Laboratory studies on intraguild predation and cannibalism among coccinellid larvae (Coleoptera: Coccinellidae)

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Abstract. Intraguild predation (IGP) and cannibalism occur in the field and could affect the dominance structure of guilds of coccinellid species. The exotic biological control agent *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) is now well established in most areas of Northern and Central Italy, but it is unclear what effect this species could have on native dominant and non-dominant coccinellids with which it co-occurs. In order to predict the trophic interactions in coccinellid guilds and the likely effect of *H. axyridis*, the incidence of IGP and cannibalism among the following six species were evaluated under laboratory conditions: *H. axyridis*, three native dominant species, *Adalia bipunctata* (L.), *Oenopia conglobata* (L.) and *Coccinella septempunctata* L. and two native non-dominant species, *Platynaspis luteorubra* (Goeze) and *Scymnus apetzi* (Mulsant). Unfed and fed fourth instar larvae of the above species were paired in an experimental arena and the incidence of predation recorded over a period of 24 h. In absence of aphids, the survival probabilities (SP) of *A. bipunctata* and *O. conglobata* were lowest when paired with either *C. septempunctata* or *H. axyridis* (< 0.20 SP after 24 h). The SP of *C. septempunctata* was similar if paired with either a conspecific larva or *H. axyridis* (< 0.34 SP after 24 h) and that of *H. axyridis* was reduced similarly if paired with either a conspecific larva or *C. septempunctata* (> 0.71 SP after 24 h). The SP of *P. luteorubra* was lower when paired with *A. bipunctata* and *C. septempunctata* (< 0.07 SP after 24 h) than with other species and that of *S. apetzi* was greatly reduced when paired with all the dominant and exotic species (< 0.27 SP after 24 h). In presence of aphids no predatory events occurred in most combinations. *H. axyridis* acted as a strong predator of native dominant and non-dominant coccinellids when the aphids are scarce. We did not find any evidence, however, that the incidence of IGP among exotic and native species is higher than either IGP or cannibalism in native species. The likelihood of IGP occurring in the field is discussed.

INTRODUCTION

The exotic coccinellid *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) was intentionally introduced into Northern Italy in the 1990s for the biological control of aphids and psyllids (Bazzocchi et al., 2004; Burgio et al., 2008). At present this species is established in several areas of Northern and Central Italy and is spreading (Burgio et al., 2008; Croci et al., 2010).

Several factors account for the success of the invasion by *H. axyridis* (Majerus et al., 2006; Roy & Wajnberg, 2008). Among these, the high incidence of intraguild predation (IGP) by this species of native ladybirds is one of the most studied both in the Nearctic (Kajita et al., 2000; Michaud, 2002; Snyder et al., 2004; Yasuda et al., 2004) and Palearctic regions (Burgio et al., 2002; Hautier et al., 2008; Ware & Majerus, 2008). Laboratory and field assessments suggest that *H. axyridis* may be a top predator of several native species and the cause of a decrease in guild diversity (Nault & Kennedy, 2003; Roy et al., 2006; Snyder & Evans, 2006; Pell et al., 2008; Brown et al., 2011).

H. axyridis feeds on a wide range of different kinds of prey (e.g. aphids, psyllids, coccids) in several habitats, such as trees and herbaceous crops (Hodek & Honek,

1996; Koch, 2003; Majerus et al., 2006). As *H. axyridis* is polyphagous it tends to co-occur with other ladybirds and compete for the same resources (Pell et al., 2008). Differences in body size, mobility of the larvae and prey specific defences determine the outcome (Michaud, 2002; Lucas, 2005; Labrie et al., 2006; Provost et al., 2006; Pell et al., 2008).

The aim of this study is to describe in the laboratory the predatory relationship in the new coccinellid guilds occurring in Central Italy. In particular, by comparing the incidence of IGP by *H. axyridis* of native species with that of IGP and cannibalism among native species, in order to assess the effect this exotic species may have on coccinellid guilds.

Due to their widespread occurrence and importance in suppressing aphid populations the native coccinellids selected for this study are, respectively, dominant [*Adalia bipunctata* (L.), *Oenopia conglobata* (L.) and *Coccinella septempunctata* L.] or non-dominant [*Platynaspis luteorubra* (Goeze) and *Scymnus apetzi* (Mulsant)] species in agro-ecosystems in Central Italy.

