Intraguild predation between syrphids and mirids: who is the prey? Who is the predator?

Bruno FRÉCHETTE[1], Santos ROJO[3], Oscar ALOMAR[2] and
Éric LUCAS[1,2,*]

[1]*Département des sciences biologiques, Université du Québec à Montréal (UQAM),
Groupe de Recherche en Écologie Comportementale et Animale (GRECA), C.P. 8888,
Succ. Centre-Ville, Montréal, Québec, H3C 3P8, Canada;* [2]*Departament de Protecció
Vegetal, Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Centre de
Cabrils, E-08348, Cabrils, Barcelona, Spain;* [3]*Universidad de Alicante, Instituto
Universitario CIBIO − Dpto de Ciencias Ambientales, Apto 99, E-03080,
Alicante, Spain*
*Author for correspondence (e-mail: lucas.eric@uqam.ca)

Abstract. The mirid *Macrolophus caliginosus* Wagner (Hemiptera: Miridae), and the syrphids, *Sphaerophoria rueppellii* (Wiedemann), *Sphaerophoria scripta* (L.), and *Episyrphus balteatus* (DeGeer) (Diptera: Syrphidae), belong to the aphidophagous guild, feeding on aphids (Hemiptera: Aphididae) in Mediterranean vegetable crops. The direction, symmetry, and intensity of intraguild predation between different instar combinations of syrphids and mirid were studied in an arena without plants. Moreover, predatory interactions between syrphids and mirids on plants were also evaluated. The results obtained in the arena without plants demonstrated mutual intraguild predation, i.e., syrphid eggs were highly susceptible to predation, whereas mirid nymphs and adults were attacked by syrphid larvae. All syrphid species showed the same propensity to predation, which was unaffected by parasitism of syrphid larvae by *Diplazon laetatorius* (Fabricius) (Hymenoptera: Ichneumonidae). *Sphaerophoria scripta* eggs were less susceptible to predation than those of the two other syrphid species. The experiment performed on plants showed different results. Predation by syrphid larvae on mirids never exceeded 10%, while 100% of syrphid eggs were preyed upon after 48 h. Intraguild predation rates were not influenced by the presence or absence of aphids on the plants. This study demonstrated that results obtained from studying intraguild predation in arenas that are highly artificial should be interpreted cautiously. Depending on the colonization history of a particular habitat in the field, syrphids should be more vulnerable to predation by mirids than vice versa.

Key words: Aphidophaga, biological control, *Diplazon laetatorius*, *Episyrphus balteatus*, intraguild predation, *Macrolophus caliginosus*, Miridae, omnivory, *Sphaerophoria rueppellii*, *Sphaerophoria scripta*, Syrphidae

Introduction

Predation between organisms that belong to the same guild (i.e., intraguild predation, or IGP) may involve complex interactions. Contrary to classical predation, the organisms involved in IGP do not always have well defined roles; the same organism may be either predator or prey, depending on a variety of factors (Polis et al., 1989). The outcomes of such interactions are usually influenced by the relative size, mobility and density of the organisms, as well as by their feeding specificity and morphology, and by the densities of extraguild prey (Sengonca and Frings, 1985; Polis et al., 1989; Lucas et al., 1998; Hindayana et al., 2001; Lucas, 2005).

Most insects experience a considerable increase in body size as they develop, and considerable modifications of morphology, physiology and/or behavior may also occur. Those changes may affect considerably the intraguild interactions between two organisms and thus their propensity for (or susceptibility to) IGP (Polis et al., 1989). For example, a species whose larvae are mainly intraguild prey may become an intraguild predator in the adult stage. Moreover, most holometabolous insects are highly vulnerable during their immobile pupal stage (Lucas et al., 2000).

Aphidophagous syrphid flies, like all holometabolous insects, are organisms experiencing drastic modifications of body size, morphology, and behavior over the course of their life cycle. The vermiform larvae feed on soft-bodied Hemiptera (Sorensen et al., 1995) and aphids are the preferred prey of most species (Rojo et al., 2003). In contrast, winged adults feed mainly on nectar and pollen. Females typically lay their eggs on leaves, usually near aphid colonies (Bombosch and Volk, 1966; Chandler, 1966; Kan, 1988). This adaptive behavior enables neonate larvae to rapidly find a first meal, but also exposes eggs to increased risk of intraguild predation. However, older larvae of some species have been observed preying on other aphidophagous predators (Hindayana et al., 2001).

