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ORIGINAL ARTICLE

Intraguild predation and competitive displacement between *Nesidiocoris tenuis* and *Dicyphus maroccanus*, 2 biological control agents in tomato pests

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Abstract *Dicyphus maroccanus* Wagner and *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) are 2 biological control agents in tomatoes. Through the crop seasons, a natural shift in the occurrence of both mirids in favor of *N. tenuis* has been observed at the end of the cropping cycle in eastern Spain. To better optimize their conservation, the reasons for the observed change, such as intraguild interactions (IGP) or the influence of environmental conditions, are worth elucidating. To do this, we first studied the IGP of adult females on heterospecific nymphs in the laboratory. We next studied exploitative competition between adults and nymphs of each species when feeding on *Ephestia kueniella* Zeller (Lepidoptera: Pyralidae) eggs in the laboratory. Finally, to analyze the competitive displacement between both mirids, we conducted a semifield experiment in which both predators were released together. All experiments were conducted at 2 temperature regimes (20 and 25°C). Adult-to-nymph intraguild interactions occurred only at 25 ºC at very low levels, showing that *N. tenuis* attacked and consumed a greater proportion of heterospecific nymphs. *Nesidiocoris tenuis* was a better competitor than *D. maroccanus* when feeding on the shared prey in the presence of its heterospecific nymph at 25 ºC. In semifield conditions, *N. tenuis* showed a competitive advantage over *D. maroccanus* at both temperatures. We conclude that there is not direct interference between both species, however, *N. tenuis* has a greater ability to outcompete, since it is best adapted to higher temperatures and it is able to remove food sources for *D. maroccanus*.

Key words competition; Mediterranean crops; Miridae; temperature; tomato

Introduction

Trophic guild interactions are common in food webs, especially those comprising biological control agents (Rosenheim *et al.*, 1995; van Veen *et al.*, 2006; Moreno-Ripoll *et al.*, 2012). When using a combination of arthropod species to control a pest, the potential direct and indirect effects that could arise among them are important aspects to be considered. Among those ecological interspecific interactions, competition and intraguild

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predation are clearly recognized as affecting the structure and dynamics of natural enemies and thus influencing the outcome of biocontrol success (Rosenheim *et al.*, 1995; Snyder & Wise, 1999; Lucas & Alomar, 2002; Boivin & Brodeur, 2006). The former implies interactions (*via* exploitation or interference) between competitors through a shared resource, while the latter occurs between consumers belonging to the same guild engaged in a predator–prey interaction (IGP predator–IGP prey) and sharing an alternative (extra-guild) prey (Lucas, 2012). Intraguild predation can be categorized as "coincidental," which occurs when the IGP predator attacks a herbivore that has previously been attacked by a parasitoid or pathogen (called the intermediate predator), and "omnivorous" when one predator encounters and consumes another predator and share the same herbivore (Polis *et al.*, 1989; Rosenheim & Harmon, 2006). Therefore, studies to assess these interspecific interactions should evaluate the foraging behavior of entomophagous arthropods towards possible inter- or intraguild prey.

The literature on the combined action of cooccurring natural enemy species in biological control includes synergistic, neutral and antagonistic effects (Nóia *et al.*, 2008; Gagnon *et al.*, 2011). The outcome varies depending on several factors, such as the life history, behavioral and morphological characteristics, population structure, environmental conditions, and guild structure of the organisms involved, among others (Finke & Denno, 2002; Lucas & Rosenheim, 2011; Perdikis *et al.*, 2014). A meta-analysis by Rosenheim and Harmon (2006) found that different intraguild predators seem to have very different effects on herbivore population suppression, at least in short-term experiments. These authors concluded that additional work is needed to provide additional observations on predator-predator interactions and how they are influenced by physical environmental features.

In this context, cropping cycles can also have an effect on the displacement of natural enemies in the field. In many cases, changes in abiotic and biotic factors along the cycles may be responsible for the replacement of species or the temporal segregation of their distributions by influencing biological parameters, and, consequently affecting biocontrol outcomes (Mills, 1999; Welch & Hardwood, 2014).