Under laboratory conditions, the incidence of IGP and cannibalism between fourth instar larvae of the above six species were quantified under two different feeding regimes, which were limiting or not limiting in terms of

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TABLE 1. Number of replicates (n = 15) in which predation occurred when either unfed or fed larvae of *Adalia bipunctata* (L.), *Oenopia conglobata* (L.), *Coccinella septempunctata* L., *Harmonia axyridis* (Pallas), *Platynaspis luteorubra* (Goeze) and *Scymnus apetzi* (Muls.) were paired with one another for 24 h. For the prey species in each combination (columns) the different superscripts indicate significantly different survival curves (see Fig. 1) when paired with different predator species (rows). The difference between survival curves was assessed using logrank tests and Holm's procedure to adjust for multiplicity, setting the family wise error rate to 0.05. Combinations where a species was never the prey (–) were excluded from the comparison.

Treatment	Predator species	Prey species					
		A. bipunctata	*O. conglobata*	*C. septem-punctata*	*H. axyridis*	*P. luteorubra*	*S. apetzi*
Unfed larvae	*A. bipunctata*	5 [b]	5 [b]	–	–	15 [a]	11 [b]
	O. conglobata	3 [b]	9 [b]	–	–	5 [b]	14 [ab]
	C. septempunctata	15 [a]	15 [a]	11 [a]	2 [a]	14 [a]	15 [a]
	H. axyridis	12 [a]	15 [a]	9 [a]	4 [a]	5 [b]	14 [ab]
	P. luteorubra	–	–	–	–	–	–
	S. apetzi	–	–	–	–	4 [b]	–
Fed larvae	*A. bipunctata*	–	–	–	–	1	3 [a]
	O. conglobata	–	–	–	–	–	–
	C. septempunctata	–	–	–	–	–	6 [a]
	H. axyridis	–	–	–	–	–	6 [a]
	P. luteorubra	–	–	–	–	–	–
	S. apetzi	–	–	–	–	–	–

larval development. Larvae of these species overlap both temporally and spatially throughout spring and summer in a variety of crops in Central Italy (Ricci & Rondoni, unpubl. data).

There are reports of *H. axyridis* adults and larvae feeding on the eggs of other coccinellids (Cottrell & Yeargan, 1998). While adults are highly mobile and frequently move between different habitats, the larvae are more likely to remain in the same place in the field, which makes it more likely they will compete for food resources and be involved in the IGP of other coccinellids (Obrycki et al., 1998). Among the coccinellid developmental stages, the fourth instar larvae are known to be the most voracious (Yasuda & Ohnuma, 1999; Lee & Kang, 2004; Cabral et al., 2006), so this instar was used in the experiments reported here. Both adults of *H. axyridis* and larvae of *C. septempunctata* have been recorded eating conspecifics in the field (Rondoni & Ricci, pers. observ.), so we included it in the experiments. The presence or absence of extraguild prey influences the intensity of the interactions (Agarwala & Dixon, 1992; Rosenheim et al., 1995; Lucas et al., 1998; Hindayana et al., 2001; Meyhöfer, 2001). The black bean aphid, *Aphis fabae* Scop., was selected as the extra-guild prey because it is a moderately suitable prey for the larval development of the species studied or a common prey item in the habitats studied (Hodek & Honek, 1996; Stathas et al., 2001; Soares et al., 2004; Barbagallo & Ricci, 2006).

MATERIAL AND METHODS

Insect rearing

The coccinellid species tested were *H. axyridis, A. bipunctata, O. conglobata, C. septempunctata, P. luteorubra* and *S. apetzi.* The larvae of these six species were obtained from eggs laid by laboratory reared females. *H. axyridis* was reared from individuals collected near Turin, Italy in 2007. Adults of the other species were collected in the hills near Perugia, Italy during 2009.

Adults of the six species were reared in plexiglass cages (13 × 20 × 30 cm), with holes in the walls covered with fine mesh to permit gas exchange, containing a pot (10 cm diam.) with 30–40 *Vicia faba minor* L. sprouts moderately infested with *A. fabae* and absorbent paper or cotton as a substrate for oviposition. The eggs were collected daily and transferred to clean Petri dishes. The larvae of all the species were reared in smaller cages (10 × 12 × 20 cm) and fed horse bean sprouts infested with aphids. Insects were kept in a climatic chamber (25 ± 1°C, 70 ± 5% RH, 14L : 10D). The seeds of horse bean were sown in pots containing horticultural soil, watered daily and grown under the same controlled environmental condition as above. 2–3 days after the emergence of the seedlings the plants were infested with *A. fabae*.

Experimental set up

To assess how the feeding status of larvae affects the incidence of IGP between coccinellids, pairs of larvae that were either starved or well fed were placed in an arena in one of the 21 possible combinations of the six species including a conspecific one for each species, with each replicated 15 times.

