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Intraguild predation among three aphidophagous predators

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Abstract

In biological control the combined use of natural enemies has been suggested as a strategy to enhance pest regulation. Therefore, studying intraguild predation (IGP) effects offers valuable information in the optimal use of multiple biological control agents. In this work, IGP interactions and their consequences in prey consumption were investigated among three aphidophagous predators and their instars in combinations of two or three species i.e *Adalia bipunctata* (2nd, 3rd and 4th larval instar), *Macrolophus pygmaeus* (2nd and 5th nymphal instar) and *Aphidoletes aphidimyza* (2nd and 3rd larval instar) in the absence and presence of extraguild prey (the aphid *Myzus persicae*). In the absence of extraguild prey, larvae of *A. bipunctata* always preyed upon and nymphs of *M. pygmaeus* killed a high proportion of the larvae of *A. aphidimyza*. Direct IGP between *A. bipunctata* and *M. pygmaeus* was not recorded but another experiment revealed that *M. pygmaeus* preyed readily upon the eggs of *A. bipunctata*. In presence of aphids there was no adverse effect and even more, when released all the three species together in several cases the observed predation rates were significantly higher than the expected. Finally, partial aphid consumption rates showed evidence for IGP interactions between *A. aphidimyza* and *M. pygmaeus.*

Key words: intraguild predation, *Adalia bipunctata*, *Aphidoletes aphidimyza*, *Macrolophus pygmaeus*, *Myzus persicae*, biological control, aphid, multiplicative risk model.

Introduction

Intraguild predation (IGP) occurs in food webs where a member of the guild (all species exploiting a similar resource, regardless of their nutrition mode, ecology, or taxonomic position) preys upon another member of the same guild (Polis *et al.*, 1989; Janssen *et al.,* 2007). Intraguild interactions involves a competitor or aggressor (IG predator), a victim predator (IG prey) and their shared prey (extraguild prey). Intraguild interactions are common among biological control agents (Rosenheim *et al.*, 1995; van Veen *et al.*, 2006) and may largely influence their effectiveness in pest control (Rosenheim *et al.*, 1993; 1995; Snyder and Wise, 1999; Ferguson and Stiling, 1996; Lucas *et al.*, 1998; Nóia *et al.*, 2008). The intensity of the IG interactions is expected to be stronger on smaller size individuals (Hindayana *et al.*, 2001; Lucas, 2012; Rondoni *et al.*, 2014), less mobile individuals (Lucas *et al.*, 1998; Hindayana *et al.*, 2001; Frechette *et al.*, 2008), on less complex environments and less availability rate of extraguild prey (Polis and Holt, 1992; Lucas *et al.*, 1998; Finke and Denno, 2002; Yasuda *et al.*, 2004; Chacón and Heimpel, 2010; Lucas and Rosenheim, 2011).

Specialist and generalist natural enemies may show complementary ecological adaptations that may increase their effect in pest suppression when act in concert rather than when used singly (Snyder and Ives, 2003; Straub *et al.*, 2008). In protected crops, combination of natural enemies in augmentation biological control programs may offer control of a set of co-occurring pests (Chow *et al.*, 2008; Colomer *et al.*, 2011; Chailleux *et al.*, 2013), earlier colonization and higher efficacy to reduce high numbers of pests (Messenlink *et al.*, 2013). Therefore, studies exploring IGP offer valuable insights in the optimization of biological control strategies in greenhouse crops (Enkegaard and Brødsgaard, 2006; van Lenteren, 2012).

The aphid predators *Adalia bipunctata* (L.) (Coleoptera Coccinellidae), *Macrolophus pygmaeus* (Rambur) (Hemiptera Miridae) and *Aphidoletes aphidimyza* (Rondani) (Diptera Cecidomyiidae) commonly co-exist on vegetable crops and are commonly released to control aphids in greenhouse crops. *A. bipunctata* is a major natural enemy of *Myzus persicae* (Sulzer) (Hemiptera Aphididae) (Jalali *et al.*, 2009; 2010; Jalali and Michaud, 2012) and is used in augmentative biological control in greenhouses (Wyss *et al.*, 1999a; 1999b; De Clercq *et al.*, 2005; Robledo Camacho *et al.*, 2009). Research has focused on its IGP interactions with other ladybird species (Hentley *et al.*, 2016). *A. bipunctata* IGP behaviour has been widely studied around the world, either in its native area (Burgio *et al.*, 2002; Ware and Majerus, 2008) or in Japan where it failed to invade after its introduction (Kajita *et al.*, 2000; 2006).

M. pygmaeus is a zoophytophagous predator effective against whiteflies, aphids and Lepidoptera in protected and open-field tomato and eggplant crops (Perdikis *et al.*, 2008; 2014; Arnó *et al.*, 2009; Urbaneja *et al.*, 2009; Trotta *et al.*, 2015) and is commonly used in augmentative biological control programs in Europe (van Lenteren, 2012). In addition to prey, *M. pygmaeus* also shows phytophagous habits developing successfully and ovipositing when feeding only on leaves of tomato or eggplant (Perdikis and Lykouressis, 2000). Its common use and polyphagy has triggered studies investigating its possible interference with other natural enemies such as *Diglyphus isaea* (Walker) (Hymenoptera Eulophidae), *Encarsia formosa* Gahan (Hymenoptera Aphelinidae), syrphids, *Orius majusculus* (Reuter) (Hemiptera Anthocoridae), *Nesidiocoris tenuis* Reuter (Hemiptera Miridae) and *Dicyphus tamaninii* Wagner (Hemiptera Miridae) (Nedstam and Johansson-Kron, 1999; Lucas and Alomar, 2002; Jakobsen *et al.*, 2004; Fréchette *et al.*, 2007; Moreno-Ripoll *et al.*, 2014; Perdikis *et al.*, 2014; Trotta *et al.*, 2015). Another member of the guild of aphidophagous predators on vegetable crops is a specialist one, the gall midge *A. aphidimyza*. This is an effective predator widely used in aphid biological control in greenhouse crops (Messelink *et al.*, 2013; Higashid *et al.*, 2016; Watanabe *et al.*, 2016). Its larvae creep and paralyze their victim before extracting its body contents. This is considered a predator particularly vulnerable to IGP due to its slow moving and defenceless nature (Lucas *et al.*, 1998; Hindayana *et al.*, 2001).

Overall, the three above mentioned predatory species have variable ecological adaptations and traits i.e. different mouthparts, slow or fast moving larvae. Feeding by predator species with different foraging behaviour may result in an increase in pest suppression due to complementarity of resource use (Soluk and Collins, 1988; Losey and Denno, 1998). However, and despite their wide use in biological control, IGP studies involving those predators are scarce. Evidence on this can be derived from a recent study where the IG interactions were searched between *M. pygmaeus* and *A. bipunctata* (Trotta *et al.*, 2015) indicating that IGP was dependent on the extraguild prey density, and when occurred was asymmetrical with *M. pygmaeus* being always the IG prey. Vellekoop (2008) studied the combined effects of *M. pygmaeus* and *A. aphidimyza* on aphid populations on eggplants. However, as far as we know, IGP between *A. bipunctata* and *A. aphidimyza* and among all the three predator species when used simultaneously have not yet been reported. Furthermore, IGP interactions are usually explored between two natural enemies; as far as we know, very few have explored three-way interactions (but see Rahmani *et al.*, 2015).

