

Alien vs. Predator – the native lacewing *Chrysoperla carnea* is the superior intraguild predator in trials against the invasive ladybird *Harmonia axyridis*

Oldřich NEDVĚD^{1,2}, Xenia FOIS³, Dita UNGEROVÁ¹, Plamen KALUSHKOV⁴

¹Faculty of Sciences, University of South Bohemia, České Budějovice, Czech Republic

²Institute of Entomology, Biology Center, České Budějovice, Czech Republic

³Istituto per lo Studio degli Ecosistemi CNR, Sassari, Italy

⁴Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria

Abstract

The alien invasive ladybird *Harmonia axyridis* (Pallas) (Coleoptera Coccinellidae) is a biological control agent of aphids and in the larval stage it is a very voracious and superior intraguild predator over most native ladybirds studied, except the large species *Anatis ocellata* (L.). We report the first aphidophagous insect - lacewing *Chrysoperla carnea* (Stephens) (Neuroptera Chrysopidae) - which is a superior intraguild predator, despite its smaller size, over the aggressive invasive ladybird *H. axyridis* in larval stage. We also observed high survival rate of hoverfly larvae *Episyrphus balteatus* (De Geer) and *Epistrophe eligans* (Harris) (Diptera Syrphidae), when exposed to ladybird larvae. Ladybird larvae were killed by lacewing larvae, individually paired in an empty Petri dish without food and water, in 50% of the cases when second instar larvae of both species were tested, in 94% of the cases with third instar larvae, and in 52% of the cases when third instar larvae of the lacewing were paired with much heavier fourth instar ladybird larvae. Larvae of the hoverflies *E. balteatus* were partially (27% of cases) and *E. eligans* strongly (76% of cases) protected against intraguild predation (= were not killed during experiment) by *H. axyridis*, but they never killed ladybird larvae. These results suggest that high biological diversity could be retained in crops and natural habitats, with possible synergistic effects on pests.

Key words: Coccinellidae, Chrysopidae, Syrphidae, aphid, IGP, multicolored Asian ladybird.

Introduction

Concerns about intraguild predation (IGP) of native aphid predators by the invasive ladybird *Harmonia axyridis* (Pallas) (Coleoptera Coccinellidae) in North America and Europe (Majerus *et al.*, 2006) and its effect on the overall biological control of aphids (Rosenheim *et al.*, 1995) has led to a number of attempts to quantify the impact of the invader on native aphidophagous insects. In laboratory interactions, *H. axyridis* was generally the dominant predator (Koch, 2003; Koch and Galvan, 2008; Ware and Majerus, 2008; Rondoni *et al.*, 2012). Long term studies in several European countries demonstrated significant decline of several native ladybird species after the arrival of *H. axyridis* (Roy *et al.*, 2012). However, adverse effects on the biological control of aphid pests due to IGP have not been reported.

Larvae of *H. axyridis* are larger and more aggressive than the larvae of the same instar of most other species of ladybirds (Cottrell and Yeorgan, 1998; Michaud, 2002; Felix and Soares, 2004; Yasuda *et al.*, 2004; Rondoni *et al.*, 2012). When paired with a larger larva of a different species, *H. axyridis* can win [e.g. against *Cycloneda sanguinea* (L.), Michaud, 2002] but often loses [e.g. against *Coleomegilla maculata* (DeGeer), Cottrell and Yeorgan, 1998; *Anatis ocellata* (L.), Ware and Majerus, 2008]. Snyder *et al.* (2004) suggested that the relative size of *H. axyridis* compared to its prey is not of great importance. Felix and Soares (2004) showed that increase in body weight of the intraguild predator (*H. axyridis*) did not significantly increase the rate of predation on another ladybird, *Coccinella undecimpunctata* L. The greater success of *H. axyridis* against *Coccinella*

septempunctata L. was attributed to its higher attack rates and greater escape ability (Yasuda *et al.*, 2001). The defensive chemistry of *H. axyridis* may make them unpalatable to other predatory insects (Hough-Goldstein *et al.*, 1996): no first instar larvae of *H. axyridis* were killed by the fourth instar larvae of *Adalia bipunctata* (L.) over a period of 10 minutes (Sato *et al.*, 2009).

