

Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): The role of intra and extraguild prey densities

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Abstract

Laboratory cages were used to evaluate the influence of extraguild (EGprey) and intraguild prey (IGprey) densities on the direction, symmetry and magnitude of the intraguild predation (IGP) of the aphidophagous *Harmonia axyridis* Pallas on *Coccinella undecimpunctata* L. and vice versa. In order to understand the role of competition between IGprey, the experiments included treatments with one IGpredator, with one or four IGprey and EGprey (*Aphis fabae* Scopoli) ranging from zero to sufficient aphids to satiate the predators for 12, 24 or 48 h. Increases in EGprey and IGprey densities did not alter the direction, but decreased the magnitude and symmetry of IGP. Predation on one individual of IGprey decreased from more than 80%, in the absence of EGprey, to from 6% to 53%, at higher EGprey densities. Decrease in IGP was less when *H. axyridis* was the IGpredator. Even at high EGprey densities, eggs and 2nd larval stages of *C. undecimpunctata* were vulnerable to IGP and the level of predation was 40% and 53%. The presence of more than one IGprey increased the magnitude of IGP mainly at EGprey densities sufficient to satiate the predators for 12 and 24 h, suggesting that competition between the IGpredator and IGprey may be one of the processes promoting IGP. These results and those of other authors suggest that *H. axyridis* has the potential to be an IGpredator, mainly of the most vulnerable stages of IGprey. Thus, *H. axyridis* may negatively affect the survival of *C. undecimpunctata*, when these two species exploit the same resources.

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Keywords: *Harmonia axyridis*; *Coccinella undecimpunctata*; Intraguild predation; Extraguild and intraguild prey densities; Competition

1. Introduction

The term intraguild predation (IGP) is used to define the interaction between predators that share the same resource, independently of their mode of nutrition, ecology and taxonomic position (Lucas, 2005). Polis et al. (1989) define IGP as the death and consumption of species that use the same resources (food/space), which, are sometimes limiting. The predator is defined as the intraguild predator, the prey (competitor) as the intraguild prey and their common resource as the extraguild prey. They distinguish it from competition by the fact that IGP reduces exploitative

competition (Polis et al., 1989). Lucas (2005) recently extended the ambit of the concept to include interspecific death, that is, when prey is killed but not consumed. However, it is not clear from the literature whether the eating of IGprey by an IGpredator is primarily to obtain resources or eliminate potential competitors.

Intraguild predation has direct implications for the fitness of the species implicated, the IGpredator, IGprey and EGprey, and potentially, for the structure and dynamics of populations and communities (Polis et al., 1989; Polis and Holt, 1992). For this reason, IGP can lead to changes in the morphological, behavioral and evolutionary characteristics of the protagonists (Polis et al., 1989). From a practical point of view, it can limit the effectiveness of biological control. Despite the apparent advantage of

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releasing several species of predators, the pest may increase in abundance as a result of unpredictable interactions between the predators (Rosenheim et al., 1995; Lucas, 2005).

There are several factors that may alter the direction, symmetry and magnitude of IGP, such as, the environment, host plant characteristics, predator and prey characteristics, the EGprey and factors related to the protagonists' life histories (Lucas, 2005). The presence or absence of EGprey influences the intensity of the interaction (Johansson, 1993; Rosenheim et al., 1995; Lucas et al., 1998; Hindayana et al., 2001; Meyhöfer, 2001; Burgo et al., 2002; Félix and Soares, 2004). However, the effect of simultaneous influence of extraguild and IGprey densities, on the magnitude, direction and symmetry of the IGP, is unknown. The purposes of this experiment were: (i) to determine the influence of EGprey (*Aphis fabae* Scopoli) and IGprey densities on the direction, magnitude and symmetry of IGP between the aphidophagous ladybeetles *Harmonia axyridis* Pallas and *Coccinella undecimpunctata* L. and (ii) to determine the effect of competition on the magnitude of IGP. If the IGprey is a potential competitor then an increase in the number of IGprey will result in an increase in IGP events. The invasive Asian ladybeetle *H. axyridis* is now a major problem in Europe and its spread across this continent will continue (Roy and Wajnberg, 2008; Soares et al., 2008). This study, thus, may help predict its potential impact on *C. undecimpunctata*, which is one of the most widely distributed ladybeetles in the world, including Europe (Iablokoff-Khnzorian, 1982), where both of these occupy similar habitats.

