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ORIGINAL PAPER

New parasitoid-predator associations: female parasitoids do not avoid competition with generalist predators when sharing invasive prey

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Abstract Optimal habitat selection is essential for species survival in ecosystems, and interspecific competition is a key ecological mechanism for many observed species association patterns. Specialized animal species are commonly affected by resource and interference competition with generalist and/or omnivorous competitors, so avoidance behavior could be expected. We hypothesize that specialist species may exploit broad range cues from such potential resource competitors (i.e., cues possibly common to various generalist and/or omnivorous predators) to avoid costly competition regarding food or reproduction, even in new species associations. We tested this hypothesis by studying short-term interactions between a native larval parasitoid and a native generalist omnivorous predator recently sharing the same invasive host/prey, the leaf miner *Tuta absoluta*. We observed a strong negative effect of kleptoparasitism (food resource stealing) instead of classical intraguild predation on immature parasitoids. There was no evidence that parasitoid females avoided the omnivorous predator when searching for oviposition sites, although we studied both long- and short-range known detection mechanisms. Therefore, we conclude that broad range cue avoidance may not exist in our biological system, probably because it would lead to too much oviposition site avoidance which would not be an efficient and, thus, beneficial strategy. If confirmed in other parasitoids or specialist predators, our findings may have implications for population dynamics, especially in the current context of increasing invasive species and the resulting creation of many new species associations.

Keywords Interspecific interactions · *Tuta absoluta* · *Stenomesius japonicus* · *Macrolophus pygmaeus* · Foraging behavior · Biological control · Kleptoparasitism

Introduction

Optimal foraging theory focuses on decisions that animals make when foraging for resources and that contribute to maximizing their fitness (Stephens and Krebs 1986). Among the different behavioral strategies studied, optimal habitat choices and time investment decisions are likely complicated by spatial and temporal dynamic variations in factors affecting habitat quality, such as food resource quantity and quality, predation and competition intensity, as well as microclimatic conditions (e.g., Gustafsson 1987; Robinson et al. 1995; Sinervo and DeNardo 1996; Martin 2001; Shima and Osenberg 2003; Marshall and Cooper 2004). Among these factors, interspecific competition is commonly considered to be one of the primary explanations for observed ecological and evolutionary patterns (Connell 1980, 1983; Schoener 1983; Gurevitch et al. 1992; Schluter 2001; Eccard and Ylonen 2003). However, the role of competition may depend on the type of competitive interaction involved (Morris 1999). Resource competition usually involves two types of interaction. Exploitative competition implies indirect negative interactions arising as a result of the use of a common resource (e.g., Case and Gilpin 1974). In contrast, interference competition involves direct negative interactions arising from

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territoriality, overgrowth, predation, or chemical competition (Schoener 1983), where consumers might alter each other's ability to exploit the resource at a certain level of abundance (e.g., Vance 1984). As the competition affecting a species increases, the likelihood that this species will avoid an area hosting a competitor will concomitantly increase.

Several studies have reported that animal species often avoid the detrimental effects of competition by temporally or spatially segregating their niches (Rosenzweig 1995; Morris 1999). Avoidance of conspecific competitors has been reported for parasitoid species, but few studies have focused on avoidance of heterospecific competitors. In arthropods, avoidance of heterospecific competitors has been demonstrated in bark beetles (Byers 1993), phytophagous mites (Pallini et al. 1997), predatory mites (Janssen et al. 1997; Gnanvossou et al. 2003), and parasitoids (Janssen et al. 1995; Tamo et al. 2006; Cancino et al. 2012). However, avoidance is not always systematic (Janssen et al. 1999) and avoidance mechanisms are often not clearly identified. In parasitoids, interspecific host discrimination has been observed mainly for closely related species that avoid multiparasitism (when the same host is parasitized by different parasitoid species) (Vet et al. 1984; van Baaren et al. 1994; Pijls et al. 1995; Royer et al. 1999; Agboka et al. 2002; Ardeh et al. 2005). This could be the result of the use of the same cues as those used to avoid superparasitism (when the same host is parasitized by different females of the same species), but the mechanisms by which parasitoids recognize competitors are largely unknown.