The experimental arena used was a Petri dish (14 cm diam.) in the lid of which there was a hole covered with netting for ventilation. The bottom of the dish was lined with absorbent paper (14 cm diam.) moistened with tap water on which there were three clean sprouts of *V. faba minor*.

In the first experiment (unfed larvae) recently moulted (5 ± 4 h) fourth-instar larvae of the six species were kept singly and starved for 15 h in clean 5 cm Petri dishes. In this case the lids of the dishes had holes covered with netting as above but they were lined with dry absorbent paper. Then using a fine bristle brush we placed one larva at one side and the other larva at the opposite side of the dish.

In the second experiment (fed larvae) recently moulted fourth instar larvae were isolated for 15 h in 5 cm Petri dishes and fed an excess of *A. fabae*. Then two larvae were transferred to the experimental arena containing three *V. faba minor* sprouts each infested with ~100 *A. fabae* (a high aphid density often
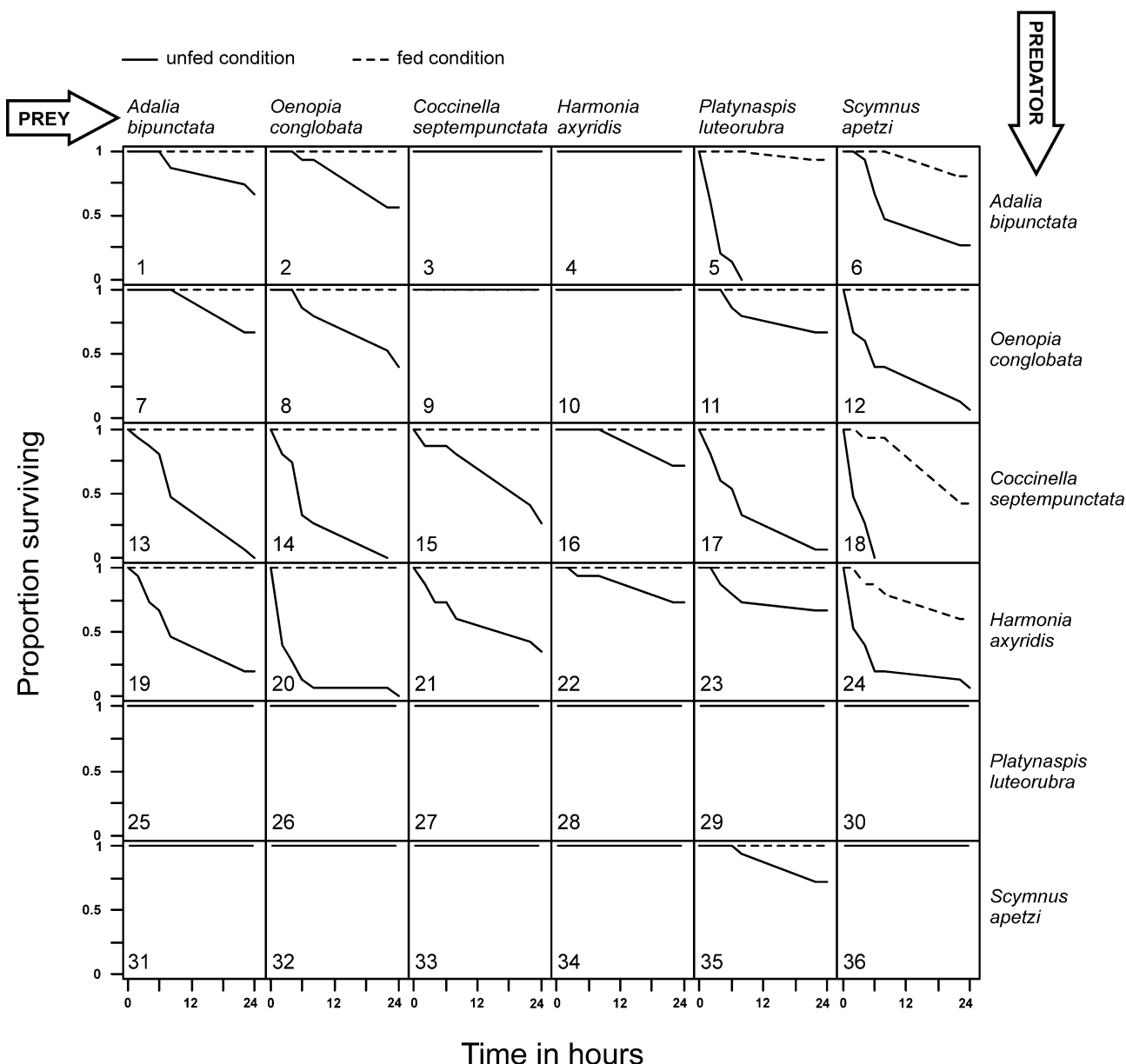
Fig. 1. The proportions of unfed (continuous line) and fed (dashed line) larvae of *Adalia bipunctata* (L.), *Oenopia conglobata* (L.), *Coccinella septempunctata* L., *Harmonia axyridis* (Pallas), *Platynaspis luteorubra* (Goeze) and *Scymnus apetzi* (Muls.) that survived when they were considered the prey (columns) in the 21 combinations.

