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### Resource quality, resource availability, and intraguild predation among omnivorous mirids

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## RESEARCH ARTICLE

### Resource quality, resource availability, and intraguild predation among omnivorous mirids

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Intraguild predation (IGP) among predatory species can influence many plant-arthropod associations. However, the relevance of IGP is poorly understood for truly omnivorous species such as those that can complete development on both animal and plant diets. Here we test the hypothesis that IGP among two omnivorous mirids is more common when extraguild food is either absent or not suitable. Laboratory experiments were performed in experimental cages in order to determine the effect of intraguild prey densities and diet availability on direction and intensity of IGP between *Dicyphus tamaninii* and *Macrolophus caliginosus* (Heteroptera: Miridae). Intraguild predation was symmetrical between the two mirid species in the absence of alternative food. Increasing densities of intraguild prey enhanced drastically the incidence of IGP. Intraguild predation was reduced when mirids were in the presence of green or red tomato fruits, but the presence of any other extraguild resources had no impact on IGP level. However, when given before the experiments, all resources with the exception of tomato leaves significantly reduced IGP. A second experiment was performed on live plants to compare the results of the previous trials with that obtained in a more natural setting. No IGP was observed when both mirid species were present on a plant. However, development of the intraguild prey (the more vulnerable stage) was hindered by the presence of the intraguild predator. The potential of such results is discussed from community ecology and biological control perspective.

**Keywords:** intraguild predation; omnivory; zoophytophagy; extraguild resource quality; Heteroptera; Miridae

#### Introduction

Development of effective biological control programs involving more than one natural enemy species requires an understanding of their interactions. For example, the impact of two natural enemy species on a shared prey could either be synergistic, additive, or disruptive (Losey and Denno 1998; Colfer and Rosenheim 2001; Cardinale, Harvey, Gross, and Ives 2003; Powell and Webster 2004; Prasad and Snyder 2004).

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Intraguild predation, or IGP, is defined as predation between species that share a similar resource (Lucas 2005). Intraguild predation is a widespread interaction in natural communities (Arim and Marquet 2004), and it could be particularly important among arthropods exploiting ephemeral and patchily distributed resources (Lucas 2005). Some authors have suggested that IGP could be triggered by a need for specific nutritional requirements such as protein (Polis, Myers, and Holt 1989) or nitrogen (Matsumura et al. 2004). Even though this hypothesis remains unvalidated, it has been observed that IGP intensity usually decreases as the quantity and/or quality of the extraguild (shared) resource increases (Polis et al. 1989; Lucas, Coderre, and Brodeur 1998).

Intraguild predation has been documented in systems where both intraguild predators and intraguild prey are predators (Polis and McCormick 1987; Lucas, Coderre, and Brodeur 1997; Lucas et al. 1998), detritivores (King and Dawson 1973; Wissinger, Sparks, Rouse, Brown, and Steltzer 1996), or herbivores (LeCato 1978; Herrera 1984). However, IGP between true omnivorous species has received less attention, and the link between omnivory and IGP has not been well established (Gillespie and Roitberg 2006). True omnivory (i.e., the act of feeding on both plant and animal resources) is widely encountered in the arthropod kingdom (Coll and Guershon 2002). It is notably common among Heteropteran predators (Lygaeidae, Miridae, Pentatomidae) (Strawinski 1964; Fauvel 1999; Eubanks and Styrsky 2005) where the occurrence and benefits of phytophagy depends on prey, plant, and water availability (Naranjo and Gibson 1996; Sanchez, Gillespie, and McGregor 2004; Sinia, Roitberg, McGregor, and Gillespie 2004). Heteropteran predators that frequently feed on plant material are often subdivided as phytozoophagous or zoophytophagous according to the relative degree of plant and prey consumption (Strawinski 1964; Alomar 2002; Coll and Guershon 2002).

The effects of true omnivory on competitors are poorly understood (Wiedenmann and Wilson 1996; Gillespie and Roitberg 2006). Availability of extraguild prey (i.e., the shared prey resource) or of plant tissues could alter interactions between omnivorous species. For example, Laycock, Camm, Van Laerhoven, and Gillespie (2006) demonstrated that extraguild prey availability and host plant species influenced intraspecific interactions (cannibalism) in the omnivorous mirid *Dicyphus hesperus* Knight. Similarly, omnivorous species may avoid IGP by feeding on extraguild resources of animal or plant origin.

Studying IGP among biological control agents is particularly important when trying to establish the compatibility between biodiversity conservation and biological control programs (Straub, Finke, and Snyder 2008). Here we explore the interactions between two omnivorous mirids, *Macrolophus caliginosus* Wagner and *Dicyphus tamaninii* Wagner. Both species are biological control agents native of the Mediterranean area (Wagner 1970), and coexist in both natural and agricultural ecosystems (Albajes and Alomar 1999; Alomar, Goula, and Albajes 2002) where they can be abundant (Alomar 1994). Both species are mainly predacious as nymphs and adults, feeding on whiteflies (Barnadas, Gabarra, and Albajes 1998), aphids (Alvarado, Balta, and Alomar 1997), spider mites (Foglar, Malausa, and Wajnberg 1990), leafminers (Nedstam and Johansson-Kron 1999), lepidopteran eggs (Salomero, Gabarra, and Albajes 1987), and thrips (Gabarra, Castañe, and Albajes 1995; Castañe, Alomar, and Riudavets 1996). However, both species also consume plant resources (Foglar et al. 1990; Alomar and Albajes 1996), and *D. tamaninii* can even

complete its development on a phytophagous diet alone (Lucas and Alomar 2001). This system is of special interest since both mirids (true omnivores) may feed (1) on their shared herbivorous prey, (2) on the same host plant as their herbivorous prey, and (3) among each other (Figure 1). For zoophytophagous animals, plant feeding may do more than provide additional nutrients. For example, plant consumption may at least in part be a means of obtaining water in omnivorous mirids, which is essential for extra-oral digestion (Sinia et al. 2004).

