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Effect of size, extraguild prey and habitat complexity on intraguild interactions: a case study with the invasive ladybird *Harmonia axyridis* and the hoverfly *Episyrphus balteatus*

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Abstract Intraguild predation (IGP) is a widespread interaction between predatory arthropods, and is influenced by several factors. The harlequin ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae), has frequently been reported as an intraguild predator of other Coccinellidae, but little is known about its interactions with other aphidophagous predators, including syrphids. This study investigated the incidence of IGP between *H. axyridis* and *Episyrphus balteatus* (Diptera: Syrphidae), the most abundant hoverfly species in Europe and a commercially available aphid biocontrol agent. The influence of size, presence of extraguild prey and habitat complexity were investigated through laboratory experiments in Petri dishes and on potted broad bean plants. In both types of arenas, IGP between *H. axyridis* and *E. balteatus* was found to be asymmetric, with the coccinellid in the majority of cases being the intraguild predator. There was a significant effect of size on the frequency of IGP. The efficiency of *H. axyridis* as an intraguild predator increased with the developmental stage. Early instars of *E. balteatus* were the most vulnerable to IGP. Pupae of either species were not attacked. In the presence of extraguild prey, the frequency of IGP was substantially reduced. However, IGP still occurred, mainly in combinations of older larvae of *H. axyridis* with first or second instars of *E. balteatus*. The size of the arena affected the incidence of IGP in combinations with second instars of *E. balteatus*, but not in combinations with third instars. Field research is needed to elucidate the ecological relevance of IGP among these predators.

Keywords Coccinellidae · *Harmonia axyridis* · Syrphidae · *Episyrphus balteatus* · Intraguild predation · IGP

Introduction

Intraguild predation (IGP) occurs when one predator consumes another predator of the same guild (i.e. a predator competing for the same prey) (Polis et al. 1989). The aggressor is called the intraguild predator, the victim the intraguild prey, and their common resource the extraguild prey. IGP can be asymmetric when one species always preys on the other, or symmetric when there is mutual predation between the two species (Polis et al. 1989; Lucas 2005; Pell et al. 2008). It is a very common and widespread interaction, that occurs frequently in a variety of ecosystems (Arim and Marquet 2004). IGP interactions affect the intraguild predator, intraguild prey

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and the extraguild prey, at the individual, the population and the community level. In the case of the intraguild predator, IGP does not only provide an additional food source, but also reduces inter- and intraspecific competition (Polis et al. 1989; Lucas 2005).

Both theoretical and empirical studies have addressed several factors that could influence IGP interactions between predators. According to Polis et al. (1989), relative body size is one of the most important factors influencing the frequency and direction of IGP. In general, the largest of the two competing predators will act as an intraguild predator on the other. This is confirmed by several studies with aphidophagous arthropod predators (Sengonca and Frings 1985; Lucas et al. 1998; Phoofolo and Obrycki 1998; Hindayana et al. 2001; Félix and Soares 2004). In some cases, however, larger individuals are eaten by smaller predators (Polis et al. 1989).

A second factor influencing IGP interactions is the abundance of extraguild prey (i.e. the shared resource of the interacting predators). A decreasing abundance of extraguild prey can cause the frequency of IGP to both increase or decrease. An increase in IGP could be passive (i.e. IGP increases just because the ratio of intraguild:extraguild prey is higher), or might be caused by active behavioral shifts. In the latter case, hungry predators might expand their diet to include guild members. Alternatively, they might move around more in search of food, increasing the number of contacts between intraguild predators and prey (Polis et al. 1989; Lucas et al. 1998). In studies with aphidophagous arthropod predators, there was in general an increase in IGP when the abundance of extraguild prey decreased (Sengonca and Frings 1985; Obrycki et al. 1998; Kajita et al. 2000; Hindayana et al. 2001).

The frequency of IGP and its impact on a community is also influenced by the habitat structure and complexity. In their meta-analysis on the influence of habitat complexity on IGP, Janssen et al. (2007) found that an increase in habitat complexity often leads to a decrease in IGP. One effect of habitat complexity might be that it decreases encounter rates between the intraguild predator and prey. Furthermore, a more structured habitat could provide refuges for the intraguild prey.

The harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is a predator of different aphid species and other soft-bodied arthropods (Hodek and Honek 1996; Koch 2003). It is native to China, Japan, Korea, Mongolia and Siberia, and can occupy many different habitats (Brown et al. 2008). As its larvae are voracious predators of different pests, *H. axyridis* has been used as a biological control agent in North America and Europe (Koch 2003; Adriaens et al. 2008). Introductions for biological control purposes (Gordon 1985; Coutanceau 2006), unintentional introductions via international trade (Day et al. 1994) or a combination of both (Lombaert et al. 2010), have led to the establishment of this coccinellid outside of its native range. *H. axyridis* is now spread in North and South America (Koch 2003; Koch et al. 2006), Europe and some parts of Africa (Brown et al. 2008; Lombaert et al. 2010). Besides its benefits as a biological control agent (Koch 2003; Pervez and Omkar 2006), the establishment of *H. axyridis* in North America and Europe has been noted to cause adverse impacts. Some studies state that it may be associated with the decline of native aphid predators in North America, in particular native coccinellids (Colunga-Garcia and Gage 1998; Michaud 2002; Alyokhin and Sewell 2004; Majerus et al. 2006). A possible indirect mechanism that could explain these declines, is interspecific competition for the same limited resources, since *H. axyridis* is a more voracious predator than other coccinellids (Michaud 2002). A more direct mechanism that is likely to contribute to the displacement of native natural enemies is IGP.