The design we used in our experiment was accepted and regularly used (Noia *et al.*, 2008; Ware and Majerus, 2008; Rondoni *et al.*, 2012), but does not allow extrapolation to the field. It is unrealistic in terms of size of the arenas and the long time that predators are exposed to each other. The magnitude of IGP in nature would be much smaller, but its asymmetric nature is likely to be similar. Larvae of *Chrysoperla carnea* (Stephens) (Neuroptera Chrysopidae) were the superior intraguild predators against larvae of the ladybird *C. maculata*, winning 89% of contests in Petri dishes, while the asymmetry decreased to 63% in microcosms with plant material (Noppe *et al.*, 2012). The size of the arena affected the incidence of IGP in combinations of *H. axyridis* with second instars of *Episyrphus balteatus* (De Geer), but not in combinations with third instars (Ingels and De Clercq, 2011). Increase in extraguild prey (aphids) and intraguild prey (*C. undecimpunctata*) density did not alter the direction, but also decreased the magnitude and asymmetry of IGP (Noia *et al.*, 2008). Thus, real IGP in nature might be milder than suggested by the results of combats between two starving larvae in a Petri dish.

Sloggett *et al.* (2009) highlighted an effect that has remained hidden, due to the methodological approach used in earlier studies: defensive alkaloids of certain native ladybirds may be toxic, although laboratory evi-

dence suggests that *H. axyridis* readily attacks this prey. Eggs of the ladybird *Calvia quatuordecimguttata* (L.) appeared to be chemically well-protected from the attack by *H. axyridis* (Ware et al., 2008), while eggs of *C. maculata* were attacked but not much suitable for development (Sloggett et al., 2009).

The lacewing *C. carnea* (and related cryptic species) is a relatively common predator of aphids and is also an intraguild predator. Fremlin (2007) found that *C. carnea* attacks larvae and pupae of *H. axyridis* in the field. Reciprocal predation of eggs is known to occur. Feeding on eggs of the lacewing *C. carnea* by larvae of *H. axyridis* lead to the same developmental time and survival as when fed on aphids (Phoofolo and Obrycki, 1998). *C. carnea* also feeds on eggs of *H. axyridis* (Phoofolo and Obrycki, 1998), although *H. axyridis* eggs are not suitable alone for the larval development of *C. carnea* (Santi and Maini, 2006). *H. axyridis* has been recorded to feed on various stages of the lacewing *C. carnea* (Gardiner and Landis, 2007). Lacewings were detected over much of the season in several locations in Florida dominated by *H. axyridis*, while no other predators or parasitoids were detected (Mizell, 2007).

Fremlin (2008) also observed predation by *H. axyridis* adults on a larva of hoverfly *Syrphus ribesii* L. (Diptera Syrphidae). Syrphid flies [especially *Pseudodoros clavatus* (F.)] were important predators of brown citrus aphid, *Toxoptera citricida* (Kirkaldy), in Florida, alongside with two ladybird species, *C. sanguinea* and *H. axyridis* (Michaud, 1999). The influence of body size, presence of aphid prey and arena size (Petri dishes and potted broad bean plants) on IGP were investigated between *H. axyridis* and the hoverfly *E. balteatus* (Ingels and De Clercq, 2011). The ladybird was the intraguild predator in the majority of cases and its efficiency increased with the developmental stage. Pupae of either species were not attacked. Eggs and larvae of *E. balteatus* faced high IGP by *H. axyridis* in laboratory which was considered important for possible decline in *E. balteatus* population following *H. axyridis* invasion (Alhmedi et al., 2010).

Pell et al. (2008) suggested that research that would test the symmetry of the relationship between those predators would be of value. Thus, the aim of this study was to characterize the direction, symmetry and strength of the IGP between larvae of native predators, the lacewing *C. carnea* and hoverflies *E. balteatus* and *Epistrophe eligans* (Harris), and the alien ladybird *H. axyridis*. This is the first report of aphidophagous insect which is a superior intraguild predator in confrontations with *H. axyridis* despite its smaller size.

Materials and methods

Experimental animals

Adult ladybirds *H. axyridis* were collected on shrubs in June in České Budějovice, Czech Republic (49°00'N, 14°27'E), and laboratory stocks were established using the most common *succinea* colour morph of this polymorphic species. Pairs of ladybirds were maintained in 9 cm Petri dishes at 20 °C, 60% RH and 18L:6D photo-

period; they were fed with pea aphids, *Acyrtosiphon pisum* (Harris), and provided with water in a small vial plugged with cotton. Eggs were removed daily from the dishes, and larvae were reared under the same conditions as their parents.