Unlike syrphids, plant bugs are hemimetabolous and thus do not undergo drastic morphological modifications in the course of their life history. The plant bug *Macrolophus caliginosus* Wagner is an omnivorous mirid (Lucas and Alomar, 2001) that naturally colonizes Mediterranean vegetable crops, both in the field (Alomar et al., 2002) and in greenhouses (Castañé et al., 2004). Even though this species seems mainly associated with whiteflies (Riudavets et al., 1995; Riudavets and Castañé, 1998), aphids may also account for an important

proportion of its diet (Fauvel et al., 1987; Alvarado et al., 1997), presumably in periods of whitefly scarcity (Enkegaard et al., 2001). Moreover, syrphids and *M. caliginosus* are also found in aphid colonies of *Uroleucon inulae* (Fischer) on false yellowhead *Dittrichia viscosa* (L.) Greuter (O. Alomar, unpublished data). Hence syrphids and *M. caliginosus* both belong to the same aphidophagous guild.

In Northeastern Spain, omnivorous mirids (*M. caliginosus*) and syrphids such as *Sphaerophoria rueppellii* (Wiedemann), *Sphaerophoria scripta* (L.), and *Episyrphus balteatus* (DeGeer) are commonly encountered in potato fields preying on the potato aphid, *Macrosiphum euphorbiae* (Thomas). However, potential intraguild interactions between these predators have never been described. A previous experiment performed in an arena without plants demonstrated that *M. caliginosus* nymphs and females were susceptible to predation by *Sphaerophoria* spp. larvae, but potential interactions between other developmental stages of these organisms have not been investigated (Lucas and Alomar, 2000).

The first aim of this paper was to characterize the interactions between various life stages of the three syrphid species and the mirid in an arena without plants. According to the classic rule of size (Sengonca and Frings, 1985; Lucas et al., 1998; Hindayana et al., 2001; Sato et al., 2003), it is predicted that the larger syrphid larvae should mostly act as the intraguild predators, while the smaller mirid should serve as the intraguild prey.

Whereas many laboratory experiments seemingly demonstrate that intraguild predation between aphidophagous predators is very frequent, it is widely recognized that the simplified arenas used for laboratory experiments probably induce intraguild interactions at higher rates than occur in natural situations. Particularly, niche partitioning between intraguild predators in both space and time (Coderre et al., 1987) and the availability of refuges may reduce the intensity of intraguild interactions in the field.

The second goal of this experiment was to evaluate the occurrence of IGP between syrphids and mirids on plants. It was hypothesized that the possibility for intraguild prey to find a refuge and the increased opportunity for niche partitioning should lead to a reduction in intraguild interactions.

Materials and methods

Mirid cultures were established from individuals collected in the spring of 1999 at the Institute for Food and Agricultural Research

and Technology (IRTA) in Cabrils (Barcelona, Spain). Colonies were kept in $40 \times 50 \times 50$ cm rearing cages placed in growth chambers set at 25 ± 2 °C, 16L:8D, and 80−90% RH. Adult and immature mirids were raised together in a cage on tobacco plants, *Nicotiana tabacum* L., and supplied with eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) and nymphs of *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae). Field collected mirids were introduced in the stock culture on a regular basis (2−4 times/year) in order to preserve genetic diversity.

Adults of the three syrphid species, *S. scripta, S. rueppellii* and *E. balteatus*, were captured with sweep nets over potato fields and nearby vegetation. The colony of *S. scripta* was however started with a few individuals from a stock culture of the University of Alicante (Spain). Syrphids were raised in the same climatic conditions as described above for mirids. Each syrphid species was reared separately. Adult flies were given water, crushed commercial pollen in a Petri dish, a bouquet of field collected wild flowers, and 70% diluted honey painted on a Post-it® paper (3 M España S.A., Madrid, Spain). Potato, *Solanum tuberosum* L., and wheat plants, *Triticum aestivum* L., infested, respectively with the aphids *M. euphorbiae* and *Sitobion avenae* (Fabricius) were also provided as needed. Syrphid eggs and larvae used for the experiment were taken from the plants and larvae were fed *ad libitum* with *M. euphorbiae* and *S. avenae* when needed.