It seems that avoidance behavior occurs between closely related species with a marked overlap in diet (Vet 1999) (i.e., between specialist species). In predators behaving both as generalist and omnivorous predators (called hereafter "generalist omnivorous predators," following the term "generalist omnivores" used in the review article of Symondson et al. (2002)), having a broad diet breadth, overlap with other species diet is frequent, but the extent of competition is less than between specialist competitors as one of the two competitors has access to a non-shared resource. However, generalist omnivorous predators may have a highly detrimental effect on specialist species via food resource competition since (i) through exploitative competition, they could reduce the prey density, even at very low levels, since they withstand low shared prey levels by feeding on other prey or other trophic levels, and (ii) the competition may be increased by additional interactions (i.e., interference competition) between the two species, such as intraguild predation or kleptoparasitism [stealing already procured food from competitors (Curio 1976)] (e.g., Chailleux et al. 2013a, b).

Mechanisms that may lead to avoidance of generalist omnivorous competitors have not yet been clearly identified in parasitoid species. It is known that parasitoid wasps can be affected by a high level of inter- and intraspecific competition and that this can drive parasitoid communities and niches (Harvey et al. 2013). Indeed, laboratory studies have shown that, in the presence of potential competitors, parasitoids alter the sizes of their foraging niches (Harvey et al. 2013). It is also known that competition pressure in parasitoids can lead to the evolution of chemical cue avoidance (Vet 1999). Interspecific competitor avoidance between parasitoids involves oviposition cue avoidance since they chemically mark the hosts after oviposition (Vet 1999). However, in competition with predators, the cues differ since they do not arise from oviposition behavior. It is likely that these mechanisms are the same as those involved in prey avoidance of generalist predators and could be specific to one competitor species or instead allow the detection of a wide range of potentially competitive carnivorous species. Mechanisms involved in generalist predator avoidance by prey have now been studied in detail: prey can recognize feces (Agarwala et al. 2003) and chemical cues (Dicke and Grostal 2001) either volatile or not (e.g., Ninkovic et al. 2013) using their olfactory ability or they can use predator visual detection (Sendoya et al. 2009).

We thus hypothesize that (i) parasitoids, which are frequently affected by both exploitative and interference competition from generalist omnivorous predators, may have developed avoidance mechanisms to a broad range of this type of competitor in order to increase their fitness and (ii) these avoidance mechanisms may occur via cues that are common to a broad range of generalist omnivorous competitors (called hereafter broad range cues).

We tested these hypotheses on a new generalist predator-parasitoid association that occurs on the invasive pest *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) which has recently invaded the Mediterranean Basin (Desneux et al. 2010, 2011). The parasitoid species used was *Stenomesius japonicus* Ashamed (Hymenoptera: Eulophidae), a native specialist parasitoid of leaf miner larvae that behaves as a solitary idiobiont ectoparasitoid (Zappala et al. 2013; Chailleux et al. 2014). It parasitizes the four *T. absoluta* larvae instars, with a preference for the second and third instars (Chailleux et al. 2014). The predator *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) is a native generalist omnivorous predator that feeds on eggs and occasionally on *T. absoluta* young larvae by extracting hemolymph through the larva cuticle (through a stylet mouthpart) (Urbaneja et al. 2009; Jaworski et al. 2013). The objectives of this study were (i) to characterize interference competition between the larval parasitoid and the generalist omnivorous predator and (ii) to assess any predator avoidance behavior by naive parasitoid females which had never previously encountered the generalist omnivorous predator.