In this work IGP interactions were investigated among *A. bipunctata*, *M. pygmaeus* and *A. aphidimyza* in pair wise combinations of different instars and when all the three predators species were acting together. Particular emphasis was given to their interactions: (1) in the absence and presence of the shared extraguild prey the aphid *M. persicae* and (2) among their developmental instars of variable age. Effects on prey consumption and partial prey consumption were recorded since complicated interactions with positive or negative results to biological control may appear in mixtures of natural enemies (Janssen *et al.*, 1998; Messelink *et al.*, 2012; Roubinet *et al.*, 2015).

Materials and methods

Plants and insects

The extraguild aphid prey, *M. persicae,* was reared on potted egg plants (cv. Bonica, General Fitotechniki S.A., Athens, Greece). A culture of *M. pygmaeus* was established with individuals collected in Boeotia, Greece (38.346952N 23.175667E) and maintained in eggplants providing eggs of *Ephestia kuehniella* Zeller (Lepidoptera Pyralidae) (Entofood™ Koppert B.V., The Netherlands). *A. bipunctata* and *A. aphidimyza* (Bio-Insecta, Thessaloniki, Greece) were reared on *M. persicae* in eggplants. Insect rearings were kept in wood framed cages (length 80 cm × width 80 cm × height 70 cm), in an air-conditioned glasshouse maintained at 23 ± 2.5 °C (mean ± SD), 65 ± 5% RH, under natural lighting.

The plants were developed individually in pots (12 cm diameter) with a mixture of peat:perlite 5:1 and were watered two/three times per week. The plants had not been fertilized or treated with any chemical, were visually inspected 3 times a week and any pest found was removed. Eggplants (cv. Bonica), with 4-5 fully developed leaves were used for the experiments.

Experiments

The experiments were carried out in plastic Petri dishes (9 cm diameter, 1.5 cm height) with a mesh-covered hole in their lid (3 cm diameter), in order to reduce the build-up of humidity inside the dish. An eggplant leaf with its lower surface facing upwards was placed in the dish. The periphery of the leaf was firmly attached to the base of the dish with a stripe of wet cotton, so that to prevent aphid or predators' movement to the underside of the leaf.

The IGP intensity was inspected using larvae of *A. bipunctata* of the 2nd, 3rd and 4th (last) instar, nymphs of *M. pygmaeus* of the 2nd and 5th (last) instar and larvae of *A. aphidimyza* of 2nd and 3rd (last) instar. The predators were used singly and in all combinations of two or all the three species together. The effect of extraguild prey on IGP was investigated by testing each combination both in the absence and presence of aphid prey. In the experiments always 24h starved nymphs (or larvae) of the predators were used. For this purpose they were provided with an eggplant leaf in a dish for 24h prior to their use in the experiments. Each treatment was replicated 20 times (a dish was a replication). For starvation, movement less sluggish larvae (1st or 2nd or 3rd instar) were selected and kept individually with aphids in Petri dish and next day morning the fresh active new instar larvae were selected and kept for starvation. Larvae moulted during the experiment were discarded and replaced by new ones. Dishes with predators were kept at 25 ± 1 °C, 65 ± 5% RH and a photoperiod of 16L:8D.

Intraguild interactions between predators without extraguild prey

IG interactions were searched in the absence of aphid prey. The predators were used in all pair-wise combinations of all the three species and their instars as described before. After 24h from their release in the dish, the predators' survival was recorded in each dish.

IGP between *M. pygmaeus* and *A. bipunctata* were further investigated studying the predation rate of *M. pygmaeus* nymphs on eggs of *A. bipunctata*, following identical methodology as above. For this purpose, 20 eggs (one day after their laying) in a single cluster were placed on the eggplant leaf in each Petri dish. A single *M. pygmaeus* 5th instar nymph was released in each dish. After 24h the egg consumption was recorded. The experiment was replicated 15 times.

IGP effects in extraguild prey presence

The predation by individuals of each predator species and instar placed singly in the dish was recorded. On each eggplant leaf in the dish, 50 *M. persicae* nymphs of 3rd and 50 nymphs of the 4thinstar were placed gently and left undisturbed for 1h to settle before the release of predator. After 24h the predator was removed and the numbers of alive and killed aphids in each dish were recorded. Aphids that were entirely consumed by *A. Aphidimyza* or *M. pygmaeus* were completely emptied and only their cuticle remained. Preliminary experiments showed that it was possible to distinguish the aphids preyed upon by *M. pygmaeus* or *A. aphidimyza* since the cuticle of the aphid consumed by the former predator was reddish but when consumed by the latter, it obtained a blackish colour. *A. bipunctata* consumes the whole aphid and thus any aphids missed were considered to be preyed upon by that predator. Our preliminary records showed that *A. bipunctata* did not consume the aphid skins that remain after *M. pygmaeus* or *A. aphidimyza* feeding. In another experiment and aiming to quantify the predation rate of each predator species in a short period after its introduction in the dish, the prey consumption of each instar when used singly was recorded a) after a period of 6h and b) after a period of 24h from their release in the dish, using the same methodology as described before.

Prey partially consumed (sucked but a part of its body mass remained unconsumed) as well as prey killed but left totally unconsumed were also recorded in each dish. This was done because partial prey consumption by *A. aphidimyza* and *M. pygmaeus* has been reported (Uygun, 1971; Fantinou *et al.*, 2008; Lykouressis *et al.*, 2016).

The IGP effects on aphid consumption were examined in all pair-wise combinations of all the three predator species and the respective instars, as described before. In addition, their interactions when using simultaneously one individual of each of the three species were studied.

In all the cases the predators were introduced in the middle of the light cycle at the above-mentioned conditions. In control experiments, the mortality of *M. persicae* without predators and that of each predator instar when placed singly in the dish was also recorded under the conditions of the experiments. It was found that after 24h the mortality of predators was zero and the aphid mortality was negligible (less than 0.5%).

Statistical analysis

The predation rates recorded when each predatory species used singly did not follow the assumptions of ANOVA (Shapiro-Wilk normality test failed, $P < 0.05$), and were compared with Kruskal-Wallis One Way Analysis of Variance on Ranks and median values were separated with Dunn's method. The same procedure was followed to compare the percentage of the total prey consumption that occurred in the first 6 hours for each species and instar. The partial aphid prey consumption rates were compared among treatments with χ^2 test.