Omnivorous predators belonging to the family Miridae (Hemiptera) are common natural enemies of pests in several agroecosystems (Coll & Ruberson, 1998). The species composition varies from region to region, although they belong mainly to the genera *Macrolophus*, *Dicyphus* and *Nesidiocoris* (Castañé *et al.*, 2004). These predators are present in open field and greenhouse crops, and adjacent natural ecosystems (Lucas & Alomar, 2001). It has been reported that they commonly engage in intraguild predation by feeding on other entomophagous organisms (McGregor & Gillespie, 2005). Particularly in tomato crops, mirids are considered the main biocontrol agents against a variety of pests, such as whiteflies, aphids, mites, and, recently, the invasive tomato borer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Calvo *et al.*, 2012; Moreno-Ripoll *et al.*, 2012; Urbaneja *et al.*, 2012). In southeastern Spain, IPM in tomato includes the use of selective pesticides, and releases and/or conservation of either *Macrolophus pygmaeus* (Rambur) or *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) (Arno & Gabarra, 2011; Calvo *et al.*, 2012; Urbaneja *et al.*, 2012). The adoption of IPM strategies opened the door to other mirid species present in southeastern Spain to spontaneously colonize tomato crops. This is the case for *Dicyphus maroccanus* Wagner (Hemiptera: Miridae), which was first reported preying on the eggs and young larvae of *T. absoluta* in the Valencia region (eastern Spain) (Mollá *et al.*, 2010; González-Cabrera *et al.*, 2011; Urbaneja *et al.*, 2012; Abbas *et al.*, 2014; Perez-Hedo & Urbaneja, 2015).

In tomatoes planted at the end of winter and ended at the end of summer (a typical crop cycle followed in open tomato crops in the Valencia region), it has been noted that *D. maroccanus* colonizes the crop earlier (March to May) than *N. tenuis*, which appears somewhat later in the system. Both predators coexist in the crop during a certain period, but *N. tenuis* populations rise rapidly until the end of the crop, whereas *D. maroccanus* progressively decreases. Explanations for the observed shift in predator occurrence could come from either intraguild or competitive interactions between the 2 species or from changing seasonal environmental factors during the cropping cycle. Therefore, in this paper, the IGP of adult females on heterospecific nymphs and the exploitative competition between adults and nymphs of each species when feeding on a shared prey (*Ephestia kuehniella* Zeller [Lepidoptera: Pyralidae] eggs) were studied in the laboratory. In addition, the competitive displacement between both mirid species when released together was studied in a semifield experiment.

Materials and methods

Plants and insects

The plants used in all experiments were seedlings of pesticide-free tomato cv. Optima (Seminis Vegetable Seeds, Inc.; Almería, Spain), approximately 30 cm high. *Nesidiocoris tenuis* adults were obtained from a commercial supplier (NESIBUG; Koppert Biological Systems, S.L., Águilas, Murcia, Spain). *D. maroccanus* nymphs and adults were obtained from established colonies in the IVIA laboratory (Pérez-Hedo & Urbaneja, 2015). Frozen eggs of *E. kuehniella* were used as an artificial source of prey for the mirids.

Environmental conditions

To know the influence of temperature on the above mentioned interactions, all experiments were conducted at 2 constant temperatures, 20°C and 25°C, which could represent the mean temperature at the end of spring and at summer registered in the Mediterranean coastal districts of Spain where open air tomatoes are grown. The laboratory experiments were conducted in 2 climatic cabinets set at each of the corresponding experimental temperature conditions (±1°C), while relative humidity and photoperiod were held constant at 65% ± 5% RH and 14 : 10 h (L : D). The semifield experiments were maintained in a glasshouse located at IVIA. Two independent cubicles in the greenhouse were selected (A and B) and acclimatized at 20 and 25°C (±1°C), respectively. Relative humidity was 65% ± 10% and the photoperiod was natural (approximately 14 : 10 h L : D) in both cubicles. Environmental conditions were controlled and recorded using a Mithra clima (ver. 1.01.03, Priva nutricontrol Ibérica S.L) datalogger.

IGP on nymphs

Intraguild predation for female adult predators exposed to a heterospecific nymph prey was assessed as a direct lethal attack, that is, by fighting and killing it. Two treatment effects were considered: *N. tenuis–D. maroccanus* and *vice versa*; and 2 control treatments (each mirid species presented with its monospecific nymph) were carried out.

