Three Neotropical mirid predators attack and consume *Tetranychus urticae* spider mites, even in the presence of preferred *Bemisia tabaci* nymphs

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Abstract

Mirid predators are powerful candidates for the control of many different pest species. We studied the prey spectrum of three Neotropical mirids - *Macrolophus basicornis* (Stal), *Engytatus varians* (Distant) and *Campyloneuropsis infumatus* (Carvalho) - and showed that of the 29 pest species occurring on tomato in Brazil, 16 are preyed upon by these mirids. One of the key pests on tomato, the spider mite *Tetranychus urticae* Koch, is difficult to control by predatory mites due to a high density of both glandular and non-glandular trichomes, while these predatory mites are very effective on other crops. Therefore, we were interested if Neotropical mirids would prey on spider mites. The three mirid species were exposed to juvenile and adult spider mites in no-choice and choice tests, and to adult spider mites and nymphs of the whitefly *Bemisia tabaci* Gennadius, a preferred prey species, in a choice test. Results of the no-choice and choice tests reveal that, based on prey acceptance rates, the mirids prefer adult over juvenile spider mites. The choice tests with adult mites versus whitefly nymphs showed a clear preference for whiteflies above spider mites. During all tests, the behaviour of the predators was continuously observed, which indicated, among others, that they apparently do not see or smell the prey, and only attack after touching it with their rostrum. However, we did observe that they paralyse spider mite prey, because attempts of the mites to escape quickly disappeared and they became quiet after they were pierced by the stylets of the mirid. This study clearly shows that the three Neotropical mirid predators attack and feed on nymphs and adults of the spider mite *T. urticae* on tomato. The predators continue to do so even in the presence of a preferred prey, nymphs of the whitefly *B. tabaci*, and might, thus, be used for the control of spider mites on tomato.

Key words: predation rate, prey selection, prey range of mirids, non-target effects, *Macrolophus basicornis*, *Campyloneuropsis infumatus*, *Engytatus varians*, *Tuta absoluta*.

Introduction

Predatory hemipterans are increasingly used in biological control of various arthropod pests (Urbaneja *et al*., 2022; van Lenteren *et al*., 2021a). Their popularity is based on their great predation capacity of many different prey species (Pineda *et al*., 2020; Yao *et al*., 2022) and their ability to search for prey on plants with sticky and poisonous trichomes like tomato (Voigt and Gorb, 2010; Voigt *et al*., 2007; Wheeler and Krimmel, 2015, Bueno *et al*., 2019). Many hemipteran mirids are zoophytophagous and feed on important pest species, but may also cause plant and fruit damage when prey availability is low (Pérez-Hedo and Urbaneja, 2016). Also, due to their very broad prey spectrum, one would expect that they might prey upon other beneficial organism or on species of conservation interest. Preying by hemipteran predators on other natural enemies has been documented, particularly on prey with developing stages of egg parasitoids (Rosenheim and Harmon, 2006; Cabello *et al*., 2015; Calvo *et al*., 2012; Bueno *et al*., 2023a). Mirid predators are known to prey upon different species of Lepidoptera, but data on potential consumption of species of conservation concern are not yet available in the literature. In preliminary experiments we have exposed eggs of four Brazilian lepidopteran species of conservation concern (*Actinote carycina* Jordan, Lepidoptera Nymphalidae, *Caligo illioneus* Cramer, Lepidoptera Nymphalidae, *Dione juno juno* (Cramer), Lepidoptera Nymphalidae, *Papilio* (*Heraclides*) *anchisiades* Esper, Lepidoptera Papilionidae) to the Neotropical mirid *Macrolophus basicornis* (Stal) (Heteroptera Miridae), and observed that the predator contacted the eggs but could not pierce the egg shell and, thus, did not consume and kill these eggs (F.C. Montes, personal observation 2024). This is a promising result, but many more species need to be tested before a reliable conclusion can be drawn concerning negative side effects. If mirid species are considered for import and release in areas where they are not endemic, an extensive environmental risk analysis should be performed to determine whether negative side effects occur (Paula *et al*., 2021).