Intraguild interactions between *H. axyridis* and different native ladybirds have been widely examined (Yasuda et al. 2001; Burgio et al. 2002; Félix and Soares 2004; Hoogendoorn and Heimpel 2004; Sato and Dixon 2004; Cottrell 2005; Kajita et al. 2006; Ware and Majerus 2008). In most of these studies, *H. axyridis* was the dominant IG predator, because of its relatively large size, higher attack rates and greater escape ability (Yasuda et al. 2001; Ware and Majerus 2008). Studies on interactions between *H. axyridis* and non-coccinellid predators are less frequent. Phoofolo and Obrycki (1998) and Gardiner and Landis (2007) found that *H. axyridis* engaged in IGP with *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) and *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). De Clercq et al. (2003) found that interactions between *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) and *H. axyridis* were asymmetric in favour of the pentatomid.

Episyrphus balteatus DeGeer (Diptera: Syrphidae) is the most common hoverfly in Europe, where it can occupy many different habitats (Verlinden and Decleer 1987; Tenhumberg and Poehling 1995; Stubbs and Falk 2002). Its larvae are voracious predators of many species of aphids (Sadeghi and Gilbert 2000). *E. balteatus* is an important biological control agent in different agro-ecosystems, especially in cereals (Tenhumberg 1995; Tenhumberg and Poehling 1995). This hoverfly has been observed to co-occur with the exotic coccinellid *H. axyridis* in different crops and in semi-natural habitats (Alhmedi et al. 2007, personal observations). However, little is known on the intraguild interactions between *E. balteatus* and *H. axyridis*. Putra et al. (2009) and Alhmedi et al. (2010) observed IGP by larvae of *H. axyridis* on those of *E. balteatus*, but the former study only used first and last instars of both predators, whereas the latter only performed experiments in the presence of extraguild prey.

The first objective of this study was to investigate the incidence, direction and magnitude of IGP between all developmental stages of *H. axyridis* and *E. balteatus* in the laboratory. Furthermore, the effect of relative size of the predators, presence of extraguild prey, and habitat complexity on the frequency of IGP was studied. Insight into the influence of these parameters on IGP interactions between the *H. axyridis* and *E. balteatus* should provide an important first step towards understanding the ecological relevance of IGP between both predators.

Materials and methods

Insects

In April 2008 and April 2009, individuals from an established wild population of *H. axyridis* were collected in a park in Ghent, Belgium. From the collected ladybirds, only the non-melanic *succinea* individuals were used to establish a laboratory population, since this morphotype is the most common in Europe (Brown et al. 2008). Individuals from up to the 10th generation of rearing were used for the experiments. *H. axyridis* was reared on frozen *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs, as described by De Clercq et al. (2003) and Berkvens et al. (2008). The eggs of *E. kuehniella* were obtained from Koppert BV (Berkel en Rodenrijs, The Netherlands).

A culture of *E. balteatus* was established with individuals collected in July 2008 and July 2009 in cabbage fields in Sint-Katelijne-Waver, Beitem and Kruishoutem, Belgium. Adults were kept in Plexiglas cages (60 × 60 × 60 cm) and provided with pollen and honey water. Broad bean plants (*Vicia faba* L.) infested with the pea aphid *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), were placed in the cages to allow syrphid oviposition. Emerged larvae were individually transferred to small Petri dishes (5 cm in diameter, 1.5 cm high) and fed with *A. pisum*. Pea aphids used in the experiments were obtained from Koppert BV. All colonies and experiments were maintained at 23 ± 1°C, 65 ± 5% RH and a 16:8 h (L:D) photoperiod.

Effect of size and presence of extraguild prey on IGP

The incidence, direction and magnitude of IGP were investigated between single individuals of either species. To understand the effect of the developmental stage on IGP, intraguild interactions were investigated between the four larval instars, pupae and adult females of non-melanic *H. axyridis* and the three larval instars and pupae of *E. balteatus*. As there are no interactions between pupae, this resulted in 23 different combinations. In order to examine the influence of extraguild prey on intraguild interactions, each combination of both predators was tested in the absence as well as in the presence of *A. pisum*. That way, 46 different combinations were tested. Each combination was replicated 20–30 times.

Because aphid consumption increases for each successive instar of *H. axyridis* and *E. balteatus* (Koch 2003, personal observations), the aphid density in treatments with *A. pisum* was dependent on the developmental stage of both predators. For every first or second instar present, 15 aphids were supplied. For every third or fourth instar or adult, 30 aphids were provided. A combination of a first and third instar, for example, thus resulted in a density of 45 aphids. Consumed aphids were not replenished during the experiment. In all cases, a mixture of late larval instars and adults of *A. pisum* were supplied.