For all experiments, statistical analyses were performed with the statistical package JMP IN® (SAS Institute, 2001).

Direction, symmetry, and intensity of intraguild predation in an arena without plants

Intraguild predation between mirids and syrphids in an arena without plants

Intraguild predation between the syrphid, *S. scripta*, and the mirid, *M. caliginosus*, was investigated in the arena without plants in order to determine their respective susceptibility. Nearly all possible relevant combinations of immature stages were tested (see Figure 1). For both species, 1st instar larvae were not used due to their ephemeral duration. *Macrolophus caliginosus* eggs were not used since they are laid within plant tissues, particularly stems (Montserrat et al., 2004). Tests were carried out in growth chambers under the same physical conditions used for the stock cultures.
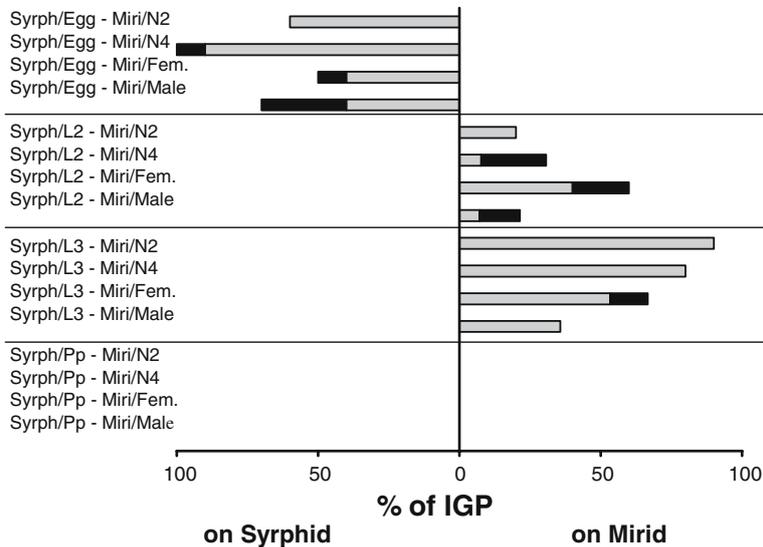
Figure 1. Percentage of intraguild predation (IGP) during the first (gray bars) and the second day (black bars) between various developmental stages of *Sphaerophoria scripta* and *Macrolophus caliginosus* in an arena without plants. The percentage of predation on *S. scripta* is presented on the left side while that on *M. caliginosus* is on the right side. Syrph, Syrphid; L2, second instar larva; L3, third instar larva; Pp, pupa; Miri, Mirid; N2, second instar nymph; N4, fourth instar nymph; Fem, female.

The arena without plants consisted of a transparent plastic cage (Ø: 75 mm × H: 32 mm) with a layer of agar (20 ml, 5%) at the bottom. The cage was covered with a plastic lid which had a meshed opening (muslin) to permit ventilation. Water was provided by a moistened cotton wick in an Eppendorf vial. A potato leaf disk (Ø: 34 mm) was deposited on the agar surface with the abaxial surface upward. The agar layer served to prevent leaf disk desiccation and contributed to maintain suitable humidity within the cage. Preliminary tests demonstrated that agar did not constitute a food source for either mirids or syrphids. After each experimental trial, the agar layer was removed, and both the cage and the Eppendorf vial were washed before a new experimental arena was set up.

At the beginning of the experiment, one individual of each species was released into the cage (see Figure 1 for the combinations tested). Syrphid pupae were gently deposited using soft pincers, while syrphid eggs were deposited with a wet camel hair brush or by cutting and transferring small pieces of leaves where eggs had been laid. After 24 and 48 h, predators were recovered and examined under a stereo microscope, and the occurrence of IGP was determined (n = 10 for

each combination tested). The mortality of immobile stages (eggs and pupae) in the absence of predators was measured as a control.

Predation on syrphid eggs: species susceptibility
A second experiment performed in the arena without plants aimed at evaluating the relative susceptibility of eggs of the three syrphid species to IGP by mirids. A piece of potato leaf onto which two eggs of either *S. rueppellii, S. scripta* or *E. balteatus* had been naturally laid was placed on the agar surface. Either one mirid male or one mirid female was then introduced to the arena. Intraguild predation was assessed by observation under a binocular microscope after 24 and 48 h. Each test was replicated 10 times and 10 replicates without mirids were observed in order to control for natural mortality. The proportions of eggs eaten by mirid males and females were compared with Likelihood Ratio *G*-tests (Sokal and Rohlf, 1981).