Here we report on a series of experimental cage studies used to determine the impact of different extraguild resources on the direction and intensity of IGP. Cage experiments were performed to control both the animal and plant food present, despite the fact that *M. caliginosus* and *D. tamaninii* will not typically encounter each other away from plant material in nature. We predicted that the presence of highly suitable food items should reduce IGP rate when compared to the presence of low quality food or food absence. Because cage experiments may overestimate IGP levels by forcing the predators to stay in the arena (see Fréchette, Rojo, Alomar, and Lucas 2007), we also evaluated occurrence of IGP in a more natural setting in order to estimate the reliability of the results obtained in experimental cages. We expected that intraguild predation should be reduced on complex substrates (such as plants) that provide refuges.

**Methods**

**Biological material**

Mirids were obtained from permanent colonies established in the Institut de Recerca i Tecnologia Agroalimentàries 4 years before the experiments. The mirid colonies were periodically refreshed with insects collected from tomato fields. *Macrolophus caliginosus* and *D. tamaninii* were reared on tobacco plants (*Nicotiana tabacum* L.) and fed with eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) and nymphs of *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae), at 25 ± 2°C, 16 h L:8 h D. The aphid *Macrosiphum euphorbiae* Thomas (Homoptera: Aphididae) which was used in the experiments, and the whitefly *T. vaporariorum* both came from colonies established on tomatoes (*Lycopersicon esculentum* Mill. cv. Carmelo).

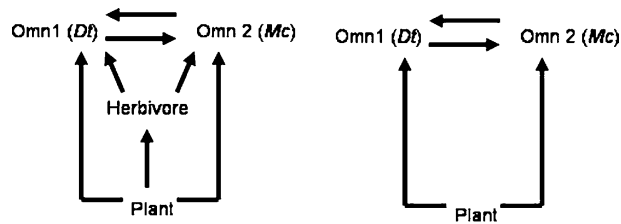


Figure 1. Simplified food web between two true omnivores that share a common resource plant, with or without a shared herbivore present. Omn, omnivore; Dt, *Dicyphus tamaninii*; Mc, *Macrolophus caliginosus*.

### **Characterization of IGP**

Direction and intensity of IGP in the absence of extraguild resources was determined for different combinations of nymphal and adult stages (see Figure 1). Eggs were not tested as potential intraguild prey, since both species usually oviposited within plant tissue. Second nymphal instars of both species have similar size and were used as 'young nymphs' in our experiment. *Macrolophus caliginosus* fifth nymphal instar and *D. tamaninii* fourth nymphal instar have similar size and were used as 'older nymphs' in our experiment. Adult males and females (2–7-days-old) were tested separately since their behaviour and voracity differ (Sengonca and Saleh 2002; Saleh and Sengonca 2003; É. Lucas, personal observations).

Trials were conducted in growth chambers ( $25 \pm 2^\circ\text{C}$ , 16 h L:8 h D) where the experimental setup consisted of a transparent plastic cage ( $32 \times 75$  mm,  $H \times \varnothing$ ) covered by a lid with a meshed opening (muslin). The bottom of the cage was lined with a 5 mm layer of agar (5 g/L). Agar maintained humidity and prevented insect desiccation. Preliminary tests showed that both mirid species do not feed on agar.

Experiments started with the introduction of one individual of each species within the cage. Intraguild predation was then determined after 24 and 48 h. The combinations were replicated 17–25 times. Dead insects were examined under a stereo microscope to confirm predation as the source of mortality. While predation on young nymphs was easily assessed since the body fluids were obviously sucked out, the occurrence of predation on adults and older nymphs was more difficult to assess. Intraguild predation was thus assessed by subtracting the mortality observed in the control to that observed in the experimental treatments. As negative IGP is impossible, negative data were rounded to zero.

For each species, development stages were compared according to their vulnerability (proportion of replicates when they are victims of IGP) and to their predatory behaviour (proportion of replicates when they did IGP). The overall vulnerability of each species was also evaluated by pooling all data together. Proportions were compared with the likelihood ratio *G*-test (Sokal and Rohlf 1981) computed on the statistical software JMP (SAS Institute 2001).

### **Effect of intraguild prey density on IGP occurrence**

A second experiment, performed in the same set-up as described above, was used to test the effect of intraguild prey density on IGP occurrence. Results of the first experiment demonstrated that second nymphal instars of both predators were rarely intraguild predators. Second nymphal instars were thus selected as intraguild prey for this experiment. Intraguild predation was evaluated over a 48 h period using one intraguild predator and either one (low density) or three (high density) intraguild prey. The combinations tested were (1) *D. tamaninii* female vs. *M. caliginosus* second nymphal instar, (2) *D. tamaninii* male vs. *M. caliginosus* second nymphal instar, (3) *D. tamaninii* fourth nymphal instar vs. *M. caliginosus* second nymphal instar, (4) *D. tamaninii* second nymphal instar vs. *M. caliginosus* female, (5) *D. tamaninii* second nymphal instar vs. *M. caliginosus* male, (6) *D. tamaninii* second nymphal instar vs. *M. caliginosus* fifth nymphal instar, and finally (7) *D. tamaninii* second nymphal instar vs. *M. caliginosus* second nymphal instar. All combinations were replicated 10–12 times. For every combination, the proportion of replicates where IGP occurred

was compared between low and high intraguild prey densities using the likelihood ratio *G*-test. In order to control for potential cannibalism, tests using only three intraguild prey of each species alone were carried out: no cannibalism was observed in those controls.

### ***Effect of extraguild resources on IGP***

A third experiment was conducted to determine impact of extraguild resource presence on IGP. The experimental set-up and conditions were the same as previously described. In all treatments, each replicate used three *M. caliginosus* second nymphal instars as intraguild prey and one *D. tamaninii* adult female as intraguild predator. This combination was selected due to its high IGP potential. Moreover, *D. tamaninii* females are more voracious than males (Sengonca and Saleh 2002; Saleh and Sengonca 2003), and we anticipated that their need for nutrients would maximise IGP.

