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Original Article

Interaction effect between two mirid predatory species (Hemiptera: Miridae) on the prey *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae)

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Efecto de la interacción entre dos especies de miridos depredadores (Hemiptera: Miridae) en la presa *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae)

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ABSTRACT: Studies on systems with multiple predatory species have shown that species interactions may not be predictable and are largely dependent on individual behavioral traits, species density, and habitat complexity. The interactions of the mirid predators *Macrolophus basicornis* (Stal) and *Engytatus varians* (Distant) (both Hemiptera: Miridae) with the pest *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) were examined, and the positive or negative effects of their combined use were estimated by a multiplicative risk model (MRM). The efficacy of single and mixed mirid species against eggs and larvae of the pest was estimated through 24-hours predation rates under laboratory conditions. Both mirid species preferred eggs and first instar larvae of *T. absoluta*. Their combined use was positive when their feeding was on these stages of the pest, but negative when it was on second instar larvae. Our results, based on predation rates, showed that *M. basicornis* had a higher predatory capacity than *E. varians* on first instar larvae of *T. absoluta*, but both mirids were good candidates as biocontrol agents against *T. absoluta* on tomato.

Key word: Biological control, predators, trophic interaction, tomato, *Tuta absoluta*.

RESUMEN: Los estudios sobre sistemas con múltiples especies depredadoras han demostrado que las interacciones entre especies pueden no ser predecibles y dependen, en gran medida, de los rasgos de comportamiento individuales, la densidad de las especies y la complejidad del hábitat. Se examinaron las interacciones de dos míridos depredadores: *Macrolophus basicornis* (Stal) y *Engytatus varians* (Distant) (Hemiptera: Miridae) con la plaga *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), estimando los efectos positivos o negativos de su combinación mediante un modelo de riesgo multiplicativo (MRM). Se estimó la eficacia de las especies de míridos, individualmente y mixtas, contra los huevos y las larvas de la plaga, mediante las tasas de depredación durante 24 horas en condiciones de laboratorio. Ambas especies de míridos prefirieron los huevos y las larvas de primer estadio de *T. absoluta*. Su combinación fue positiva al alimentarse de estos estadios de la plaga, pero negativa en el segundo estadio larvario. Los resultados, basados en las tasas de depredación, mostraron que *M. basicornis* tiene una mayor capacidad de depredación en comparación con *E. varians* sobre las larvas de primer estadio de *T. absoluta*, pero ambos míridos son buenos candidatos como agentes de control biológico de *T. absoluta* en el cultivo del tomate.

Palabras clave: Control biológico, depredadores, interacción trófica, tomate, *Tuta absoluta*.

INTRODUCTION

The tomato leaf miner (TLM), *Tuta absoluta* (Meyrick), is an important native pest on tomato (*Solanum lycopersicum* L.) in South America (1). This specie was reported in eastern Spain in late 2006 (2) and, since then, it has spread to various countries in Europe, Africa, Middle, East and Asia (3, 4). In the western hemisphere, it was reported in Panama (2011) and Costa Rica (2014) (5) and, more recently, in a Caribbean country such as Haiti (6). The species has a huge economic impact, and yield losses of up to 100 % and reduction in fruit quality have been reported both in open field and greenhouse crops, mainly where control methods have not been applied (7, 8).

Several approaches were implemented to manage *T. absoluta* in its area of origin, mainly by using insecticides, but with limited success due to insect resistance (9). Insecticides proved not to be a sustainable control method (10) due to the pest resistance caused in some populations (11, 12), as well as to high mortality of natural enemies of the pest (7, 13).

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There is an increasing interest in mirid predators as biocontrol agents of *T. absoluta* and other tomato pests. *Nesidiocoris tenuis* (Reuter) and *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) are successfully marketed and used in the biological control of *T. absoluta* and *Bemisia tabaci* in Europe (14, 15). Both *M. pygmaeus* and *N. tenuis* can prey 60-70 eggs and 2-3 larvae of first and second instar of TLM in 24 hours (16). These predators coexist by feeding the same prey. Their interaction and the intraguild predation (IGP) were studied by Moreno-Ripoll et al. (17), Lampropoulos *et al.* (18), and Perdikis *et al.* (19). However, this information is not available for other mirid species.