Predation on syrphid pupae: effect of pupal age
A third experiment was done in the arena without plants in order to evaluate whether the age of the syrphid pupa affects its susceptibility to IGP by mirids. Pupae were therefore grouped into three age classes: (1) pre-pupa, the period when the 3rd instar larva immobilizes itself and begins to elaborate the physical structure of the pupa (easily identified by the white color of the pupa), (2) pupa proper, when the pupa is fully formed and sclerotized (which occurs about 24 h after the beginning of pupa formation, and is recognized by the brown color of the pupa), and (3) post-pupa, which begins 48−72 h before the imago emerges from the pupa (distinguishable when aspects of adult morphology become visible through the puparium). One *S. scripta* pupa was placed in the arena without plants along with either a male or a female of *M. caliginosus* (n = 10). After 48 h, the mirid was removed and the pupa was kept in the same conditions until the imago came out. Unemerged pupae were kept for a maximum of 2 weeks, at which point they were considered dead. Pupal mortality due to intraguild predation was assessed by comparing the observed mortality with that of control pupae not exposed to intraguild predators.

Propensity of syrphid species for intraguild predation
A fourth experiment was carried out in the laboratory in order to determine possible differences among the three syrphid species in their propensity for IGP. A 3rd instar larva of one of the three syrphid species (*S. scripta, S. rueppellii* and *E. balteatus*) was placed in the

arena without plants with either a male or female adult mirid. Predation on mirids was recorded after 24 and 48 h (n = 10 for each sex). The proportions of mirid males and females preyed upon by the three syrphid species were compared with Likelihood Ratio *G*-tests.

Predation by parasitized syrphid larvae

The fifth experiment evaluated the influence of parasitism on the propensity of syrphid larvae to prey on *M. caliginosus*. Parasitized syrphid larvae continue feeding and develop until pupation. However, Hazell et al. (2005) have demonstrated that *E. balteatus* larvae parasitized by *Diplazon laetatorius* (Fabricius) (Hymenoptera: Ichneumonidae) eat fewer aphids, possibly due to a lower mobility. It was thus hypothesized that parasitism could alter intraguild interactions between syrphids and mirids.

The parasitoid *D. laetatorius* was originally obtained from field collected *S. scripta* pupae. Upon emergence, *D. laetatorius* adults were fed with a honey−water solution provided on a cotton wick. Parasitoid sex was not determined, but were assumed to be females since males are only rarely observed in the Palearctic. Parasitized syrphids were obtained by placing 20 *S. scripta* and *S. rueppellii* 2nd instar larvae (2−3 days old) on potato plants together with 5 *D. laetatorius* adults (less than one-week old) for a period of 48 h. Syrphid larvae were then used for the experiments. Parasitization of the syrphid larvae was later confirmed by keeping the used larvae (one larva per Petri dish in the same growth chamber conditions as described above) until an adult parasitoid emerged from the syrphid pupa. Syrphids from which no adult parasitoid emerged were excluded from the analysis. Since only one parasitoid adult was recovered from each parasitized syrphid pupae, it is assumed that multiple parasitism did not occur. The control treatment consisted of a group of 10 syrphid larvae of both species which were placed in the same conditions as described above, but without parasitoids.

After molting, each 3rd instar larva, parasitized or unparasitized, was placed individually in the arena without plants together with a mirid female. Intraguild predation was recorded after 24 and 48 h. Proportions of mirids preyed upon were compared with Likelihood Ratio *G*-tests.