The predatory mirid *Nesidiocoris tenuis* (Reuter) (Heteroptera Miridae) is commercially used on a large scale in Europe for control of various pests, including the worldwide invasive pest South American tomato leaf miner *Tuta absoluta* (Meyrick) (= *Phthorimaea absoluta*, Chang and Metz, 2021) (Lepidoptera Gelechiidae) on tomato crops (Ferracini *et al*., 2019). As *T. absoluta* is also a serious pest in Latin America, including Brazil, we searched for native natural enemies of this pest in the state of Minas Gerais (Brazil) (Bueno *et al*., 2013), which resulted in finding, among others, three zoophytophagous mirids:

Campyloneuropsis infumatus (Carvalho), *Engytatus varians* (Distant) and *M. basicornis*. Compared to *N. tenuis*, life table and greenhouse studies of the three Neotropical mirids show important advantages: a higher pest kill rate than *N. tenuis* (van Lenteren *et al*., 2019; 2021b), and no or very limited plant injury (Silva *et al*., 2017; van Lenteren *et al*., 2018). Also, these three mirids not only attack *T. absoluta*, but a range of other Lepidoptera, Diptera, whitefly, aphid, spider mite and thrips species (see Table 4 in Bueno *et al*., 2023b). On tomato, 29 pest species may cause damage in Brazil (Pratissoli and Carvalho, 2015), and up to five weekly pesticide sprays during the tomato production cycle are needed to be able to harvest marketable tomatoes (Guedes and Picanço, 2012). The potential importance of using mirid predators for pest control in tomatoes is that 16 of its pest species are known to be preyed upon by Neotropical mirids (Bueno *et al*., 2023b), in contrast to only eight species parasitized by *Trichogramma pretiosum* Riley (Hymenoptera Trichogrammatidae), which is currently used for control of *T. absoluta* in Brazil (Bueno *et al*., 2023b).

Until recent, it was unknown if the three Neotropical mirids mentioned above would attack and consume spider mites. Spider mites are considered one of the most serious tomato pests (van Lenteren *et al*., 2020; Cardoso *et al*., 2024). On other crops, spider mites are effectively controlled by predatory mites, but due to a high density of both glandular and non-glandular trichomes, predatory mites show low effectivity on tomato (Drukker *et al*., 1997). We became interested whether the Neotropical mirids we found might attack and consume *Tetranichus urticae* Koch (Acari Tetranychidae) spider mites and, thus, might be used in mite control in Latin America. In Europe it is known that *Macrolophus pygmaeus* (Rambur) (Heteroptera Miridae) preys on spider mite eggs (Enkegaard *et al*., 2001) and this mirid predator is now commercially used for mite control.

In order to determine if native Brazilian mirids will attack and consume *T. urticae* spider mites when occurring alone or in combination with preferred nymphs of the whitefly *Bemisa tabaci* Gennadius (Hemiptera Aleyrodidae), we performed behavioural observations to record the number of contacts and feeding events when offering juvenile and adult spider mites, as well as whitefly nymphs. We decided for behavioural observations because in contrast to some immobile prey like lepidopteran eggs and whitefly nymphs, spider mites are mobile and might be able to try to escape from attacks by mirids. Knowledge of spider mite predation in the presence of a preferred alternative prey is important to be able to judge whether spider mite control by the mirids would still be possible in the presence of a preferred other pest species.

Materials and methods

Plant, spider mite, whitefly and mirid rearing

Tomato plants, *Solanum lycopersicon* L. cv. Santa Clara were grown in a greenhouse in 3L pots containing a substrate mixed with 200 g of NPK 4-14-8 fertilizer under natural light, temperature and humidity conditions in a greenhouse.

T. urticae spider mite populations were maintained in the laboratory at 24 ± 1 °C, 70 ± 10% RH and 12 hours photophase). Rearing of mites was carried out in Petri dishes (15 cm) with thick moistened foam (1 cm) covering the bottom of the Petri dish in order to maintain the turgidity of the jack bean, *Canavalia ensiformis* (L.), leaf placed on the foam. Next mites were added to the jack bean leaf and moistened cotton was placed around a piece of leaf to prevent mites from escaping. New Petri dishes with leaves and mites were prepared every week or whenever needed.