To set up the experiment, single females of either *N. tenuis* or *D. maroccanus* (less than 3 d old) were randomly selected, isolated individually in Petri dishes (55 mm in diameter and 10 mm in height), and starved for 24 h with access only to water soaked in a cotton ball. During the starvation period, dishes were stored at the 2 temperature conditions for acclimation. After that period, 1 heterospecific 1st instar nymph was offered to each female (IG predator) as IG prey. To obtain 1st instar nymphs, 8 adult couples (<4 d old) of the corresponding mirid species were released into a methacrylate cage (40 cm × 40 cm × 40 cm) containing 4 tomato plants. *Ephestia kuehniella* eggs were offered as food *ad libitum* every 2 d. After 1 week, plants bearing predator eggs were removed, cut into small sections, and placed in Petri dishes (60 mm in diameter) lined with filter paper to avoid excess humidity. The dishes were checked daily for newly hatched nymphs. Newly emerged nymphs (≤24 h old) were used in the IGP experiments described above. Each IG predator–prey combination was replicated 20 times.

Visual observations of the predation act were made at 4 periods as follows: (i) during the first 30 min, at each 1- to 3-min interval, (ii) each 5- to 10-min interval to complete a 5-h period, (iii) every 30 min up to 7 h, and (iv) at 24 h. Period intervals were chosen following the work of Abad-Moyano *et al.* (2009). The experiment was ended when the nymph was either killed by the IG predator or it survived after 24 h. The number of surviving nymphs was recorded.

Exploitative competition

To test the effect of the interaction between both mirid species in the presence of prey, and the influence of temperature conditions (20 and 25°C) on the interaction, an experiment was designed considering 3 treatments: in treatment 1 (T1), 1 adult female of each species was introduced simultaneously into a plastic Petri dish arena 55 mm in diameter × 10 mm high containing 20 *E. kuehniella* eggs presented as prey on a tomato leaflet; in treatment 2 (T2), 1 female adult and 1 heterospecific 1st instar nymph were introduced simultaneously into the unit with 20 *E. kuehniella* eggs as described above, and in treatment 3 (T3), 1 adult female of each mirid species and 1 of each respective heterospecific nymph and 20 *E. kuehniella* eggs were combined together in the same unit. The control treatment consisted of 1 female adult of each mirid species placed alone in the arena and provided with 20 *E. kuehniella* eggs. All mirids used were taken randomly from the stocks, isolated individually in Petri dishes (55 mm in diameter and 10 mm in height), and starved for 24 h at the corresponding experimental temperature with access only to water soaked in a cotton ball. The experiment was held under 2 temperature conditions while the relative humidity and photoperiod remained constant (65% ± 5% RH and 14 : 10 h L : D). Each treatment was replicated 20 times. The number of eggs eaten by each predator species was recorded firstly by visual counting of the preying act throughout a 60-min period, and later by checking under the microscope signs of suctioned eggs.

Competitive displacement between D. maroccanus and N. tenuis

Both species, *D. maroccanus* and *N. tenuis,* were simultaneously released into a 60 cm × 60 cm ×

60 cm plastic cage (BugDorm-2; MegaView Science Co. Ltd.; Taichung, Taiwan, China). Groups of 8 30-cm tall potted tomato plants were placed. Two adult *N. tenuis* and 2 *D. maroccanus* were released for each tomato plant (total = 16 couples per cage). Throughout the experiment, *E. kuehniella* eggs were sprinkled on plants every 48 h (approximately 0.1 g of *E. kuehniella* eggs per plant) (Urbaneja-Bernat *et al.*, 2015). To exclude any other cause of displacement, but competition, separate populations of each predator species were monitored under the same conditions as described above. In this case only 2 adults of either *N. tenuis* or *D. maroccanus* were released for each tomato plant (total = 8 couples per cage). As mentioned above, 2 temperature conditions were considered, 20 and 25°C, and each treatment was replicated 3 times.