The effect of interactions among the predators (*A. bipunctata*, *M. pygmaeus* and *A. aphidimyza*) on their aphid prey consumption when used individually and in combination was assessed by using the multiplicative risk model (Soluk and Collins, 1988; Soluk, 1993; Sih *et al.*, 1998, Lampropoulos *et al.*, 2013). This model is considered to account for prey removal, because a prey individual eaten by one predator is no longer available to the other predators. If predators have independent effects then:

$$E_{p1+2} = P_1+P_2-(P_1\times P_2) \qquad (A)$$

where E_{p1+2} is the expected proportion consumed in the two-predator treatments and P_1, P_2 are the mean observed proportions consumed in the single-predator treatments. We extended equation (A) to include a third predator by adding the term P_3 as described by Nilsson *et al.* (2006):

$$E_{p1+2+3} = P_1+P_2+P_3-(P_1\times P_2)-(P_1\times P_3)-(P_2\times P_3)+(P_1\times P_2\times P_3) \qquad (B)$$

The expected rates were calculated for each individual. The observed and the expected rates for the individuals of each treatment were compared with unpaired t-test. The Bonferroni adjustment was used. In cases that normality test (Shapiro-Wilk) failed ($P < 0.05$) the data were compared using a Mann-Whitney Rank Sum Test. Analyses were conducted with the statistical package SigmaPlot 12.0 (Systat Software, 2012).

Results

Intraguild interactions between predators without extraguild prey

When *A. bipunctata* (2nd, 3rd and 4th instar larvae) and *M. pygmaeus* (2nd and 5th instar nymphs) were used together in pair wise combinations, without aphids, no killed individual was observed. *M. pygmaeus* 5th instar consumed in average 15.33 ± 0.50 eggs of *A. bipunctata* when provided in clusters of 20 eggs.

A. bipunctata (2nd, 3rd and 4th instar) always consumed *A. aphidimyza* (2nd and 3rd instar) (figure 1). *M. pygmaeus* 2nd instar nymphs did not consume any instars of *A. aphidimyza*. However, *M. pygmaeus* 5th instar nymphs consumed *A. aphidimyza* 2nd and 3rd instar larvae at a percentage of 70% and 60% respectively (figure 1).

IGP effects in extraguild prey presence

Intraguild mortality

Killing events were not recorded between *A. bipunctata* and *M. pygmaeus.* However, *A. bipunctata* 3rd instar consumed *A. aphidimyza* 3rd instar larvae at a percentage of 20%. *A. bipunctata* (4thinstar) consumed *A. aphidimyza* 2nd and 3rd instar larvae at a percentage of 15% and 25%, respectively. *M. pygmaeus* (5th instar) consumed *A. aphidimyza* (3rd instar) larvae at a percentage of 15% (figure 1). When *A. aphidimyza* 2nd instar used together with either *A. bipunctata* 4th instar and *M. pygmaeus* 5th instar or with *A. bipunctata* 3rd instar and *M. pygmaeus* 5th instar, then was found dead in two and a single replicate, respectively.

Extraguild prey consumption

The results of the aphid consumption when each predator was used singly were significantly dependent of the predator species and its instar ($H = 123.56$, $df = 6$, $P < 0.001$) (figure 2). The highest consumption recorded when *A. bipunctata* 4th instar larvae were used, followed

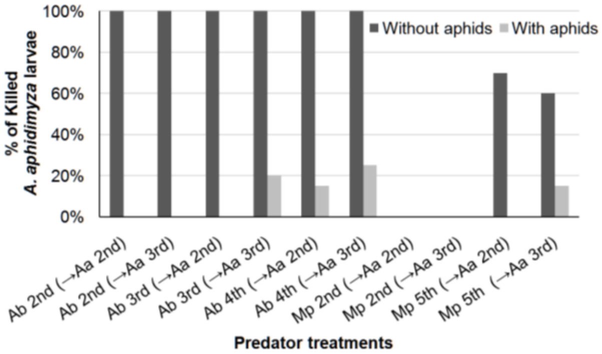

Figure 1. Percentage of the replicates in each pairwise IGP treatment in which *A. aphidimyza* (Aa, 2nd and 3rd instars) were found killed by *A. bipunctata* (Ab, 2nd, 3rd and 4th instars) or *M. pygmaeus* (Mp, 2nd and 5th instars) as recorded without or with extraguild prey (i.e. the aphid *M. persicae*).

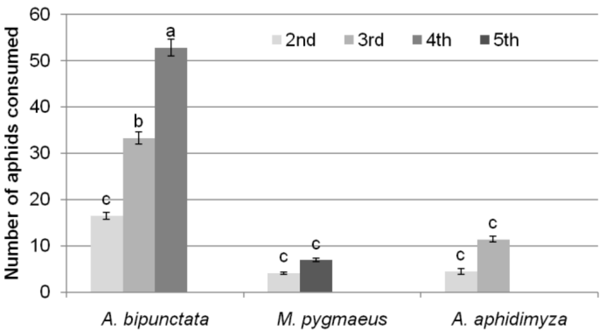

Figure 2. Consumption (mean ± SE) of *M. persicae* nymphs by single 24h starved nymph or larva of variable instar, of each of three predator species, *A. bipunctata*, *M. pygmaeus* and *A. aphidimyza*, as recorded 24h after introduction of each larva or nymph in a Petri dish at 25 °C. Columns with different letter are significantly different (Kruskal-Wallis test, $P < 0.05$).

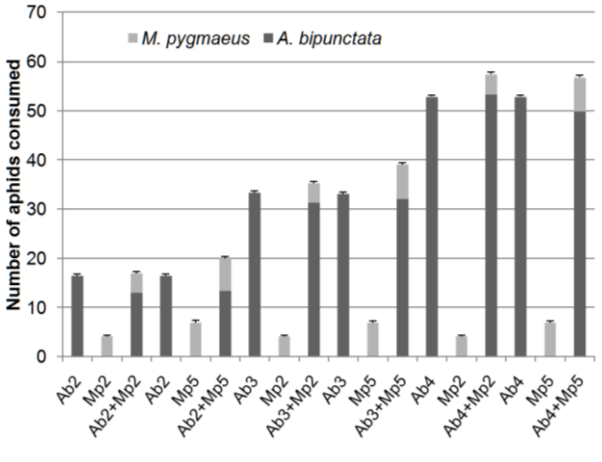

Figure 3. Consumption (mean ± SE) of *M. persicae* nymphs by *A. bipunctata* (Ab, 2nd, 3rd and 4th instars) and *M. pygmaeus* (Mp, 2nd and 5th instars) when used individually and in the respective treatments when used together, 24h after their introduction in Petri dishes at 25 °C.

by that of its 3rd and 2nd instar larvae. The latter fed on more aphids than *A. aphidimyza* 3rd or *M. pygmaeus* 5th, however there was no significant difference in their predation rates and to the predation rates of the other predators' instars.

The aphid consumption recorded when the three predator species were used in pair wise combinations is shown in figures 3-5. The total observed consumption rates were compared with the expected ones when the predator species were used in pairs and are shown in the figure 6. There were no significant differences between the expected and the observed values. The observed and the expected total consumption rates when the three predator species were used together are shown in the figure 7. The observed values were significantly higher than expected one in the cases of *A. bipunctata* 4th, *A. aphidimyza* 2nd and *M. pygmaeus* 5th instars ($t = 2.98$, $df = 8$, $P = 0.005$) and *A. bipunctata* 3rd, *A. aphidimyza* 3rd and *M. pygmaeus* 2nd instars ($t = 2.95$, $df = 8$, $P = 0.005$).