2. Materials and methods

2.1. Biological material

Harmonia axyridis and *C. undecimpunctata* individuals came from a stock culture and were reared at 22 ± 1 °C, with $75 \pm 5\%$ RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips Ref.: TDL 23W/54 and TDL 18W/54). In order to avoid food adaptation and consanguinity ladybeetles were fed *ad libitum* on a mixed diet of the aphids *A. fabae* Scopoli and *Myzus persicae* (Sulzer), and eggs of *Ephestia kuehniella* Zeller and field collected ladybeetles were added regularly to the stock culture.

2.2. Intraguild predation experiments

2.2.1. Influence of the extraguild prey density on the direction, magnitude and symmetry of intraguild predation

To assess the influence of EGprey density on the magnitude, direction and symmetry of IGP between *H. axyridis* and *C. undecimpunctata*, five experiments were carried out. Three experiments were used to assess the effect of EGprey density when *H. axyridis* was the IGpredator [(i) 4th larval stage of *H. axyridis* vs eggs of *C. undecimpunctata*, (ii) 4th larval of *H. axyridis* vs 2nd larval stage of *C.*

undecimpunctata, (iii) 4th larval of *H. axyridis* vs 4th larval stage of *C. undecimpunctata*] and two experiments when *C. undecimpunctata* was the IG predator [(iv) 4th larval stage of *C. undecimpunctata* vs eggs of *H. axyridis* and (v) 4th larval stage of *C. undecimpunctata* vs 1st larval stage of *H. axyridis*].

2.2.2. The effect of extraguild and intraguild prey densities on the direction, magnitude and symmetry of intraguild predation

To assess the effect of extraguild and IGprey densities, two experiments were performed. In one *H. axyridis* was the IGpredator [(vi) 4th larval of *H. axyridis* vs four individuals of the 4th larval stage of *C. undecimpunctata*] and in the other *C. undecimpunctata* [(vii) 4th larval stage of *C. undecimpunctata* vs four individuals of the 1st larval stage of *H. axyridis*]. IGP between these two ladybeetles is asymmetrical (Félix and Soares, 2004).

Each experiment consisted of four treatments with different densities of EGprey (apterous females of *A. fabae*). The prey densities were as follows: (i) absent, (ii) sufficient to meet the food requirements of the predators for 12 h, (iii) sufficient for 24 h and (iv) sufficient for 48 h. The amount of prey provided in each treatment was based on the results of Soares et al. (2004) and Moura et al. (2006).

The methodology used is that of Félix and Soares (2004). Larvae and eggs were 24 h old. Larvae were starved for 24 h before the experiments, except first instar individuals (to avoid a high rate of mortality). One individual was placed with one (or four) of the other species in a 2L transparent plastic box containing a potted broad bean plant (approximately 15 cm tall) with a particular number of aphids. Five eggs were provided in the combinations that used eggs. Eggs were placed on plant leaves and larvae at the base of the plant. The second individual (or the four individuals) was released after the first larva had moved up the stem. Twenty-four hours later, the box was checked to determine which individuals had survived. There were 15 replicates of each treatment. The natural mortality of each instar and occurrence of cannibalism in the two species when kept in similar conditions, but in the absence of the other ladybeetle, were used as a control. These results were used in the calculation of IGP for both species. All experiments were carried out at 20 ± 1 °C, $75 \pm 5\%$ of RH and a photoperiod of 16L:8D, under fluorescent lamps (Philips Ref.: TDL 23W/54 and TDL 18W/54).

IGP levels were estimated from the rates of predation (that is the proportion of replicates where IGP has occurred) for *H. axyridis* (RPha) and *C. undecimpunctata* (RPcu), which were calculated as follows:

To determine influence of the EGprey density,

$$RPha = [(Pcu, ha) SRcu/N]100$$

$$RPcu = [(Pha, cu) SRha/N]100$$

To determine the effect of extraguild and intraguild prey densities,

$$RPha = [P(\text{cu, ha}) \text{SRcu} \text{SRcu4}/N]100$$

$$RPcu = [P(\text{ha, cu}) \text{SRha} \text{SRha4}/N]100$$

where “ $P(\text{cu, ha})$ ” is the number of individuals of *C. undecimpunctata* killed, “ $P(\text{ha, cu})$ ” is the number of individuals of *H. axyridis* killed, “SRcu” and “SRha” are the survival rate of *C. undecimpunctata* and *H. axyridis* in control, “SRcu4” and “SRha4” are the survival rate of *C. undecimpunctata* and *H. axyridis*, respectively, in control for cannibalism and “ N ” is the number of replicates. Survival rates (SRcu and SRha) were calculated for the replicates in which single individuals were placed on plants for 24 h, the controls.