Direction, symmetry, and intensity of intraguild predation on plants

These tests were conducted for a period of 48 h on potato plants in the presence or the absence of potato aphids. The experimental setup

used was composed of a Plexiglas cylinder (Ø: 20 cm × H: 31 cm) covered with muslin. The bottom of the cylinder was sealed with silicone to a plastic lid. A potted potato plant (3 weeks old) was placed in a hole drilled in the plastic lid, so that the pot could draw up water contained in an underlying recipient. Four scenarios were compared: (1) two eggs of the syrphid *E. balteatus* and one female *M. caliginosus* in the absence of aphids; (2) two eggs of the syrphid *E. balteatus* and one female *M. caliginosus* in the presence of 10 late instar (3rd−4th) aphids; (3) three females of *M. caliginosus* and a 3rd instar larva of the syrphid *S. scripta* in the absence of aphid prey; (4) three females of *M. caliginosus* and a 3rd instar larva of the syrphid *S. scripta* in the presence of 10 late instar (3rd−4th) aphids (n = 10). Syrphid eggs were collected from the stock culture by cutting the leaf area (< 1 cm^2) supporting the eggs. The leaf section was then glued to the undersurface of a potato leaf 4 h before the introduction of the mirids, in order to allow the glue to dry. The glue used was carboxymethylcellulose which is an odorless modified cellulose gum. For treatments 2 and 4, plants were infested with aphids 1 h before the introduction of mobile stages. Mobile predators were introduced into the setup on different parts of the plant. Predation was recorded after 24 and 48 h using a stereo microscope.

Results

Direction, symmetry, and intensity of intraguild predation in an arena without plants

Intraguild predation between mirids and syrphids in an arena without plants

Intraguild predation was mutual, both species preying on the other (Figure 1). Nevertheless all interactions were asymmetrical, each life stage of a species being exclusively a predator, a prey, or neither. While syrphid eggs were eaten by all mobile stages of the mirid, syrphid pupae (48 h old) and larval stages were never preyed upon. On the other hand, syrphid larvae preyed on all mobile stages of the mirid, the 3rd instar generating the higher levels of predation (61.2 and 65.3% predation of mirids after 24 and 48 h, respectively). Adult males of the mirid were preyed upon by 2nd instar syrphid larvae less often than females ($\chi^2_{24 h}$ = 3.898, df = 1, p = 0.048; $\chi^2_{48 h}$ = 3.747, df = 1, p = 0.053) but there was no difference with 3rd instar larvae ($\chi^2_{24 h}$ = 0.915, df = 1, p = 0.339; $\chi^2_{48 h}$ = 2.823, df = 1,

$p = 0.093$). Control treatments showed that there was no natural mortality for all tested life stages.

Predation on syrphid eggs: species susceptibility

Eggs of the 3 syrphid species were preyed upon by both male and female mirids (Figure 2). The eggs of *S. scripta* were less susceptible to predation by mirid females after 24 and 48 h ($\chi^2_{24\,h} = 12.634$, df $= 2$, $p = 0.002$; $\chi^2_{48\,h} = 13.171$, df $= 2$, $p = 0.001$) than those of the other syrphid species. *Sphaerophoria scripta* eggs were also less susceptible to predation by mirid males after 24 h ($\chi^2_{24\,h} = 12.315$, df $= 2$, $p = 0.002$), but no significant difference was observed after 48 h ($\chi^2_{48\,h} = 4.773$, df $= 2$, $p = 0.092$). No egg mortality was observed in the control treatment after 48 h.

Predation on syrphid pupae: effect of pupal age

Despite their absence of mobility, syrphid pupae were generally not victims of intraguild predation by *M. caliginosus*. One pre-pupa died as a result of predation by a mirid female, but all the other pupae
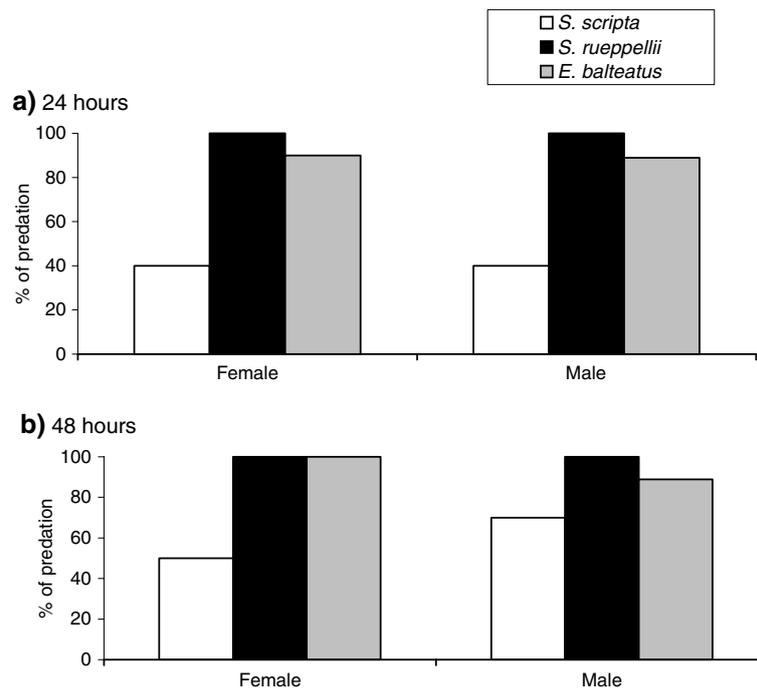