One day before the experiment, experimental mirids were kept on *T. vaporariorum* infested tomato plants. Mirids were then randomly assigned to one of the nine following treatments: (1) *Tomato leaf treatment*, where a tomato leaf disk ( $\varnothing$  34 mm) was put on the agar layer (abaxial surface up) just before agar solidification; (2) *Red tomato fruit treatment*, where a slice of ripe tomato fruit outer surface (34 × 7–10 mm,  $\varnothing$  × H) was used, with the external surface upward and the basis slightly submerged in hot wax in order to prevent agar degradation and fungus colonization. The waxed disk was then put in the agar, so that only the external surface emerged (that ensured that the same research area was available than in the previous treatment); (3) *Green tomato fruit treatment*, where an unripe tomato slice was prepared using the same methodology as in the previous treatment; (4) *Whitefly treatment*, where 20 mg of *T. vaporariorum* pupae (1–3-days-old) were put in the centre of the cage within a circle of ca. 34 mm; (5) *Aphid treatment*, where three *M. euphorbiae* adults were introduced into the cage 5 min before the mirids; (6) *Dicyphus treatment*, where three *D. tamaninii* second nymphal instars were added into each cage. This treatment was conducted to evaluate IGP intensity when conspecific prey is present. Intraguild predation between nymphs was assessed in a control by placing only three *M. caliginosus* second nymphal instars and three *D. tamaninii* second nymphal instars together without adults: only one predation event on *D. tamaninii* was observed in this control; (7) *Ephestia treatment*, where 20 mg of *E. kuehniella* eggs were put in the centre of the cage within a circle of ca. 34 mm; (8) *No resource treatment*, where no extraguild resource was present; and (9) *Control treatment*, where only three *M. caliginosus* second nymphal instars were present, in order to evaluate *M. caliginosus* mortality in the absence of *D. tamaninii*. These treatments systematically vary the extraguild resource available.

According to Lucas and Alomar (2001), the animal resources tested (*T. vaporariorum*, *M. euphorbiae*, *E. kuehniella* eggs, and *M. caliginosus* nymphs) are high quality food items for *D. tamaninii* nymphs. A diet of either red or green tomato fruits enables similar survival rates than the animal resources, but decreases growth rate and adult weight. Tomato fruits are thus considered of lower quality than the animal resources. Tomato leaves are unsuitable as no *D. tamaninii* nymphs were able to reach adulthood on this diet.

Intraguild predation was recorded after 24 h. Each treatment was replicated 12 times. The proportions of replicates where IGP occurred were compared with a likelihood ratio *G*-test and *post-hoc G*-tests (Sokal and Rohlf 1981). The mean number of nymphs killed was compared with a Kruskal–Wallis test and *post-hoc* Tukey-type tests for non-parametric data.

### ***Effect of recently eaten food items on IGP***

The propensity to engage in IGP could be influenced by the nutritional status of a predator. We tested this hypothesis by determining the impact of recently eaten food items on IGP occurrence in the same experimental set-up and conditions. As in the previous experiment, *D. tamaninii* females were used as intraguild predators and *M. caliginosus* second nymphal instars as intraguild prey. The diets were the same as in the previous experiment; the aphid and the intraspecific diet were however omitted, and a diet of six frozen *M. caliginosus* second to third nymphal instars was added. Each intraguild predator was first confined during 5 days on each of the treatment, and diets were refreshed after 2 days. Water was provided with a moistened cotton wick in an Eppendorf vial. Afterwards, each predator was transferred to a new cage with only the agar layer, a moistened cotton wick, and three *M. caliginosus* second nymphal instars. Intraguild predation was recorded after 24 h. Treatments were replicated 10–15 times. The proportions of replicates where IGP occurred were compared with a likelihood ratio *G*-test and *post-hoc* tests. The mean number of nymphs killed was compared with one-way ANOVA and *post-hoc* Tukey tests on transformed data (log data + 1).

### ***IGP on plants***

Cage experiments can overestimate IGP levels (Fréchette et al. 2007). Survival of *M. caliginosus* second nymphal instars in the presence of *D. tamaninii* adults was thus evaluated on plants over a 7-day period. The experimental set-up used was composed of a Plexiglas cylinder (31.0 × 19.9 cm, H × Ø) covered with muslin. The bottom of the cylinder was sealed with silicone to a plastic lid. A pot with a 3-week-old tomato plant was placed in a hole at the bottom of the cage, so that the base of the pot was soaked in water.

We varied extraguild resources using: (1) no prey; (2) whitefly nymphs in excess (plants were infested with whitefly adults for 2 days and eggs were left to develop to second to third instar nymphs before the test); and (3) *E. kuehniella* eggs in excess (80–100 mg per plant, deposited on the upper side of leaves). For each extraguild resource type, experiments were run either: (1) in the presence of intraguild predators (a male and a female *D. tamaninii*), or (2) in the absence of intraguild predators.

At the beginning of this experiment, six *M. caliginosus* second nymphal instars were placed on each plant. After 7 days, the number of live mirids was recorded. Impact of treatments on intraguild prey development was also evaluated by recording the number of *M. caliginosus* exuviae using a stereo microscope. The six experimental treatments were replicated 12 times. Proportions of surviving nymphs were squared root arcsin transformed. Since the distribution of residuals was not normal, data were ranked, and a two-way ANOVA was performed on the ranked data (presence/absence of adults and extraguild prey) (Zar 1999). Significant differences were detected using a

Tukey–Kramer HSD test. Numbers of exuviae were ranked and compared between treatments using a two-way ANOVA.