In Brazil, the mirid species *Macrolophus basicornis* (Stal) and *Engytatus varians* (Distant) were found in the tobacco (20) and tomato crops (7). The results of these species provide elements to consider them as promising potential candidates for the biological control of *T. absoluta* (21, 22, 23, 24). In laboratory conditions, *M. basicornis* and *E. varians* reached predation rates of 92-101 eggs of *T. absoluta* in 24 hours (7, 22). In addition, these mirids were able to prey eggs of *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae) known as “small tomato borer”, which co-occurs with *T. absoluta* in the tomato crop (25). In the Caribbean, the presence of *Macrolophus basicornis*, *E. varians*, and *N. tenuis* showed a level of incidence higher than 50 % in Cuban crop systems such as tomato and tobacco (26).

In any agricultural system, it is difficult to determine the exact role of a given natural enemy of a pest in actually suppressing its host/prey population. Therefore, these effects need to be characterized and quantified, including possible key determinants on the prey population size (27). In this sense, the studies related to the Multiple Predator Effects (MPEs) help to analyze the possible effects due to predators. In order to identify an emergent MPE, the observed impacts of multiple predators must be compared with an expected effect. These expectations depend on the knowledge of the system complexity. For example, for two predator types, A and B, the expected MPE is the sum of their individual effects; an emergent MPE is then defined as one that differs from this (28).

The use of two types of models, additive and substitutive, can help to know multiple predator effects on predation rates (or prey mortality or survival) (29, 28). In the former, the additive design, compares the observed predation rates of individuals in each species with the predation rates of the predators when they are mixed. However, the additive expectation makes no sense when major impacts on prey by predators are expected and prey shortage is not prevented since it allows prey to be killed twice, which is unrealistic. To solve this overestimation of predation, a Multiplicative Risk Model (MRM) was proposed by Sih (28). The second model, the substitutive design, relies on the total number of interacting individuals, which is constant while richness of the involved predator species changes (18).

The aim of the present study was to define how the predation rates and the interaction of the mirid predators *M. basicornis* and *E. varians* behave when they fed on eggs and larvae (1st and 2nd instars) of *T. absoluta.* Predation rates of each mirid predators (alone or mixed) were determined and their effects, positive (increased prey consumption) or negative (decreased prey consumption, prey risk reduction), were assessed by using the MRM.

MATERIALS AND METHODS

Insect rearing

In order to have an available stock colony of the pest, tomato plants infested with eggs, larvae, and pupae of TLM were collected from cultivated areas in the campus of the Federal University of Lavras (Minas Gerais, Brazil). In the laboratory, the emerged adults were fed with tomato plants (cv. Santa Clara) in mesh cages (90 cm x 70 cm x 70 cm), where fresh tomato plants were regularly introduced to obtain individuals for the experiments.

Similarly, nymphs and adults of mirid predators were collected from tobacco plantations located in the municipalities of Ribeirão Vermelho (21°11′29″S and 45°03′45″W, at about 790 m altitude) and Lavras, (21°14′43″S and 44°59′59″W, at about 920 m altitude) Minas Gerais State, Brazil. The insects were taken to the laboratory and their stock colonies were reared in acrylic cages (60 x 30 x 30 cm). The predators were maintained on tobacco plants (*Nicotiana tabacum* L., cv TNN) and fed with eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) *ad libitum,* following the methodology described by Bueno *et al.* (7) and Silva *et al.* (21). The female mirids used in the experiments were taken from this stock colony with the aid of a compressor-vacuum pump equipment (FANEM®) used for sucking small insects.

All stock colonies were kept under the same environmental conditions in a room at 25±2ºC, 60±10 % r.h., and 12 h photoperiod.