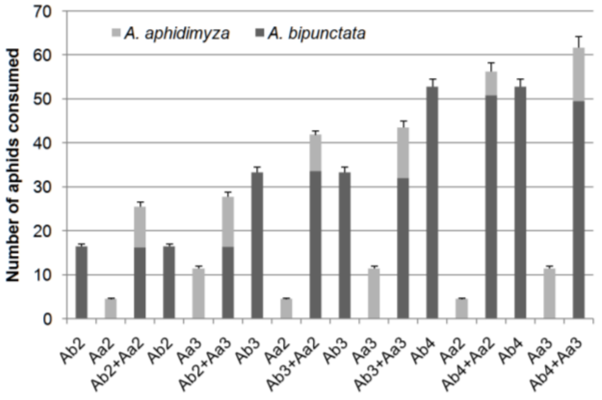

Figure 4. Consumption (mean ± SE) of *M. persicae* nymphs by 2nd, 3rd and 4th nymphal instars of *A. bipunctata* (Ab) and *A. aphidimyza* (Aa) 2nd and 3rd larval instars, when used individually and in the respective treatments when used together 24h after their introduction in Petri dishes at 25 °C.

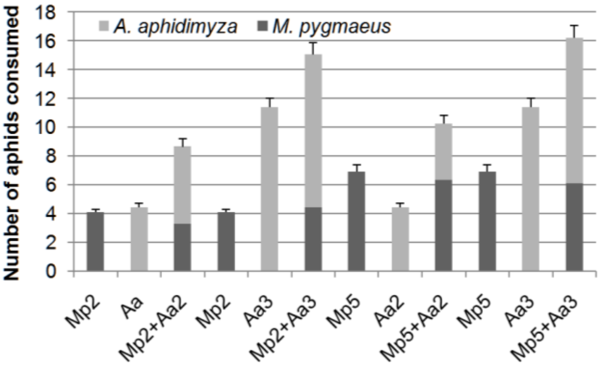

Figure 5. Consumption (mean ± SE) of *M. persicae* nymphs by 2nd and 5th nymphal instars of *M. pygmaeus* (Mp) and *A. aphidimyza* (Aa) (2nd and 3rd larval instars) when used individually and in the respective treatments when used together, 24h after their introduction in Petri dishes at 25 °C.

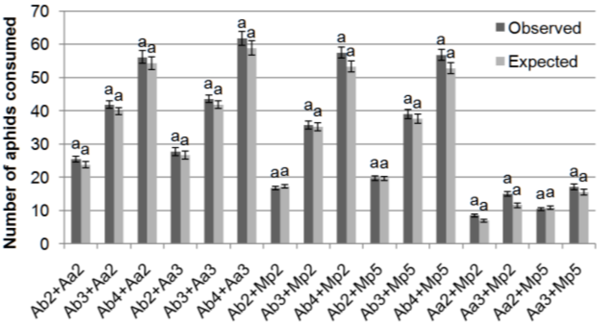

Figure 6. Consumption of *M. persicae* nymphs (mean ± SE) observed and the respective expected ones as derived by the multiplicative model, when predator individuals (*A. bipunctata* 2nd, 3rd and 4th instars, *A. aphidimyza* 2nd and 3rd larval instars, and *M. pygmaeus* 2nd and 5th nymphal instars) foraged in pairwise combinations in Petri dishes at 25 °C. Columns with different letter are significantly different within each predator combination (t-test or Mann-Whitney Rank Sum Test, P < 0.05).

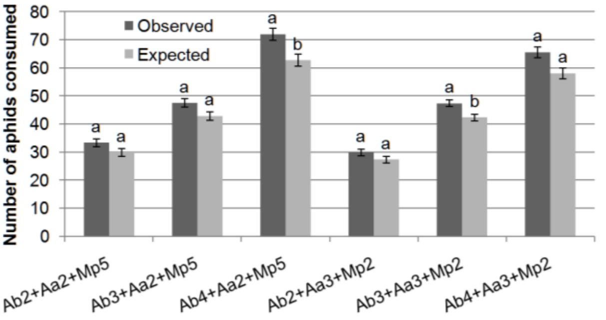

Figure 7. Consumption of *M. persicae* nymphs (mean ± SE) observed and the respective expected ones as derived by the multiplicative model when predator individuals (*A. bipunctata* 2nd, 3rd and 4th instars, *A. aphidimyza* 2nd and 3rd larval instars, and *M. pygmaeus* 2nd and 5th nymphal instars) foraged in combinations of 3 (one larva or nymph of each species) in Petri dishes at 25 °C. Columns with different letter are significantly different within each predator combination (t-test or Mann-Whitney Rank Sum Test, P < 0.05).

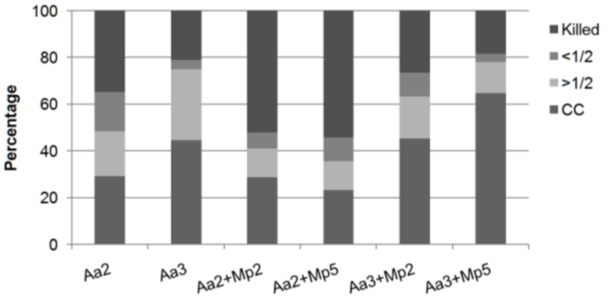

Figure 8. The allocation (%) of total aphid predation to completely (CC), more than half (>1/2) or less than half (<1/2) consumed aphids and aphids killed but not consumed at all (killed), by *A. aphidimyza* 2nd and 3rd instars when used together with 2nd or 5th instar nymphs of *M. pygmaeus*.

Interestingly, the consumption during the first 6h of *A. bipunctata* was much more intense than the other predator species (37 ± 8%, 41 ± 3%, and 44 ± 2% of the total aphid consumption in a 24h period for 2nd, 3rd and 4th instars, respectively), in comparison to the 2nd and 5th nymphal instars of *M. pygmaeus* (6 ± 3% and 14 ± 4%, respectively) and the 2nd and 3rd larval instar of *A. aphidimyza* (3 ± 1% and 16 ± 3%, respectively) (H = 91.82, df = 6, P < 0.001).

Partial aphid prey consumption

The partial aphid prey consumption was observed in the case of *A. aphidimyza* when used singly or together with *M. pygmaeus* or *A. bipunctata*. The percent of aphids completely, more than half, less than half consumed and killed but not consumed by *A. aphidimyza* when used with *M. pygmaeus* is shown in figure 8. More killed but left unconsumed aphids were recorded when *A. aphidimyza* 2nd instar was used together with *M. pygmaeus* 5th instar although non-significantly higher than those in the other cases (χ^2 test, P > 0.05). Partial aphid prey consumption was observed in the case of *M. pygmaeus*, too, but at very low incidence.