**Results**

**Characterization of IGP**

With all treatments pooled together, *D. tamaninii* and *M. caliginosus* were equally susceptible to IGP in the first 24 h ( $G_{1,42} = 1.5, P = 0.219$ ). Intraguild predation was thus symmetrical between the two species and occurred in 5.8% of the tests during the first 24 h. However, after 48 h, *M. caliginosus* was significantly more often victim of IGP than *D. tamaninii* ( $G_{1,135} = 4.7, P = 0.031$ ). Intraguild predation occurred in a further 10.5% of the tests, for a total of 16.4% after 48 h (Figure 2).

Relative susceptibility of both species was influenced by their development stage. *Macrolophus caliginosus* second instars and adult females were more vulnerable to IGP than the other stadia of this species, both after 24 h ( $G_{3,308} = 18.8, P = 0.001$ ), and after 48 h ( $G_{3,308} = 26.4, P = 0.001$ ). *Macrolophus caliginosus* adult males were rarely preyed upon (1.53%). All stages of *D. tamaninii* were equally vulnerable to predation after 24 h ( $G_{3,308} = 5.8, P = 0.12$ ), while second and fourth nymphal instars were more susceptible than adults after 48 h ( $G_{3,308} = 27.5, P = 0.001$ ). Adult males of *D. tamaninii* were never preyed upon.

Predation propensity was the same for all development stages of *M. caliginosus* ( $G_{3,308} = 5.8, P = 0.12$ ) and *D. tamaninii* ( $G_{3,308} = 5.3, P = 0.15$ ).

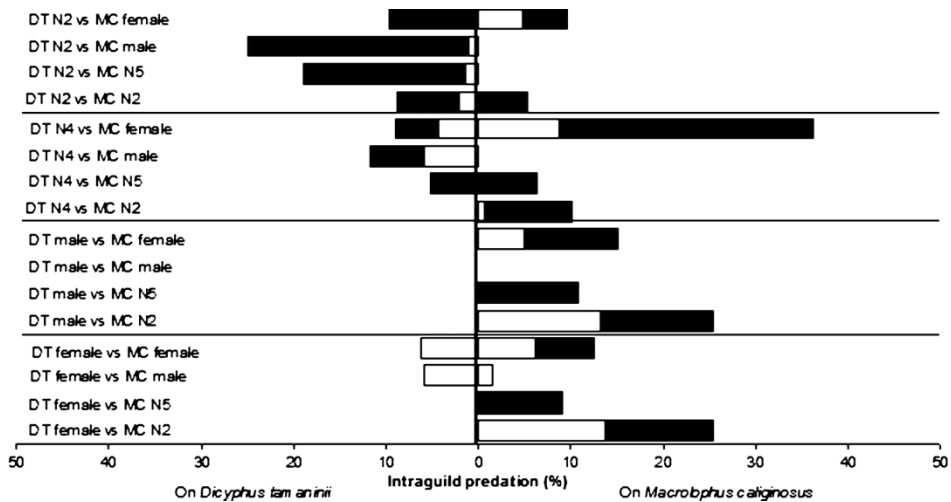


Figure 2. The percentages (%) of replicates where IGP occurred after 24 h (open bars) and 48 h (solid bars) between various stadia of *Dicyphus tamaninii* and *Macrolophus caliginosus* in the absence of extraguild resource. Predation on *D. tamaninii* is presented on the left side and predation on *M. caliginosus* is presented on the right side. DT, *D. tamaninii*; MC, *M. caliginosus*; N2, second nymphal instar; N4, fourth nymphal instar; N5, fifth nymphal instar; fem., adult female; male, adult male.



### Effect of intraguild prey density on IGP occurrence

For every combination tested, occurrence of IGP increased in treatments with high intraguild prey density ( $G$ -test,  $P < 0.050$ ; Figure 3), the only exception being *D. tamaninii* male vs. *M. caliginosus* second nymphal instars ( $G_{1,16} = 0.8$ ,  $P = 0.39$ ). Second instars of both species never killed older stadia, i.e., intraguild prey never killed intraguild predator. The highest level of IGP (>90%) was however observed when intraguild prey density was highest, i.e., when second instars of both species were present together (a total of six second nymphal instars).

Excluding the treatment where second instars of both species were present, IGP occurred in 14.7% (low intraguild prey density) and 70% (high intraguild prey density) when *D. tamaninii* was the intraguild prey, and 20.7% (low intraguild prey density) and 65.6% (high intraguild prey density) when *M. caliginosus* was the intraguild prey when data were pooled across treatments.

### Effect of extraguild resources on IGP

The impact of alternative resources on IGP varied according to resource type ( $G_{8,99} = 21.6$ ,  $P < 0.006$ ; Figure 4). The presence of red tomato fruit significantly reduced IGP occurrence ( $G_{1,46} = 9.0$ ,  $P < 0.003$ ), and no IGP was observed in the presence of green tomato fruit ( $P = 0.015$ ). However, animal resources and tomato leaves had no impact on IGP ( $G_{1,58} = 1.2$ ,  $P > 0.05$ ). No mortality was recorded in the absence of intraguild predator (*Control treatment*). Even though there was an overall significant difference in the number of nymphs killed (Kruskal–Wallis:  $\chi^2 =$