Adult lacewings, *C. carnea*, were collected outside on trees in autumn. Although they had still their summer green colour, we considered them to be in diapause, and thus we treated them with the juvenile hormone analogue methoprene (two microlitres of 1% solution in acetone) to induce reproduction (Zdarek et al., 2000). Adults were maintained in groups on a diet of honey and pollen of *Typha angustifolia* L. Eggs were removed and the lacewing larvae were reared in similar conditions as ladybird larvae, except the rearing temperature was 25 °C.

The larvae of *H. axyridis* were also paired with larvae of two species of hoverflies (Diptera Syrphidae), either *E. balteatus* or *E. eligans*. Small fly larvae collected in the field in the same place as *H. axyridis* were reared in the same conditions as lacewings and fed with *A. pisum* to attain approximately the same mass as *H. axyridis* larvae.

Contests

The second, third, and fourth (last) instar larvae were individually paired with lacewing and hoverfly larvae in clean Petri dishes in experiments. Adults were not tested because common green lacewings and hoverflies are not predaceous in the adult stage. The second and third (last) instar lacewing larvae were paired with ladybird larvae. The contests were arranged following the method by Ware and Majerus (2008), i.e. in an empty 9 cm glass Petri dish without food and water, at 20 °C, 60% relative humidity and 18L:6D photoperiod, about 2000 lux light intensity. The larvae in dishes were observed from 10 o'clock AM each hour during the photophase up to 48 hours. Time of predation and making of cocoon or pupation were noted. Larvae were weighed before the experiment using an electronic microbalance accurate to 0.1 mg. The third and fourth instar larvae of *H. axyridis* were paired with larvae of hoverflies. The conditions of the contest with hoverfly larvae were the same as above, except a piece of moist cotton was present to prevent desiccation of the fly larvae.

Data processing

Levels (IL) and symmetry (SI) of intraguild predation (IGP) were calculated following the method described by Lucas et al. (1998): IL was the proportion of replicates with IGP over total number of replicates; SI was the proportion of replicates in which a given predator was eaten over the number of replicates in which there was IGP. A symmetry greater than 0.5 means that *C. carnea* was more successful predator, while value less than 0.5 means that *H. axyridis* was the more effective predator. Yates corrected χ^2 test (Statistica 8.0 software package) was used to test whether the symmetry differed significantly from 50% and two tailed Fisher's exact test for 2 × 2 table were used to compare symmetry between instars. The time to death was compared non-parametrically using a Mann-Whitney test.

Results

The mass of the *H. axyridis* second instar larvae and mass of *C. carnea* second instar larvae before the experiment were comparable (table 1), as well as the masses of the third instars. *H. axyridis* fourth instar larvae were 2.7× heavier than *C. carnea* third instar larvae with which they were paired.

Contests between second instar larvae of *H. axyridis* and *C. carnea* had symmetric results (table 2). The average time-to-win values did not differ ($z = 0.74$, $p = 0.46$). In the contest between third instar larvae, the larva of *C. carnea* killed the larva of *H. axyridis* in most cases ($\chi^2 = 5.6$, $p = 0.02$). In a part of the contests between fourth instar larva of *H. axyridis* and third instar larva of *C. carnea*, both larvae survived until the end of experiment. In the others, *C. carnea* was more successful, but the deviation from symmetry was not significant ($\chi^2 = 1.4$, $p = 0.38$). The average time-to-win was shorter in larvae of *H. axyridis* ($z = 2.5$, $p = 0.016$). Fisher's exact test showed that the level of IGP was lower ($p = 0.04$) in the third type of contest (third against fourth instar) than in the second type (third against third instar). Symmetry in the second treatment differed from the first one (second against second instar, $p = 0.015$) but not from the third one ($p = 0.06$).

In seven of the eight cases where both last instar larvae survived, and in three cases of those 17, when the lacewing larva killed and ate the ladybird larva, the lacewing subsequently spun a cocoon and successfully pupated. More lacewing larvae pupated after additional feeding by aphids. Ladybird larvae did not attack cocoons with lacewing pupae.