Discussion

In the absence of extraguild prey IGP towards *A. aphidimyza* was asymmetric, with the gall midge always being the IG prey. Thus, our study supports the expectation that sessile and low mobility predators are generally vulnerable to IGP (Lucas *et al*., 1998). Similar findings have been reported in earlier studies where *A. aphidimyza* was proved vulnerable to IGP by *Coleomegilla maculata* (De Geer) (Coleoptera Coccinellidae) and *Chrysoperla rufilabris* (Burmeister) (Neuroptera Chrysopidae) (Lucas *et al*., 1998) or by *Harmonia axyridis* (Pallas) (Coleoptera Coccinellidae) (Gardiner and Landis, 2007). In our study, *A. bipunctata* larvae revealed high aggressiveness towards *A. aphidimyza*. Differently, *M. pygmaeus* nymphs consumed *A. aphidimyza* at a much lower rate than *A. bipunctata* larvae. However, slow moving syrphid larvae were often protected against mobile predatory ladybird larvae, probably by their slime cover (Nedvěd *et al*., 2013).

In the absence of extraguild prey incidence of direct IGP between *A. bipunctata* and *M. pygmaeus* did not occur. Their IGP interactions have been investigated in the study of Trotta *et al*. (2015) who reported that 4th instar larvae of *A. bipunctata* consumed in 32% of the cases a female of *M. pygmaeus*, when enclosed together in a small plastic cylinder (diameter: 5.5 cm, height: 7.5 cm, volume: 150 ml) without aphids.

Generally, IGP intensity may decrease with increasing extraguild prey density (e.g. Kajita *et al*., 2000; Nóia *et al*., 2008; Pérez-Guerrero, 2015; Trotta *et al*., 2015) and this was also corroborated in our study. In another work, the attacked and dead *A. aphidimyza* larvae in treatments with *M. pygmaeus* were very low and in the combined treatment the number of aphids didn't differ to the monospecific treatment where only *A. aphidimyza* had been used (Vellekoop, 2008). Although the *A. aphidi-*

myza larvae suffer from intraguild predation by other aphidophagous predators (Lucas *et al*., 1998; Hindayana *et al*., 2001), the risk is reduced in the case of aphid abundance (Lucas *et al*., 1998; Lucas and Brodeur, 2001; Christensen *et al*., 2002). These outcomes indicate that the IG prey (*A. aphidimyza*) could feed on the aphid prey likely being unnoticed by the mobile predators such as *A. bipunctata* and *M. pygmaeus*. This may happen for highly specific predators that can prey within the aphid colony without causing disturbance and profit by the dilution effect (Lucas *et al*., 1998). *A. aphidimyza* follows a furtive predation strategy (New, 1991; Lucas and Brodeur, 2001; Fréchette *et al*., 2008) and likely this may lessen the intensity of IGP interactions. Similarly to our results, Wyss *et al.* (1999b) in a system with two predator species common to ours, reported that the combined release of *A. bipunctata*, *A. aphidimyza*, and *Episyrphus balteatus* De Geer (Diptera Syrphidae) effectively controlled the rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera Aphididae) and thus their joint effect was best explained by an additive model. The reasons behind the additive effect found in our work could be associated with the fact that the aphid density was not a limiting factor. Dib *et al.* (2011) found that the interactions were additive in high aphid densities higher than satiation when compared with lower aphid densities.

Larger individuals of *A. bipunctata* and *M. pygmaeus* were stronger intraguild competitors than the smaller instars. This is consistent with the general rule of Polis *et al.* (1989) and other studies involving aphidophagous arthropod predators (Sengonca and Frings, 1985; Lucas *et al*., 1998; Phoofolo and Obrycki, 1998; Hindayana *et al*., 2001; Felix and Soares, 2004). The only strong intraguild predator smaller than its intraguild prey was 3rd instar larva of *Chrysoperla carnea* (Stephens) killing 4th instar larva of *H. axyridis* (Nedvěd *et al*., 2013).

The use of the predators in pair wise combinations indicated that there was no adverse effect on their aphid prey consumption. Even more, when released all the three species together then their total predation rate on their shared aphid prey was not reduced but instead of it, in most cases the observed values were significantly higher than the respective expected ones. Additive effects among natural enemies involved in IGP interactions may be due to searching on different plant parts (Onzo *et al*., 2004), prefer different prey instars (Calvo *et al*., 2009) or when their interactions are synergistic i.e. when a natural enemy causes changes to the behaviour of the shared prey that make the latter more vulnerable to the other natural enemy, a mechanism called 'predator facilitation' (Losey and Denno, 1998; Sih *et al*., 1998). Evidence for reasons behind the additive effects found here can be derived from the study of their predation in a 6h period (11:00 to 17:00) after their release in the Petri dish. Among the three predator species, the larvae of 2nd, 3rd and 4th instar of *A. bipunctata* were able to consume within the first 6h much higher portion of their total 24h aphid consumption than the other predator species tested. Similarly, to our results, Wyss *et al.* (1999b) also recorded that 50% of the daily aphid consumption of *A. bipunctata* larvae occurred in the first six hours of the foraging period. Although ladybird larvae can feed during the scotophase, their principal predatory activity is diurnal (Nakamuta, 1987). In contrast, *M. pygmaeus* have shown a higher feeding rate in the dark phase (Perdikis *et al*., 1999; 2004). This difference indicates a temporal separation in the activity pattern among the predator species likely enabling them to act in an independent manner. The diel activity pattern was decisive of negative interaction between spiders and *Orius laevigatus* (Fieber) (Hemiptera Anthocoridae). In that study, the extraguild prey consumption was reduced only during the night when both predators were active (Perez-Gurrero *et al*., 2015).

Records on partial aphid prey consumption revealed evidence for IGP interactions between *M. pygmaeus* and *A. aphidimyza* in aphid presence. It is possible that the observed relatively increased frequency of abandoning a prey unconsumed could be induced by disturbance of *A. aphidimyza* during feeding by the mirid predator. Anyway, partial consumption of aphids was sometimes recorded also in solitary larvae of predatory ladybirds that were not disturbed (Šenkeříková and Nedvěd, 2013). The aphid reaction to a predator's attack i.e. production of droplets (Mandour *et al*., 2006) or alarm pheromones (Almohamad *et al*., 2008) may affect the members of the guild differentially. The impact of this kind of effects in IGP intensity between those two predator species needs further evaluation.

IGP intensity is expected to elevate in small arenas or simple environments (Lucas *et al*., 1997; Dib *et al*., 2016). In our system, although simplified arenas were used, the predator species acted in an independent and additive manner as shown by their aphid prey consumption. This outcome indicates their potential for combined use in biological control under conditions of high aphid availability. In fact, *A. aphidimyza* is usually used in high aphid population levels (Blumel, 2004; Messenlink *et al*., 2013) whereas larvae of *A. bipunctata* occur only under high prey densities (Trotta *et al*., 2015) and adult coccinellids are less likely to lay eggs when aphid populations are low (Evans, 2003).