Figure 2. Percentage of *Sphaerophoria scripta*, *Sphaerophoria rueppellii* and *Episyrphus balteatus* eggs preyed upon by *Macrolophus caliginosus* adult males and females after 24 h (a) and 48 h (b).

were recovered unharmed. In the control treatment 100% of the pupae successfully reached the adult stage.

Propensity of syrphid species for intraguild predation

Predation by the three different syrphid species on both male and female *M. caliginosus* did not differ after 24 h (χ^2_{males} = 0.881, df = 2, p = 0.644; $\chi^2_{females}$ = 4.823, df = 2, p = 0.090) or after 48 h (χ^2_{males} = 0.086, df = 2, p = 0.958; $\chi^2_{females}$ = 3.892, df = 2, p = 0.143). In total, males (27.3% after 24 h and 33.3% after 48 h) tended to be slightly less susceptible to predation than females (47.1 and 55.9% after 24 and 48 h, respectively), even though the differences in proportion were not significant ($\chi^2_{24\,h}$ = 2.832, df = 1, p = 0.092; $\chi^2_{48\,h}$ = 3.477, df = 1, p = 0.062).

Predation by parasitized syrphid larvae

After 24 and 48 h, the intensity of predation by parasitized and healthy syrphid larvae on mirid females was similar for both *S. scripta* ($\chi^2_{24\,h}$ = 0.044, df = 1, p = 0.834; $\chi^2_{48\,h}$ = 0.778, df = 1, p = 0.378) and *S. rueppellii* ($\chi^2_{24\,h}$ = 1.848, df = 1, p = 0.174; $\chi^2_{48\,h}$ = 0.220, df = 1, p = 0.639). That is, parasitism affected neither the intensity nor the direction of predation. None of the syrphid larvae, parasitized or not, was victim of IGP by mirids.

Direction, symmetry, and intensity of intraguild predation on plants

Predation rate by syrphid larvae on mirid females was low (Figure 3). One mirid female (10%) had been preyed upon after 48 h in the presence of aphids, and no females had been preyed upon in the absence of aphids. On the other hand, the level of predation on syrphid eggs was very high: 100% of the syrphid eggs were preyed upon after 24 h in the presence of aphids, while all but one egg (90%) were eaten by mirids in the absence of aphids. All the syrphid eggs were preyed upon after 48 h.

Discussion

Our experiments performed in the arena without plants demonstrated that IGP between syrphids and mirids is mutual and that the direction of predation is mainly determined by the combination of developmental stages considered. While syrphid eggs are highly susceptible to predation by mirids, the subsequent syrphid developmental stages
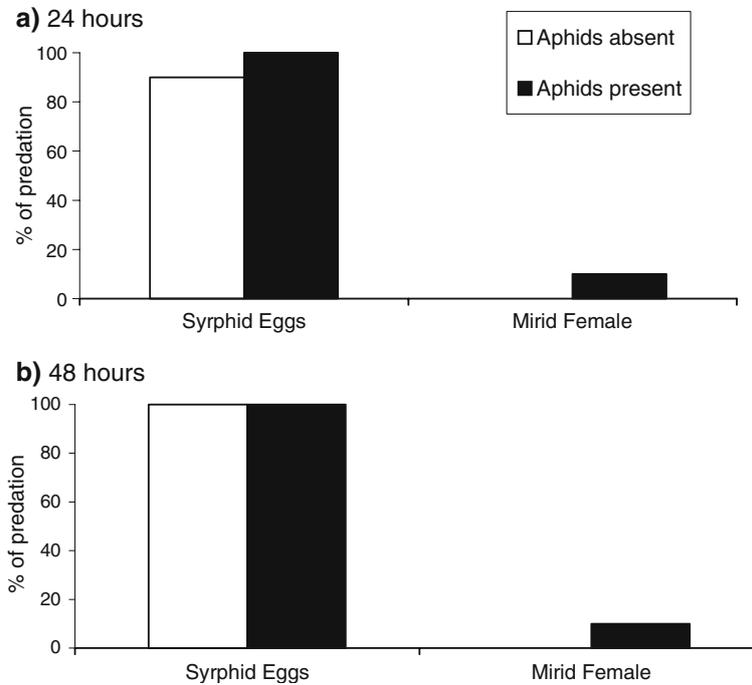
Figure 3. Percentage of *Episyrphus balteatus* eggs preyed upon by *Macrolophus caliginosus*, and of *M. caliginosus* females preyed upon by *Sphaerophoria scripta* larvae on potato plants, in the presence or in the absence of the aphid *Macrosiphum euphorbiae*, after 24 h (a) and 48 h (b).