Observations of subsequent offspring numbers began 3 weeks after the experiment was set up, and based on generation time reported for Miridae in general and for *N. tenuis* and *Dicyphus* spp., insect recording continued at 7-d intervals (Sánchez *et al.*, 2009; Mollá *et al.*, 2014). Two measurements were made. First, the number of nymphs and adults of *N. tenuis* and/or *D. maroccanus* per cage were counted inside the greenhouse, during the following 9 weeks at 20°C and 7 weeks at 25°C. After counting the adults and nymphs, 1 apical shoot per plant (approximately 10 cm in length) and per cage was removed to monitor the mirid eggs development. This part of the plant was selected because of the tendency of Miridae to oviposit there (Perdikis *et al.*, 2014). Each shoot was cut into small sections of approximately 4–5 cm, introduced into Petri dishes (9 cm in diameter), and provided with *E. kuehniella* eggs (approximately 5 eggs to N_1, 10 eggs to N_2, 15 eggs to N_3, 20 eggs to N_4, and 25 eggs to N_5; Urbaneja-Bernat *et al.*, 2015) and water soaked in a cotton ball to maintain the foliage turgid. Dishes were kept at the corresponding temperatures (20 or 25°C), and checked every 72 h to register the number of emerging nymphs and identify the species when they reach adulthood. The relative abundance of *N. tenuis* in relation to the total number of mirids counted each week (the sum of adults and nymphs on plants and the emerged nymphs on shoots) was estimated.

Statistical analyses

The survival of the nymphs after exposure to heterospecific predation was evaluated by means of Kaplan–Meier survival analyses. Nymph survival curves were plotted of the time to death to reflect the mortality due to intraguild predation by the IG adult female predator. Comparisons of the survival curves of each effect and control treatment were tested for statistical significance (Chi-square and Mantel–Cox tests). The results from the exploitative competition experiment were subjected to a two-way analysis of variance (ANOVA) in which the temperatures (20 and 25°C) and competition treatments (control, T1, T2, T3, and T4) were considered as fixed factors. Means were compared using Bonferroni's test ($P < 0.05$). Finally, a generalized linear mixed model with repeated measures (GLMM) was used to compare the numbers of mirid bugs per shoot in all of the 3 treatments in the competitive displacement experiment. Treatment was considered as a fixed factor and time as a random one. When significant differences were found, pairwise comparisons of the fixed factor levels were performed with the least significant difference (LSD) post hoc test ($P < 0.05$). Selection of the best model was based on the Akaike Information Criterion (AIC). Each GLMM used a normal distribution and identity link function.

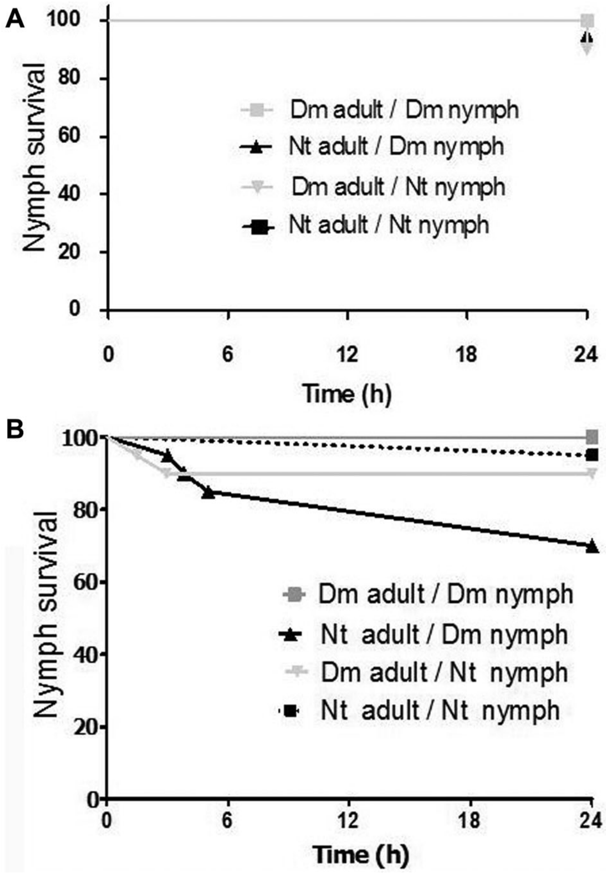

Fig. 1 Survival (%) of *N. tenuis* and *D. maroccanus* nymphs in laboratory tests after exposure for 24 h to a heterospecific adult female at (A) 20 ºC and (B) 25°C. Bullets indicate the mean time for each interval studied.