First instars of both predators used in the experiments were less than 24 h old, whereas the older instars were used up to 12 h after molting. The gender of the *H. axyridis* adults was determined using the method described by McCornack et al. (2007). The adult females used were 1–2 weeks old and had been allowed to mate. The pupae used were 1–3 days old. Before testing, the predators were transferred to individual Petri dishes only containing a moistened piece of household paper. In this manner, second instars were starved for 16 h, whereas third and fourth instars and adults were starved for 24 h.

The experimental arena consisted of a vented plastic Petri dish (5 cm in diameter, 1.5 cm high) in which a leaf disk of a broad bean plant was placed on agar (1%). During the first 90 min, the predators in the Petri dishes were observed in order to record all contacts between them. A confrontation was regarded as a contact when the opponents randomly met and separated again without any further actions. A contact became an attack when one predator tried to feed on the other. An attack was considered successful when it resulted in the death of the prey. After 24 h, the survival of both insects was recorded.

A control treatment was carried out in order to check the survival of the different stages during a 24 h period without food. For this purpose, 15 individuals of each stage were starved as described above and were transferred to an individual Petri dish containing a *V. faba* leaf disk on agar. After 24 h, survival was recorded. In the case of interactions with pupae, adult emergence from pupae that had been exposed to a predator was compared with that in the control treatment, in order to determine the incidence of IGP.

Effect of size, extraguild prey and habitat complexity on IGP

In order to investigate the influence of habitat complexity on IGP between *H. axyridis* and *E. balteatus*, intraguild interactions were also studied on potted *V. faba* plants. The experimental arena consisted of a Plexiglas cylinder (9 cm in diameter, 20 cm high), covered with mesh screen cloth. The cylinder was placed over a potted broad bean plant of approximately 15 cm high, with two to four fully developed leaves. It was pushed about 1 cm into the potting soil, and fixed onto the plant pots using Parafilm M (Picheney Plastic Packaging, Chicago, USA).

The incidence, direction and magnitude of IGP was investigated between second and third instars of *E. balteatus*, and second to fourth instars and adult females of the non-melanic population of *H. axyridis*. As there were little or no interactions in Petri dishes with first instars of the coccinellid, the combinations with this instar were not tested. The combinations involving pupae of either predator were also not considered, because attacks on pupae by larvae or adults of the other species were never observed in the Petri dish experiments. IGP in combinations with first instars of the syrphid were not tested, since preliminary tests showed that because of their small body size, dead or surviving first instars could not reliably be retrieved in the arenas after 24 h.

The effect of extraguild prey on IGP was again investigated by testing each combination both in the absence and presence of *A. pisum*. In the treatments with aphids, the broad bean plants were infested with 40 adult aphids, 24 h before the start of the tests. This resulted in an average of 150 ± 11 aphids (mean ± SE, a mixture of adults and young nymphs) present on the plants at the start of the experiments.

Prior to the experiments, the larvae and adults of both predators were treated in the same way as in the Petri dish experiment described above. Each experiment was replicated 15 times. At the start of the experiment, the larvae of *E. balteatus* were placed on one of the oldest leaves of the plant, whereas the larvae and adults of *H. axyridis* were placed at the base of the stem. After 1, 4 and 24 h, the position of both predators on the plant was noted. The survival of the predators was recorded after 24 h.

Statistical analysis

Data analyses was carried out using SPSS 15.0 (SPSS Inc. 2006). A generalized linear model was used with a Poisson error distribution and a log link function (McCullagh and Nelder 1989). Because the data showed quasi-complete separation, a bionomial error distribution could not be used (Altman et al. 2004). Analyses started each time with a saturated model and interactions and non-significant main factors were dropped at a significance level of 0.05. The most parsimonious model is reported, using likelihood ratios to assure model fit.

Results

Effect of size and presence of extraguild prey on IGP

Observations during the first 90 min of the Petri dish experiments indicated that all larval instars of *E. balteatus* used defence ploys upon attack by *H. axyridis*. These consisted of oral slime secretions and fierce body movement. Table 1 shows the average number of contacts between the different combinations of both predators, and the number and success rate of attacks by *H. axyridis*. For first and second instars of *E. balteatus* the defence mechanisms were only effective in a limited number of cases against first or second instars of the ladybird, which were smaller or of similar size. Third instars of *E. balteatus* were more difficult to capture. The slime secreted by these hoverfly larvae immobilized the larvae of *H. axyridis* temporarily, causing them to retreat for cleaning. Third instars of *E. balteatus* also tried to escape from their attacker by fiercely thrashing their body.

Attacks of *E. balteatus* against larvae of *H. axyridis* were rarely observed. Adults of the ladybird were never attacked. Except for a few first instars of *H. axyridis*, all larvae of the coccinellid were able to withstand a syrphid attack, by fiercely moving their body back and forth, or by launching a counterattack. The mean number of contacts increased with the age of both predators. Adding aphids to the Petri dishes resulted in all combinations in a strong decline of the number of contacts and attacks. With aphids present, both predators spent most of their time consuming aphids instead of moving around.