Materials and methods

Biological materials

Five-week-old tomato plants, *Solanum lycopersicum* L. cv. Betalux, were grown in climatic chambers (24±1 °C, RH 65 %, photoperiod 16L:8D) with a daily supply of nutrient solution. All insect species were reared in growth chambers (25±1 °C, RH 70±10 %, 16L:8D). A *T. absoluta* colony was established using greenhouse-collected individuals in July 2009 at INRA, Alenya, France (initial number of individuals=190). Adults were kept in cages (55×75×80 cm) containing tomato plants and fed by placing honey on one wall inside the cages. The life cycle of the *S. japonicus* parasitoid is 12–15 days at 25 °C on *T. absoluta*; eggs are deposited by females in the host mines close to the host larva and they hatch after 1.5 to 2 days. Before ovipositing, parasitoid females paralyze the *T. absoluta* larvae, which then quickly die. Parasitoids were reared in the same sized cages as those used for *T. absoluta*. In cages, a constant supply of tomato plants infested with *T. absoluta* larvae was provided to parasitoids and honey droplets were put on tomato leaves. Rearing was initiated using individuals collected in greenhouses in Spain and France ($n=11$ and $n=7$, respectively). The predator *M. pygmaeus* is widely used in European greenhouses to control whiteflies and more recently to control *T. absoluta*, and it is also able to feed on plants (Fauvel et al. 1987; Bonato 2006). *M. pygmaeus* individuals were provided by the Biotop company in France. They were reared for one generation in the laboratory in cages containing tobacco plants and fed with UV-sterilized *Ephestia kuehniella* eggs before the experiments.

All parasitoid females used in the experiments were of mixed ages and had been isolated from hosts in a transparent plastic box (*d* 9 cm, *h* 12 cm) covered with a mesh and containing a tomato trifoliate leaf for 5 days prior to the experiments, which corresponds to an optimal duration to obtain the maximum oviposition level according to preliminary experiments (see Biondi et al. 2012 for a thorough description of the design). Honey droplets were placed on the box sides. This design (hereafter called arenas) was used for all experiments except the olfactometric behavioral study. In the same way, all *M. pygmaeus* females used in the experiment had been isolated from insect food sources 24 h before the experiments using the same arenas.

Short-term negative effects of the predator on immature parasitoids

A laboratory experiment was carried out in arenas to assess the effects of the predator on the parasitoid immature stages. *S. japonicus* females were individually transferred to an arena containing a tomato trifoliate leaf infested with five *T. absoluta* third larval instars deposited on the trifoliate leaf 1 h before parasitoid release so as to enable host larvae mine digging. Parasitoid females were allowed to parasitize the hosts for 48 h in a climatic chamber (24±1 °C, RH 65 %, photoperiod 16L:8D). Parasitoids were then removed and one *M. pygmaeus* male-female pair was introduced in the arena. Natural enemy staying durations were established according to preliminary experiments. Three days after their introduction, predators were removed and the mines were opened under a binocular microscope to record the number of parasitoid offspring. The number of living *T. absoluta* larvae was also noted. The same design was used but without *M. pygmaeus* for comparison. Twenty replicates were performed for the two treatments.

A second experiment consisting of direct behavioral observations was carried out because a negative effect of the predator on the parasitoid offspring was observed in the previous experiment (i.e., fewer parasitoid offspring in the presence of the predator). Hence, in addition to potentially directly attacking the parasitoid offspring, we suspected that *M. pygmaeus* was able to feed more easily on paralyzed *T. absoluta* larvae than on healthy ones. One *T. absoluta* third larval instar was placed on a tomato leaflet in a petri dish for 1 h to ensure its establishment in a mine. Leaflet stems were planted in flower foam for watering. Parasitoid females were then allowed to oviposit individually under a binocular microscope to observe oviposition, and thus to ensure the presence of eggs in the mines without the need to open the mines. Petri dishes were kept for 2 days in a climatic chamber, corresponding to the time required for the parasitoid eggs to hatch. Then one *M. pygmaeus* female was introduced into the petri dish for 5 h. The number of *T. absoluta* larvae and parasitoid immature stages attacked by the predator were then recorded by opening the mines under a binocular microscope. Attacked *T. absoluta* larvae had sections of their body damaged by the predator. If no damage was observed, larvae were considered to not have been attacked. In addition, for *T. absoluta* larvae attacked by *M. pygmaeus*, the proportion of hemolymph sucked by the predator (¼, ½, ¾, all of the larva) was visually assessed under a binocular microscope. After the observations, parasitized larvae were kept under the same experimental conditions and controlled daily to check any parasitoid larvae mortality. As a control treatment, *M. pygmaeus* females were also released on healthy *T. absoluta* larvae using the same experimental design and at the same time as the treatment with parasitized larvae. Eleven replicates were carried out for the two treatments.