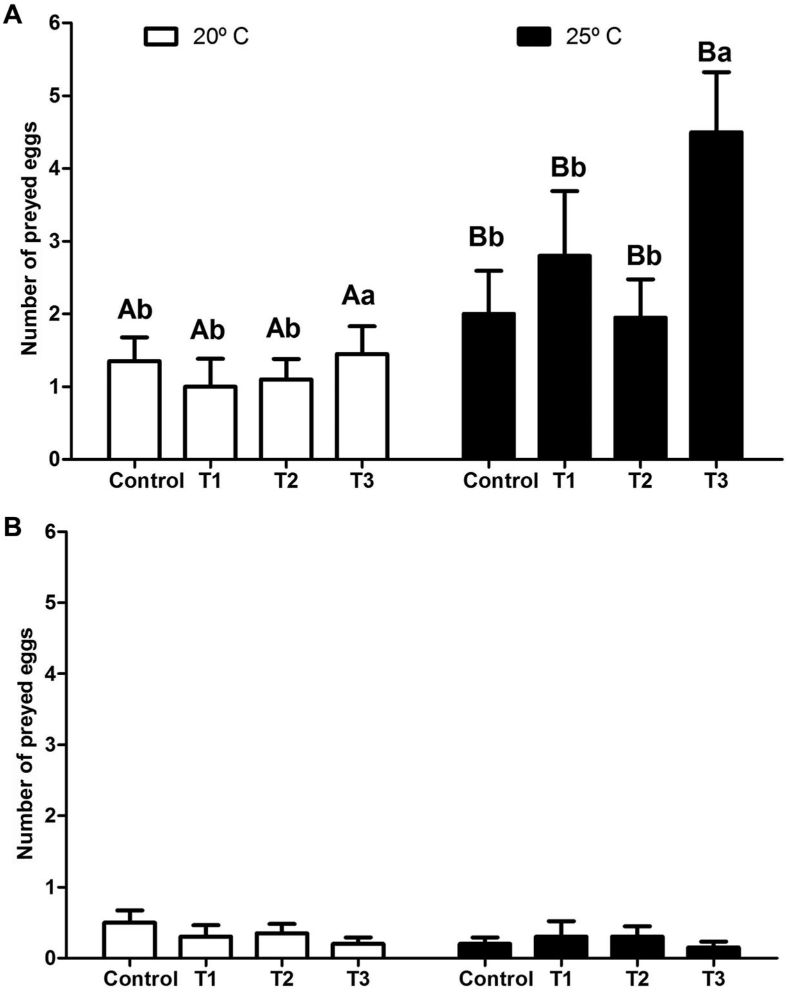

Fig. 2 Number of *E. kuehniella* eggs killed (mean ± SE) in laboratory tests, by (A) *N. tenuis* and (B) *D. maroccanus* at 20 ºC and 25°C. Control: 1 adult female of each mirid species alone in the arena provided with 20 *E. kuehniella* eggs; T1: 1 adult female of each species was introduced simultaneously with 20 *E. kuehniella* eggs as prey; T2: 1 female adult and 1 heterospecific 1st instar nymph were introduced simultaneously in the unit with 20 *E. kuehniella* eggs; and T3: 1 adult female of each mirid species along with 1 respective heterospecific nymph and 20 *E. kuehniella* eggs were combined together in the same unit. Bars with different upper case letters indicate significant differences between temperatures (20 and 25 ºC) whereas bars with different lower case letters show significant differences between competition treatments (control, T1, T2, T3 and T4) (Bonferroni; $P < 0.05$).

Results

IGP on nymphs

Intraguild predation by *N. tenuis* and *D. maroccanus* adult females against its heterospecific first-nymphal stage differed significantly with temperature (at 20°C: $\chi^2 = 3.667$, $P = 0.300$; at 25°C: $\chi^2 = 10.03$, $P = 0.018$) (Fig. 1). At 20°C, 100% of the nymphs survived predation by its opponent during 24 h. In contrast, at 25°C *D. maroccanus* nymphs suffered up to 30% predation by *N. tenuis* adults by the end of the experiment (24 h); meanwhile, predation by *D. maroccanus* adults on *N. tenuis* nymphs was lower (<5%). In addition, cannibalism was observed in *N. tenuis* (approximately 10%), whereas this was not observed for *D. maroccanus*.