The results of the Petri dish experiments are shown in Fig. 1. In the absence of extraguild prey, IGP was asymmetric, with *H. axyridis* being the intraguild predator and *E. balteatus* the intraguild prey in all but one cases. Only when third instar hoverfly larvae were paired with first instars of the coccinellid, *E. balteatus* could act as an intraguild predator in 17% of the cases. In the combinations with pupae, there was no evidence of predation after the 24 h test period. Therefore, the combinations with pupae were not included in the statistical analyses.

There was a strong two-factor interaction between intraguild predator and prey stage ($\chi^2 = 30.34$; df = 8; $P < 0.001$), between intraguild predator stage and presence of extraguild prey ($\chi^2 = 30.92$;

Table 1 Number of contacts, percentage of contacts that resulted in an attack by *H. axyridis* on *E. balteatus*, and percentage of successful attacks for each tested combination of both predators in Petri dishes, and both in the absence and the presence of the aphid *A. pisum* (means ± SE)

E. balteatus	*H. axyridis*	Without aphids			With aphids		
		Contacts	% Attacks	% Success	Contacts	% Attacks	% Success
L1	L1	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.07 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
L1	L2	2.25 ± 0.28	64.81 ± 6.50	60.00 ± 8.28	0.12 ± 0.06	33.33 ± 27.22	100.00 ± 0.00
L1	L3	1.67 ± 0.19	52.50 ± 7.90	95.24 ± 4.65	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
L1	L4	1.83 ± 0.23	32.73 ± 6.33	100.00 ± 0.00	0.07 ± 0.05	0.00 ± 0.00	0.00 ± 0.00
L1	A	2.40 ± 0.48	21.67 ± 5.32	100.00 ± 0.00	0.55 ± 0.13	6.25 ± 6.05	100.00 ± 0.00
L2	L1	1.45 ± 0.28	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
L2	L2	3.03 ± 0.37	41.76 ± 5.17	15.79 ± 5.91	0.23 ± 0.12	0.00 ± 0.00	0.00 ± 0.00
L2	L3	2.00 ± 0.28	62.07 ± 6.37	75.00 ± 7.22	0.10 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
L2	L4	1.61 ± 0.18	73.33 ± 6.59	81.82 ± 6.71	0.27 ± 0.12	33.33 ± 19.25	100.00 ± 0.00
L2	A	4.36 ± 0.85	19.67 ± 3.60	79.17 ± 8.29	0.86 ± 0.18	37.50 ± 9.88	88.89 ± 10.48
L3	L1	1.10 ± 0.24	3.03 ± 2.98	0.00 ± 0.00	0.10 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
L3	L2	4.10 ± 0.51	29.27 ± 4.10	0.00 ± 0.00	0.25 ± 0.20	0.00 ± 0.00	0.00 ± 0.00
L3	L3	4.83 ± 0.58	32.41 ± 3.89	4.26 ± 2.94	0.37 ± 0.12	18.18 ± 11.63	0.00 ± 0.00
L3	L4	3.43 ± 0.45	58.33 ± 5.03	26.79 ± 5.91	0.25 ± 0.10	0.00 ± 0.00	0.00 ± 0.00
L3	A	8.23 ± 0.90	21.05 ± 2.59	3.84 ± 2.67	1.55 ± 0.51	3.23 ± 3.17	0.00 ± 0.00

L1–L4 Larval instars 1–4, *A* adult

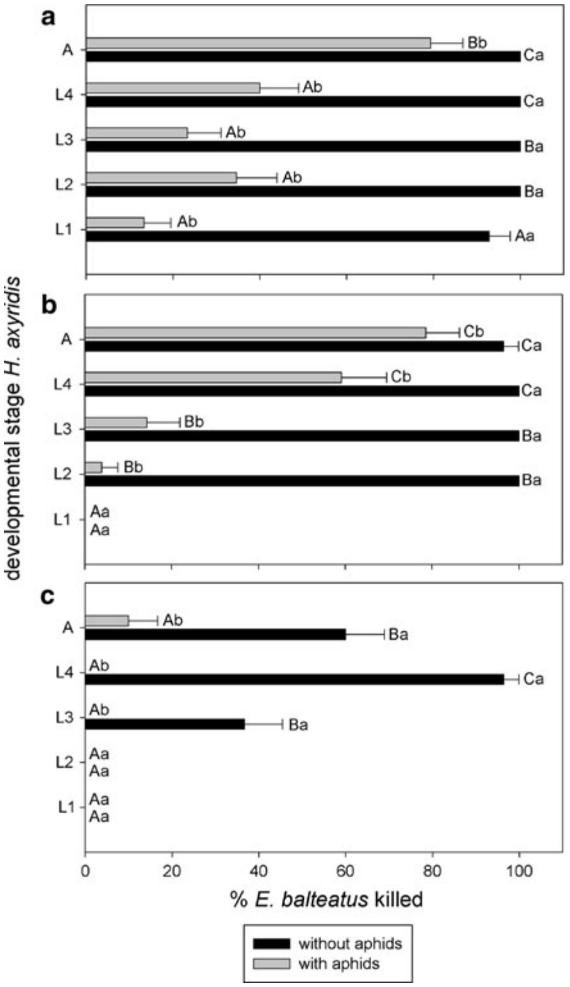

Fig. 1 Percentage of first instars (**a**), second instars (**b**) or third instars (**c**) of *E. balteatus* killed through intraguild predation by different stages of *H. axyridis* in Petri dishes, in the absence and presence of extraguild prey (aphids). *L1–L4* Larval instars 1–4, *A* adult. The effect of the IG predator stage is indicated by capital letters, the effect of the presence of extraguild prey is indicated by lowercase letters. Bars with a different letter are significantly different. Error bars represent SE