observed in the field). During the course of the experiment the number of *A. fabae* in the arena was kept relatively constant by substituting new infested sprouts when the number of aphids was about 1/3 of the initial level. As the aim of the experiment is to reproduce conditions similar to those occurring in the field when aphids are absent and abundant the larvae were not starved before pairing them in this experiment. These experiments were carried out in a climatic chamber (25 ± 1°C, 70 ± 5% RH, 14L : 10D).

Pairing of larvae started daily at 10:00 h. The larvae were monitored four times during the day (2, 4, 6, and 8 h after pairing) and twice the following day (22 and 24 h after pairing). At each observation the status of the larvae (dead or alive) was recorded. If dead the death was ascribed to either predation or starvation. When predation was not directly observed, it was ascribed to predation if the larva had clearly been injured. If predation occurred the larva that was the prey was recorded.

Time to event (predation) data were analysed using non-parametric survival analysis that is commonly applied in medical, engineering, ecological research (Caesar, 2003; Caesar et al., 2010; Meyhöfer & Hindayana, 2000) and recently in studies on IGP (Walzer & Schausberger, 2011).

In this study, the death events were never directly observed, but only known to have occurred between two successive observations (interval censored). Therefore, we used the Nonparametric Maximum Likelihood Estimator (NPMLE) of the survival function that extends the Kaplan-Meyer estimator to the case of interval censoring (Gómez et al., 2009).

NPMLEs are represented as "survival curves" depicting the time course of "survival probability" (SP), e.g. the probability that the event occurred after time *t*. For each "combination × treatment" level, we calculated two survival curves, one for each larval species, with the exception of the cannibalistic contests for which only one curve was calculated (Table 1 and the main diagonal from left to right in Fig. 1).

Differences between curves were tested using the logrank test (Clark et al., 2003) and P-values were adjusted for multiplicity by using Holm's procedure (Holm, 1979; Logan et al., 2005) and adopting an experiment wise error rate $\alpha = 0.05$. The open source R software (R Development Core Team, 2010) was used for computing the statistical analysis (package "interval") (Fay & Shaw, 2010).

RESULTS

In the experiment in which the larvae were starved, the probability of survival (SP) of *A. bipunctata* (Fig. 1, first column, continuous lines and Table 1, first column, upper part) was similarly affected by both *C. septempunctata* and *H. axyridis* (squares 13 and 19, < 0.20 SP after 24 h, $P_{Holm} = 0.52$) and more than by *O. conglobata* or by conspecific *A. bipunctata* (squares 7 and 1, in all the two pair wise comparisons with *C. septempunctata* $P_{Holm} \leq 0.0006$ and *H. axyridis* $P_{Holm} \leq 0.0145$).

The SP of *O. conglobata* (Fig. 1, second column, continuous lines and Table 1, second column, upper part) was similarly affected by the native *C. septempunctata* and exotic *H. axyridis* (squares 14 and 20, $P_{Holm} = 0.165$) and more (0.00 SP after 24 h) than by *A. bipunctata* or conspecific *O. conglobata* (squares 2 and 8, with *C. septempunctata*: $P_{Holm} \leq 0.0017$; with *H. axyridis*: $P_{Holm} \leq 0.0005$).

The SP of *C. septempunctata* (Fig. 1, third column, continuous lines and Table 1, third column, upper part) was similarly and only affected by *H. axyridis* and conspecific *C. septempunctata* (squares 21 and 15, < 0.34 SP after 24 h, P = 0.87).

H. axyridis (Fig. 1, fourth column, continuous lines and Table 1, fourth column, upper part) was similarly and only affected by *C. septempunctata* and conspecific *H. axyridis* (squares 16 and 22, > 0.70 SP after 24 h, P = 0.94).