Avoidance behavior

The ability of parasitoid adult females to avoid the predator was tested using both a choice and a non-choice experiment. In the non-choice assay, five treatments were carried out with

T. absoluta larvae associated with (1) *S. japonicus* alone, (2) *S. japonicus* + *M. pygmaeus*, (3) *S. japonicus* + *M. pygmaeus* semiochemicals, (4) *M. pygmaeus* alone, and (5) a control with *T. absoluta* alone. Five *T. absoluta* third larval instars were placed per arena 1 h before the natural enemy release, as described for the first experiment. Isolated *S. japonicus* females and/or, when needed, one *M. pygmaeus* male-female pair was added. For treatment 3, one *M. pygmaeus* male-female pair was added in the arena prior to the experiment for 24 h and removed just before the host larvae were established (i.e., 1 h before the parasitoid introduction). Despite the fact that *M. pygmaeus* semiochemicals were not specifically studied, this treatment is warranted because it is known that (i) the presence of this predator can impact parasitoid behavior (Martinou et al. 2010), (ii) hemipteran predators can leave patch marking (however such marking seems to persist for only around an hour, Nakashima et al. 2002) and sex and trail pheromones (Aldrich 1988; Nakashima and Hirose 1999; Aldrich et al. 2007), and (iii) some predatory arthropods leave semiochemicals that persist for 10 days on plant leaves (Hemptinne et al. 2001). Forty-eight hours after natural enemy introduction, mines were opened under a binocular microscope to record the number of parasitoid offspring and of *T. absoluta* living larvae. Twenty replicates were carried out per treatment.

A Y-tube olfactometer was used to study the response of female *S. japonicus* adults in a choice situation. The Y-tube consisted of a central plastic tube (*l* 8 cm, *d* 1.6 cm) connected at the two sides to the middle of arenas containing odor sources. The central tube was perforated at the center and connected to a removable tube (*l* 4 cm, *d* 1 cm). The parasitoid was first confined in this removable tube 15 min before the experiment to avoid possible decisions due to stress. Then one side of the removable tube containing the parasitoid was carefully attached to the central tube, while the other side was attached to a suction pump that generated an air flow from the two odor sources. The chosen air flow rate was 0.25 m s^{-1}, which did not disturb parasitoid movement (personal observation). The odor sources in the two arenas consisted of a tomato trifoliate infested with two *T. absoluta* third larval instars, and for one side, one *M. pygmaeus* male-female pair was added. Larvae were placed on the trifoliate 2 h before the experiment and the predators were released in the arena 1 h before the experiment, so (i) larvae were already in mines when the predators were released and (ii) predators had time to produce possible olfactory cues. Each arena was used three times and then replaced by a new one. Parasitoids that did not reach one of the two ends of the central tube after 30 min were excluded from the experiment. To obtain 20 replicates leading to a choice, 21 females were tested but one was excluded because it did not reach one of the ends of the central tube after 30 min.