Experimental set up

Predation rate of mirids on eggs and larvae of TLM: Females of each mirid species (1 to 5 days old) were individualized in 5 ml tubes containing a piece of moistened cotton (as water source) and kept starved for 24 hours. The tubes were sealed with a PVC® film to prevent them from escaping. The experimental unit made up by a uniform cohort of 120 TLM eggs was placed on tomato leaflets supported by a 1 % agarwater solution in a Petri dish (9 cm diameter). The eggs were carefully transferred to the tomato leaflets using a brush (Major Brushes® size 00). A film used to cover this experimental unit was pierced with an entomological needle to allow leaf transpiration and humidity removal from the dishes. One predator female was released into an experimental unit.

Similarly, the larvae of TLM were carefully transferred and maintained on tomato leaflets as described above. Ten and five larvae of 1st and 2nd instar were respectively placed in each experimental unit. Larval instars of *T. absoluta* was identified following the methodology described by Giustolin *et al.*(30). In the test, the number of larvae used was the same as used by Urbaneja *et al*. (16) to determine the prey suitability of *T. absoluta* larval instars with *N. tenuis* and *M. pygmaeus*. However, given the smaller size and knowing the preference of both predators for 1st instar larvae, a double quantity of this instar was offered for *M. basicornis* and *E. varians*.

Eggs and larvae were exposed to predator females for 24 hours, and the number of preys consumed was then counted under a stereomicroscope (Zeiss 40X). The prey was considered as consumed when the eggshell was present without content and the larvae were immobile and without abdominal content. The experiments on different types of prey were carried out at 25±1ºC, 70±10 % r.h., and 12h photoperiod in a climatic chamber ELECTROlab®.

The following experimental treatments were set up: (1) one *M. basicornis* female offered with TLM eggs (MB_alone), (2) one *M. basicornis* female with first instar larvae of TLM (MB_alone), (3) one *M. basicornis* female with second instar larvae of TLM (MB_alone), (4) one *E. varians* female with TLM eggs (EV_alone), (5) one *E. varians* female with first instar larvae of TLM (EV_alone), (6) one *E. varians* female with second instar larvae of TLM (EV_alone). One female of both species (*M. basicornis* + *E. varians*) with prey (i. e. (7) (MB+EV_together) with TLM eggs, (8) (MB+EV_together) with first instar larvae and (9) (MB+EV_together) with second instar larvae). Twenty-five replicates per treatment were assayed.

Multiple predation effects in interspecific interactions: Predation by the combination *M. basicornis* and *E. varians* feeding on eggs and larvae of TLM was determined and predicted. A Multiplicative Risk Model (MRM) was calculated following the methodologies proposed by Soluk (31); Soluk and Collins (29); Sih *et al*. (28); Griffen (32), Schmitz (33), and Lampropoulos *et al*. (18). According to these authors, this model applies to the additive design and it is considered to account for prey removal because an individual prey eaten by one of the species is no longer available to the other. If predators have independent effects, then the proportion of the prey that survives both predators will be:

$$(1 - \mathrm{P_a})(1 - \mathrm{P_b}) = 1 - \mathrm{P_a} - \mathrm{P_b} + \mathrm{P_aP_b} \quad [1]$$

Where P_a and P_b is the prey mortality when exposed to predator a or b singly.

The predation observed when both predators were present was estimated by

$$\mathrm{Cfs} = \mathrm{N_p}\left(\mathrm{P_a} + \mathrm{P_b} - \mathrm{P_aP_b}\right) \quad [2]$$

Where Cfs is the expected mixed consumption, N_p is the initial prey density, and P_a and P_b as described above over 24 hours of exposure.