Populations of *B. tabaci* were maintained on cabbage plants (*Brassica oleracea* L. var. *acephala* DC. cv. Manteiga) for feeding and oviposition inside mesh cages (60 × 40 × 40 cm) in a greenhouse under natural light, temperature and humidity conditions.

The rearing of mirids was carried out in the laboratory (24 ± 1 °C, 70 ± 10% RH and 12 hours photophase) according to the methodology described in Bueno *et al*. (2013). Adults were released inside acrylic cages (60 × 30 × 30 cm) containing a tobacco plant (*Nicotiana tabacum* L., cultivar TNN) as oviposition substrate. *Ephestia kuehniella* (Zeller) (Lepidoptera Pyralidae) eggs supplied by Koppert BioSystems Brazil, were offered as food for the mirid predators.

All rearings took place at the campus of the University of São Paulo/ESALQ (Piracicaba, SP, Brazil).

Prey acceptance, prey preference, predation capacity and attack behaviour of mirid predators when exposed to *T. urticae* or *B. tabaci*

To determine whether the three mirid species will be able to feed on juvenile (= protonymph + deutonymph) and adult *T. urticae*, these developmental stages were offered to each mirid species in no-choice and choice tests. In addition, choice tests were performed to evaluate the preference of all three mirid species to adult *T. urticae* or nymphs of *B. tabaci*. The treatments were: (i) 20 juvenile *T. urticae*, (ii) 20 adult *T. urticae*, (iii) 10 juvenile + 10 adult *T. urticae*, (iv) 10 nymphs of *B. tabaci* + 10 adult *T. urticae*, and (v) control, i.e. treatments i, ii, iii, iv without predator.

Individual female mirid predators of up to 7 days old were taken from the maintenance colonies with the aid of a fine brush and kept in Petri dishes without access to food but with access to water for 24 hours before carrying out the experiment. Next, they were transferred to the foraging arena, consisting of a Petri dish (9 cm in diameter) containing a leaflet of tomato cv. Santa Clara with the spider mites or *B. tabaci* nymphs on a layer of water agar (1%). To obtain whitefly nymphs, the leaflets were exposed to whitefly adults to lay eggs. After, the excess number of nymphs was removed and spider mites were added with a thin brush.

The searching and predation behaviour of mirid females was observed by using a stereomicroscope. For each predator species and each test treatment (i-iv), a total of 100 contacts between the predator and the prey were observed, consisting of 10 contacts by 10 individual females, i.e. 10 replicates. The percentage of acceptance of spider mites or whitefly was determined by dividing the number of encounters followed by feeding/total

number of encounters × 100. During the observations, the type of each contact (encounter not followed by feeding or encounter followed by feeding) was recorded. For one of the species, *M. basicornis*, the duration of the two types of contacts was recorded as well.

All tests were conducted in an air-conditioned room at 25 ± 2 °C, 70 ± 10 % RH and 12 hours photophase.

Data analysis

In the no-choice and choice prey acceptance tests, first the heteroscedasticity of the error variance and a normal distribution of the data were verified using the Bartlett and Shapirov-Wilk tests, respectively. Data regarding analyses between the three mirid species were submitted to analysis of variance of the data by ANOVA followed by Tukey's test or Kruskal-Wallis test for non-parametric analysis. The analysis of prey acceptance within mirid predators species were submitted to Mann-Witney U test.

Results

Behaviour when contacting and consuming spider mites and whiteflies

During all our observations of the searching behaviour of the three mirids, we obtained the impression that they search randomly, do not see or smell the prey and only react with attack behaviour when they have contacted a prey with their rostrum. After piercing the spider mites with their stylets, it seems that they paralyse the spider mite because attempts by the mites to escape from the attacking mirids quickly disappear and the mites became quiet.