P. luteorubra larvae were the prey in all contests in which predatory events occurred (Fig. 1, fifth column, continuous lines and Table 1, fifth column, upper part). *A. bipunctata* and *C. septempunctata* affected the SP of *P. luteorubra* similarly (squares 5 and 17, $P_{Holm} = 0.088$) and more than the other species (*A. bipunctata*: $P_{Holm} \leq 0.0004$; *C. septempunctata*: $P_{Holm} \leq 0.0121$) (with *A. bipunctata*: 0.0 SP after 8 h and *C. septempunctata*: 0.07 SP after 24 h). Differences in the survival curves of *P. luteorubra* paired with *H. axyridis*, *O. conglobata* and *S. apetzi* were not significant (squares 23, 11 and 35, $P_{Holm} \geq 0.079$). No cannibalistic events were recorded for *P. luteorubra* (square 29).

The SP of *S. apetzi* (Fig. 1, sixth column, continuous lines and Table 1, sixth column, upper part) was greatly affected by all the dominant and exotic species (squares 6, 12, 18 and 24, < 0.27 SP after 24 h, $P_{Holm} \leq 0.0011$ compared to when paired with conspecific *S. apetzi*, square 36). *C. septempunctata* affected *Scymnus* survival more than *A. bipunctata* ($P_{Holm} = 0.0003$) but none of the other comparisons were significant ($P_{Holm} \geq 0.088$) and no cannibalistic events were recorded for *S. apetzi* (square 36).

In the experiment in which the larvae were fed (Fig. 1, first to fourth column, dashed lines and Table 1, first to fourth column, lower part) the SP of *A. bipunctata*, *O. conglobata*, *C. septempunctata* and *H. axyridis* was not affected. *P. luteorubra* SP (Fig. 1, fifth column, dashed lines and Table 1, fifth column, lower part) was slightly, but not significantly ($P_{Holm} = 1$) affected by *A. bipunctata* (square 5) and that of *S. apetzi* (Fig. 1, sixth column, dashed lines and Table 1, first column, lower part) similarly affected by *C. septempunctata*, *A. bipunctata* and *H. axyridis* (squares 18,6 and 24) ($P_{Holm} \geq 0.30$).

DISCUSSION

In the absence of aphids both *H. axyridis* and *C. septempunctata* greatly reduced the probability of survival of *A. bipunctata* and *O. conglobata*. To our knowledge there are no studies on IGP involving *O. conglobata*, but our results for *A. bipunctata* are similar to those previously recorded by other authors in laboratory experiments. For example Kajita et al. (2006) found that larvae of both *H. axyridis* and *C. septempunctata* perform better when co-occurring with *A. bipunctata* than only with conspecifics. Ware & Majerus (2008) record that in contests between fourth instar larvae of *H. axyridis* and *A. bipunctata* the latter was the prey within 48 h in all the replicates. Snyder et al. (2004) based on the results of small microcosm experiments report that both *Coccinella transversoguttata* Brown and *Hippodamia convergens* Guérin-Méneville, dominant native species in agricultural fields in eastern Washington and Northern Idaho, are often the prey of either *H. axyridis* or *C. septempunctata*. However, in interpreting the results of laboratory and field experiments where predation is not directly observed, the consumption of larvae that died from starvation can represent an important source of error (Harwood & Obrycki, 2005; Moser & Obrycki, 2009).

To predict the likelihood of IGP occurring in the field the following facts need to be taken into consideration. In Italy *C. septempunctata* is generally univoltine and the larvae are likely to be found only on herbaceous crops (Hodek & Honek, 1996; Hodek & Michaud, 2008; Ricci & Rondoni, unpubl. data). *A. bipunctata* however, is usually polyvoltine with the first generation larvae occurring on trees and those of successive generations most often on herbaceous crops and weeds (Majerus, 1994; Iperti, 1999; Jansen & Hautier, 2008; Ricci & Rondoni, unpubl. data). Furthermore, Honek (1985) and Jansen & Hautier (2008) record that *A. bipunctata* is most likely to be found in habitats where aphids are abundant and *C. septempunctata* in habitats where aphid abundance is relatively low and oviposition in these two species starts at different times. In agreement with Obrycki et al. (2000) the temporal and spatial differences in the habitats of mature *C. septempunctata* and larvae of *A. bipunctata* limits the interaction between these two species as the individuals occurring in herbaceous seminatural habitats and crops make up only a part of the *A. bipunctata* population.

O. conglobata occurs in herbaceous crops and stands of weeds in France (Iperti, 1999), Pakistan (Khan et al., 2007) and the Czech Republic (Ameixa et al., 2010). In Italy the ecology of this species and its ability to develop on aphids infesting herbaceous plants is unknown, so the likelihood of this species being attacked and eaten by *C. septempunctata* larvae in the field cannot be predicted at present.