The symmetry index of Lucas et al. (1998) was used. This index is the number of replicates in which a given predator is eaten over the total number of replicates in which there was IGP, in a particular combination of predators.

2.3. Statistical analysis

The symmetry index for each combination was compared with the predicted 50% if the interaction is random, using a Chi-square test (χ^2 , $P < 0.05$) (SPSS Inc., 2004). IGP between the two species in a given combination was assessed using the χ^2 and was considered to be (i) symmetrical, when the χ^2 value was not significant, which indicates similar levels of predation on the two species, (ii) asymmetrical, when the χ^2 value was significant and (iii) not significantly asymmetrical, when the χ^2 value was not significant but the predation of the two species differed.

Predation in the different treatments was compared using the multiple comparison test for proportions (MCTP), where significant results are those with a $q_{0.05, \infty, 4}$ value > 1.92 (Zar, 1996). The relationship between rate of predation and prey density was analyzed using Spearman rank correlation and its significance using ANOVA ($P < 0.05$). All analysis were performed using SPSS, 12.0.1 for Windows (SPSS Inc., 2004). The displayed values are regular averages and standard errors.

3. Results

3.1. Influence of the extraguild prey density on the direction, magnitude and symmetry of intraguild predation

Independent of the EGprey density, the direction of IGP remained constant (Figs. 1 and 2).

Predation by the 4th larval stage of *H. axyridis* of eggs (MCTP, $P = 0.0223$), 2nd (MCTP, $P = 0.0024$) and 4th larval stage (MCTP, $P < 0.0001$) of *C. undecimpunctata* differs significantly with EGprey density (Fig. 1). There is a significant negative dependence for the predation of *H. axyridis* on the eggs but not on 2nd and 4th larval stages (Table 2). IGP was significantly asymmetrical in five combinations; 4th larval stage of *H. axyridis* with eggs in the absence of aphids and when there were sufficient aphids for the predators for 12 h, and 4th larval stage of *H. axy-*

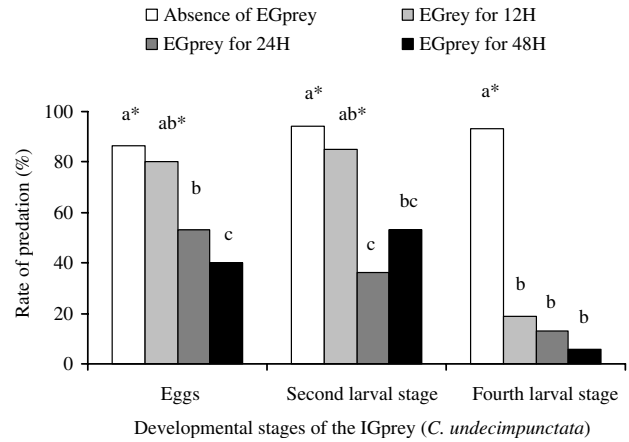


Fig. 1. Rate of predation of the 4th larval stage of *H. axyridis* on eggs, 2nd and 4th larval stages of *C. undecimpunctata* under different densities of extraguild prey. Legend: * indicates significant asymmetrical IGP (χ^2 , $df = 1$, $P < 0.05$) and different letters in the same treatment mean significant differences (MCTP, $P < 0.05$).

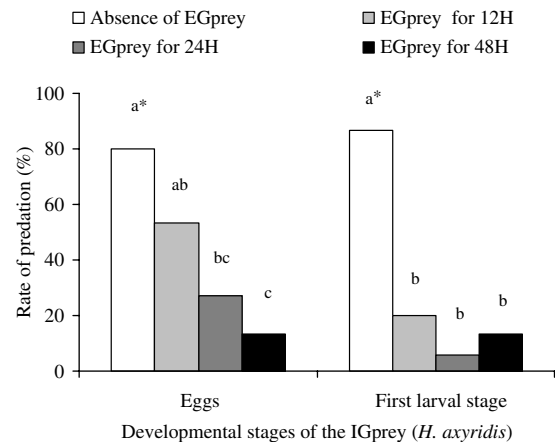


Fig. 2. Rate of predation of the 4th larval stage of *C. undecimpunctata* on eggs and 1st larval stage of *H. axyridis* under different densities of extraguild prey. Legend: * indicates significant asymmetrical IGP (χ^2 , $df = 1$, $P < 0.05$) and different letters in the same treatment mean significant differences (MCTP, $P < 0.05$).