were not observed to be intraguild prey, with the exception of one pre-pupa. On the other hand, all the mirid developmental stages studied were susceptible to predation by syrphid larvae.

Syrphids as intraguild predators/mirids as intraguild prey

In the arena without plants, syrphid larvae preyed on all *M. caliginosus* mobile stages: the three syrphid species studied attacked the mirid with similar propensity, and the 3rd instar larva was the most voracious stage.

Parasitization of syrphid larvae had no impact on their propensity to prey on mirids. Hazell et al. (2005) demonstrated that *E. balteatus* larvae parasitized by *D. laetatorius* ate fewer aphids than unparasitized ones and hypothesized that this decrease in voracity could be the result of lower mobility. For that reason, it was expected that the intensity of intraguild predation by syrphid larvae would be reduced by previous parasitization. However, no significant difference was

observed in the intensity of predation by parasitized and healthy larvae. The difference between the results of Hazell et al. (2005) and those presented here could be attributable to the arena size used in the present experiment. The small arena allowed frequent contacts between syrphids and mirids without need for the former to allocate much energy to movement.

The experiments conducted on plants showed different results than those run in the arena without plants. Mirid mortality due to predation by syrphid larvae was very low, even in the absence of aphid prey. *Macrolophus caliginosus* thus appears to escape predation from syrphid larvae on plants. Since eggs of this mirid are laid within plant tissues, they should not be available for attack by aphidophagous predators. Nymphs and adults are quite mobile, a characteristic that may facilitate evasion of predation, at least against a slower-moving predator like a syrphid larva. This inference is supported by the fact that males, that are more active than females (O. Alomar, unpublished data), tended to be less preyed upon than the slower females.

Mirids as intraguild predators/syrphids as intraguild prey

Syrphids were only susceptible to predation by mirids during the egg stage. The pupa, which is the other syrphid immobile stage, does not seem to be as susceptible to intraguild predation by *M. caliginosus*.

The susceptibility of syrphid eggs to predation by *M. caliginosus* was not uniform among the three syrphid species studied. The eggs of *S. scripta* were less susceptible to predation than those of *S. rueppellii* and *E. balteatus*. Differences in rate of egg predation among different aphidophagous predators have been previously observed (Agarwala and Dixon, 1992). Eggs of some coccinellids (Hemptinne et al., 2000; Agarwala and Yasuda, 2001; Sato and Dixon, 2004) and chrysopids (Eisner et al., 1996) are chemically protected against predation. According to Sato and Dixon (2004), predatory species that colonize aphid patches later than others are more likely to evolve chemical defense of their eggs. *Sphaerophoria scripta* colonizes Mediterranean crops from early spring to autumn (S. Rojo, unpublished data), while *S. rueppelli* and *E. balteatus* larvae are mainly active in spring. This means that *S. scripta* eggs may be laid at a moment when other aphidophagous predators are present or have reached more advanced developmental stages. Chemical or mechanical defenses could thus have evolved for the eggs of this species which could be otherwise particularly susceptible to predation. An alternative hypothesis could be that the eggs of *S. scripta* are less attractive to mirids than those

of *S. rueppellii* and *E. balteatus* due to their size and/or color. The exochorion structure of *S. scripta* eggs is different from that of eggs from other syrphid species including *E. balteatus* (e.g., Chandler, 1968; Kuznetsov, 1988). However, the egg of *S. rueppellii* remains to be described. The experiments conducted on plants confirmed that syrphid eggs were very vulnerable to predation by mirids, even on a more structurally complex substrate.