df = 4; $P < 0.001$) and between intraguild prey stage and presence of extraguild prey ($\chi^2 = 34.84$; df = 2; $P < 0.001$). In the absence of extraguild prey, a significant effect of the intraguild predator stage was found ($\chi^2 = 72.40$; df = 4; $P < 0.001$), with an increase in the frequency of IGP with the age of the *H. axyridis* larvae. In combinations with first or second instars of *E. balteatus*, first instars of the coccinellid were less successful intraguild predators than all other stages (for all contrasts $\chi^2 > 9.66$; df = 1; $P < 0.002$) (Fig. 1a and b, black bars). The frequency of IGP did not differ between combinations with second or third instars of *H. axyridis* (for all contrasts $\chi^2 < 0.13$; df = 1; $P > 0.324$). There was also no difference between combinations with fourth instars or adults of the coccinellid (for all contrasts $\chi^2 < 1.84$; df = 1; $P > 0.077$). However, IGP occurred more often in the latter combinations than in those with second or third instars of *H. axyridis* (for all contrasts $\chi^2 > 4.39$; df = 1; $P < 0{,}036$). For third instars of the hoverfly, there was no difference in the frequency of IGP events when paired with first or second instars of *H. axyridis* ($\chi^2 = 2.83$; df = 1; $P = 0.093$) (Fig. 1c, black bars). IGP in those combinations was less frequent than in those with older instars of the coccinellid (for all contrasts $\chi^2 > 4.73$; df = 1; $P < 0.03$). No differences were observed between the combinations with third instars or adults ($\chi^2 = 0.46$; df = 1; $P = 0.455$), but the frequency of IGP in those combinations was lower than in that with fourth instars of *H. axyridis* (for all contrasts $\chi^2 > 6.02$; df = 1; $P < 0.014$), showing the highest level of IGP on third instars of *E. balteatus*.

The intraguild prey stage also had a significant effect on the incidence of IGP ($\chi^2 = 74.00$; df = 2; $P < 0.001$). In the absence of extraguild prey, first instars of *E. balteatus* were more vulnerable to IGP than older hoverfly larvae (for all contrasts $\chi^2 > 4.92$; df = 1; $P < 0.026$) in combinations with all developmental stages of *H. axyridis*. Furthermore, IGP was less frequent in all combinations with third instars of *E. balteatus* than in those with second instar hoverfly larvae (for all contrasts $\chi^2 > 4.55$; df = 1; $P < 0.033$) (Fig. 1).

Adding aphids to the containers resulted in a significant decrease of IGP in all combinations where IGP occurred (for all contrasts $\chi^2 > 4.95$; df = 1; $P < 0.026$) (Fig. 1). The presence of aphids also altered the effect of the intraguild predator stage on IGP, except in the combinations with second instars of *E. balteatus*. With first instars of the hoverfly, the frequency of IGP did not differ between combinations with first to fourth instars of *H. axyridis* (for all contrasts $\chi^2 < 1.66$; df = 1; $P > 0.197$) (Fig. 1a, grey bars). However, in the combination with adults of the coccinellid, IGP was more frequent (for all contrasts $\chi^2 > 5.20$; df = 1; $P < 0.023$). With third instars of the hoverfly, no effect of the developmental stage of *H. axyridis* was found (for all contrasts

$\chi^2 < 3.77$; df = 1; $P > 0.052$) (Fig. 1c, grey bars). With aphids present, the effect of the intraguild prey stage was not significant in combinations with first, second and third instars of *H. axyridis* (for all contrasts $\chi^2 < 2.793$; df = 1: $P > 0.095$). In the combinations with fourth instars and adults of the ladybird, IGP was less frequent on third instars of *E. balteatus* than on first or second instars (for both contrasts $\chi^2 > 5.19$; df = 1; $P < 0.023$), but there was no difference between first and second instars of the hoverfly (for both contrasts $\chi^2 < 0.93$; df = 1; $P > 0.336$) (Fig. 1).

Effect of size, extraguild prey and habitat complexity on IGP

In the absence of extraguild prey, *H. axyridis* individuals were found on the Plexiglas cylinder or the soil in at least half of the observations (Table 2). Individuals of *E. balteatus*, however, were only found away from the plant in about 20% of the cases. Adding aphids to the arenas resulted in a drastic increase of individuals that were found on the plant, averaging about 80% for *H. axyridis* and 95% for *E. balteatus*.

The results of the experiments on potted broad bean plants are shown in Fig. 2. In this larger arena, IGP remained asymmetric, with *H. axyridis* being the intraguild predator and *E. balteatus* the intraguild prey. All two-factor interactions were significant (for all contrasts $\chi^2 > 4.02$; df = 1; $P < 0.04$), except for the interaction between intraguild predator stage and extraguild prey ($\chi^2 = 4.82$; df = 3; $P = 0.186$), and between intraguild predator stage and habitat complexity ($\chi^2 = 6.57$; df = 3; $P = 0.087$).