The co-occurrence of *H. axyridis* and *A. bipunctata* larvae is well documented both in trees (Ware et al., 2009) and herbaceous crops (Jansen & Hautier, 2008), and together with *O. conglobata* on willows and limes (Rondoni & Ricci, unpubl. data). So in these habitats it is likely that the abundance of these two native species is lower due to competition from *H. axyridis*.

In a laboratory experiment, Yasuda et al. (2001) record that within 1 h *H. axyridis* is more likely to attack and eat *C. septempunctata* than vice-versa. Snyder et al. (2004), using pairs of larvae of these two species, in which the fourth instar larva was the "predator" and the third instar larva the "prey", record that IGP occurred in more than 80% of the replicates but neither of the two species had an advantage over the other.

In Central Italy *H. axyridis* larvae were found together with those of *C. septempunctata* on herbaceous plants (i.e. *Urtica dioica* L., *Medicago sativa* L. and *Artemisia vulgaris* L.) (Rondoni, pers. observ.). However due to differences in the time of oviposition observed in previous studies (Hironori & Katsuhiro, 1997; Jansen & Hautier, 2008) is possible that the native species tends to develop earlier than *H. axyridis* in such habitats. In this respect *C. septempunctata* larvae can have a size-advantage over *H. axyridis* and potentially can not only escape predation but also reduce the suitability of a habitat for the invader by reducing the abundance of aphids (Evans, 2004; Snyder et al., 2004). In Utah *C. septempunctata* develops earlier than the native *Coccinella transversoguttata richardsoni* Brown and this pattern, together with the higher reproductive investment and the greater foraging ability of the former species, is thought to be responsible for the decline in the abundance of *C. transversoguttata* (Kajita & Evans, 2010).

The non-dominant species tested were very often the intraguild prey. The relatively low voracity, low mobility and small size of *Scymnus* (Agarwala & Yasuda, 2001) and *P. luteorubra* larvae possibly determine this outcome.

Scymnus larvae are covered by a thick waxy layer that enables them to feed on aphids that are attended by ants (Volkl & Vohland, 1996; Majerus et al., 2007). The presence of the waxy filaments is an adaptation against attack by ants because (a) ants find it difficult to bite the larvae through the waxy covering and (b) some waxes are sticky, which may cause ants to cease attacking in order to clean their mouthparts (Majerus et al., 2007). In our laboratory experiments we often noted that both of the above delayed the occurrence of the predatory event. For *S. nigrinus* Kugelann and *S. interruptus* (Goeze) their waxy cover, like that of *S. apetzi* larvae, is not an effective protection against attacks by large species of coccinellid (Volkl & Vohland, 1996).

P. luteorubra larva tend to deter attacking ladybirds by adhering to the substrate (e.g. plant sprouts), wrinkling the dorsal surface when inspected and quite often by reflex bleeding from several dorsal glands. The blood coagulates very rapidly and may stick to the predator's mouthparts. As in other insect families reflex bleeding in coccinellids is an important means of defense against invertebrate predators (Blum & Sannasi, 1974; Majerus & Kearns, 1989; Sato et al., 2009).

The low survival of *P. luteorubra* when paired with both *A. bipunctata* and *C. septempunctata* indicates these species may be important predators of *P. luteorubra* inhabiting both trees (e.g. *Prunus avium* L.) and weeds (*Arctium lappa* L.). The relatively higher survival of *P. luteorubra* paired with *H. axyridis* is an unexpected result. We suggest that its sticky reflex blood, coccid-like shape and ability to seek refuge in the plant sprouts could be important in its ability to avoid predation. Whether native *A. bipunctata* and *C. septempunctata* have a higher tendency to attack and eat *P. luteorubra* than *H. axyridis* remains to be investigated.

Moreover, the structure of the mandibles also determines the incidence IGP (Pell et al., 2008). Larvae of the two non-dominant species tested have piercing-sucking mouthparts (Ricci, 1979) with which they seize an antenna or leg of an aphid and then feed by means of extra-intestinal digestion. This type of feeding behaviour seems effective if the prey moves slowly but not if prey is fast moving like the larvae of ladybirds.

Moreover *P. luteorubra* and *S. apetzi* have a specific functional role in reducing the abundance of aphids. The larvae of these species are able to feed on ant-attended aphid colonies (Majerus et al., 2007) or those in rolled up leaves that are not accessible to coccinellid species whose larvae are bigger (Ricci & Rondoni, pers. observ.). Pell et al. (2008) and Volkl (1995) suggest that by associating with ants these ladybirds can escape from their natural enemies. In this way they can coexist with dominant species, which results in a synergistic effect in terms of aphid control (Losey & Denno, 1998; Pell et al., 2008).