When larva of *H. axyridis* attacked the lacewing larva, it approached it from one side or from behind and bit it on the dorsal side. The lacewing larva tried to defend itself but was overpowered. When larva of *C. carnea* attacked the ladybird larva, it pierced the soft abdominal

sternites from below (figure 1) using its jaws (mandibular-maxillary sucking complex). The ladybird larva then stayed almost motionless, and the lacewing larva was able to probe and suck the bodily contents out.

In the additional experiments with hoverflies, third and fourth instar *H. axyridis* larvae killed more than half of same size *E. balteatus* larvae; and fourth instar *H. axyridis* killed small proportion of same size *E. eligans* larvae (table 2). Some syrphid larvae defended themselves after an attack by ladybird larva, they moved and twisted. However, no syrphid ever attacked a ladybird larva, so that symmetry of intraguild predation was not calculated. Ladybird larvae often interrupted their attacks and abandoned a syrphid larva.

Discussion

The native lacewing *C. carnea* was the superior intraguild predator in trials against the invasive ladybird *H. axyridis*; two hoverfly species, *E. balteatus* and *E. eligans* defended themselves against IGP. Until now, there was only one member of the aphidophagous guild known to effectively kill *H. axyridis*, the eyed ladybird *A. ocellata*, which is larger than *H. axyridis*. *C. carnea* is the first aphidophagous insect that appeared superior to *H. axyridis* in IGP encounters despite its smaller size.



Figure 1. Third instar *C. carnea* larva biting into soft abdominal segments of its intraguild prey, fourth instar *H. axyridis* larva.

(In colour at www.bulletinofinsectology.org)

Table 1. Body mass (BM, mg) of the larvae of individual instars included in IGP contests.

Species	Instar	BM average	BM range
<i>H. axyridis</i>	second	3.1	2.6-3.4
	third	14	12-16
	fourth	35	28-38
<i>C. carnea</i>	second	2.6	2.2-2.9
	third	13	11-14

Table 2. Composition of IGP pairs, number of replications (N), number of killed individuals of *H. axyridis* (a) and second species (b), level of IGP (IL) and symmetry of IGP (SI), average time-to-win (TTW, hours) of *H. axyridis* and *C. carnea*.

<i>H. axyridis</i> instar	second species	instar	N (a, b)	IL	SI	TTW	
						<i>H. axyridis</i>	<i>C. carnea</i>
second	<i>C. carnea</i>	second	10 (5, 5)	1.00	0.50	25	20
third	<i>C. carnea</i>	third	17 (16, 1)	1.00	0.94	38	19
fourth	<i>C. carnea</i>	third	33 (17, 8)	0.76	0.68	11	23
third	<i>E. balteatus</i>	third	14 (0, 10)	0.71	0	23	
fourth	<i>E. balteatus</i>	third	20 (0, 15)	0.75	0	22	
fourth	<i>E. eligans</i>	third	17 (0,4)	0.24	0	24	