ridis with 2nd larval stage of *C. undecimpunctata* in the absence of aphids and when there were sufficient aphids for the predators for 12 h, and 4th larval stage of *H. axyridis* with 4th larval stage of *C. undecimpunctata* in the absence of aphids (Fig. 1 and Table 1). In the other combinations, IGP was not significantly asymmetrical (Fig. 1 and Table 1).

Predation of 4th larval stage of *C. undecimpunctata* on eggs (MCTP, $P = 0.0011$) and 1st larval stage (MCTP, $P < 0.0001$) of *H. axyridis* differed significantly with EGprey density (Fig. 2). There was no dependence between the predation on eggs (but on the limit of significance) and 1st larval stage and aphid density (Table 2). IGP was significantly asymmetrical in the following combinations: 4th larval stage of *C. undecimpunctata* with eggs and 1st larval stage of *H. axyridis* in the absence of aphids (Fig. 2 and

Table 1
Rate of predation (RP) and summary of the χ^2 analysis for the influence of EGprey (*A. fabae*) and IGprey densities on the magnitude, direction and symmetry of the intraguild predation between 4th instar larvae of *H. axyridis* or *C. undecimpunctata*

Combinations	Influence of the extraguild prey density																
	Absence of EGprey				EGprey for 12 h				EGprey for 24 h				EGprey for 48 h				
	IGpredator	RP	χ^2	df	P	RP	χ^2	df	P	RP	χ^2	df	P	RP	χ^2	df	P
<i>H. axyridis</i> (4th)	<i>C. undecimpunctata</i> (Eggs)	87	0.0003	1	0.014	80	0.0005	1	0.018	53	0.0047	1	0.055	40	0.1430	1	0.095
	<i>C. undecimpunctata</i> (2nd)	94	0.0002	1	0.010	85	0.0003	1	0.015	36	0.0201	1	0.113	53	0.0047	1	0.055
	<i>C. undecimpunctata</i> (4th)	93	0.0007	1	0.012	19	0.0886	1	0.234	13	0.1573	1	0.308	6	0.3173	1	0.427
<i>C. undecimpunctata</i> (4th)	<i>H. axyridis</i> (Eggs)	80	0.0005	1	0.018	53	0.0047	1	0.055	27	0.0455	1	0.169	13	0.1572	1	0.308
	<i>H. axyridis</i> (1st)	87	0.0003	1	0.014	20	0.5839	1	0.555	6	0.3428	1	0.442	13	0.1573	1	0.308
<i>Influence of the extraguild and intraguild prey densities</i>																	
<i>H. axyridis</i> (4th)	<i>C. undecimpunctata</i> (4th)	81	0.0013	1	0.029	42	0.0166	1	0.102	18	0.1168	1	0.267	6	0.3405	1	0.440
<i>C. undecimpunctata</i> (4th)	<i>H. axyridis</i> (1st)	58	0.0052	1	0.057	41	0.0194	1	0.111	36	0.0265	1	0.129	6	0.3414	1	0.441

Table 1). In the other combinations, IGP was not significantly asymmetrical (Fig. 2 and Table 1).

3.2. The effect of extraguild and intraguild prey densities on the direction, magnitude and symmetry of intraguild predation

Independent of the EGprey density, the direction of IGP remained constant (Figs. 3 and 4).

The predation by the 4th larval stage of *H. axyridis* of the four 4th larval stage of *C. undecimpunctata* differed significantly with EGprey density (MCTP, $P = 0.0001$) (Fig. 3). Predation by *H. axyridis* of the 4th larval stage was not dependent on aphid density (Fig. 3 and Table 2). IGP was significantly asymmetrical in the combination 4th larval stage of *H. axyridis* and four 4th larval stage of *C. undecimpunctata* in the absence of aphids (Fig. 3 and Table 1). In other combinations, IGP was not significantly asymmetrical (Fig. 3 and Table 1).