Exploitative competition

Nesidiocoris tenuis preyed upon significantly more *E. kuehniella* eggs at 25°C than at 20°C ($F = 15.63$; $\text{df} = 1$,

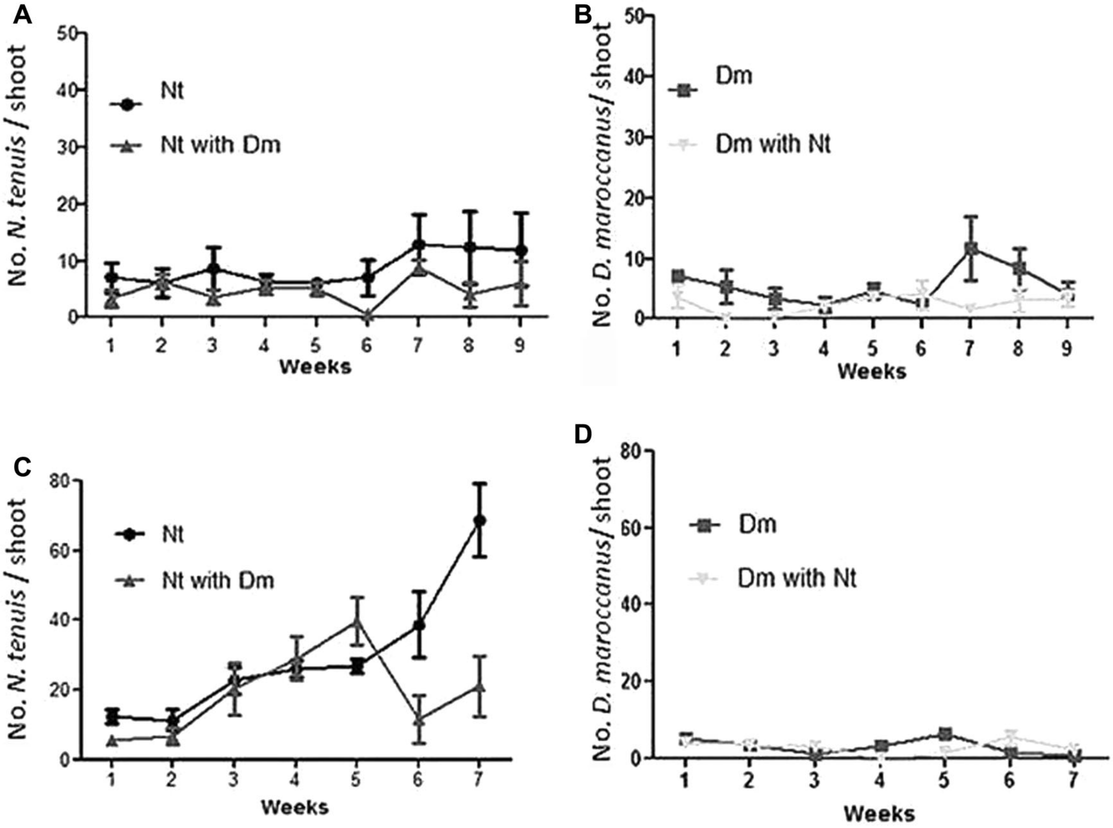

Fig. 3 Variation in the abundance of *N. tenuis* and *D. maroccanus* (adults + nymphs; mean number ± SE) per tomato shoot in mixed- and single-species treatments at 2 temperature regimes in greenhouse trials. (A) *N. tenuis* at 20 ºC; (B) *D. maroccanus* at 20°C; (C) *N. tenuis* at 25 ºC; (D) *D. maroccanus* at 25 ºC.

152; $P < 0.001$). *Nesidiocoris tenuis* consumed more *E. kuehniella* eggs in T3 (1 adult of each mirid species with its heterospecific nymph) when compared with the rest of the treatments ($F = 2.668$; df = 3,152; $P = 0.0498$), with a predation rate of 4.35 ± 0.86 eggs per hour (Fig. 2A). No interaction occurred between temperature and the experimental treatment factors ($F = 1.864$; df = 3,152; $P = 0.1381$).