For *M. basicornis*, we measured the duration of encounters with and without feeding (figure 1, supplemental material table S1). In no-choice tests, contacts with an adult spider mite not followed by consumption last on average 3.2 seconds, while an encounter followed by feeding lasts on average 3 minutes and 54 seconds. When juvenile mites are offered, a contact lasts on average 2.6 seconds and feeding lasts 3 minutes and 2 seconds. The average duration of an encounter is similar for juveniles and adults, but feeding on adult mites lasts longer than on juvenile mites (Mann-Witney U test: $P < 0.05$).

In the choice experiment with adult and juvenile mites, encounters with adults last on average 1.9 seconds and feeding 7 minutes and 7 seconds, while encounters with juveniles last 1.95 seconds and feeding lasts 2 minutes and 6 seconds (figure 2, supplemental material table S1). Thus, also in the choice test the average duration of an encounter is similar for juveniles and adults, and feeding on adult mites lasts significantly longer than on juvenile mites, like we found in the no-choice test (Mann-Witney U test: $P < 0.05$).

In the choice experiment with adult mites and nymphs of whiteflies, encounters with adult mites last 1.3 seconds and feeding lasts 2 minutes and 5 seconds, while encounters with *B. tabaci* last 1.9 seconds and feeding takes 6 minutes and 10 seconds (figure 3, supplemental material table S1). Again, duration of encounters are similar, while feeding times on *B. tabaci* are significantly longer than on adult mites (Mann-Witney U test: $P < 0.01$).
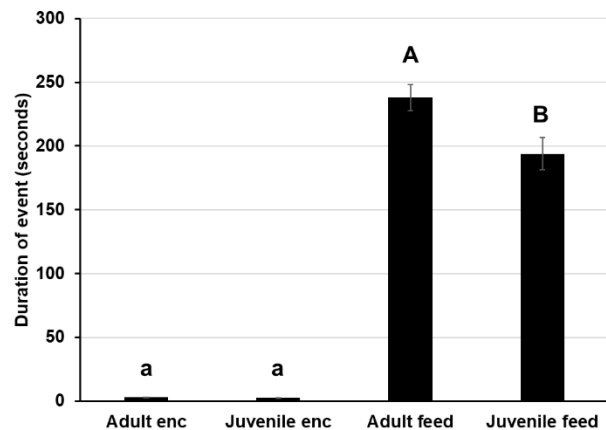

Figure 1. Average duration (± S.E.) of an encounter (enc) and a feeding (feed) event by *M. basicornis* in no-choice tests with either juvenile or adult *T. urticae*. Columns with a different letter indicate a significant difference at $P < 0.05$.
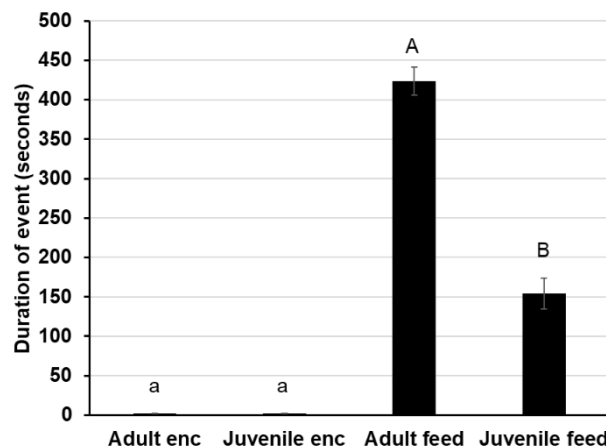

Figure 2. Average duration (± S.E.) of an encounter (enc) and a feeding (feed) event by *M. basicornis* in choice tests with juvenile and adult *T. urticae*. Columns with a different letter indicate a significant difference at $P < 0.05$.
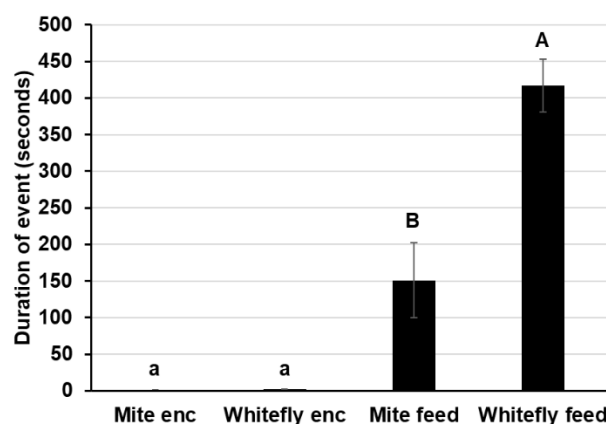

Figure 3. Average duration (± S.E.) of an encounter (enc) and a feeding (feed) event by *M. basicornis* in choice tests with adult *T. urticae* and nymphs of *B. tabaci*. Columns with a different letter indicate a significant difference at $P < 0.01$.