Predation of the 4th larval stage of *C. undecimpunctata* on 1st larval stage of *H. axyridis* differed significantly with EGprey density (MCTP, $P = 0.0268$) (Fig. 4). Predation by *C. undecimpunctata* on the 1st larval stage was dependent on aphid density (Fig. 4 and Table 2). IGP in all treatments was not significantly asymmetrical (Fig. 4 and Table 1).

In the presence of more than one IGprey intraguild predation increased. If *H. axyridis* was the IGpredator, the level of predation increased when there was sufficient EG prey for the predator for 12 h (Fig. 5A). If *C. undecimpunctata* was the IGpredator, the level of predation increased when there was sufficient EG prey for the predator for 12 and 24 h (Fig. 5B).

4. Discussion

In this study, the direction, symmetry and magnitude of IGP between *H. axyridis* and *C. undecimpunctata* was characterized. In the presence of several IGprey the direction of IGP was the same in the presence and absence of EGprey. This finding accords with what happens in Odonata predatory guilds (Johansson, 1993) and of aphidophagous insects, whether predators (larvae and adults) or parasitoids (larvae, pupae and adults) (Meyhöfer and Klug, 2002). The results indicate that *H. axyridis* was more often the IGpredator than *C. undecimpunctata*. For both predators a decreasing trend in the degree of IGP with increase in abundance of the EGprey was observed. In other guilds, the presence of EGprey also decreases predation by IGpredators (Lucas et al., 1998; Obrycki et al., 1998; Yasuda et al., 2004), and the same is observed in zooplankton guilds (Johansson, 1993). There are differences in the vulnerability of different larval stages to IGP: smaller and sessile individuals were the most vulnerable. Several authors cite these two characteristics as key factors determining vulnerability in aphidophagous guilds (Lucas et al., 1998; Hindayana et al., 2000; Félix and Soares 2004; Yasuda et al., 2004). In some

Table 2
Rate of predation (RP) and correlation analysis for the influence of EGprey (*A. fabae*) and IGprey densities on the magnitude, direction and symmetry of the intraguild predation between 4th instar larvae of *H. axyridis* or *C. undecimpunctata*

Combinations		Influence of the extraguild prey density			
IGpredator	IGprey	df	R	Slope ± SE	P
<i>H. axyridis</i> (4th)	<i>C. undecimpunctata</i> (Eggs)	3	0.96	-0.618 ± 0.128	0.04
	<i>C. undecimpunctata</i> (2nd)	3	0.72	-0.497 ± 0.342	0.28
	<i>C. undecimpunctata</i> (4th)	3	0.77	-0.606 ± 0.355	0.23
<i>C. undecimpunctata</i> (4th)	<i>H. axyridis</i> (Eggs)	3	0.95	-1.639 ± 0.397	0.05
	<i>H. axyridis</i> (1st)	3	0.71	-1.358 ± 0.94	0.29
Influence of the extraguild and intraguild prey densities					
<i>H. axyridis</i> (4th)	<i>C. undecimpunctata</i> (4th)	3	0.92	-0.294 ± 0.092	0.09
<i>C. undecimpunctata</i> (4th)	<i>H. axyridis</i> (1st)	3	0.99	-0.804 ± 0.089	0.01

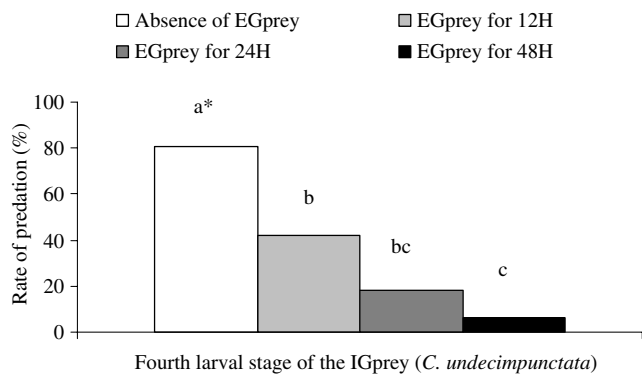


Fig. 3. Rate of predation of the 4th larvae stage of *H. axyridis* on four individuals of the 4th larval stage of *C. undecimpunctata* under different densities of extraguild prey. Legend: * indicates significant asymmetrical IGP (χ^2 , df = 1, $P < 0.05$) and different letters mean significant differences (MCTP, $P < 0.05$).

