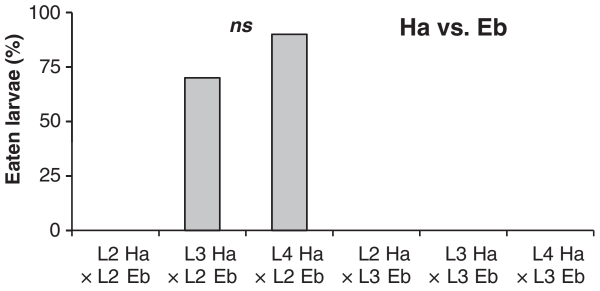

Fig. 2 Percentage of *Episyrphus balteatus* 2nd instar larvae eaten by *Harmonia axyridis* larvae when paired together on aphid-infested plants during 3 days of experiment (χ^2 test, $P < 0.05$). L, larvae; Eb, *E. balteatus*; Ha, for *H. axyridis*.

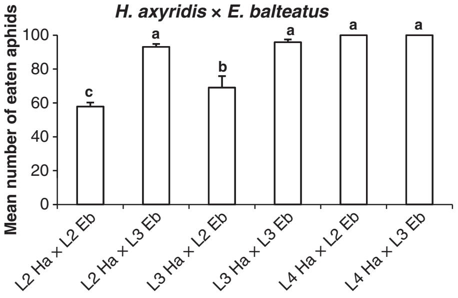

Fig. 3 Mean number (±SE) of aphids eaten by different hetreospecific larva pairings of *Harmonia axyridis* and *Episyrphus balteatus*. L, larvae; Eb, *E. balteatus*; Ha, *H. axyridis*. Different letters above the bars indicate significant differences (*t*-test, $P < 0.05$).

Impact of larval presence on oviposition

The presence of either con- or heterospecific larvae on aphid-infested plants had two negative effects on oviposition by *H. axyridis* and *E. balteatus* females: (i) it reduced the number of eggs laid by these females compared to control treatment and (ii) the eggs laid by *E. balteatus* females fell victim to IGP and cannibalism.

The presence of conspecific larvae was repellent to ovipositing *H. axyridis* females during both the first 2 h ($F_{1,18} = 46.35$ and $P < 0.001$) and the following 22 h ($F_{1,18} = 11.87$ and $P = 0.003$, fig. 4). In comparison, the presence of *E. balteatus* larvae on aphid-infested plants did not reduce *H. axyridis* oviposition significantly during the first 2 h, but did over the following 22 h ($F_{1,18} = 38.99$ and $P < 0.001$, fig. 4).

Oviposition by *E. balteatus* females was not influenced by the presence of either con- or hetreospecific larvae during the first 2 h of experiment (respectively, $F_{1,18} = 0.02$ and $P = 0.902$; $F_{1,18} = 0.18$ and $P = 0.675$, fig. 4). However, from 2 to 24 h these females laid significantly lower numbers of eggs compared to controls when either con- or heterospecific larvae were present on aphid-infested plants (respectively, $F_{1,18} = 58.47$ and $P < 0.001$; $F_{1,18} = 69.99$ and $P < 0.001$, fig. 4).

Overall, the presence of either *H. axyridis* or *E. balteatus* larvae significantly reduced the numbers of eggs laid by *H. axyridis* females ($F_{1,18} = 59.76$ and $P < 0.001$; $F_{1,18} = 20.78$ and $P < 0.001$ respectively) compared to control treatment. Similarly, *E. balteatus* females oviposited lower numbers of eggs following the presence of either *E. balteatus* ($F_{1,18} = 24.17$ and $P < 0.001$) or *H. axyridis* larvae ($F_{1,18} = 22.99$ and $P < 0.001$).

Intraguild predation and cannibalism on hoverfly eggs were both detected in this experiment (fig. 5). Overall, ladybird larvae preyed significantly on *E. balteatus* eggs during the 24-h period, compared to hoverfly larvae (respectively, 79.13% and 42.67% of total eggs laid by hoverfly females; $\chi^2 = 123.313$; d.f. = 1; $P < 0.001$).

Discussion

The biological performance of *H. axyridis* and *E. balteatus* larvae in suppressing aphid population was

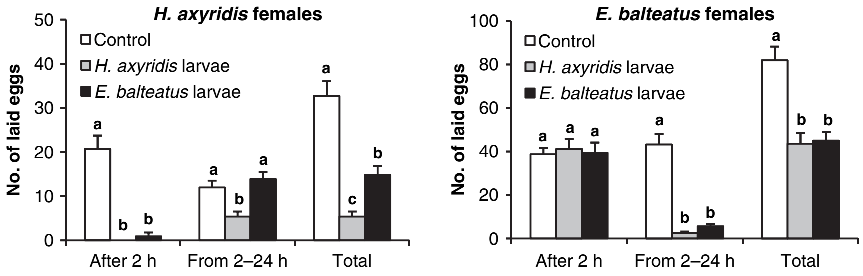

Fig. 4 Mean number (±SE) of eggs laid by *Harmonia axyridis* and *Episyrphus balteatus* females in relation with the presence of either con- or heterospecific larvae on aphid-infested plants. Control treatment was aphid-infested plant without predatory larva presence. Different letters above the bars indicate significant differences (SNK test, $P < 0.05$).