Statistical analyses

All statistical analyses were performed using R software (R Development Core Team 2009) with the "multcomp" and "agricolae" packages. For the first experiment (predator effect on immature parasitoids), the number of *S. japonicus* offspring and of living *T. absoluta* larvae were analyzed using a generalized linear model (GLM) with a Poisson distribution and a log link function. The *M. pygmaeus* situation (i.e., absence, presence) was tested as a factor in this model. For the behavioral observation experiments, a χ^2 test was performed to compare the number of larvae attacked by the predator. For the avoidance non-choice assay, a GLM with a Poisson distribution was also used to analyze the number of *S. japonicus* offspring [*M. pygmaeus* situation as a factor (i.e., presence, absence, semiochemicals)] and the number of living *T. absoluta* larvae [*M. pygmaeus* situation (i.e., presence, absence, semiochemicals) and *S. japonicus* presence (i.e., presence, absence) as factors]. When necessary, means were separated using a least significant difference post-hoc test (LSD test) for multiple comparisons. The parasitoid choice in the avoidance choice assay was analyzed using an exact binomial test.

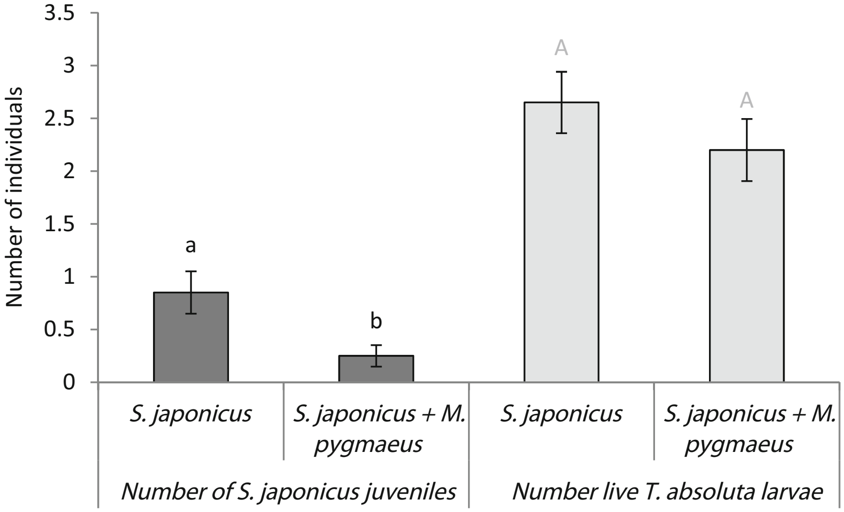
Results

Short-term negative effects of the predator on immature parasitoids

The experiment evaluating the predator impact on parasitoid immature stages showed that the number of *S. japonicus* offspring (larvae instar) recorded after 3 days was reduced by the presence of *M. pygmaeus* (Fig. 1; $F_{1,\ 38}$=8.18, P=0.007). However, the number of living *T. absoluta* larvae was not affected by the presence of *M. pygmaeus* ($F_{1,\ 38}$=1.24, P=0.273): on average, about half of the *T. absoluta* larvae were still living after 3 days in both treatments (Fig. 1). Indeed, *M. pygmaeus* was not able to feed on healthy *T. absoluta* third larval instars (but it fed on dead ones) as confirmed by the behavioral experiment (see results below).

In the behavioral observations, none of the immature parasitoids were directly attacked by the predator, so we did not observe any intraguild predation. On the contrary, *M. pygmaeus* fed on the parasitized *T. absoluta* larvae, attacking on average 81.8±11.8 % (±SE) of the parasitized larvae. Parasitoid larvae, by (i) being outside of the host larvae (as already mentioned, *S. japonicus* is an ectoparasitoid) and (ii) being very small compared to *T. absoluta* larvae, were neither directly attacked by *M. pygmaeus* nor physically affected when *M. pygmaeus* attacked *T. absoluta* larvae, according to our observations. However, when *M. pygmaeus* sucked