Prey acceptance by mirids of juvenile and adult spider mites in no-choice tests

Individual predators of the three species were exposed to 20 adult or 20 juvenile spider mites on a tomato leaflet in a Petri dish. The observation period was terminated when the predator had encountered 10 mites. The acceptance rates (encounters followed by feeding/all encounters × 100) of adult mites ranged from 36 to 46%, and were not significantly different between mirid predators (Kruskal-Wallis test: $P > 0.05$) (figure 4, supplemental material table S1-3). However, significant differences in prey acceptance were observed among mirid species when exposed to juvenile mites (ANOVA: $P < 0.001$). Specifically, *M. basicornis* demonstrated a higher percentage of encounters followed by consumption in comparison to *E. varians* (figure 4). Furthermore, when comparing juvenile and adult mite acceptance within predator species, only *E. varians* exhibited a distinct preference for adult mites (Mann-Witney U test: $P < 0.05$) (figure 4). In all control treatments, i.e Petri dishes without mirid predator, all juvenile and adult *T. urticae* individuals survived.

Prey acceptance by mirids of juvenile and adult spider mites in choice tests

The consumption of juvenile mites was similar across all predator species (Kruskall-Wallis test: $P > 0.05$), with acceptance rates ranging from 24 to 31% (figure 5, supplemental material table S1-3). Similarly, no differences were observed among the predation rates of adult mites by *M. basicornis*, *E. varians*, and *C. infumatus*, with respective percentages of prey acceptance of 45, 39, and 39% (ANOVA: $P > 0.05$) (figure 5). All three mirid predator species show a preference for adult over juvenile mites (Mann-Witney U test: $P < 0.01$) (figure 5). In all control treatments, i.e Petri dishes without mirid predator, all individuals survived.

Comparison within species of the percentages acceptance of juvenile or adult mites did not show significant differences for any of the mirid species (figure 6). (Kruskall-Wallis test: $P > 0.05$).

Prey acceptance by mirids of adult *T. urticae* and nymphs of *B. tabaci* in choice tests

The percentages acceptance of adult mites in the choice tests was similar across the three predator species (Kruskall-Wallis test: $P > 0.05$), with rates ranging from
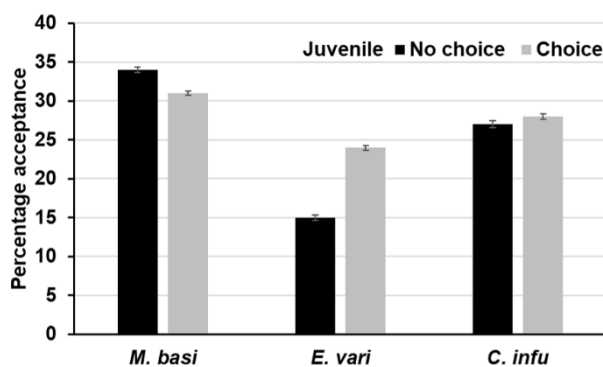

Figure 4. Percentage acceptance (± S.E.) by *M. basicornis* (*M. basi*), *E. varians* (*E. vari*) and *C. infumatus* (*C. infu*) of juvenile or adult *T. urticae* in no-choice tests. *($P < 0.05$) among the three mirid species feeding on juvenile mites; **($P < 0.05$) within mirid species.

Figure 5. Percentage acceptance (± S.E.) by *M. basicornis* (*M. basi*), *E. varians* (*E. vari*) and *C. infumatus* (*C. infu*) of juvenile and adult *T. urticae* in choice tests. **($P < 0.05$) within mirid species.