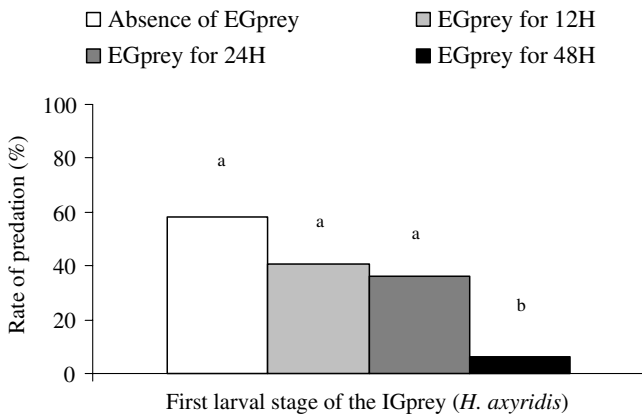


Fig. 4. Rate of predation of the 4th larvae stage of *C. undecimpunctata* on four individuals of the 1st larval stage of *H. axyridis* under different densities of extraguild prey. Legend: different letters mean significant differences (MCTP, $P < 0.05$).

experiments, although IGP was statistically insignificant, the level of predation was approximately half of that in tests where IGP occurred, e.g. when *C. undecimpunctata* was the IG predator of eggs and 4 first larval stage. When *H. axyridis* was the IG predator, the level of predation of

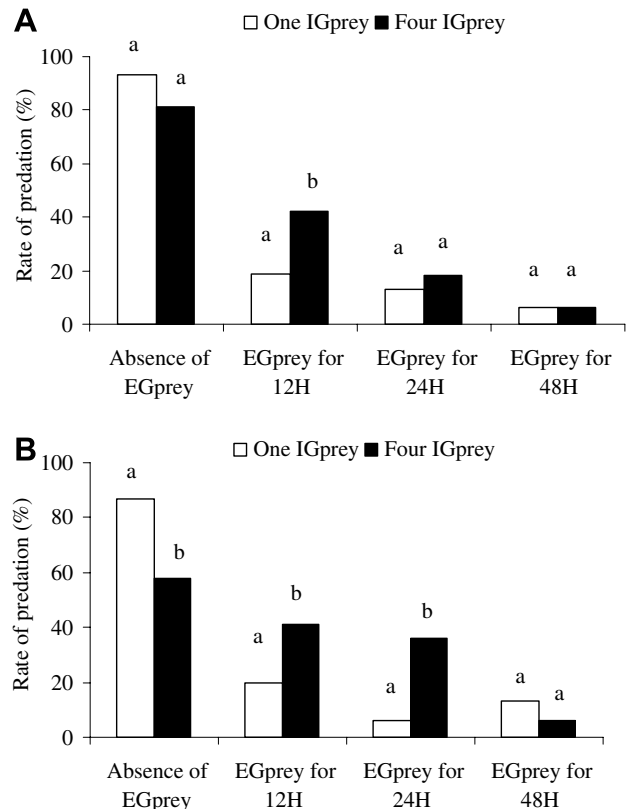


Fig. 5. Rate of predation in the treatments having one or four intraguild prey when *H. axyridis* (A) or *C. undecimpunctata* (B) were the IG predators (χ^2 , df = 1, $P < 0.05$).

eggs, 2nd and 4th larval stage was high. Obrycki et al. (1998) recorded no negative interactions between the exotic *Coccinella septempunctata* L. and the native *Coleomegilla maculata lengi* (DeGeer) at prey densities above 20 aphids per day. Negative interaction only occurred at a low prey density (1 aphid per day). As a potential IGpredator, *H. axyridis* is more aggressive than *C. undecimpunctata*, as in several coccinellid guilds it is the IG predator (Kajita et al., 2000; Yasuda et al., 2001; Brown, 2003; Sato and Dixon, 2004; Snyder et al., 2004; Yasuda et al., 2004). Félix and Soares (2004) found that even when there is only a small difference in the weight of the IGprey and

IGpredator, *H. axyridis* is more likely to be the predator than *C. undecimpunctata*.