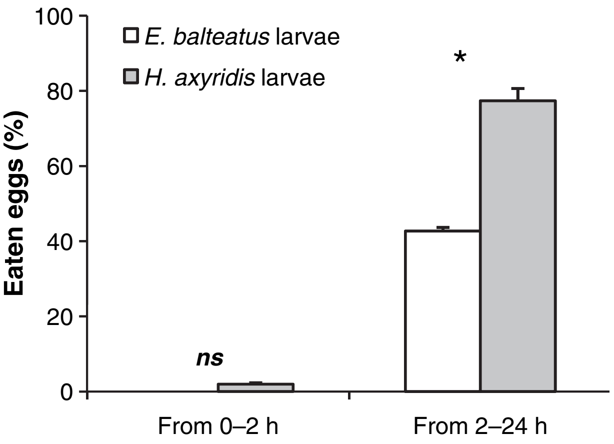

Fig. 5 Mean number (% ±SE) of *Episyrphus balteatus* eggs eaten by either *Harmonia axyridis* or *E. balteatus* larvae found in oviposition sites on aphid-infested plants. *Significant differences between treatments in the mean number of preyed eggs using chi-squared test ($P < 0.05$).

investigated in relation with larval mobility. In a short term, the hoverfly larvae showed efficiently aphid suppression, while these larvae could not consume all available aphids when they formed puparium. In a long term, the ladybird larvae were, compared to the hoverfly larvae, more efficient in suppressing aphid population in both laboratory and field conditions. The mobility of *H. axyridis* larvae played an important role in efficiently searching and controlling aphids that feed on experimental plants or those removed towards experimental cage corners, this result confirmed the finding of Osawa (2000) and With et al. (2002) focusing on the ability of *H. axyridis* larvae to control efficiently aphids in space and time. The harlequin ladybird *H. axyridis* is one of the most important generalist predators in exerting strong top–down population regulation of aphids (Hodek and Honěk 1996; Koch 2003; Costamagna and Landis 2006). Aphid mobility may also be important factors influencing aphid predation by its predators. Several studies have demonstrated that prey mobility increases searching and handling time and influences, as a consequence, prey consumption rate in predatory populations (e.g. Allan et al. 1987; Nordlund and Morrison 1990). Avoidance behaviour vs. predatory larvae was recorded in aphid populations, where some aphid individuals left the host plant and removed towards experimental cage walls and corners avoiding the predation. The ladybird larvae were recorded attacking aphids on host plants and those removed towards cage walls and corners, whereas *E. balteatus* larvae could not.

As an effective generalist predator of aphids and other pests *H. axyridis* has been a successful biological control agent. However, the very functional traits that have contributed to its success in this regard also implicate it as an intraguild predator that poses a significant risk to native beneficial species and their associated ecosystem services (Roy et al. 2006). Serious problems involving declines in beneficial populations, particularly in native coccinellids have been observed (Snyder et al. 2004; Majerus et al. 2006; Roy et al. 2006; Snyder and Evans 2006; Pell et al. 2008) but no data has been reported on the impact of *H. axyridis* on aphidophagous hoverfly larvae. This study examined the nature of IGP between immatures of *H. axyridis* and *E. balteatus* and its impact on aphid suppression. The common hoverfly species *E. balteatus* was considered to be a direct competitor of *H. axyridis* potentially co-occurring on aphid-infested plants in temperate regions (Alhmedi et al. 2006, 2007); thus intraguild interactions between them are expected. In these experiments, IGP occurred frequently between either 3rd or 4th instars of *H. axyridis* and 2nd instars of *E. balteatus* with asymmetric results; *E. balteatus* was always the IGP prey and never the predator. *Harmonia axyridis* is well documented as an intraguild predator (Evans 1991; Cottrell and Yeargan 1999; Kajita et al. 2000; Snyder and Ives 2003), and several authors have suggested that IGP might be facilitating invasion by this ladybird (Evans 1991; Cottrell and Yeargan 1999; Yasuda and Ohnuma 1999; Michaud 2002). A covering of thick dorsal spines present in all instars *H. axyridis* has already been posited to explain some of the IGP advantages of this species (Michaud and Grant 2003; Ware and Majerus 2008).

The outcome of IGP between larvae is known to be influenced by the relative size of protagonists (Polis et al. 1989; Lucas et al. 1998; Felix and Soares 2004); the larger species generally acting as predator and the smaller as prey. It is also reported that the size, larval stage, mobility and intraguild prey are important factors in determining the strength of IGP (Polis et al. 1989; Lucas et al. 1998; Rosenheim et al. 2004; Straub et al. 2008). The susceptibility of different instars of *E. balteatus* to IGP is likely affected by the nature of their physical defences such as mouth parts and their mobility (Hindayana et al. 2001), in addition to their size relative to the IG predator. *Episyrphus balteatus* 3rd instar larvae seemed to defend themselves well against *H. axyridis* 3rd or 4th instar larvae. Moreover, *H. axyridis* were unable to prey on *E. balteatus* 3rd instar larvae even after all aphids on the plant had been consumed. These latter were already detected showing a symmetrical predation with the ladybird *C. septempunctata* (Hindayana et al. 2001).