Fig. 1 Mean number (±SE) of *S. japonicus* offspring produced per parasitoid female in 48 h (*dark gray*) and mean number (±SE) of living *T. absoluta* (*light gray*), recorded after 3 days with and without *M. pygmaeus* being present (after *S. japonicus* female oviposition) under laboratory conditions. Values with the same *letters* (lower case for parasitoid offspring and upper case for *T. absoluta* larvae) are not significantly different at $P<0.05$



the hemolymph of parasitized *T. absoluta* larvae, which was also the food resource of the immature parasitoid, this was considered to be food robbing (i.e., kleptoparasitism). Hemolymph sucking of parasitized *T. absoluta* larvae by the predator took on average 48.3±26.3 % of the total larva hemolymph content. *M. pygmaeus* did not attack the immature parasitoids, but all of them died 2 days after the experiment, probably because of the lack of food resources caused by the predator robbing. No healthy *T. absoluta* larvae were attacked by the predators in the control treatment; thus, the presence of the parasitoid significantly affected the number of larvae attacked by *M. pygmaeus* ($\chi^2=12.03$, $d.f.=1$, $P<0.001$).

Avoidance behavior

In the non-choice experiment, the number of *S. japonicus* offspring produced was not significantly affected by the presence of *M. pygmaeus* (Fig. 2; $F_{1,\ 58}=0.47$, $P=0.497$). Overall, an average of 2.33±0.41 offspring was produced in 48 h. The number of living *T. absoluta* larvae after the experiment (Fig. 3) was significantly affected by the presence of *S. japonicus* ($F_{1,\ 98}=112.21$, $P<0.001$). Conversely, the presence of *M. pygmaeus* had no significant effect on this parameter ($F_{2,\ 97}=1.65$, $P=0.197$). In the choice experiment, parasitoids did not significantly avoid the predator (binomial exact test: $P=0.824$); 55±0.11 % of the parasitoids chose the odor source without *M. pygmaeus*.

Discussion

We obtained evidence of a negative effect of the generalist omnivorous predator *M. pygmaeus* on immature stages of the parasitoid *S. japonicus*. The observations inferred that it was not intraguild predation but rather kleptoparasitism. The predator fed on *T. absoluta* larvae attacked by parasitoid females, thus robbing immature parasitoids of the food resource, which may have contributed to their death. However, in our experiments, parasitoid females did not refrain from attacking *T. absoluta* larvae when the predators or their semiochemicals were present in non-choice tests, and they also did not avoid the predators in choice tests. Hence, contrary to our former hypothesis, parasitoid females apparently did not exhibit any kind of long- or short-range avoidance behavior. This suggests that parasitoid females apparently did not recognize (or at least did not respond to) any cues (odor or physical cues, visual detection) that would have allowed them to avoid exploitative and interference competition risks with the predator.

These results could mainly be explained by the time-saving hypothesis. Indeed, whether egg or time is the principal limiting factor of fitness in parasitoids has been a topic of

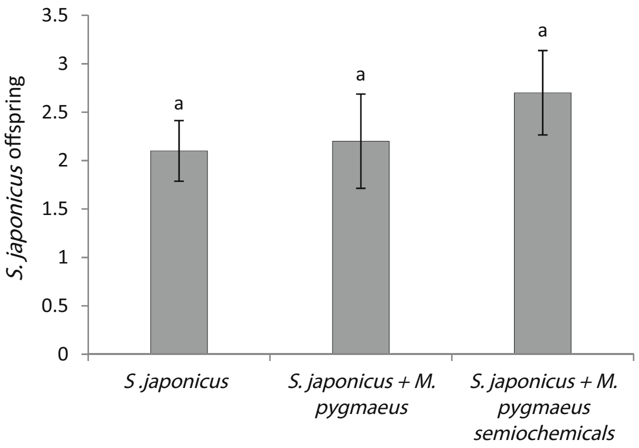
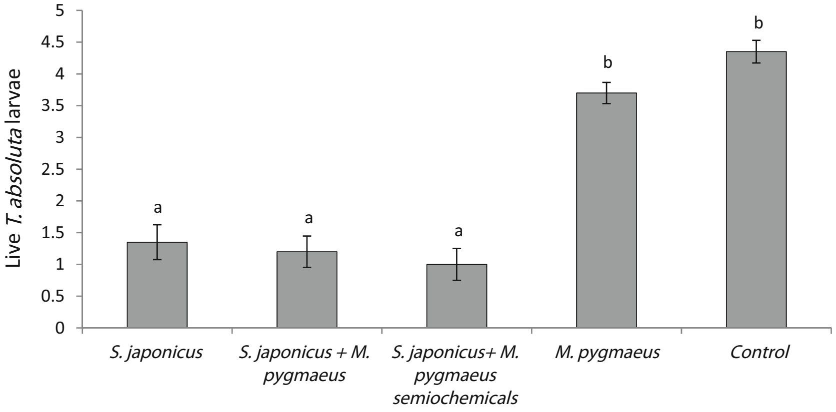