Dicyphus maroccanus exhibited a lower consumption rate at both temperatures compared with *N. tenuis*. The differences between the treatments ($F = 0.5821$; df = 3, 152; $P = 0.6276$) and temperatures ($F = 0.9635$; df = 1,152; $P = 0.3279$) were not significant (Fig. 2B). *D. maroccanus* ate a minimum of 0.2 ± 0.1 *E. kuehniella* eggs per hour at 20°C in T3 and up to 0.3 ± 0.1 in T1 and T2 at 25°C. No interaction occurred between temperature and the experimental treatment factors ($F = 2.152$; df = 3,152; $P = 0.7236$). Interference competition, that is, direct attacks between *N. tenuis* and *D. maroccanus*, was not observed.

Competitive displacement between D. maroccanus and N. tenuis

The density (number of individuals per shoot) of both species of Miridae was affected by the presence of its heterospecific at the 2 temperature conditions assessed (Fig. 3). At 20°C, the number of *N. tenuis* and *D. maroccanus* per shoot in the competition treatment was lower than in the "alone treatment" for each species throughout the study period: 9 weeks ($F = 4.316$; df = 2,78; $P = 0.017$ and $F = 13.545$; df = 2,78; $P \leq 0.001$, respectively). At the end of the experiment, *N. tenuis* reached higher densities than *D. maroccanus* in the competition treatment (6.33 ± 1.20 and 3.66 ± 1.52 individuals per tomato shoot, respectively) (Figs. 3A and B).

At 25°C *N. tenuis* and *D. maroccanus* densities were also lower in the competition treatment than in the "alone treatment" over the 7-week period of observations ($F = 13.545$; df = 2,78, $P \leq 0.001$ and $F = 34.081$; df = 2,78; $P < 0.001$, respectively). When released simultaneously, *N.*

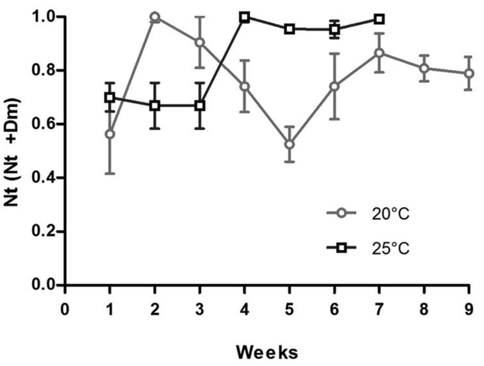

Fig. 4 Variation in the relative abundance of *N. tenuis* expressed as number of Nt/(number of Nt + number of Dm) in mixed-species semifield releases at 2 temperatures in tomato greenhouse trials. Nt: *Nesidiocoris tenuis*; Dm: *Dicyphus maroccanus*.

tenuis achieved up to 39.66 ± 6.89 individuals per shoot, while *D. maroccanus* attained only 3.66 ± 0.66 (Figs. 3C and D).

When comparing the variations in relative abundance of the mirid species in the competition treatment over the study period and for both temperature conditions, *N. tenuis* was favored over *D. maroccanus* (Fig. 4).