Ecological and biological control implications

Although many authors mention various organisms, such as spiders and ants, as occasional syrphid predators, their interactions with Hemiptera have seldom been documented. Koehler (1948) and Jessup (1964) showed that diets of the predaceous Hemiptera *Troilus luridus* Fabricius (Pentatomidae) and *Nabis capsiformis* Germar (Nabidae) may include syrphids. Moreover, some soft-bodied Hemiptera, such as aphids, are able to kill syrphid larvae and other aphidophagous predators through specialized 'soldiers' (e.g., Foster, 1990; Tanaka and Ito, 1995). Mirid predation on syrphid larvae has only been anecdotally reported (Wheeler, 2001). As regards to syrphid predation on mirids, Wheeler (2001) and Rojo et al. (2003) reveal two African syrphid species preying on mirids, i.e., *Allograpta nasuta* (Macquart) feeding on *Helopeltis* sp. in cotton (Lean, 1926; Cotterell, 1928) and *Melanostoma annulipes* (Macquart) on *Psallus impictus* Odhiambo (= *Moissonia importunitas* Distant) colonies in *Crotalaria agatiflora* Schweinfurth (Schmutterer, 1974). The syrphid *Ischiodon aegyptius* (Wiedemann) has also been reported to attack *Helopeltis* sp. nymphs during ecdysis, but only on rare occasions (da Silva Barbosa, 1959). Otherwise, syrphid predation on mirids has also been reported anecdotally (Varis, 1972). That is, the results presented here are thus a contribution to this little known aspect of syrphid and mirid biology.

Predation of syrphid eggs by mirids could be of ecological significance in natural situations. In the experiment on plants, more than 90% of the syrphid eggs were preyed upon by mirids after only 24 h. Mirids are ubiquitous and abundant in both natural and agroecosystems and their omnivorous feeding habits enable them to persist on plants even in the absence of prey. Egg predation by mirids could thus be a significant mortality factor for syrphids. Due to mirid omnivory and mobility, both aphidozetic (i.e., species that oviposit only in the presence of aphids) and phytozetic syrphids

(i.e., species not as closely associated with aphids) could be negatively affected. Those results are particularly interesting since, to the authors' knowledge, syrphid egg predation by mirids has only been reported by Petherbridge and Husain (1918, in Wheeler 2001) and by Carroll and Hoyt (1984).

No experiments were carried out to evaluate the susceptibility of syrphid 1st instar larvae, but this small and early stage may also be vulnerable to predation by omnivorous mirids (see Hindayana et al., 2001). Differences in susceptibility of early instars between species would be expected due to different mobility (Chandler, 1969; Rojo et al., 1996).

Omnivorous mirids appear to be very efficient (or specialized) on small, sessile prey like whiteflies and aphids, and IGP directed toward eggs deposited onto plants might be very common. In the literature, many cases of mirids preying on insect eggs have been reported (for example Strawinski, 1964; Wheeler, 2001). This study confirms the extreme vulnerability of insect eggs laid in exposed locations (see Hinton, 1981; Branquart et al., 1997; Lucas et al., 1998), and underscores the adaptive value of defensive tactics such as laying eggs within plant tissues.

One very important conclusion of this study is that one should be very cautious when extrapolating laboratory results. In an arena without plants, mirids were highly vulnerable to predation by syrphid larvae; however, on plants, predation rate on the same mirid was relatively low. Being unable to escape in the arena without plants, mirids were deprived of their primary defense − evasion. Theories of IGP generally propose that mobility is an important determinant and that less mobile stages of development should be more vulnerable to predation (Polis et al., 1989). This study tends to support this hypothesis. All predation tests should be carried out in as close to a natural situation as possible.

Intraguild predation between biological control agents might be important in Mediterranean greenhouses and field crops in which several aphid predators are often released simultaneously. Both syrphids (*E. balteatus*) and mirids are commercially available for biological control purposes, and can also share the same reservoir plants used in habitat management programs. Intraguild predation could potentially hinder biological control programs that rely on the combined use of those two organisms, something warranting a more thorough examination in field situations.

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