A. bipunctata interactions with *A. aphidimyza* indicate their little potential to be combined in prey shortage or preventive releases. Between *A. bipunctata* and *M. pygmaeus* there were no IGP effects but the results showed evidence for interference and avoidance behaviour between them. Additional evidence for understanding the intensity of IGP effects between them is derived from the study of IGP effects among the immature stages. In this context, in the current study, *M. pygmaeus* consumed a high number of the eggs of *A. bipunctata*. In contrast, *O. laevigatus* showed a clear avoidance behaviour and denied to consume eggs of *A. bipunctata* in Petri dishes (12 cm in diameter) (Santi and Maini, 2006). The efficient consumption of *A. bipunctata* eggs by *M. pygmaeus* indicates that their interactions at long time scale should be further examined. Finally, additional potential avoidance behaviour i.e. that of females when selecting oviposition sites should be considered (Putra *et al*., 2009; Almohamad *et al*., 2010). The evidence of IGP between *A. bipunctata* and *M. pygmaeus* may be examined in future studies to understand the role of IGP in shaping their efficacy in aphid regulation and their optimal use in biological control.

Overall, the present laboratory study indicates that the three aphidophagous species act in an additive way when foraging under high extraguild prey densities; however, in extraguild prey absence they can engage in IGP interactions of variable level. The release of *A. aphidimyza* together with *A. bipunctata* in aphid prey shortage needs caution whereas the evidence obtained showed that *A. bipunctata* and *M. pygmaeus* may not systematically engage in IGP and *A. aphidimyza* and *M. pygmaeus* may be combined without strong IGP effects. The instar of the involved predators showed significant effects in IGP interactions. Taken together, the present study has possible consequences for pest biological control with practical interest particularly in cases when additional means are required to control high aphid densities.

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References

ALMOHAMAD R., VERHEGGEN F. J., FRANCIS F., LOGNAY G., HAUBRUGE E., 2008.- Emission of alarm pheromone by non-preyed aphid colonies.- *Journal of Applied Entomology*, 132: 601-604.

ALMOHAMAD R., VERHEGGEN F. J., FRANCIS F., HAUBRUGE E, 2010.- Intraguild interactions between the predatory hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) and the Asian ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae): effect of larval tracks.- *European Journal of Entomology*, 107: 41-45.

ARNÓ J., SORRIBAS R., PRAT M., MATAS M., POZO C., RODRÍGUEZ D., 2009.- *Tuta absoluta*, a new pest in IPM tomatoes in the northeast of Spain.- *IOBC/WPRS Bulletin*, 49: 203-208.

BLUMEL S., 2004.- Biological control of aphids on vegetable crops, pp. 297-312. In: *Biocontrol in protected culture* (HEINZ K. M., VAN DRIESCHE R. G., PARRELLA M. P., Eds).- Ball Publishing, Batavia, USA.

BURGIO G., SANTI F., MAINI S., 2002.- On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae).- *Biological Control*, 24: 110-116.

CALVO F. J., BOLCKMANS K., BELDA J. E., 2009.- Development of a biological control-based integrated pest management method for *Bemisia tabaci* for protected sweet pepper crops.- *Entomologia Experimentalis et Applicata*, 133: 9-18.

CHACÓN J. M., HEIMPEL G. E., 2010.- Density-dependent intraguild predation of an aphid parasitoid.- *Oecologia*, 164: 213-220.

CHAILLEUX A., BEAREZ P., PIZZOL J., AMIENS-DESNEUX E., RAMIREZ-ROMERO R., DESNEUX N., 2013.- Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest, *Tuta absoluta*.- *Journal of Pest Science*, 86: 533-541.

CHOW A., CHAU A., HEINZ K. M., 2008.- Compatibility of *Orius insidiosus* (Hemiptera: Anthocoridae) with *Amblyseius* (*Iphiseius*) *degenerans* (Acari: Phytoseiidae) for control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse roses.- *Biological Control*, 44: 259-270.

CHRISTENSEN R. K., ENKEGAARD A., BRØDSGAARD H. F., 2002.- Intraspecific interactions among the predators *Orius majusculus* and *Aphidoletes aphidimyza*.- *IOBC/WPRS Bulletin*, 25: 57-60.

COLOMER I., AGUADO P., MEDINA P., MARÍA HEREDIA R., FERERES A., EDUARDO BELDA J., VINUELA E., 2011.- Field trial measuring the compatibility of methoxyfenozide and flonicamid with *Orius laevigatus* Fieber (Hemiptera: Anthocoridae) and *Amblyseius swirskii* (Athias-Henriot) Acari: Phytoseiidae) in a commercial pepper greenhouse.- *Pest Management Science*, 67: 1237-1244.

DE CLERCQ P., BONTE M., VAN S. K., BOLCKMANS K., DEFORCE K., 2005.- Development and reproduction of *A. bipunctata bipunctata* (Coleoptera: Coccinellidae) on eggs of *Ephestia kuehniella* (Lepidoptera: Phycitidae) and pollen.- *Pest Management Science*, 61: 1129-1132.

DIB H., JAMONT M., SAUPHANOR B., CAPOWIEZ Y., 2011.- Predation potency and intraguild interactions between generalist (*Forficula auricularia*) and specialist (*Episyrphus balteatus*) predators of the rosy apple aphid (*Dysaphis plantaginea*).- *Biological Control*, 59: 90-97.

DIB H., SAUPHANOR B., CAPOWIEZ Y., 2016.- Effect of management strategies on arthropod communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in south-eastern France.- *Agriculture, Ecosystems and Environment*, 216: 203-206.

ENKEGAARD A., BRØDSGAARD H. F., 2006.- Biocontrol in protected crops: is lack of biodiversity a limiting factor?, pp. 91-122. In: *Ecological and societal approach to biological control* (EILENBERG J., HOKKANEN H. M. T., Eds).- Springer, Dordrecht, The Netherlands.

EVANS E. W., 2003.- Searching and reproductive behaviour of female aphidophagous lady birds (Coleoptera: Coccinellidae) a review.- *European Journal of Entomology*, 100: 1-10.

FANTINOU A. A., PERDIKIS D., MASELOU D. A., LAMBROPOULOS P. D., 2008.- Prey killing without consumption: does *Macrolophus pygmaeus* show adaptive foraging behaviour?- *Biological Control*, 47: 187-193.

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.

FERGUSON K. I., STILING P., 1996.- Non-additive effects of multiple natural enemies on aphid populations.- *Oecologia*, 108: 375-379.

FINKE D. L., DENNO R. F., 2002.- Intraguild predation diminished in complex structured vegetation: implications for prey suppression.- *Ecology*, 83: 643-652.

FRECHETTE B., ROJO S., ALOMAR O., LUCAS E., 2007.- Intraguild predation among mirids and syrphids: who is the prey? Who is the predator?- *BioControl*, 52: 175-191.

FRÉCHETTE B., FRANÇOIS L., LUCAS E., 2008.- *Leucopis annulipes* larvae (Diptera: Chamaemyiidae) use a furtive predation strategy within aphid colonies.- *European Journal of Entomology*, 105: 399-403.

GARDINER, M., LANDIS D., 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.

HENTLEY W. T., VANBERGEN A. J., BECKERMAN A. P., BRIEN M. N, HAILS R. S, JONES T. H., JOHNSON S. N., 2016.- Antagonistic interactions between an invasive alien and a native coccinellid species may promote coexistence.- *Journal of Animal Ecology*, 85: 1087-1097.