Statistical analysis

Normal distribution of data was corroborated by the Shapiro-Wilk test for all the experiments. The effect of treatments the predation rate (in per cent) during 24 h was analyzed using a two-way ANOVA with predators as the first factor with three levels: each predator released individually and mixed. The second factor, also with three levels, was type of prey: eggs and larvae of 1st and 2nd instar, respectively. In addition, the interaction between factors was included in the model. Taking into account the significant differences obtained for interaction term, the predation rates reached by predator combinations between treatments was compared for each type of prey separately using a one-way ANOVA test. The comparisons between means were performed using Tukey HSD post-hoc tests (p<0.05).

The comparisons between predation rates observed and predicted from the MRM to test emergent multiple predator effects (MPEs) with *M. basicornis* and *E. varians* mixed were analyzed by a two-way ANOVA followed by two factors: a) type of data, observed versus predicted predation rates, and b) type of prey (i.e. eggs and 1st and 2nd instar larvae). In addition, the interaction between factors was included in the model. Data used in the analysis were log transformed. The comparisons between means were performed by Tukey HSD post-hoc test (p<0.05). The statistical analyses were carried out with R v.3.6.3 (34). The standard error for all mean values (mean ± SE) was provided.

RESULTS

Predation rate of mirids on eggs and larvae of TLM

The predation rate of *M. basicornis* and *E. varians* on eggs and larvae of *T. absoluta* significantly differed among predator combinations ($F_{2, 216} = 19.53$, $P < 0.0001$), type of prey ($F_{2, 216} = 205.50$, $P < 0.0001$), and prey-predator interaction ($F_{4, 216} = 11.99$, $P < 0.0001$). Both predators individually reached similar predation rates on eggs with no significant differences; however, their combination significantly increased their eggs consumption (for *M. basicornis*: $F_{2,\ 72}$ = 14.37, $P < 0.001$ and for *E. varians*: $F_{2,72}$ = 14.37, $P < 0.0001$) (Fig. 1).

Feeding on first^{t} instar larvae of *T. absoluta* by each mirid species individually differed significantly ($F_{2,\ 72}$ = 18.39, $P < 0.0001$). *Macrolophus basicornis* reached the highest predation rate of, which did not differ from that observed when both predators were present and in contrast with the response obtained by *E. varians* ($F_{2,72}$ = 18.39, $P < 0.0001$). However, predation on the second instar larvae of the pest did not show significant differences between treatments ($F_{2,\ 72}$ = 3.09, $P = 0.051$), but the adjustment of the p-values showed no differences between the predator combinations on this type of prey (Fig. 1).

Interspecific interaction effects on the predation efficacy

Differences between observed and predicted predation rates were shown by the MRM (OP-rates) and type of preys (TP) (Table 1.). No interaction between the factors was shown by their analysis using the two-way ANOVA.

The analysis of multiple predator effects (MPEs) indicated that when both mirid predators were present feeding on eggs (P = 0.987) or 1st instar larvae (P = 0.995), the results were positive because of the similarity between the observed and predicted values estimated by the model (MRM), without significant differences (Fig. 2). In contrast, the effect of both mirids feeding on 2nd instar larvae was negative, as the observed predation rate was significantly lower than the estimated by the MRM ($P = 0.009$) (Fig. 2).

DISCUSSION

The efficacy of the two neotropical mirids on eggs and larvae of the pest is known (21, 24). However, our results show their preference for eggs and the 1st instar larvae, in contrast with what was observed for the 2nd instar. Our results are in agreement with those observed by Urbaneja *et al.* (35) with other mirid species such as *N. tenuis* and *M. pygmaeus* .