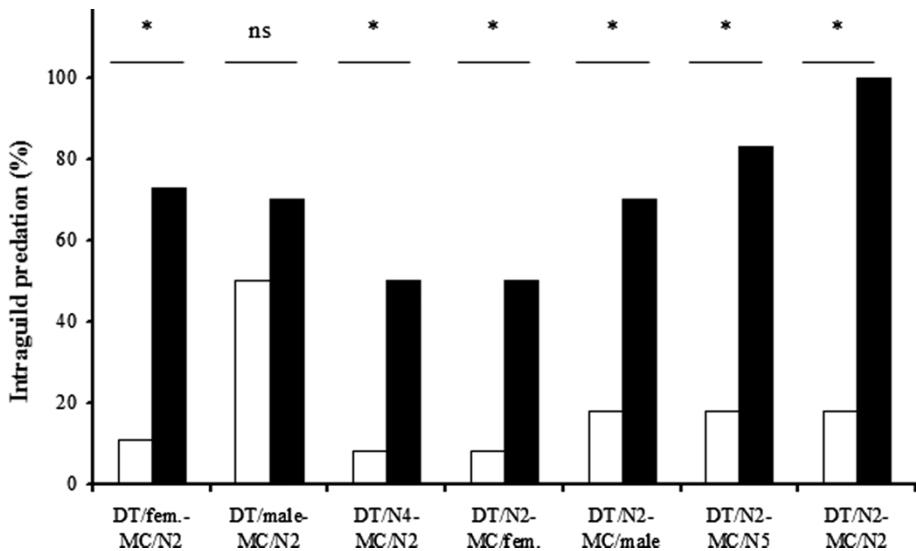


Figure 3. Effect of intraguild prey density on IGP between *Dicyphus tamaninii* and *Macrolophus caliginosus* for a 48 h observation period. Bars represent the percentage (%) of replicates where IGP occurred in the presence of low (open bars) and high (solid bars) intraguild prey densities. An asterisk (\*) indicate significant difference between low and high intraguild prey density ( $P < 0.05$ ). DT, *D. tamaninii*; MC, *M. caliginosus*; N2, second nymphal instar; N5, fifth nymphal instar.

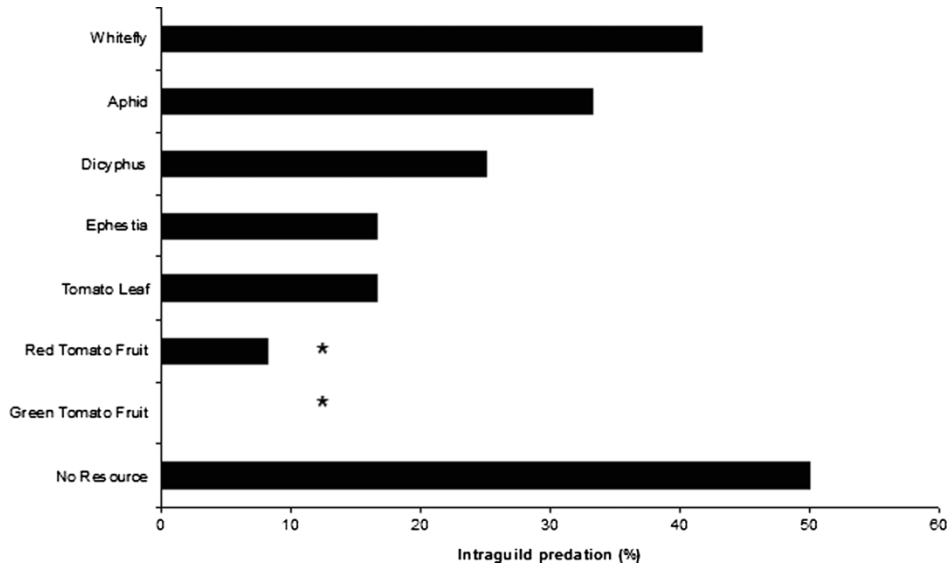


Figure 4. Effect of extraguild resource on IGP, expressed as the percentage (%) of replicates where IGP occurred in the presence of different extraguild resources. Percentages followed by an asterisk (\*) are significantly different from the *No resource* treatment ( $P < 0.05$ ).

16.29,  $df = 8$ ,  $P = 0.038$ ), *post-hoc* tests showed no difference between treatments ( $P > 0.05$ ). That is, the highest number of nymphs killed was observed in the *No resource* treatment ( $0.58 \pm 0.19$ ) and the lowest *Green tomato fruit* treatment ( $0 \pm 0.00$ ). In the *Aphid* treatment, all aphids were preyed upon, suggesting that their density may have been insufficient to fully assess their impact on IGP.

#### ***Effect of recently eaten food items on IGP***

In the *No resource* treatment, *M. caliginosus* nymphs were highly susceptible to IGP by *D. tamaninii* females: IGP occurred in 90.91% of the replicates (Figure 5a). The proportion of replicates where IGP occurred was similar (70%) when females were previously fed with tomato leaves ( $G_{1,19} = 1.5$ ,  $P = 0.22$ ). However, all other resources (animal or plant) provided before the experiment significantly reduced IGP occurrence ( $< 60\%$ ) ( $G_{7,84} = 20.9$ ,  $P = 0.004$ ). The mean number of *M. caliginosus* nymphs killed differed among treatments (Kruskal–Wallis:  $\chi^2 = 17.34$ ,  $df = 7$ ,  $P = 0.015$ ). The mean number of dead *M. caliginosus* nymphs was significantly lower when intraguild predators were absent (*Control* treatment) than in the presence of starved *D. tamaninii* females (*No resource* treatment), ( $P < 0.05$ ). However, the numbers of *M. caliginosus* nymphs killed were similar among all other combinations ( $P > 0.05$ ) (Figure 5b).

#### ***IGP on plants***

Survival of *M. caliginosus* nymphs on plants was not influenced by the presence of *D. tamaninii* adults ( $F$  ratio = 0.56,  $df = 1$ ,  $P = 0.46$ ; Figure 6a). However, extraguild