Higashid A., Yano E., Nishikawa S., Shuiji O., Okuno N., Sakaguchi T., 2016.- Reproduction and oviposition selection by *Aphidoletes aphidimyza*, (Diptera Ceccidomyiidae) on the banker plants with alternative prey aphids or crop plants with pest aphid.- *Applied Entomology and Zoology*, 51: 445-456.

Hindayana D., Mayhöfer R., Scholz D., Poehling H.-M., 2001.- Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators.- *Biological Control*, 20: 236-246.

Jakobsen L., Enkegaard A., Brodsgaard H. F., 2004.- Interactions between two polyphagous predators, *Orius majusculus* (Hemiptera: Anthocoridae) and *Macrolophus caliginosus* (Heteroptera: Miridae).- *Biocontrol Science and Technology*, 14: 17-24.

Jalali M. A, Michaud J. P., 2012.- Aphid-plant interactions affect the suitability of *Myzus* spp. as prey for the two spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae).- *European Journal of Entomology*, 109: 345-352.

Jalali M. A., Tirry L., De Clercq P., 2009.- Food consumption and immature growth of *A. bipunctata bipunctata* (Coleoptera: Coccinellidae) on a natural prey and a factitious food.- *European Journal of Entomology*, 106: 193-198.

Jalali M. A., Tirry L., De Clercq P., 2010.- Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*.- *BioControl*, 55: 261-269.

Janssen A., Pallini A., Venzon M., Sabelis M. W., 1998.- Behaviour and indirect interactions in food webs of plant inhabiting arthropods.- *Experimental and Applied Acarology*, 22: 497-521.

Janssen A., Sabelis M. W., Magalhaes S., Montserrat M., van der Hammen T., 2007.- Habitat structure affects intraguild predation.- *Ecology*, 88: 2713-2719.

Kajita Y., Takano F., Yasuda H., Agarwala B. K., 2000.- Effects of indigenous lady-bird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance.- *Applied Entomology and Zoology*, 35: 473-479.

Kajita Y., Takano F., Yasuda H., Evans E.W., 2006.- Interactions between introduced and native predatory ladybirds (Coleoptera, Coccinellidae): factors influencing the success of species introductions.- *Ecological Entomology*, 31: 58-67.

Lampropoulos P. D., Perdikis D. C., Fantinou A. A., 2013.- Are multiple predator effects directed by prey availability?- *Basic Applied Ecology*, 14: 605-613.

Losey J. E., Denno R. F., 1998.- Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations.- *Ecology*, 79: 2143-2152.

Lucas E., 2012.- Intraguild interactions, pp. 343-374. In: *Ecology and behaviour of the ladybird beetles (Coccinellidae)* (Hodek I., van Emden H. F., Honek A., Eds).- John Wiley & Sons Ltd., Chichester, UK.

Lucas E., Alomar O., 2002.- Impact of the presence of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on whitefly (Homoptera: Aleyrodidae) predation by *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae).- *Biological Control*, 25: 123-128.

Lucas E., Brodeur J., 2001.- A fox in sheep's clothing: furtive predators benefit from the communal defence of their prey.- *Ecology*, 82: 3246-3250.

Lucas E., Rosenheim J. A., 2011.- Influence of intermediate prey density on intraguild predation by heteropteran predators: a review of the evidence and a case study.- *Biological Control*, 59: 61-67.

Lucas E., Coderre D., Vincent C., 1997.- Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*.- *Entomologia Experimentalis et Applicata*, 85: 151-159.

Lucas E., Coderre D., Brodeur, 1998.- Intraguild predation among aphid predators: characterization and influence of extraguild prey density.- *Ecology*, 79: 1084-1092.

Lykouressis D., Perdikis D., Mandarakas I., 2016.- Partial consumption of different species of aphid prey by the predator *Macrolophus pygmaeus* (Hemiptera: Miridae).- *European Journal of Entomology*, 113: 345-351.

Mandour N. S., El-Basha N. A. S., Liu T. X., 2006.- Functional response of the ladybird, *Cydonia vicinanilotica* to cowpea aphid, *Aphis craccivora* in the laboratory.- *Insect Science*, 13: 49-54.

Messelink G. J., Sabelis M. W., Janssen A., 2012.- Generalist predators, food web complexities and biological pest control in greenhouse crops, pp. 191-214. In: *Integrated pest management and pest control - current and future tactics* (Larramendy M. L., Soloneski S., Eds).- InTech, Rijeka, Croatia.

Messenlink G. J., Bloemhard C. M., Sabelis M. W., Janssen A., 2013.- Biological control of aphids in the presence of thrips and their enemies.- *BioControl*, 58: 45-55.

Moreno-Ripoll R., Gabarra R., Symondson W. O. C., King R. A., Agustí N., 2014.- Do the interactions among natural enemies compromise the biological control of the whitefly *Bemisia tabaci*?- *Journal of Pest Science*, 87: 133-141.

Nakamuta K., 1987.- Diel rhythmicity of prey-search activity and its predominance over starvation in the lady beetle, *Coccinella septempunctata bruckii*.- *Physiological Entomology*, 12: 91-98.

Nedstam B., Johansson-Kron M., 1999.- *Diglyphus isaea* (Walker) and *Macrolophus caliginosus* Wagner for biological control of *Liriomyza bryoniae* (Kaltenbach) in tomato.- *Bulletin Section Regionale Ouest Palaearctique, Organisation Internationale de Lutte Biologique*, 22: 185-187.

Nedvěd O., Fois X., Ungerová D., Kalushkov P., 2013.- Alien vs. Predator - the native lacewing *Chrysoperla carnea* is the superior intraguild predator in trials against the invasive ladybird *Harmonia axyridis*.- *Bulletin of Insectology*, 66: 73-78.

New T. R., 1991.- *Insects as predators*.- New South Wales University Press, New South Wales, Australia.

Nilsson E., Hertonsson P., Stenberg M., Brodersen J., Olsson K., Stenroth P., Lakowitz T., Brönmark C., Nyström P., McIntosh A. R., 2006.- Facilitation and interference among three predators affect their consumption of a stream-dwelling mayfly.- *Freshwater Biology*, 51: 1507-1514.

Nóia 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 intermediate prey densities.- *Biological Control*, 46: 140-146.

Onzo A., Hanna R., Janssen A., Sabelis M. W., 2004.- Interactions between two neotropical phytoseiid predators on cassava plants and consequences for biological control of a shared spider mite prey: a screenhouse evaluation.- *Biocontrol Science and Technology*, 14: 63-76.

Perdikis D., Lykouressis D., 2000.- Effects of various items, host plants and temperatures on the development and survival of *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae).- *Biological Control*, 17: 55-60.

Perdikis D., Lykouressis D., Economou L., 1999.- The influence of temperature, photoperiod and plant type on the predation rate of *Macrolophus pygmaeus* Rambur on *Myzus persicae* (Sulzer).- *BioControl*, 44: 281-289.