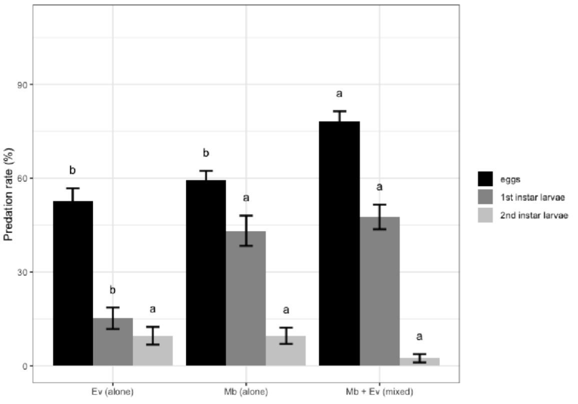

Figure 1. Predation rate (in percentage) on eggs and larvae of *Tuta absoluta*. (mean ± SE) by females of *Macrolophus basicornis* (MB) or *Engytatus varians* (EV) (alone and/or mixed) *Different letters on bars indicate significant differences and bars followed by ns are not statistically different (ANOVA followed by Tukey HSD post-hoc test: $p<0.05$)./ Tasa de depredación (en porcentaje) sobre huevos y larvas de *Tuta absoluta*. (media ± SE) por hembras de *Macrolophus basicornis* (MB) o *Engytatus varians* (EV) (solas y/o mezcladas) *Las letras diferentes en las barras indican diferencias significativas y las barras seguidas de ns no son estadísticamente diferentes (ANOVA seguido de la prueba post-hoc de Tukey HSD: $p<0,05$).

The positive response of the two mirid species used together against eggs and first instar larvae of TLM, and their negative response on second instar larvae is related to main mechanisms of 'multiple predator effects' (MPEs). According to Sih *et al.* (28) the negative response occurs when the prey defense effects against one predator are greater than against the other one.

Interactions between predators (e.g., cooperation, competition or intraguild predation), as well as antipredator responses by prey, can lead to emergent MPEs, where prey consumption rates by multiple predators foraging together cannot be predicted by knowing the independent effects of each predator on prey survival (36). Predator-prey interactions are known to be an important factor in shaping populations of organisms in nature, including the size, type, and dispersion altering the intensity of herbivore-plant interactions (37). Predators may induce an antipredator behavior of prey that affects feeding and dispersal of mobile prey (38, 39).

Table 1. Results of the comparative analysis of the predation rates observed and predicted by the multiplicative risk model (OP-rates) when *Macrolophus basicornis* and *Engytatus varians* were mixed against different type of prey (TP) by using a two-way ANOVA. / Resultados del análisis comparativo de las tasas de depredación observadas y predichas por el modelo de riesgo multiplicativo (OP-tasas) cuando *Macrolophus basicornis* y *Engytatus varians* fueron mezclados contra diferentes tipos de presas (TP) utilizando un ANOVA de dos vías. Source *df* SS *F P*

Sourse	*df*	SS	*F*	*P*
OP-rates	1	0.201	7.125	0.008
TP	2	11.964	212.047	<.0001
OP-rates x TP	2	0.158	2.792	0.064
Residuals	144			

In order to explain the reaction of TLM larvae on predation rate of mirids, behavior of the predators and prey during the experiment was observed. The larvae of *T. absoluta* showed an escape and defense behavior after the first contact with the predators and reacted against the predators with strong movements (first and second instars) and evasion. In addition, when *M. basicornis* and *E. varians* were mixed for feeding on larvae, the number of encounters between both predators was very rare. After their interaction, they evaded each other by moving in opposite directions. Sometimes, *E. varians* remained immobile compared to *M. basicornis*. These observations suggest that *E. varians* perceives the presence of another predator species and reacts by displaying this pattern. Olson *et al*. (40) evidenced that predatory confusion or a relatively simple limited perception could have persistent evolutionary effects on prey behavior, sensorial mechanisms of the predators, and interaction between them.

The tests involving TLM larvae as prey suggest an interspecific predator interaction with an additional prey-predator interaction, as motile larvae are more likely to escape predation. This interference showed a reducing effect on the predation rate, which was more evident with second instar larvae as prey. These larvae are larger and can vigorously defend themselves.

However, the reaction of the encounter between predators could stimulate the consumption of eggs and first instar larvae because the mirids would need to move and cover a major area on the leaflets, with higher possibilities for encountering intact prey. Perdikis et al. (19) did not observe aggressive contacts between the predators when they studied the behavioral activities of *M. pygmaeus* and *N. tenuis,*, but *N. tenuis* was affected by the presence of *M. pygmaeus.* A similar result was obtained with *M. basicornis* and *E. varians* in this study*,* where an aggressive behavior was not observed.