20 to 34% (figure 7, supplemental material table S1-3). Also, no differences were observed among the predation rates of the whitefly *B. tabaci* by the three mirids, with respective percentages of acceptance of 65, 57, and 53% (ANOVA: $P > 0.05$) (figure 7). However, all three mirid predator species show a preference for nymphs of *B. tabaci* over adult *T. urticae* (Mann-Witney U test: $P < 0.01$) (figure 7). In all control treatments, i.e Petri dishes without mirid predator, all individuals survived.

Figure 6. Percentage acceptance (± S.E.) by *M. basicornis* (*M. basi*), *E. varians* (*E.vari*) and *C. infumatus* (*C. infu*) of juvenile or adult *T. urticae* in no-choice and choice tests.
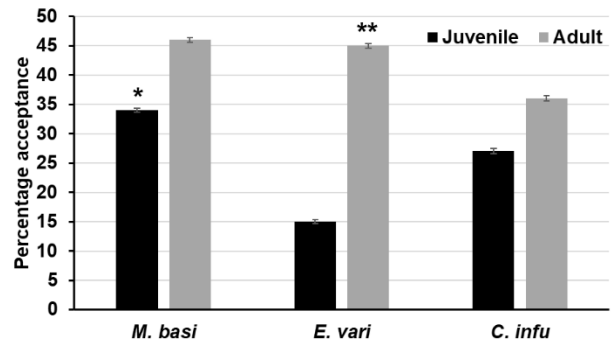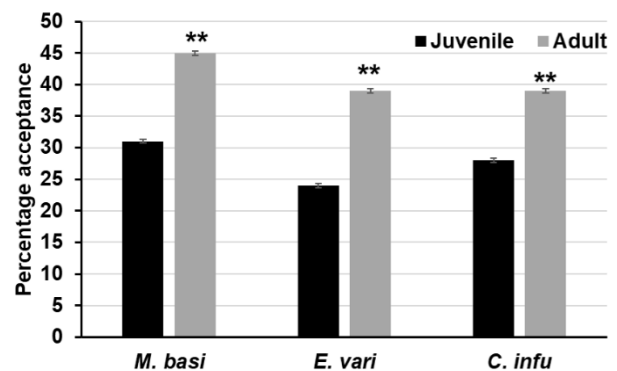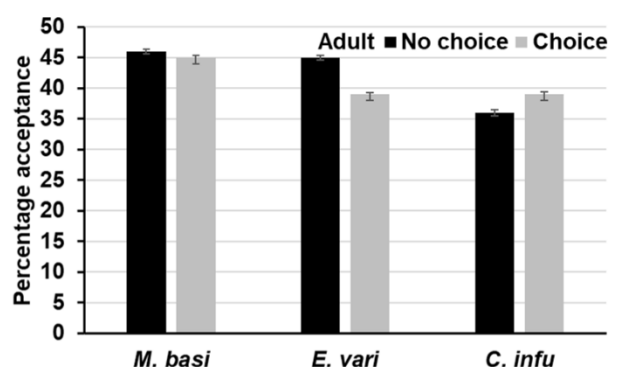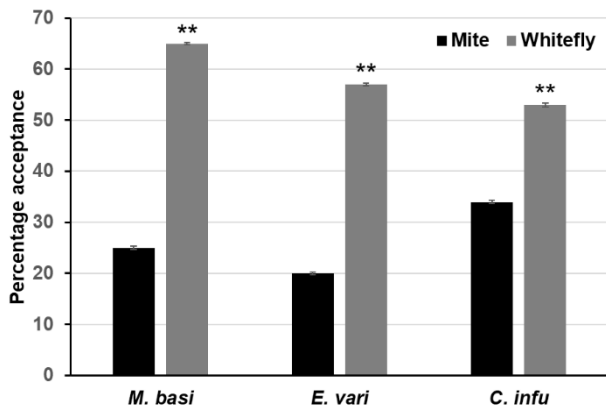
Figure 7. Percentage acceptance (± S.E.) by *M. basicornis* (*M.basi*), *E. varians* (*E.vari*) and *C. infumatus* (*C. infu*) of adult *T. urticae* and nymphs of *B. tabaci* in choice tests. **(P < 0.05) within mirid species.