On potted plants, the effect of the intraguild predator stage was significant ($\chi^2 = 25.73$; df = 3; $P < 0.001$), and independent of the presence of aphids. In the combinations with second instars of *E. balteatus*, no differences in the frequency of IGP could be detected between second, third and fourth instars of *H. axyridis* (for all contrasts $\chi^2 < 1.56$; df = 1; $P > 0.212$) (Fig. 2a). However, the level of IGP in combinations of these hoverfly larvae with adult coccinellids was different from the combinations with the larval stages of *H. axyridis* (for all contrasts $\chi^2 > 8.57$; df = 1; $P < 0.003$). When the coccinellid was paired with third instars of the hoverfly, IGP occurred less frequently with second instars of the ladybird than in combinations with other stages (for all contrasts $\chi^2 > 7.30$; df = 1; $P < 0.007$) (Fig. 2b). There were no differences in IGP between third and fourth instars and adults of the coccinellid (for all contrasts $\chi^2 < 1.04$; df = 1; $P > 0.308$).

The intraguild prey also had a significant effect on the incidence of IGP ($\chi^2 = 46.08$; df = 1; $P < 0.001$). In the absence of aphids, IGP was more frequent in combinations with second instars compared to third instars of *E. balteatus*, and this for all

Table 2 Percentage of the total number of observations (means ± SE) in which individuals of *H. axyridis* or *E. balteatus* were found on or off the broad bean plant, for each tested combination of both predators, and both in the absence and presence of the aphid *A. pisum*

E. balteatus	*H. axyridis*	Location *H. axyridis*				Location *E. balteatus*			
		Without aphids		With aphids		Without aphids		With aphids	
		On plant	Off plant	On plant	Off plant	On plant	Off plant	On plant	Off plant
L2	L2	47.7 ± 7.5	52.3 ± 7.5	77.8 ± 6.2	22.2 ± 6.2	80.0 ± 7.0	20.0 ± 7.0	100.0 ± 0.0	0.0 ± 0.0
L2	L3	44.4 ± 7.4	55.6 ± 7.4	91.1 ± 4.2	8.9 ± 4.2	55.0 ± 11.1	45.0 ± 11.1	100.0 ± 0.0	0.0 ± 0.0
L2	L4	26.7 ± 6.6	77.3 ± 6.6	64.4 ± 7.1	35.6 ± 7.1	100.0 ± 0.0	0.0 ± 0.0	100.0 ± 0.0	0.0 ± 0.0
L2	A	44.4 ± 7.4	55.6 ± 7.4	77.8 ± 6.2	22.2 ± 6.2	76.9 ± 11.7	23.1 ± 11.7	91.6 ± 4.6	8.1 ± 4.6
L3	L2	38.6 ± 7.3	61.4 ± 7.3	91.1 ± 4.2	8.9 ± 4.2	86.7 ± 5.1	13.3 ± 5.1	95.6 ± 3.1	4.4 ± 3.1
L3	L3	40.0 ± 7.3	60.0 ± 7.3	84.3 ± 5.1	15.7 ± 5.1	81.4 ± 5.9	18.6 ± 5.9	100.0 ± 0.0	0.0 ± 0.0
L3	L4	40.0 ± 7.3	60.0 ± 7.3	70.6 ± 6.4	29.4 ± 6.4	82.9 ± 5.9	17.1 ± 5.9	98.0 ± 2.0	2.0 ± 2.0
L3	A	31.1 ± 6.9	68.9 ± 6.9	84.4 ± 5.4	15.6 ± 5.4	58.5 ± 7.7	41.5 ± 7.7	88.4 ± 4.9	11.6 ± 4.9

L2–L4 Larval instars 2–4, *A* adult

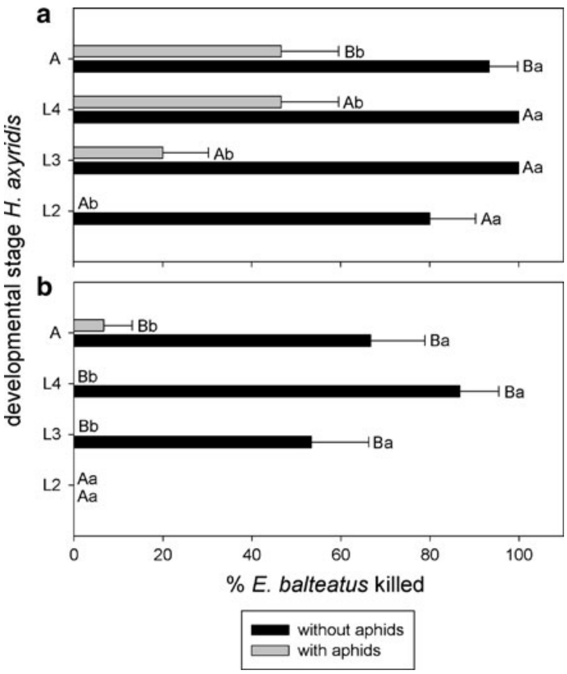

Fig. 2 Percentage of second instars (**a**) or third instars (**b**) of *E. balteatus* killed through intraguild predation by different stages of *H. axyridis* on potted broad bean plants, in the absence and presence of extraguild prey (aphids). *L2–L4* Larval instars 2–4, *A* adult. The effect of the IG predator stage is indicated by capital letters, the effect of the presence of extraguild prey is indicated by lowercase letters. Bars with a different letter are significantly different. Error bars represent SE