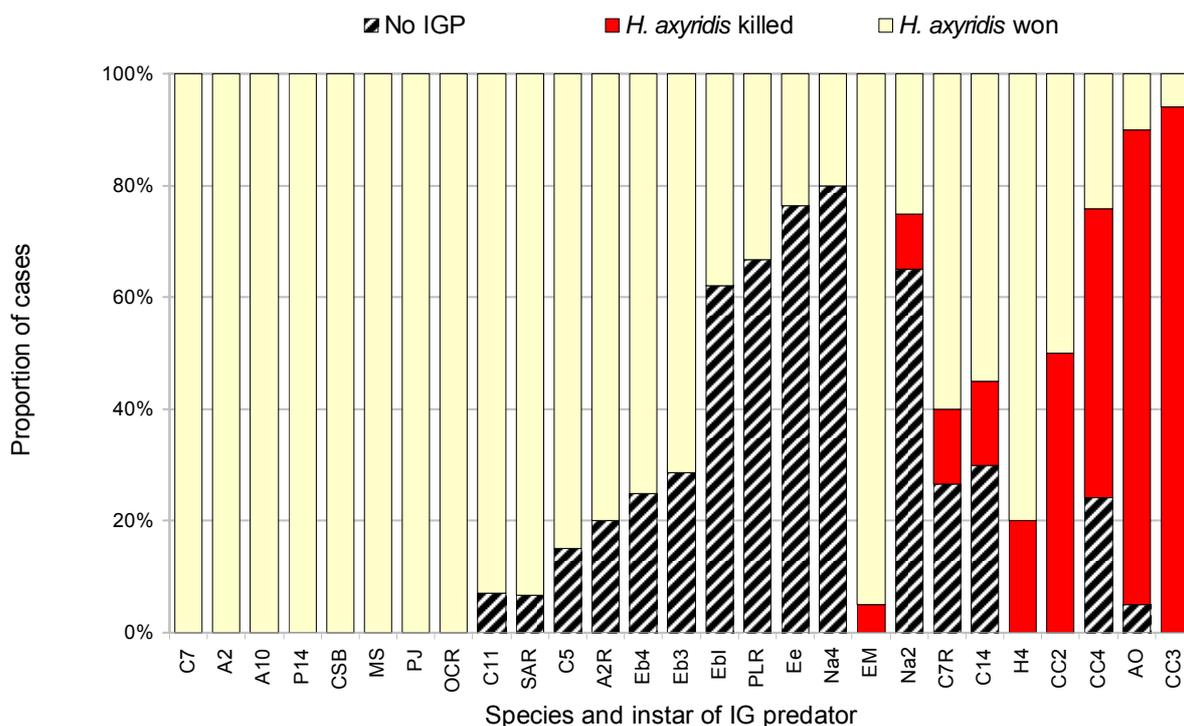


Figure 2. Review of so far studied cases of intraguild predation between *Harmonia axyridis* and other aphidophagous insects ordered according to the symmetry of the result of combat. Twelve results originate from the study by Ware and Majerus (2008): larvae of the fourth instars of ladybirds (Coleoptera Coccinellidae); C7 = *Coccinella septempunctata*, A2 = *Adalia bipunctata*, A10 = *Adalia decempunctata*, P14 = *Propylea quatuordecimpunctata*, C5 = *Coccinella quinquepunctata*, H4 = *Harmonia quadripunctata*, C14 = *Calvia quatuordecimguttata*, AO = *Anatis ocellata*, CSB = *Coccinella septempunctata brucki*, MS = *Menochilus sexmaculatus*, PJ = *Propylea japonica*, EM = *Eocaria muiri*; one case comes from Noia *et al.* (2008): fourth instar of ladybird C11 = *Coccinella undecimpunctata*; five cases from Rondoni *et al.*, 2012: fourth instar larvae of A2R = *A. bipunctata*, OCR = *Oenopia conglobata*, C7R = *C. septempunctata*, PLR = *Platynaspis luteorubra*, SAR = *Scymnus apetzzi*; one from Ingels and De Clercq (2011): Eb1 = third instar larvae of hoverfly (Diptera Syrphidae) *Episyrphus balteatus* with third instar of *H. axyridis*; two from Takizava and Snyder (2012): Na2 = *Nabis alternatus* larva with second instar of *H. axyridis*, Na4 = *N. alternatus* larva with fourth instar of *H. axyridis*; other cases were achieved in this study: Eb3 = larvae of hoverfly *E. balteatus* with third instar of *H. axyridis*, Eb4 = larvae of *E. balteatus* with fourth instar of *H. axyridis*, Ee = larvae of hoverfly *Epistrophe eligans* with fourth instar of *H. axyridis*, CC2 = larvae of the second instar of *Chrysoperla carnea* (Neuroptera Chrysopidae) and *H. axyridis*, CC3 = larvae of the third instar of *C. carnea* and *H. axyridis*, CC4 = larvae of the third instar of *C. carnea* and the fourth instar of *H. axyridis*. (In colour at www.bulletinofinsectology.org)

Since the time to win was shorter for ladybird larvae as predators, we agree with previous authors (Yasuda *et al.*, 2001; Snyder *et al.*, 2004; Nedvĕd *et al.*, 2010) who emphasized the high aggressiveness of *H. axyridis*. It exhibits high attack rates or great ability to capture intraguild prey and can avoid predation. The properties of lacewing larvae that enable them to survive these attacks and capture ladybird larvae should be investigated.

Some lacewing larvae carry a protective shield (made of pieces of plant material, exuviae or dead prey) on its dorsal side, but this is not the case of *C. carnea*. Puffs of long hairs (trichomes) on thorax and abdomen may help in defence, although they are not dense enough. Chemical defence in lacewings is not well-known, but an abdominal secretion is believed to be smeared on enemies. In any case, lacewing larvae are highly mobile and may simply escape from similar predators. The trash package carried on the dorsal side of body of *Mallada desjar-*

dinsi (Navas) larvae did not protect them against prevalent IGP by *C. carnea* third instar larvae (Mochizuki *et al.*, 2006).