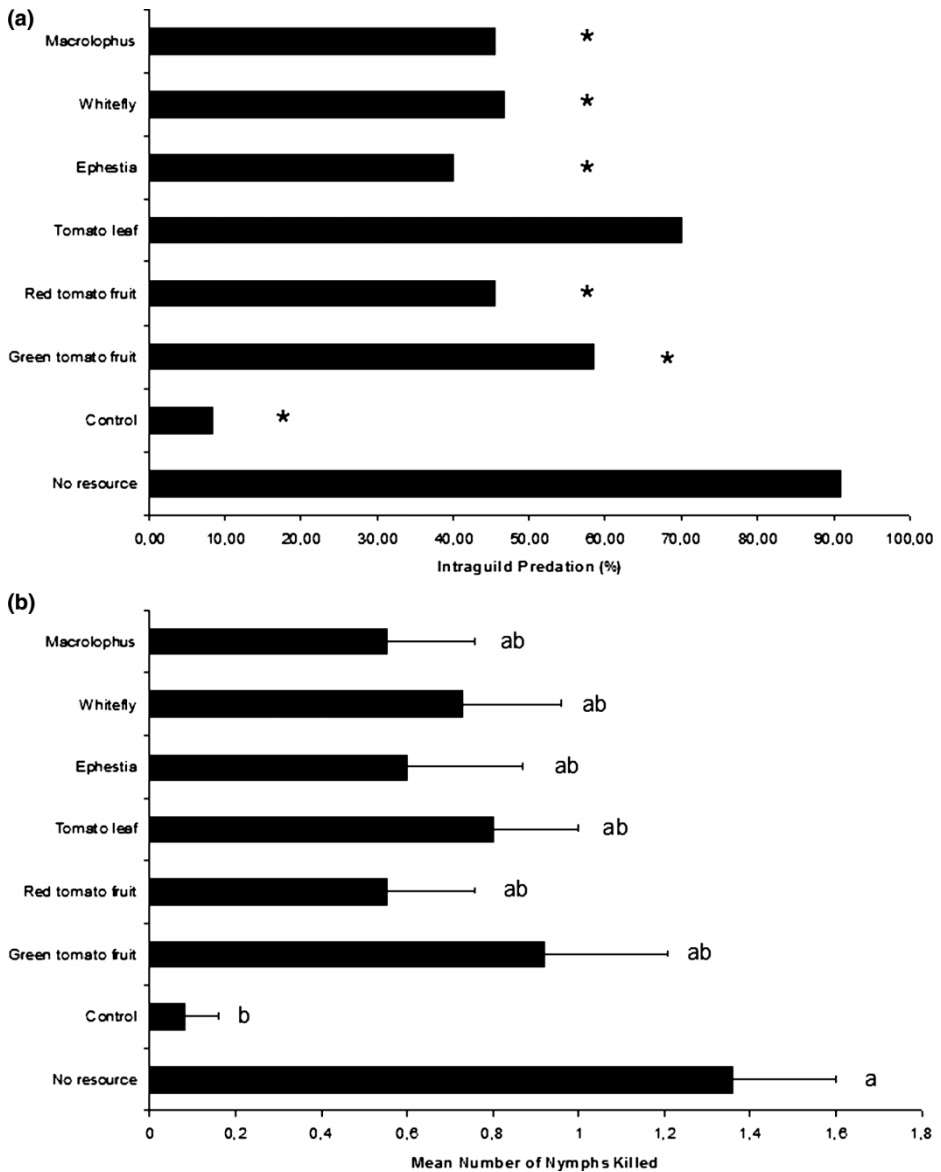


Figure 5. Effect of recently eaten food items on IGP occurrence. (a) Effect of recently eaten food items on the percentages (%) of replicates where IGP occurred. Percentages followed by an asterisk (\*) are significantly different from the *No resource* treatment ( $P < 0.05$ ). (b) Effect of recently eaten food items on the mean number of *Macrolophus caliginosus* nymphs killed by the intraguild predator. Means followed by different letters are significantly different ( $P < 0.05$ ).

prey availability significantly affected *M. caliginosus* nymphs survival ( $F$  ratio = 16.51,  $df = 2$ ,  $P < 0.0001$ ), and treatments differed from each other ( $P < 0.05$ ). Highest survival was observed in the presence of *E. kuehniella* eggs, intermediate survival occurred in the presence of whiteflies, and the lowest survival was observed