Fig. 2 Mean number (±SE) of *S. japonicus* offspring produced per parasitoid female in 48 h when alone with *T. absoluta* larvae, when *M. pygmaeus* was present, and when only *M. pygmaeus* semiochemicals were present under laboratory conditions. Values with the same *letters* are not significantly different at $P<0.05$

Fig. 3 Mean number (±SE) of living *T. absoluta* larvae per arena after 48 h in five treatments under laboratory conditions: (1) *S. japonicus* female alone, (2) *S. japonicus* females + *M. pygmaeus*, (3) *S. japonicus* females + *M. pygmaeus* semiochemicals, (4) *M. pygmaeus* alone, and (5) control with *T. absoluta* larvae alone. Values with the same *letters* are not significantly different at $P<0.05$



considerable discussions in recent decades (Rosenheim 1996; Sevenster et al. 1998). Under natural conditions, the average lifespan of solitary parasitoids such as *S. japonicus* is often considered to be too short for the females to deposit all their eggs (Rosenheim 1999). Based on simulation models (e.g., Turlings et al. 1985) or field studies (Janssen 1989), some authors suggest that as long as she is not egg-limited and oviposition is not overly time-consuming, a female parasitoid should accept a host already parasitized by another species, even if the chance of offspring survival is small. Similar hypotheses could explain that female parasitoids should not avoid generalist omnivorous predators via broad range cues. Indeed, avoiding many generalist omnivorous predators may lead them to avoid too many oviposition sites because such predators are abundant in agroecosystems, as hypothesized by Dicke and Grostal (2001) for prey attacked by generalist predators. In addition to this first explanation (i.e., (i) the competition cost is too low to induce avoidance mechanisms), two others could be proposed: (ii) detection mechanisms of broad range cues that would allow parasitoid avoidance of many generalist omnivorous predators may not exist or (iii) broad range cues exist and could be detected by parasitoids but the studied predator species did not exhibit these broad range cues.

Our experiments did not allow us to identify the relevant hypothesis, so this remains to be tested on other biological models. It is not clearly known which cues *S. japonicus* parasitoid females are able to detect, but these two latter explanations are dependent on this factor. Nevertheless, before *T. absoluta* invasion, *S. japonicus* females must have already competed with species relatively close to *M. pygmaeus* (e.g., from the same Hemiptera order) because hemipteran predators bear a stylet that allows them to attack larvae inside the mine. In line with this, most *T. absoluta* larvae predators that have been recorded were hemipterans (Zappala et al. 2013; Bueno et al. 2013; Speranza et al. 2014). In addition, some Eulophidae parasitoids are known to detect olfactory stimuli from conspecific or heterospecific parasitoids (e.g., Silva-Torres et al. 2005) and it is known that larval parasitoids are able to detect odors, visual cues, and vibrations from their hosts, but it is unknown whether they are able to use these types of cues to detect competitors (Sugimoto et al. 1988; Fischer et al. 2001). Only chemical cues have been shown to be used by female parasitoids to avoid intraguild predation risks for their offspring (Nakashima et al. 2004; Meisner et al. 2011). Based on the abovementioned knowledge, it seems that (i) considering the complexity of the host location for leaf miner parasitoids, these species are capable of detecting many cues, but possibly only in a very specific way, and (ii) it is probable that *M. pygmaeus* shares some cues (i.e., feces composition, semiochemicals, visual shape, etc.) with the arthropod predatory species generally competing with *S. japonicus*, since these predators are from the same order. Therefore, the time-saving hypothesis seems to be the most relevant.