Hoverfly larvae *E. balteatus* were partially and *E. eligans* strongly protected against IGP. They defended themselves both actively by rapid movements and passively by their slimy surface. Among IGP prey species published to date, coccinellid *Platynaspis luteorubra* (Goeze) seems to be also protected in some way (Rondoni *et al.*, 2012) (figure 2) against *H. axyridis* but not against *A. bipunctata* and *C. septempunctata*. Larvae of *P. luteorubra* lack mechanical protection found in other ladybirds such as scoli or senti. The waxy exudations of larvae of *Scymnus* species do not protect them against *H. axyridis* predation (Nedvĕd *et al.*, 2010; Rondoni *et al.*, 2012; figure 2).

It was hypothesised (Sloggett *et al.*, 2009) that native ladybirds may be toxic to *H. axyridis*, although labora-

tory experiments suggest *H. axyridis* readily attacks these prey. Whether lacewing and hoverfly larvae possess chemical compounds effective against attack or decreasing survival and increasing developmental time remain to be tested.

Fourth instar larvae of several European and Japanese ladybirds were ineffective against *H. axyridis* (Ware and Majerus, 2008), except *A. ocellata* and partially *Harmonia quadripunctata* (L.) and *C. quatuordecimguttata* (figure 2). The results of encounters between first instar larvae were more symmetrical, similarly to our second instar trial.

The ability of lacewing larva to kill larva of *H. axyridis* can be mainly attributed to the long mandibulo-maxillar piercing complex. Long spiny protuberances on the dorsal side of *H. axyridis* larvae do not protect them against lacewing long mouthparts, and the lacewing larva can even reach soft smooth ventral side of the body, which was already reported by Fremlin (2007). The fact that ladybird larva stayed motionless soon after the lacewing larva attacked suggests an existence of unknown paralysing compound in the saliva of the lacewing.

Although the chemical defence of *H. axyridis* is effective against many predators including other ladybirds, lacewing *C. carnea* was apparently not repelled, neither subsequently affected by these toxic compounds. Lacewing larvae successfully pupated after substantial feeding on the ladybird. We do not know whether they would be able to complete entire developmental cycle on the diet consisting only from *H. axyridis*. On the other hand, ladybird larvae often abandoned a hoverfly larva probably because its slimy soft surface.

In a microcosm experiment (Gardiner and Landis, 2007), adult *H. axyridis* removed an average of 1.07 ± 0.28 individual lacewing larva within 3 h of foraging, leaving on average 1.67 ± 0.29 lacewing larvae. However, another intraguild prey, the fly *Aphidoletes aphidimyza* (Rondani) was reduced much more strongly. This may be because *C. carnea* are larger, more mobile, or less preferred intraguild prey than *A. aphidimyza*. However, in the field, Brown (2003) found no decrease in the abundance of *A. aphidimyza* and various chrysopid species after the establishment of *H. axyridis*. Among four ladybird species tested, *H. axyridis* was the least susceptible to intraguild predation by the predatory bugs *Nabis alternatus* Parshley and *Geocoris bullatus* (Say) and was the most likely to consume the bugs (Takizava and Snyder, 2012).

Niche overlap between large generalist *H. axyridis* and smaller or specialized aphidophagous species may be small not only in space but also in time; large species exploiting larger or abundant prey (Sloggett, 2008) and being later (Honěk *et al.*, 2008). When *H. axyridis* dominated observed plants, most other aphidophagous insects were out competed or killed, only lacewings survived and contributed in suppression of aphids (Mizell, 2007). This observation supports the relevance of our laboratory findings.

Although it was shown that *H. axyridis* caused decline in abundance and distribution of several native ladybird species in Europe (Roy *et al.*, 2012) through competi-

tion and IGP, the loss of biodiversity and of ecosystem services may not be as strong as the laboratory experiments suggest. This is because of the lower magnitude of IGP under natural conditions, and because the ladybird has some powerful native competitors (*A. ocellata*, *C. carnea*) in Europe. Several species of aphidophagous predators including alien *H. axyridis* and native *C. carnea* and syrphid flies probably function synergistically in the biological control of aphids.