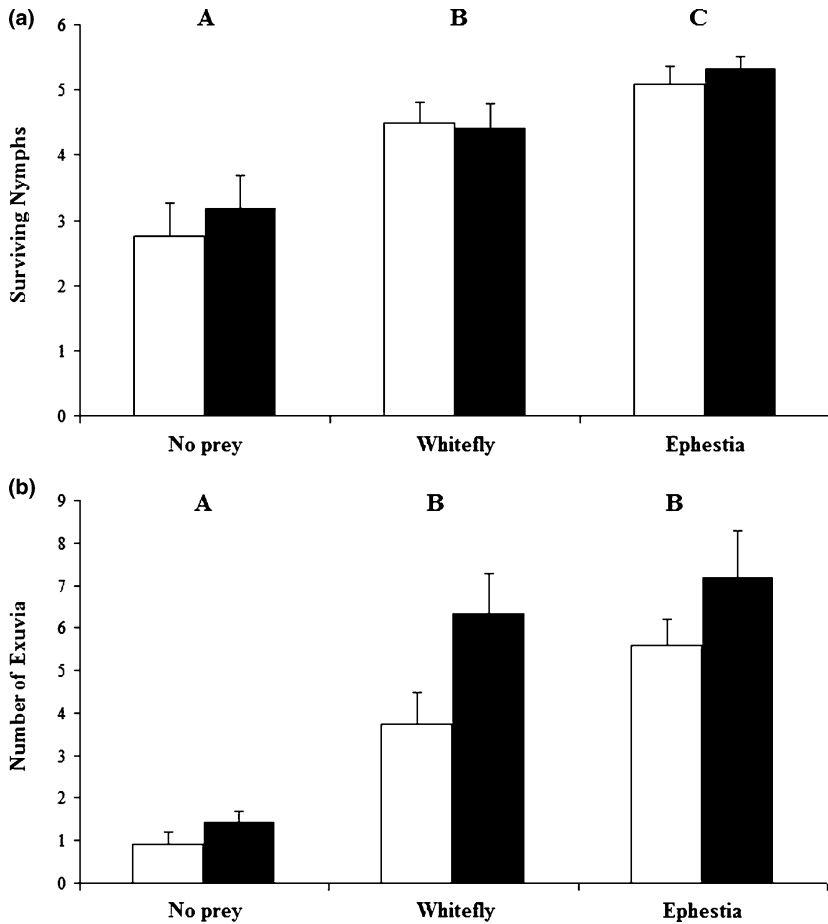


Figure 6. Effect of *Dicyphus tamaninii* adults presence (open bars) or absence (solid bars), and extraguild resource (no prey, *Trialeurodes vaporariorum* nymphs or *Ephestia kuehniella* eggs) on *Macrolophus caliginosus* nymph survival. (a) Number of surviving *M. caliginosus* nymphs. Different letters indicate significant differences between extraguild resource types ( $P < 0.05$ ). No difference was observed according to *D. tamaninii* presence/absence ( $P > 0.05$ ). (b) Number of *M. caliginosus* exuvia collected. Different letters indicate significant differences between extraguild resource types ( $P < 0.05$ ). More exuviae were collected when *D. tamaninii* was absent ( $P < 0.05$ ). DT, *D. tamaninii*.

in the absence of extraguild prey. There was no significant interaction between *D. tamaninii* adult presence/absence and extraguild prey availability ( $F$  ratio = 0.062,  $df = 2$ ,  $P = 0.94$ ). However, the number of *M. caliginosus* exuvia was significantly affected by both intraguild predator presence ( $F$  ratio = 5.51,  $df = 1$ ,  $P = 0.022$ ; Figure 6b) and extraguild resource availability ( $F$  ratio = 34.57,  $df = 2$ ,  $P < 0.0001$ ). There was a significant increase in the number of *M. caliginosus* exuvia collected when *D. tamaninii* adults were absent ( $P < 0.05$ ). Presence of extraguild prey (whiteflies or *E. kuehniella* eggs) resulted in more exuvia than when intraguild prey were absent ( $P < 0.05$ ), but whiteflies and *E. kuehniella* did not differ in their

impact on the number of *M. caliginosus* exuviae ( $P > 0.05$ ). Both animal resources were provided in excess and were still present on plants at the end of the tests. No interactions occurred between *D. tamaninii* adult presence/absence and extraguild prey availability ( $F$  ratio = 0.70,  $df = 2$ ,  $P = 0.50$ ).

## Discussion

Our experimental cage studies demonstrate that *D. tamaninii* and *M. caliginosus* were involved in IGP, and that both species could either act as intraguild predator or as intraguild prey depending upon the stadia confronted. These experiments also demonstrated that occurrence of IGP increased with intraguild prey density. Certain types of extraguild resources provided before or during the experiments also influenced IGP. When provided before the experiment, all diets significantly decreased IGP level compared to the *No resources treatment*, the only exception being tomato leaves that did not affect IGP. However, only the presence of green and red tomato fruits as part of the experimental setup decreased IGP when starved predators were used. This result is surprising since aphids and whiteflies, which are considered high quality food items, did not significantly decrease IGP, while green and red tomato fruits, which are considered low quality food items, significantly reduced IGP.

These results seem to indicate that satiation is an important driving force promoting IGP between *D. tamaninii* and *M. caliginosus*. The fact that tomato leaves provided before the experiment did not lower IGP levels in the same way that the other extraguild resources was expected as tomato leaves are poor quality food items that do not allow *D. tamaninii* to complete its development (Lucas and Alomar 2001).

To better assess impacts of recent food items on IGP, a regression line was fitted between the observed IGP intensities under different food resource treatment (the *effect of recently eaten food items* experiment in this study) and the fitness associated with same resource from a related study (see Lucas and Alomar 2001) (Figure 7). The regression indicates that IGP intensity decreases as the fitness associated with a resource increases ( $r^2 = 0.7044$ ). The decrease in IGP observed with both animal and plant resources should be more pronounced in true omnivores: plant resources should have less effect on IGP (or cannibalism) in more zoophagous omnivores, and animal resources should not reduce IGP (or cannibalism) in true herbivorous species (Figure 8).

The fact that only tomato fruits decreased the level of IGP when starved *D. tamaninii* individuals are present with both intraguild prey and extraguild resources may confirm the fruit-feeding habits of this species on tomato plants (Lucas and Alomar 2002). Continuous access to tomato fruits in those treatments may have concentrated *D. tamaninii* foraging on those fruits, therefore reducing their foraging time and reducing IGP opportunities. Conversely, in the presence of tomato leaves (which are an inappropriate diet) or scattered prey, females may have foraged more actively thus enhancing the encounter probabilities with intraguild prey.

Observed IGP intensity in this study was very low (5.8% after 24 h, and 16.4% after 48 h) compared to what was observed by Lucas et al. (1998) with aphidophagous species: 51% of IGP after 24 h between the ladybeetle *Coleomegilla maculata lengi* Timberlake and the lacewing *Chrysoperla rufilabris* Burmeister, 72%

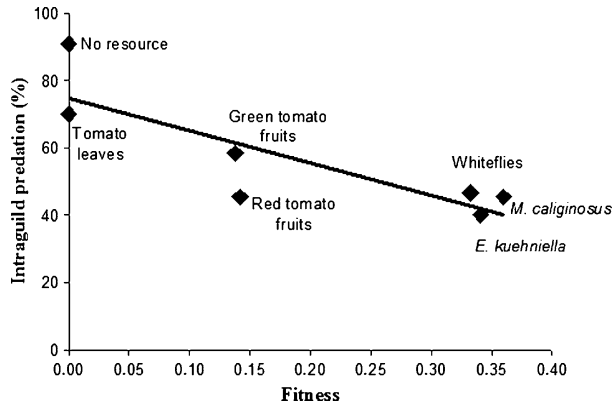


Figure 7. Effect of resource quality on the percentage of replicates where IGP occurred. Intraguild predation data are from the current work (*effect of recently food items* experiment). Resource quality was evaluated with a composite index of fitness using Lucas and Alomar (2001) data, where  $r = \{\ln [(adult\ weight) (\% \text{ nymphal development survival})]\} / (\text{days from first instar to adult moult})$  (Broberg and Bradshaw 1995). The index values were 0.000 for tomato leaves or in the absence of resource, 0.138 for green tomato fruits, 0.142 for red tomato fruits, 0.333 for whiteflies, 0.341 for *E. kuehniella* eggs, and 0.360 for *M. caliginosus* nymphs.