stages of *H. axyridis* (for all contrasts $\chi^2 > 4.06$; df = 1; $P < 0.044$) (Fig. 2). When aphids were added, the same differences were found, except for the combinations with fourth instars of *H. axyridis* where no significant difference in IGP between second and third instars of *E. balteatus* was found ($\chi^2 = 1.85$; df = 1; $P = 0.174$).

Adding extraguild prey to the arena resulted again in a significant decrease in IGP events ($\chi^2 = 27.17$; df = 1; $P < 0.001$) (Fig. 2). The effect of habitat complexity was independent of the stage of *H. axyridis*. In combinations with third instars of *E. balteatus*, the frequency of IGP did not differ between Petri dishes and potted plants, both in the absence and the presence of extraguild prey (for both contrasts $\chi^2 < 1.93$; df = 1; $P > 0.164$). In combinations with second instars of the hoverfly, habitat complexity affected the incidence of IGP, again both in the absence or presence of extraguild prey (for both contrasts $\chi^2 > 3.89$; df = 1; $P < 0.049$).

Discussion

In the present laboratory study, IGP between *H. axyridis* and *E. balteatus* occurred frequently, and was always asymmetric. The coccinellid acted as the intraguild predator and the syrphid as the intraguild prey in all but one cases. Our study corroborates the findings of Putra et al. (2009) and Alhmedi et al. (2010), who reported that IGP between larvae of *H. axyridis* and *E. balteatus* was in the majority of cases asymmetric in favour of the coccinellid.

In our study, there was a significant effect of the developmental stage of both interacting species on the frequency of IGP. Early instars of *E. balteatus* were most vulnerable to IGP, and older larvae and adults of *H. axyridis* were the strongest intraguild predators. This effect was the clearest in Petri dishes and in the absence of aphids. Furthermore, in most of the tested combinations, the larger individuals behaved as intraguild predators on the smaller intraguild prey, which is consistent with the general rule of Polis et al. (1989). In other IGP studies with *H. axyridis*, this ladybird also acted as an intraguild predator on smaller opponents. Moreover, when larvae of the ladybird were combined with predators of similar size, *H. axyridis* remained the intraguild predator in most of the cases (Cottrell and Yeargan 1998; Kajita et al. 2000; Snyder and Ives 2003; Félix and Soares 2004; Gardiner and Landis 2007; Ware and Majerus 2008). Larvae of *E. balteatus* were found to act as intraguild predators on smaller nymphs of *Macrolophus caliginosus* (Hemiptera: Miridae) (Frechette et al. 2007), and on smaller larvae of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) (Hindayana et al. 2001).

However, not in all confrontations studied here did the larger individuals act as the intraguild predators. When the larvae of *E. balteatus* were larger than those of *H. axyridis* they were paired with, they did not act as intraguild predators. This indicates that, besides body size, other factors such as behavioral or morphological attributes can affect the outcome of intraguild interactions (Lucas et al. 1998; Hindayana et al. 2001; Ware and Majerus 2008). Larvae of *H. axyridis* frequently attacked those of *E. balteatus*, whereas attacks by hoverfly larvae were rarely observed. All larval instars of *E. balteatus* showed defence ploys, but they were not very effective against *H. axyridis*. On the other hand, larvae of the ladybird could easily withstand attacks by hoverfly larvae. Larvae of *H. axyridis* possess thick dorsal spines, which protect them against potential predators (Michaud and Grant 2003; Ware and Majerus 2008). Such dorsal spines are also present, but not as pronounced, on young larvae of *C. septempunctata* (Ware and Majerus 2008), which may in part explain why third instars of *E. balteatus* could kill smaller larvae of the latter ladybird in the study of Hindayana et al. (2001), but not those of *H. axyridis* in the current study.

Our results show that adding extraguild prey to the experimental arena resulted in a decrease of the level of IGP, independent of the size of the arena. However, IGP still occurred in most of the combinations, and the symmetry and direction of the interactions was never altered. The presence of extraguild prey has been reported to increase or decrease the intensity of IGP, or to have no effect (Lucas et al. 1998). A decrease of IGP in the presence of extraguild prey, can be explained by several mechanisms. First, this may be the result of a difference in prey preference, due to differences in quality between the intraguild and extraguild prey related to a higher nutritional value, or lower energy expenses or damage during hunting, or both.