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References

- ALHMEDI A., HAUBRUGE E., FRANCIS F., 2010.- Intraguild interactions and aphid predators: biological efficiency of *Harmonia axyridis* and *Episyrphus balteatus*.- *Journal of Applied Entomology*, 134: 34-44.
- BROWN M. W., 2003.- Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*.- *BioControl*, 48: 141-153.
- COTTRELL T. E., YEARGAN K. V., 1998.- Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae).- *Journal of Kansas Entomological Society*, 71: 159-163.
- FELIX S., SOARES A. O., 2004.- Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera : Coccinellidae): the role of body weight.- *European Journal of Entomology*, 101: 237-242.
- FREMLIN M., 2007.- Intra-guild predation of harlequin ladybird larvae by lacewing larvae.- *Bulletin of Amateur Entomological Society*, 66: 110-116.
- FREMLIN M., 2008.- Intra-guild predation of hoverfly larvae by harlequin ladybirds.- *Bulletin of Amateur Entomological Society*, 67: 148-150.
- GARDINER M. M., LANDIS D. A., 2007.- Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies.- *Biological Control*, 40: 386-395.
- HARMON J. P., STEPHENS E., LOSEY J., 2007.- The decline of native ladybirds (Coleoptera: Coccinellidae) in the United States and Canada.- *Journal of Insect Conservation*, 11: 85-94.
- HONEK A., DIXON A. F. G., MARTINKOVA Z., 2008.- Body size and the temporal sequence in the reproductive activity of two species of aphidophagous coccinellids exploiting the same resource.- *European Journal of Entomology*, 105: 421-425.
- HOUGH-GOLDSTEIN J., COX J., ARMSTRONG A., 1996.- *Podisus maculiventris* (Hemiptera: Pentatomidae) predation on ladybird beetles (Coleoptera: Coccinellidae).- *Florida Entomologist*, 79: 64-68.
- INGELS B., DE CLERCQ P., 2011.- 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*.- *BioControl*, 56: 871-882.
- KOCH R. L., 2003.- The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control and non-target impacts.- *Journal of Insect Science*, 3: 116.