In conspecific larval pairings of *H. axyridis*, no cannibalism was recorded on aphid-infested plants, though larval cannibalism is considered to be a common phenomenon in *H. axyridis* in both laboratory and field findings (e.g. Osawa 1993; Koch 2003; Michaud 2003; Santi et al. 2003; Burgio 2005). Similarly, no *E. balteatus* larval cannibalism was detected in conspecific larval pairings, confirming previous findings by Hindayana (2001). The aphid densities provided in these experiments were probably not sufficiently low to induce larval cannibalism in either species as demonstrated in this study, particularly when low density of conspecific predatory larvae was available.

In the second larval interaction experiment, prey suppression was high despite IGP. In general, IGP between the IG predator and the IG prey generates variable impacts on shared prey population suppression. These impacts may be disruptive (Snyder and Wise 1999; Prasad and Snyder 2004) or synergistic (Losey and Denno 1998; Lucas 2005), but they may be additive (Weisser 2003; Janssen et al. 2006). Under conditions of this study, aphid suppression was not influenced by the IGP between *H. axyridis* and *E. balteatus* larvae when the ladybird larva was in the 4th instar. However, IGP between *H. axyridis* 3rd instar larvae and *E. balteatus* 2nd instar larvae negatively influenced the suppression of aphid colonies. The high ability of *H. axyridis* to suppress prey population particularly 4th larval stages seemed to be among the important reasons reducing the impact of IGP on aphid suppression (Hodek and Honěk 1996; Koch 2003; Gardiner and Landis 2007).

Gravid female predators responded negatively to the presence of either con- or heterospecific larvae and laid fewer eggs compared to control treatments where the predatory larvae were absent. Putra et al. (2009) found in oviposition preference experiments that *E. balteatus* females tend to adjust their rate of eggs laying in response to the presence of ladybird larvae; they laid fewer eggs in aphid colonies with a ladybird larva (specially 4th instar larvae) than without the larva. In previous study, Hemptinne et al. (1992) found that in the presence of conspecific larvae *A. bipunctata* females would leave an aphid colony without ovipositing. Yasuda et al. (2000) reported that gravid females of *H. axyridis* were deterred from ovipositing on plants hosting conspecific larval tracks, but not with heterospecific (larvae of *C. septempunctata*) tracks. Interestingly, these predatory larvae colonising oviposition sites not only influenced the number of eggs laid by the ovipositing females but they also engaged in IGP and cannibalism against *E. balteatus* eggs; significant numbers of hoverfly eggs were eaten by predatory larvae. This scenario may be explained by the defensive chemistry of *H. axyridis* eggs which has been previously implicated as central to the observed resistance of *H. axyridis* eggs to cannibalism (Magro et al. 2007) or predation by other aphidophagous insects (Alam et al. 2002; Sato and Dixon 2004). Ladybird eggs are most likely protected from predation by defensive alkaloids, pyrazines and quinolenes. The alkaloids are synthesized by ladybirds and are reported to be found in all developmental stages (Ayer and Browne 1977; Hemptinne et al. 2000a,b; Agarwala and Yasuda 2001; Ware et al. 2008). This would help to explain why *H. axyridis* eggs are escaped from predation by hoverfly larvae on aphid-infested plants compared with *E. balteatus* eggs (Cottrell and Yeargan 1998a,b). Cannibalism and predation against ladybird eggs are most often associated with larval stages (Dixon 2000; Cottrell 2007) and, for some species, may be affected inversely by the relative abundance of extraguild prey (Sato et al. 2003). Therefore, 2nd instar larvae seemed to be unable to engage in cannibalism for *H. axyridis* eggs while prey is available on host plants; whereas, 4th instar larvae, for example, of *H. axyridis* have been already engaged in cannibalism against conspecific eggs (Yasuda and Ohnuma 1999; Yasuda et al. 2001; Lanzoni et al. 2004). This study shows that under controlled laboratory conditions, hoverfly eggs suffered from both cannibalism and IGP whereas, IGP was the larger threat to *E. balteatus* eggs. *Episyrphus balteatus* larvae are known to cannibalize conspecific eggs regardless of the presence of aphids (Chandler 1969; Branquart et al. 1997).

In summary, the results of this study reveal differing strengths of interactions between the native European hoverfly *E. balteatus* and the exotic ladybird *H. axyridis*. Thus, although a number of factors may be important in the biological efficiency of *E. balteatus* to control aphids and spread well in its native range, one such factor may be IGP by *H. axyridis*. Conversely, asymmetric IGP may promote the establishment of *H. axyridis* in Belgium. This laboratory study provides some useful insights and important first steps in evaluating the potential importance of IGP. As Lucas et al. (2002) point out, however, *in situ* studies in natural systems are now needed to more fully assess the importance of interspecific interactions such as IGP in determining the success or failure of either introductions of species such as *H. axyridis* or native species such as *E. balteatus* that we have studied here in aphid biocontrol programs.

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