Perdikis D., Lykouressis D., Economou L., 2004.- The influence of light-dark phase, host plant, temperature and their interaction on predation rate in an insect predator.- *Environmental Entomology*, 33: 1137-1144.

Perdikis D., Kapaxidi E., Papadoulis G., 2008.- Biological control of insect and mite pests in greenhouse solanaceous crops.- *The European Journal of Plant Science and Biotechnology*, 2 (Special Issue 1): 125-144.

Perdikis D., Lucas E., Garantonakis N., Giatropoulos A., Kitsis P., Maselou D., Panagakis S., Lampropoulos P., Paraskevopoulos A., Lykouressis D., Fantinou A., 2014.- Intraguild predation and sublethal interactions between zoophytophagous mirids (*Macrolophus pygmaeus* and *Nesidiocoris tenuis*).- *Biological Control*, 70: 35-41.

Pérez-Guerrero S., Gelanbenga A., Vargas-Osuna E., 2015.- Compatibility of *Orius laevigatus* and *Cheiracanthium pelasgicum* for predation on *Helicoverpa armigera* eggs: effects of density and day/night activity on intraguild predation.- *BioControl*, 60: 783-793.

Phoofolo M. W., Obrycki J., 1998.- Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae.- *Entomologia Experimentalis et Applicata*, 89: 47-55.

Polis G. A., Holt R. D., 1992.- Intraguild predation: the dynamics of complex trophic interactions.- *Trends in Ecology & Evolution*, 7: 151-154.

Polis G. A., Myers C. A., Holt R. D., 1989.- The ecology and evolution of intraguild predation: potential competitors that eat each other.- *Annual Review of Ecology and Systematics*, 20: 297-330.

Putra N. S., Yasuda H., Sato S., 2009.- Oviposition preference of two hoverfly species in response to risk of intraguild predation.- *Applied Entomology and Zoology*, 44: 29-36.

Rahmani H., Daneshmandi A., Walzer A., 2015.- Intraguild interactions among three spider mite predators: predation preference and effects on juvenile development and oviposition.- *Experimental and Applied Acarology*, 67: 493-505.

Robledo-Camacho A., van der Blom J., Sánchez-Martínez J. A., Torres-Giménez S., 2009.- *Control Biológico en Invernaderos Hortícolas*.- Asociación Coexphal-FAECA, Almería, Spain.

Rondoni G., Ielo F., Ricci C., Conti E., 2014.- Intraguild predation responses in two aphidophagous coccinellids identify differences among juvenile stages and aphid densities.- *Insects*, 5: 974-983.

Rosenheim J. A., Wilthoit L. R., Armer C. A., 1993.- Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population.- *Oecologia*, 96: 439-449.

Rosenheim J. A., Kaya H. K., Ehler L. E., Marois J. J., Jaffee B. A., 1995.- Intraguild predation among biological-control agents: theory and evidence.- *Biological Control*, 15: 303-335.

Roubinet E., Straub C., Jonsson T., Staudacher K., Traugott M., Ekbom B., Jonsson M., 2015.- Additive effects of predator diversity on pest control caused by few interactions among predator species.- *Ecological Entomology*, 40: 362-371.

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.

Sengonca C., Frings B., 1985.- Interference and competitive behaviour of the aphid predators, *Chrysoperla carnea* and *Coccinella septempunctata*, in the laboratory.- *Entomophaga*, 30: 245-251.

Šenkeříková P., Nedvěd O., 2013.- Preference among three aphid species by predatory ladybird beetle *Harmonia axyridis* in laboratory.- *IOBC/WPRS Bulletin*, 94: 123-130.

Sih A., Englund G., Wooster D., 1998.- Emergent impacts of multiple predators on prey.- *Trends of Ecological Evolution*, 13: 350-355.

Snyder W. E., Ives A. R., 2003.- Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol.- *Ecology*, 84: 91-107.

Snyder W., Wise D., 1999.- Predator interference and the establishment of generalist predator populations for biocontrol.- *Biological Control*, 15: 283-292.

Soluk D. A., 1993.- Multiple prey effects: predicting combined functional response of stream fish and invertebrate predators.- *Ecology*, 74: 219-225.

Soluk D. A., Collins N. C., 1988.- Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators.- *Oikos*, 52: 94-100.

Straub C. S., Finke D. L., Snyder W. E., 2008.- Are the conservation of natural enemy biodiversity and biological control compatible goals?- *Biological Control*, 45: 225-237.

Systat Software, 2012.- *SigmaPlot for Windows*. Version 12.0.- Systat Software Inc., Germany.

Trotta V., Durán Prieto J., Fanti P., Battaglia D., 2015.- Prey abundance and intraguild predation between *Adalia bipunctata* (Coleoptera: Coccinellidae) and *Macrolophus pygmaeus* (Hemiptera: Miridae).- *European Journal of Entomology*, 112: 862-865.

Urbaneja A., Montón H., Mollá O., 2009.- Suitability of the tomato borer *Tuta absoluta* as prey for *M. pygmaeus* and *Nesidiocoris tenuis*.- *Journal of Applied Entomology*, 133: 292-296.

Uygun N., 1971.- Der Einfluss der Nahrungsmenge auf Fruchtbarkeit und Lebensdauer von *Aphidoletes aphidimyza* (Rond.) (Diptera: Itonididae).- *Zeitschrift für Angewandte Entomologie*, 69: 234-258.

van Lenteren J. C., 2012.- The state of commercial augmentative biological control: plenty of natural enemies but a frustrating lack of uptake.- *Biocontrol*, 57: 1-20.

van Veen F. J. F., Morris R. J., Godfray H. C. J., 2006.- Apparent competition, quantitative food webs, and the structure of phytophagous insect communities.- *Annual Reviews of Entomology*, 51: 187-208.

Vellekoop R., 2008.- Effect of generalist predatory bugs on aphid control by *Aphidoletes aphidimyza*. 32 pp. *Thesis*, Laboratory of Entomology, Wageningen University, The Netherlands.

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.

Watanabe H., Yano E., Higashida K., Hasegawa S., Takabayashi J., Ozawa R., 2016.- An attractant of the aphidophagous gall midge *Aphidoletes aphidimyza* from honeydew of *Aphis gossypii*.- *Journal of Chemical Ecology*, 42: 149-155.

Wyss E., Villiger M., Müller S. H., 1999a.- The potential of three native insect predators to control the rosy apple aphid, *Dysaphis plantaginea*.- *BioControl*, 44: 171-182.

Wyss E., Villiger M., Hemptinne J. L., Müller S. H., 1999b.- Effects of augmentative releases of eggs and larvae of the two-spot ladybird beetle, *Adalia bipunctata*, on the abundance of the rosy apple aphid, *Dysaphis plantaginea*, in organic apple orchards.- *Entomologia Experimentalis et Applicata*, 90: 167-173.

Yasuda H., Evans E. W., Kajita Y., Urakawa K., Takizawa T., 2004.- Asymmetric larval interactions between introduced and indigenous ladybirds in North America.- *Oecologia*, 141: 722-731.

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