- KOCH R. L., GALVAN T. L., 2008.- Bad side of a good beetle: the North American experience with *Harmonia axyridis*.- *BioControl*, 53: 23-36.
- LUCAS E., CODERRE D., BRODEUR J., 1998.- Intraguild predation among aphid predators: characterization and influence of extraguild prey density.- *Ecology*, 79: 1084-1092.
- MAJERUS M. E. N., STRAWSON V., ROY H. E., 2006.- The potential impacts of the arrival of the halloween ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain.- *Ecological Entomology*, 31: 207-215.
- MICHAUD J. P., 1999.- Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*.- *BioControl*, 44: 347-367.
- MICHAUD J. P., 2002.- Invasion of the Florida Citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*.- *Environmental Entomology*, 31: 827-835.
- MIZELL R. F., 2007.- Impact of *Harmonia axyridis* (Coleoptera: Coccinellidae) on native arthropod predators in pecan and crape myrtle.- *Florida Entomologist*, 90: 524-536.
- MOCHIZUKI A., NAKA H., HAMASAKI K., MITSUNAGA T., 2006.- Larval cannibalism and intraguild predation between the introduced green lacewing, *Chrysoperla carnea*, and the indigenous trash carrying green lacewing, *Mallada desjardinsi* (Neuroptera : Chrysopidae), as a case study of potential nontarget effect assessment.- *Environmental Entomology*, 35: 1298-1303.
- NEDVĚD O., KALUSHKOV P., FOIS X., UNGEROVÁ D., ROZSYPALOVÁ A., 2010.- *Harmonia axyridis*: six-legged alligator or lethal fugu?- *IOBC/wprs Bulletin*, 58: 65-68.
- NOIA M., BORGES I., SOARES A. O., 2008.- Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): The role of intra and extraguild prey densities.- *Biological Control*, 46: 140-146.
- NOPPE C., MICHAUD J. P., DE CLERCQ P., 2012.- Intraguild predation between lady beetles and lacewings: outcomes and consequences vary with focal prey and arena of interaction.- *Annals of the Entomological Society of America*, 105: 562-571.
- PELL J. K., BAVERSTOCK J., ROY H. E., WARE R. L., MAJERUS M. E. N., 2008.- Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives.- *BioControl*, 53: 147-168.
- PHOOFOLO M. W., OBRYCKI J. J., 1998.- Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae.- *Entomologia Experimentalis et Applicata*, 89: 47-55.
- RONDONI G., ONOFRI A., RICCI C., 2012.- Laboratory studies on intraguild predation and cannibalism among coccinellid larvae (Coleoptera: Coccinellidae).- *European Journal of Entomology*, 109: 353-362.
- ROSENHEIM J. A., KAYA H. K., EHLE L. E., MAROIS J. J., JAFFEE B. A., 1995.- Intraguild predation among biological control agents: theory and evidence.- *Biological Control*, 5: 303-335.
- ROY H. E., ADRIAENS T., ISAAC N., KENIS M., ONKELINX T., SAN MARTIN G., BROWN P. M. J., HAUTIER L., POLAND R., ROY D. B., COMONT R., ESCHEN R., FROST R., ZINDEL R., VAN VLAENDEREN J., NEDVĚD O., RAVN H. P., GRÉGOIRE J. C., DE BISEAU J.-C., MAES D., 2012.- Invasive alien predator causes rapid declines of native European ladybirds.- *Diversity and Distributions*, 18 (7): 717-725.
- SANTI F., MAINI S., 2006.- Predation upon *Adalia bipunctata* and *Harmonia axyridis* eggs by *Chrysoperla carnea* larvae and *Orius laevigatus* adults.- *Bulletin of Insectology*, 59: 53-58.
- SATO S., YASUDA H., EVANS E. W., DIXON A. F. G., 2009.- Vulnerability of larvae of two species of aphidophagous ladybirds, *Adalia bipunctata* Linnaeus and *Harmonia axyridis* Pallas, to cannibalism and intraguild predation.- *Entomological Science*, 12: 111-115.
- SLOGGETT J. J., 2008.- Weighty matters: Body size, diet and specialization in aphidophagous ladybird beetles (Coleoptera: Coccinellidae).- *European Journal of Entomology*, 105: 381-389.
- SLOGGETT J. J., HAYNES K. F., OBRYCKI J. J., 2009.- Hidden costs to an invasive intraguild predator from chemically defended native prey.- *Oikos*, 118 (9): 1396-1404.
- SNYDER W. E., CLEVINGER G. M., EIGENBRODE S. D., 2004.- Intraguild predation and successful invasion by introduced ladybird beetles.- *Oecologia*, 140: 559-565.
- STATSOFT INC., 2008.- *STATISTICA (data analysis software system), version 8.0.*- Tulsa, USA.
- TAKIZAWA T., SNYDER W. E., 2012.- Alien vs. predator: Could biotic resistance by native generalist predators slow lady beetle invasions?- *Biological Control*, 63: 79-86.
- WARE R. L., MAJERUS M. E. N., 2008.- Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird *Harmonia axyridis*.- *BioControl*, 53: 169-188.
- WARE R. L., RAMON-PORTUGAL F., MAGRO A., DUCAMP C., HEMPTINNE J. L., MAJERUS M. E. N., 2008.- Chemical protection of *Calvia quatuordecimguttata* eggs against intraguild predation by the invasive ladybird *Harmonia axyridis*.- *BioControl*, 53: 189-200.
- YASUDA H., KIKUCHI T., KINDLMANN P., SATO S., 2001.- Relationship between attacks and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds.- *Journal of Insect Behaviour*, 14: 373-384.
- YASUDA H., EVANS E. W., KAJITA Y., URAKAWA K., TAKIZAWA T., 2004.- Asymmetrical larval interactions between introduced and indigenous ladybirds in North America.- *Oecologia*, 141: 722-731.
- ZDAREK J., CTVRTECKA R., HOVORKA O., KOSTAL V., 2000.- Activation of gonads and disruption of imaginal diapause in the apple blossom weevil, *Anthonomus pomorum* (Coleoptera : Curculionidae), with juvenoids in laboratory and field trials.- *European Journal of Entomology*, 97: 25-31.

Authors' addresses: Oldřich NEDVĚD (corresponding author: nedved@prf.jcu.cz), Dita UNGEROVÁ, Faculty of Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic; Xenia FOIS, Istituto per lo Studio degli Ecosistemi CNR, sede di Sassari, Italy; Plamen KALUSHKOV, Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Blvd. Tzar Os-voboditel, 1000 Sofia, Bulgaria.

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