Second, the presence of extraguild prey may affect the foraging behavior of a predator (Hindayana et al. 2001). In our study, in the presence of extraguild prey, both predators focused on the consumption aphids rather than moving around in search for food. This reduced the chance of them encountering, even in the small Petri dish arena’s, and thus leading to a lower level of IGP. Furthermore, the percentage of contacts leading to an attack was lower compared to the same combination without aphids. The intraguild predators may have been satiated by feeding on aphid prey, and more reluctant to take the risk of injury associated with attacking another predator. Together with a lack of prey preference or a preference for the extraguild prey, this would lead to fewer attacks on the intraguild prey.

Third, Yasuda et al. (2004) showed that at higher levels of food supply the growth rate of the intraguild prey increased, reducing the incidence of IGP in interactions between ladybirds. A similar effect was observed in our experiments, especially in the case of third instars of *E. balteatus*. In the control treatment, all third instars of the hoverfly survived a 48 h starving period, but showed only limited activity at the end of this period. In contrast, when those larvae were allowed to feed on aphids, they had grown and were much more active, resulting in a greater vigour and ability to withstand attacks by *H. axyridis*.

The size of the experimental arena did not have a significant effect on the frequency of IGP in combinations with third instars of *E. balteatus*. However, in combinations with second instars of the hoverfly, habitat complexity did affect IGP. In a number of previous studies the size of the arena had a clear effect on the intensity of IGP, with smaller and more simple arenas generating higher levels of IGP. For example, Chang (1996) found that, although *C. carnea* and *C. septempunctata* larvae consumed each other in Petri dishes, they did not affect one another’s impact on aphid populations on potted broad bean plants. In the experiments of Hindayana et al. (2001), IGP still occurred between *E. balteatus*, *C. carnea* and *C. septempunctata* on broad bean plants, but it was reduced approximately fivefold compared with that in Petri dishes. Conversely, in interactions between *H. axyridis* and *P. maculiventris* without extraguild prey, there was no lower incidence of IGP on potted broad bean plants than in Petri dishes (De Clercq et al. 2003).

According to Kajita et al. (2006) and Janssen et al. (2007), habitat structure can influence IGP through different mechanisms. First, predators have more opportunity in larger arenas to avoid contact with each other, reducing encounter rates. In the experiments of Hindayana et al. (2001), the volume and searching area of the arena increased by 200 and 40 times, respectively, when plants were used compared to Petri dishes. This resulted in a significant decrease of IGP between *E. balteatus* and *C. septempunctata* larvae. In our experiments, the increase in volume and searching area was only 43 and 20 times, and did not result in a significant decrease in IGP on third instars of *E. balteatus*. On the other hand, *H. axyridis* is a more voracious ladybird and a stronger intraguild predator than *C. septempunctata* (Ware and Majerus 2008), which complicates a comparison of the findings of our study with those of Hindayana et al. (2001).

A second way to avoid confrontation is by hiding in refuges. In a highly structured habitat, more refuge patches may be present (Denno and Finke 2006). The effect on IGP would be the clearest if different refuges are used by predator and prey, protecting the prey from predation (Janssen et al. 2007). Second instars of *E. balteatus* are smaller than third instars, which could enable them to hide in refuges (e.g. leaf axils) more effectively. This may explain why in our experiments there was an effect of arena size on IGP on second instars of the hoverfly, but not on third instars.

Petri dishes constitute a small and very artificial environment. This kind of arena serves only to show the potential outcome of predatory interactions between two species and to estimate the effectiveness of attack and defence mechanisms (Levin 1992). Plants are an improvement over Petri dish arenas, but they may still have important limitations. As Kajita et al. (2006) pointed out, only one species of host plant is included in such experiments, whereas results could vary among host plant species. The outcome of IGP experiments could also vary if more than one plant of the same species is provided. The intraguild prey could then avoid plants or extraguild prey patches that are occupied by intraguild predators, leading to spatial segregation between the predators (Janssen et al. 2006). Furthermore, migration away from the plant is prevented by the enclosure, which can be an important behavioral response of ladybird larvae when prey become scarce (Shellhorn and Andow 1999; Sato et al. 2003). In the present plant experiments, *H. axyridis* was observed more frequently on the Plexiglas cylinder or on the soil in the absence of extraguild prey compared to when aphids were provided. Finally, IGP experiments involving immature stages do not consider potential avoidance behaviors of adult females when selecting oviposition sites. Putra et al. (2009) and Almohamad et al. (2010) demonstrated that *E. balteatus* females laid significantly fewer eggs on leafs contaminated with larval tracks of *H. axyridis*, thus reducing the risk of predation to their progeny. An appropriate selection of oviposition sites by *E. balteatus* is crucial given the limited mobility of its larvae, preventing migration when prey become scarce. Given the above limitations, it is difficult to extrapolate the results from plant cage experiments to predict the incidence of IGP between two given predators in the field.

In conclusion, the present laboratory study indicates that *H. axyridis* can act as an intraguild predator of larvae of *E. balteatus*, with the young syrphid larvae being the most vulnerable to IGP. However, in order to determine whether the widescale establishment of the harlequin ladybird in Europe could negatively impact on native populations of the hoverfly, field studies are needed to improve our understanding of the interactions among both predators. More realistic studies are also warranted to unveil the impact of IGP interactions between the studied species on their role in regulating aphid populations. The development of effective molecular tools will be instrumental to assess the ecological relevance of intraguild predation by *H. axyridis*.

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