In the present study, although the combined use of both predators increased consumption of eggs and first instar larvae of the pest, no significantly for *M. basicornis* in the latter case, and revealed the potential of both predators, the implications of their coexistence in crop areas are still in discussion. In this sense, Tylianakis *et al*. (41) and Tylianakis and Romo (42) suggested that more complex habitats could increase the positive effects of multiple predators; for this reason, it would be very interesting to find out whether the effect of the presence of individuals of these two predator species in the field is complementary or competitive on prey regulation. In the context of biological control, the coexistence of natural enemies and the role they play by competition are very important. Indeed, niche competitions have been considered a key mechanism associated with the prey regulation by predator biodiversity (43, 44).

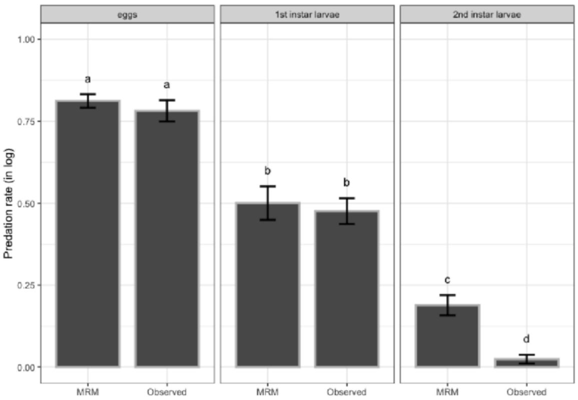

Figure 2. Proportion of the consumption of eggs and larvae of *Tuta absoluta* observed and predicted by the Multiplicative Risk Model (MRM) with *Macrolophus basicornis* and *Engytatus varians* mixed. *Different letters on bars indicate significant differences (ANOVA, followed by Tukey HSD post-hoc test, $p<0.05$)./ Proporción del consumo de huevos y larvas de *Tuta absoluta* observada y predicha por el Modelo de Riesgo Multiplicativo (MRM) con *Macrolophus basicornis* y *Engytatus varians* mezclados. *Las letras distintas en las barras indican diferencias significativas (ANOVA, seguido de la prueba posthoc de Tukey HSD, $p<0,05$)

The density dependent effects of a single species is as important as those of multiple species. Especially given by the fact that many predators occupy a specific niche on a plant or crop (19). However, our first findings on how these predators when used together may react to control *T. absoluta* under laboratory conditions are the basis for future research, as both predators are being widely studied as potential biocontrol agents of this target and other pests in tomato (25) and their preference for a specific niche could change and share the same plant stratum under different temperature scenarios (Author's personal communication).

On the other hand, intraguild predation (IGP) occurs when a predatory species attacks other competing species (45). Therefore, the potential implications of our results should be considered for biological control. Further studies are imperative to understand IGP interactions between *E. varians* and *M. basicornis* and their implications in the regulation of *T. absoluta* as it is known for other mirid predators of this prey. For example, *M. pygmaeus* nymphs completed their development to the adult stage only when the alternative prey (eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) was present, while in the presence of *N. tenuis* adults, a greater number of dead *M. pygmaeus* nymphswere observed with their body fluids totally sucked out, indicating an interaction of intraguild predation (19).

CONCLUSION

Our findings showed the efficacy of *E. varians* and *M. basicornis* simultaneously on *T. absoluta* as prey, where the predators achieved suppression of its immobile and mobile stages (*i.e.,* eggs and larvae) alone or mixed. According to the MRM, the mirids in combination showed a positive (additive) effect when preying on eggs and first instar larvae, but a negative effect on second instar larvae. Although *M. basicornis* has a greater predatory capacity compared to *E. varians* on first instar larvae of the pest, both mirids are good candidates as biocontrol agents against *T. absoluta* on tomato.

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