There are studies indicating that *H. axyridis* can negatively affect other species in nature. The interaction between *H. axyridis* 4th larval stage and 4th and 2nd larval stage of North American indigenous species (*C. transversoguttata richardsoni* Brown and *Hippodamia convergens* Guerin) studied by Yasuda et al. (2004) was highly asymmetrical, and *H. axyridis* was seldom the IGprey when EGprey was scarce. Snyder et al. (2004) report that *H. axyridis* (3rd and 4th larval stages) is more frequently the IGP than the other species studied (one exotic, *C. septempunctata*, and two native, *C. transversoguttata* and *H. convergens*), and in combinations when it was the smaller species it was very good at avoiding being eaten. Kajita et al. (2000) results support the hypothesis that the introduction of exotic species leads to a decrease in the abundance of indigenous species. *H. axyridis* (2nd and 4th larval stages) is more aggressive than other species (larvae of *Adalia bipunctata* L. and *C. septempunctata*) and the survival percentage of an indigenous species in the U.S.A. (*A. bipunctata*) is low when reared with the exotic *C. septempunctata*. *H. axyridis* has had an obvious impact on the abundance of *C. septempunctata* in the U.S.A. (Horn, 1996; LaMana and Miller, 1996; Brown and Miller, 1998; Brown, 2003). *Cycloneda sanguinea* L., previously the predominant aphidophagous coccinellid in Florida, declined in abundance with the increase in abundance of *H. axyridis* (Michaud, 2002). Studies conducted by Félix and Soares (2004) and Soares and Serpa (2007) suggest that this species might have negative impact on *C. undecimpunctata* populations, which is supported by the present study. However, a field cage study, conducted on sweet corn in the Minnesota, shows that *H. axyridis* larvae weighed more when kept with *C. maculata* than when kept with equal number of conspecific, suggesting that intraspecific competition is stronger for *H. axyridis* than interspecific competition with *C. maculata* (Hoogendoorn and Heimpel, 2004). The cages used on the previous experiments were larger than those used on our experiments. This may have allowed spatial niche separation of both predator species, and thus decreasing the interaction.

In addition to IGP there are several other factors that influence the interactions within a community, such as cannibalism. Cannibalism was relatively high in the controls. This may enable coccinellids to survive when food is scarce (Schellhorn and Andow, 1999; Michaud, 2003). In the *H. axyridis* controls cannibalism occurred at all prey densities, which indicates the benefits of larval cannibalism for this species, as by eating conspecific larvae they can increase their probability of survival (Snyder et al., 2000). Cannibalism in the *C. undecimpunctata* controls only occurred in the absence of aphids (85%), which suggests that this coccinellid does not resort to cannibalism in the presence of EGprey.

An interesting result of this study is the impact that an increase in IGprey density had upon predation. That is,

in experiments involving *H. axyridis* 4th larval stage and *C. undecimpunctata* 4th larval stage and by *C. undecimpunctata* 4th larval stage and *H. axyridis* 1st larval stage, when the *A. fabae* densities were sufficient to satiate the two predators for 12 and 24 h, an increase in the number of IGprey leads to an increase in predation by the IG predator. This supports the possibility of occurrence of both of the two hypothetical IGP scenarios: the protective and/or competitive (Lucas, 2005). In the protective scenario 4th larval stage intensify predation of the IG prey in order to decrease the probability of being eaten before achieving the vulnerable pupal stage. The pupae of aphidophagous predators are frequently victims of IGP. In the competitive scenario it serves to eliminate potential competitors. The latter scenario is supported by the fact that an increase in IGP occurred when the number of IGprey was highest and the number of *A. fabae* was sufficient to satiate all the predators for 12 and 24 h. In addition, the results also might suggest that IGP has a nutritive role, that is, when the nutritive value of the IGprey is superior to that of the EGprey (Lucas, 2005), then even in the presence of an *ad libitum* quantity of EGprey, this type of interaction is advantageous. The high nutritive value of IGprey is cited by other authors (Yasuda and Ohnuma, 1999). Predation by *C. undecimpunctata* and *H. axyridis* on four IGprey (in absence of EGprey) was lower than expected, although it was not significantly lower for the latter. Based on these results we may hypothesize that a higher number of predators inside the guild may lead to an increase in walking what would be advantageous for IGprey in order to avoid being preyed. This hypothesis should be however tested.

The results of this study suggest that *H. axyridis* is an IGpredator, mainly of the most vulnerable stages of IGprey, even when aphids are present. Moreover, the results also suggest that the increase in competition between IGpredator and IGprey when there is an increase in the number of EGprey may promote the occurrence of IGP.

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