between *C. maculata* and the midge *Aphidoletes aphidimyza* Rondani, and 96% between the *C. rufilabris* and *A. aphidimyza*. This difference may reflect a lower tendency for IGP by the two omnivorous mirids studied. Since IGP may be accompanied with injury or mortality risk, and since omnivorous mirids can survive on plant resources, selection may not have favoured a strong tendency for IGP in the species studied (and possibly in other true omnivorous species). Moreover, mirids seem to be more efficient when attacking sessile or low-mobile prey (Kullenberg 1944; Dolling 1991). According to Kullenberg (1944), even though mirids were observed cannibalizing or preying on nymphs of other mirid species, feeble, sick or dying individuals are usually selected.

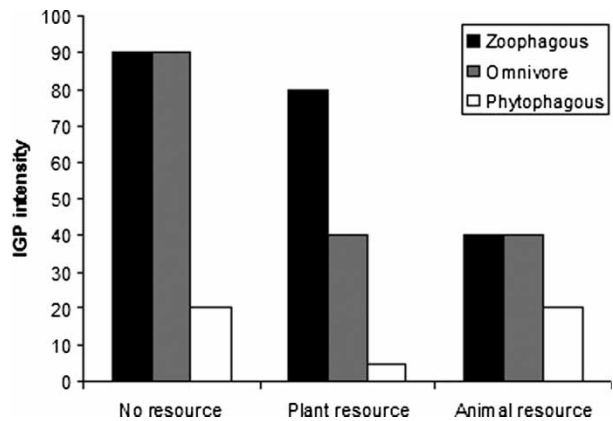


Figure 8. Theoretical figure representing the expected impact of different food types on IGP intensity in zoophagous, omnivorous, and phytophagous species.

Mirids are highly mobile and fleeing is their main defence strategy against predation (Kullenberg 1944; Dolling 1991; Fréchette et al. 2007). Females may even flee away from males several times before mating (Gemeno, Alomar, Riudavets, and Castañe 2007). As was observed with aphidophagous species (Lucas et al. 1998), our works also suggest that symmetry of IGP is more influenced by this mobility than by individuals' relative size. Adult males of both mirid species, which are especially mobile, were much less preyed upon than the larger and less mobile females. Also, *M. caliginosus* females were more susceptible to IGP than smaller but more mobile fourth nymphal instars. Finally, IGP was not related to predator size, as no stadium was identified to achieve a higher level of predation.

The experiment performed on plants tends to confirm that IGP may be rare in the field between the two species studied. Survival of *M. caliginosus* second nymphal instars on plants was not influenced by the presence of *D. tamaninii* adults, even in the absence of extraguild prey and after 7 days of interaction. This could be related to the fact that plants represent a more complex substrate than experimental cages and provide hiding places for intraguild prey. Also, even if tomato plants are low quality food items, they still can provide water (Gillespie and McGregor 2000), reducing the need for IGP and decreasing predator foraging time. That is, natural populations may reach higher density than what was tested in this experiment: as a consequence, IGP opportunity on plant could be higher when intraguild predator and prey reach higher densities.

Nevertheless, the experiment performed on plant also stresses the fact that the results of IGP experiments performed in artificial arenas should be interpreted cautiously; our experiments may have overestimated the occurrence of IGP by forcing the predators to stay in the artificial arena. A similar conclusion was reached by Fréchette et al. (2007) in an experiment exploring the occurrence of IGP between omnivorous mirids and aphidophagous syrphids. Other studies have also demonstrated the effect of plants on interactions between insects (Elsey 1974; Carter, Sutherland, and Dixon 1984; Grevstad and Klepetka 1992; Giroux, Duchesne, and Coderre 1995; Messina, Jones, and Nielson 1997; Clark and Messina 1998; Cortesero, Stapel, and Lewis 2000). By increasing the predator foraging surface and by providing refuge to the prey, plants usually decrease interaction intensities. This impact of plant should be even more important when omnivorous species are involved since plants may also be a food source, reducing foraging motivation.

Even though IGP was not observed in the plant experiment, IGP risk may have lead to a slower intraguild prey development rate since exuviae were less numerous in the presence of the intraguild predator (Figure 5b). Thus, even if IGP level was low, intraguild predators had significant sub-lethal effect on intraguild prey. The slower development rate of *M. caliginosus* nymphs in the presence of *D. tamaninii* had already been observed in an earlier greenhouse cage study (Lucas and Alomar 2002). The reason for this still has to be explored, but could be the result of competition for resources and/or niche displacement through enemy (intraguild predator) avoidance.

Currently, *M. caliginosus* is successfully used in combination with parasitoids to control whiteflies in tomato greenhouses (Gabarra and Besri 1999; Avilla, Albajes, Alomar, Castañe, and Gabarra 2004). This species also shows potential for the control of whiteflies in greenhouse melons (Alomar, Riudavets, and Castañe 2006). This study suggests that *M. caliginosus* could be used together with *D. tamaninii* as biological control agents since IGP level is low between these species. For example,

the natural colonization of crops by *D. tamaninii*, which is common in the Spanish Mediterranean area (Castañe, Alomar, Goula, and Gabarra 2004; Gabarra, Alomar, Castañe, Goula, and Albajes 2004), should not disrupt the establishment of *M. caliginosus* populations released for biological control purposes. However, the possibility that the presence of both species leads to behavioural disturbance and thus lowers the predation impact on the extraguild (shared) prey should be further investigated.

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