From an applied standpoint, our study obtained the first evidence of kleptoparasitism between biological control agents at the intraguild level. However, cases of intra- and interspecific kleptoparasitism have been reported in vertebrates (Dominey and Snyder 1988; Di Bitetti and Janson 2001; Garrido et al. 2002; Honer et al. 2002), marine invertebrates (Morissette and Himmelman 2000), and arthropods (e.g., Michener 1974; Crespi and Abbot 1999; Sivinski et al. 1999; Whitehouse et al. 2002; Reader 2003; Kronauer 2004; Richard et al. 2004; LaPierre et al. 2007). Interspecific kleptoparasitism has never been reported in predatory Hemiptera, but scavenger behavior has (Sugiura and Yamazaki 2006). In our study, kleptoparasitism was similar to scavenging because (i) the host (here the juvenile parasitoid) was almost immobile and unable to defend its food sources and (ii) the robbed *T. absoluta* larvae were dead and even sometimes decaying specimens. *M. pygmaeus* seemed to adopt an opportunistic behavior when it encountered a parasitized *T. absoluta* larva. The latter represents a rich food source as compared to *T. absoluta* eggs, which is almost the only *T. absoluta* stage that the predator can individually fed on, apart from occasional attacks on the youngest *T. absoluta* larval instars, which would be costlier for the predator than kleptoparasitizing dead larvae. Indeed, parasitized larvae are easier to attack for the predator because healthy *T. absoluta* larvae adopt a squirming defensive behavior in response to attack (personal observation): squirming larvae usually get out of the mine, fall into the undergrowth, and can then escape (also observed by Tautz and Markl 1978).

The predator behavior thus meets most of the requirements to be considered as facultative kleptoparasitism: (i) the benefits of additional food exceed the cost associated with theft, (ii) the host (here the *S. japonicus* parasitoid) is negatively affected by the loss of food, (iii) the kleptoparasite (here *M. pygmaeus*) does not injure the hosts in any direct way, and (iv) typical habitats of the host and the kleptoparasite are congruent (Iyengar 2008). These observations highlight that the large group of idiobiont ectoparasitoids might present a substantial opportunity for food-stealing because they typically consume their hosts in several days, therefore increasing the likelihood of having their food items stolen by a kleptoparasite (Iyengar 2008). Indeed, when externally feeding on their hosts, if idiobiont ectoparasitoids are not directly attacked by the predator, then attacks on their hosts do not represent intraguild predation, contrary to endoparasitoids which are generally consumed by the intraguild predator while consuming parasitized hosts. Intraguild predation and kleptoparasitism may lead to different responses from the parasitoid being attacked. It should be noted that neither of the two negative interactions reported in our experiment (exploitative competition on a stage-structured prey and kleptoparasitism on immature parasitoid stages) directly affects adult females. Since the two competitors attack different stages, they never meet trying to use the same individual resource at the adult stage simultaneously. Hence, we believe that it is unlikely that the two interactions observed in our study would induce adaptive avoidance behavior via learning. In such a case, if the strong negative effects on parasitoid fitness arising from this new association are confirmed under natural conditions, the evolution of any avoidance mechanism would require natural selection over parasitoid generations and would likely only occur on a long-term scale.

The findings of our study support the conclusion that parasitoids do not use broad range cues to avoid generalist omnivorous predators. This may have implications for population dynamics, especially in case of invasions that create many new species associations. Further studies should be carried out to depict generalist-specialist interactions and the fitness consequences of the different strategies. Such studies are currently lacking in the literature even though generalist-specialist associations are very frequent in nature.

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