Englund (1997) emphasizes the importance of spatial scale and prey movements in determining the response of predators. In natural conditions it is possible to escape and so reduce the risk of IGP (Sato et al., 2005). We observed, both in the field and laboratory, that the larvae of *Scymnus* drop off plants in order to avoid predator attacks. This behaviour however leads to a drastic reduction in their waxy covering, which increases their risk of being attacked by predators as waxless *Scymnus* larvae are more vulnerable (Agarwala & Yasuda, 2001). This may account for the low probability of survival of *S. apetzi* in the presence of aphids. If this is the case then increasing the dimension of the experimental cage is likely to result in a higher probability of survival of the *Scymnus* larva as it reduces the probability of their encountering other larva.

No predation was recorded in most of the combinations supplied with aphids. This was possibly due to (i) the low mobility of well fed larvae resulting in them encountering one another less frequently (Agarwala & Dixon, 1992; Dixon, 2000); (ii) a faster rate of growth of the intraguild prey (Lucas, 2005) and (iii) an increase in food selectivity as aphids are qualitatively better and may be less risky in terms of being attacked and eaten compared to intraguild prey (Schoener, 1971; Pastorok, 1980; Ernsting & van der Werf, 1988; Montserrat et al., 2006). Previous works on ladybirds (Kajita et al., 2000), lacewings (Phoofolo & Obrycki, 1998) and pentatomids (De Clercq et al., 2003) report a reduction in IGP when extraguild prey was present in the experimental arena. When the same larval stages are paired a reduction in IGP by *H. axyridis* is reported for the hoverfly *Episyrphus balteatus* DeGeer (from 100 to 5% of second instar larvae by adding 30 pea aphids) (Ingels & De Clercq, 2011) and *A. bipunctata* (from 76 to 60% in 24 h by adding 50 cowpea aphids) (Kajita et al., 2000). Cannibalism by fourth instar larvae of *A. bipunctata* is reduced from 36 to 0% by the addition of extraguild prey (Kajita et al., 2000).

It is difficult to predict the consequences of the arrival of an exotic species, especially one that is a generalist predator (Wallner, 1996; Roy & Wajnberg, 2008; Roy et al., 2011). Other IGPs, competition for resources and enemy release hypothesis (ERH) are driving factors affecting the population dynamics and the relationship among species (Snyder & Evans, 2006). Mooney & Cleland (2001) list the potential consequences for invaded communities of the establishment of a new species. They include competitive exclusion, niche displacement, predation and ultimately extinction. Kenis et al. (2010) propose a risk assessment of the threat of *H. axyridis* to the principal native ladybird species in Europe. Using data on the likelihood of encounter in the field, consequences of competition for food and predation it is predicted that the species most at risk from *H. axyridis* will be *A. bipunctata*, *Adalia decempunctata* (L.), *Calvia decemguttata* (L.) and *O. conglobata*. Brown & Miller (1998) report the displacement of several native coccinellids (including *A. bipunctata*) from apple orchards by *C. septempunctata*, which dominated the Coccinellini fauna from 1989 to 1994 in Virginia. Subsequently *H. axyridis* invaded apple agro-ecosystems, displacing *C. septempunctata* and becoming the dominant species in apple orchards. In South Dakota the structure of native coccinellid guilds in field crops changed after the arrival of *C. septempunctata* in 1987 (Elliott et al., 1996). In 2004 both *C. septempunctata* and *H. axyridis* were dominant in field crops in South Dakota (Hesler & Kieckhefer, 2008). In Europe the establishment of *H. axyridis* is linked to a decline in native aphidophagous ladybirds, notably *A. bipunctata* and *A. decempunctata* in Belgium (Adriaens et al., 2010) and *A. bipunctata*, *C. septempunctata* and *Propylea quatuordecimpunctata* (L.) in the UK (Brown et al., 2011). All these studies indicate that when *C. septempunctata* and *H. axyridis* become established in a new area the dominance structure of invaded communities of coccinellids changes.

In our case (Italy) the results do not necessarily mean that the indigenous ladybirds are currently at risk of extinction as a result of their interactions with *C. septempunctata* or in the future with *H. axyridis*.