Discussion

Previous studies showed that the absence of alternative prey is a key condition for engaging in intraguild predation. Perdikis and Lykouressis (2000) first reported that ca. 25% of *M. pygmaeus* nymphs did not complete their development in the presence of *N. tenuis* adult females, without any prey remaining on tomato leaves, although their study was not intended to prove IGP between those species. Perdikis *et al.* (2009), Moreno-Ripoll *et al.* (2012), and Perdikis *et al.* (2014) later observed that *M. pygmaeus* nymphs were vulnerable to predation by *N. tenuis* adult females in the absence of alternative prey (i.e., the shared prey resource, *E. kuehniella* eggs) on tomato crops. It has been noted that IG predation can be an evolved trait to reduce the number of competitors by killing them (Rosenheim *et al.*, 1995; Félix & Soares, 2004). In this study, we demonstrate that the *N. tenuis* adult female can behave as IG predator on the juveniles of another mirid species that naturally occurs on tomato crops in the region, *D. maroccanus*. To our knowledge, this is the first study to explore intraguild predation in the *N. tenuis–D. maroccanus* system. Nevertheless, our results demonstrate that IGP is not the responsible for the shift in the occurrence of both mirids because even with a long period of starvation IGP is quite low (virtually zero at 20°C and about 30% at 25°C). Furthermore, *N. tenuis* and *D. maroccanus* avoided preying on each other in the presence of alternative prey, that is, they preferred the extraguild prey at the 2 temperatures tested. Lampropoulos *et al.* (2013) found that prey consumption in the *N. tenuis–M. pygmaeus* system was driven by prey availability. Thus, when prey becomes scarce, predation pressure intensifies, while at greater prey densities, this effect is diminished and the 2 species behave as if they were acting independently. The egg density offered to *N. tenuis–D. maroccanus* in this study could be sufficient for each species to prevent competition for prey, but the presence of 4 individual predators (nymphs and adults of both mirid species) in the same experimental unit and a higher temperature may have increased the ability of *N. tenuis* to outcompete *D. maroccanus*, with that being the cause of the increased consumption rather than the availability of prey.

We also found that interactions between these 2 mirids were different at the temperature conditions tested. *Nesidiocoris tenuis* predation behavior was stimulated only at 25°C in the presence of 1 heterospecific adult, 1 heterospecific nymph, 1 conspecific nymph, and alternative prey. Notably, *D. maroccanus* did not feed and spent more time resting in the presence of *N. tenuis*. It is known that *N. tenuis* is best adapted to high temperatures than *D. maroccanus* (Pérez-Hedo & Urbaneja, 2015). Because temperature thresholds for both species may be different, the increase of *N. tenuis* populations may be greater at higher temperatures than those of *D. maroccanus*, being this 1 possible explanation of why interactions between both species increase in favor of *N. tenuis* at higher temperatures.

Another possible explanation for the difference in numbers between the 2 species may be the antibiosis effect for one of the species (in our case on *D. maroccanus*), which could be induced by the plant feeding of another species (in our case by *N. tenuis*). It is known that mirids can activate the same defense mechanisms as strict herbivores (Pérez-Hedo *et al.*, 2015a). Pérez-Hedo *et al.* (2015b) demonstrated that tomato plants punctured by *N. tenuis* were less attractive to the whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) and to the lepidopteran *T. absoluta*, whereas plants punctured by *D. maroccanus* did not repel *B. tabaci* and, more interestingly, became more attractive to *T. absoluta*. Some of these differences were attributed to the capacity of *N. tenuis* to activate abscisic acid (ABA) signaling pathways in tomato plants which made them less attractive to the whitefly *B. tabaci*. In contrast, *D. maroccanus* was not able to up-regulate ABA. Therefore, one might think that these plant responses could also have a role in the interactions between these 2 mirids. However, this knowledge remains unknown; hence, further studies are required.

In the semifield study reported here, *N. tenuis* reached higher densities at both temperatures than *D. marocannus*. Both species were significantly affected by the presence of the heterospecific antagonist, with a population growth trend for *N. tenuis* populations and a decreasing trend for *D. maroccanus* to almost its extinction in the study period.

In general, the consequences of interspecific competition are studied in fixed-time experiments and thus may not be detected immediately (Snyder & Wise, 1999; Mills, 1999). However, competitive displacement may be an effect that is manifested gradually over time. The displacement of natural enemies used in the biological control of insect pests has been often reported, and it has even been associated with increased suppression of the pest population. Lucas & Alomar (2002) and later Castañé *et al.* (2004) proved that interactions between the mirids *Macrolophus caliginosus* (Wagner) and *D. tamaninii* did not decrease the control of the whitefly *T. vaporariorum*. Although *M. caliginosus* represents a high-quality resource for *D. tamaninii* (Lucas & Alomar, 2001), the intraguild interactions among them are not intensive. Similar results were obtained by Perdikis *et al.* (2014) for *M. pygmaeus* and *N. tenuis.* In the context of the biological control of tomato pests, further studies should evaluate the outcome of pest suppression if the competitive displacement of *N. tenuis* against *D. maroccanus* takes place in tomato crops at spatially larger and temporally longer term scales.

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