The spatial distributions and seasonal timing of occurrence and reproduction of coccinellids in habitats are very complex in agricultural and natural landscapes (Elliott et al., 1996). There are many ecological studies on refuges that can be used to escape from predators as they play an important role in maintaining a high diversity of predators (Forrester & Steele, 2004; Denno & Finke, 2006). Thus, as pointed out by Elliott et al. (1996), if competition is an important factor in determining coccinellid assemblages, refuges from competition probably exist for most species of coccinellid at plant (Schellhorn & Andow, 1999), field (Hampton, 2004) and landscape levels (Gardiner et al., 2009). In particular, Evans et al. (2011b) review several examples of native coccinellids that show a niche-shift that allows them to survive in territories invaded by an exotic species of ladybird. In Italian agroecosystems invaded by *H. axyridis* there are probably refuges from competition for the native species. For example, in *A. bipunctata* (like *A. decempunctata*) there is an alkaloid (adaline) that is toxic for both *H. axyridis* (Sloggett & Davis, 2010) and *C. septempunctata* (Agarwala & Dixon, 1992). Although *H. axyridis* feeds on *Adalia* spp. in the field (Hautier et al., 2011), it is likely that it prefers other tree-dwelling species, like *O. conglobata* (Rondoni & Ricci, unpubl. data), which is not strictly aphidophagous and can feed and develop on various stages of leaf beetles (Hodek & Honek, 1996) and psyllids (Erler, 2004). Perhaps, in areas where *H. axyridis* becomes established, *O. conglobata* will be selected to feed more on non aphid pests and in effect show a strategic niche shift.

In herbaceous agro-ecosystems *H. axyridis* and *C. septempunctata* could became co-dominants in the same habitats. Perhaps the invader will develop more on trees and only later in the year colonize the herbaceous layer, potentially at a time when the immature stages of *C. septempunctata* are no longer present. Moreover, when they co-occur in alfalfa for example, the two species may feed mainly on other suitable preys, such as weevils, when aphids are scarce (Obrycki & Kring, 1998; Evans, 2004; Evans & Gunther, 2005).

P. luteorubra and *S. apetzi* are niche specialists. Even though their niches overlap those of the dominant species they frequently feed where there are no other species of predator. According to Pell et al. (2008) it is possible that in the presence of *H. axyridis* these non-dominant species will become even better adapted at exploiting their specific niches.

Thus it is reasonable to hypothesize that these natural enemies will coexist but the local abundance of the native species will be reduced. For example, in Western North America native ladybirds are no longer recorded in alfalfa field due to competition from *C. septempunctata*, but are recorded in refuge habitats and reappear in high numbers

in alfalfa fields heavily infested with aphids (Evans, 2004; Evans et al., 2011b).

There is a possibility of a worse scenario as pointed out recently by many authors (for example, Dukes & Mooney, 1999; Walther et al., 2009; Evans et al., 2011a). They stress that habitat fragmentation and changes in climate can increase the adverse effect of invasive species by reducing the number of refuge habitats for native species in which they can avoid exploitative competition and direct predation from the invaders.

In the context of biological control Mills (2006) suggests that all cases of competitive displacement due to invasive species are associated with an increase in pest suppression. In North America the establishment of *H. axyridis* has resulted in a reduction in native coccinellid abundance and surprisingly also an augmentative suppression of pests in apple and potato crops (Brown & Miller, 1998; Alyokhin & Sewell, 2004; Brown, 2004). In particular, a diversity of natural enemies that each use plant space differently is associated with good pest suppression (Straub & Snyder, 2008). Thus, if *C. septempunctata* and *H. axyridis* could be co-dominants in herbaceous crops because of the differences in their temporal niche partitioning or presence of alternative food when aphids are scarce a better biological control of the aphids might be realized.

In conclusion, the results of this study indicate that in the absence of aphids *H. axyridis* is a strong intraguild predator of several native coccinellids. In addition to adding *O. conglobata*, *P. luteorubra* and *S. apetzi* to its list of potential preys we also corroborate the findings of other studies on *A. bipunctata* and *C. septempunctata*. The overall effect of the exotic predator on native species was similar to that of *C. septempunctata* and sometimes that of *A. bipunctata* and *O. conglobata* on non-dominant species. This suggests that other factors, like niche partitioning and differences in resource exploitation allow several species of indigenous coccinellids to coexist in the habitats studied. It is suggested that the niche of *H. axyridis* overlaps those of both *A. bipunctata* and *O. conglobata*, and therefore it is likely that these native species will be negatively affected by *H. axyridis*. In fact *H. axyridis* can dominate arboreal coccinellid guilds (Brown et al., 2011) and therefore it is likely that niche dislodgment will occur in these habitats.

Further research will focus on defining the biology and habitat utilization by *H. axyridis* and native coccinellids at the landscape level in Central Italy. In particular, comparison of the coccinellid assemblages at invaded and non-invaded sites will provide a better understanding of the effect of the exotic species on other ladybirds. Field observations carried out in parallel with analysis of gut-contents will provide more accurate information about the important trophic relationships in coccinellid assemblages and their role in the suppression of pests in agro-ecosystems.

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