Figure 8. Percentage acceptance (± S.E.) by *M. basicornis* (*M. basi*), *E. varians* (*E. vari*) and *C. infumatus* (*C. infu*) of adult *T. urticae* in no-choice tests, in choice tests with juvenile mites and in choice tests with nymphs of *B. tabaci*. **(P < 0.05) within mirid species.

M. basicornis and *E. varians* exhibited significantly lower rates of acceptance of adult mites (P < 0.05) in choice tests where *B. tabaci* nymphs were present than in no-choice tests and choice tests with juvenile and adult mites (figure 8, supplemental material table S1-3). However, *C. infumatus* showed no significant difference (P > 0.05) in adult mite acceptance across all three scenarios (figure 8).

As can be seen in figures 1-8 and in supplemental material table S1-3, most averages only show small variation (expressed as standard error of the mean), with the exception of the variation in the average time used for feeding (figures 1-3). The low variation for the average percentages acceptance indicates consistent prey choice behaviour.

Discussion

Prey searching and attack behaviour towards spider mites

Information about the foraging behaviour of mirid predators is limited. Wheeler (2001) wrote that mirids seem to search unsystematically and discover prey by touching it with their antennae and/or tip of the rostrum, although it is now known that several Palearctic and Neotropic species make use of herbivore-induced plant volatiles in prey finding (Molla, 2013; Lins *et al*., 2014; Silva *et al*., 2018). More recently, we found that the Neotropic species *M. basicornis* contacted significantly fewer old, *T. pretiosum* parasitized eggs of *T. absoluta* than recently parasitized eggs. Moreover, olfactometer tests revealed that *M. basicornis* could smell differences between volatiles of tomato leaves infested with eggs of different qualities, i.e. unparasitized, recently or old parasitized *T. absoluta* eggs, to locate suitable prey (van Lenteren *et al*., 2023). The results of the current experiments with behavioural observations of *M. basicornis* when exposed to juvenile and adult *T. urticae*, and to nymphs of *B. tabaci* did not indicate that they saw or smelled the 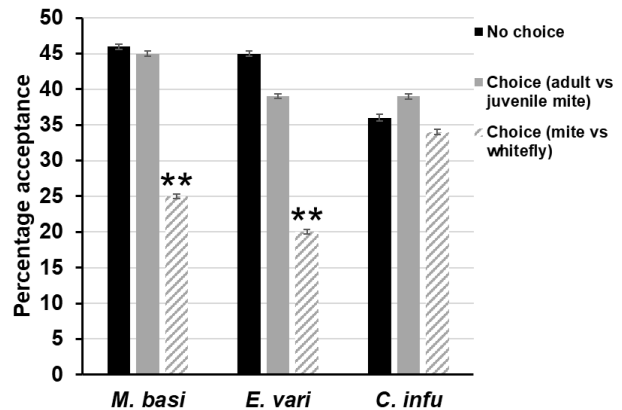prey, and only reacted with attack behaviour after contacting a prey with their rostrum. However, we did observe that this predator apparently paralyses spider mite prey, because attempts of the mites to escape quickly vanished and they became quiet after they were pierced by the stylets of the mirid. Broekhuizen (2017) detected similar behaviour when observing *M. basicornis* attacking *Helicoverpa armigera* Hubner (Lepidoptera Noctuidae) larvae. When checking the literature, we found the following sentence in Wheeler (2001): "Although … mirids tend to lack the salivary enzymes that carnivorous heteropterans such as reduviids and members of some aquatic families use to immobilize their prey, *Stethoconus japonicus* Schumacher (Heteroptera: Miridae) causes almost immediate prey paralysis or death of lace bugs." Wheeler (2001) obtained this information from Neal *et al*. (1991), who, in the legend of Figure 3, mention that *S. japonicus* immobilizes male azalea lace bugs *Stephanitis pyrioides* (Scott) (Heteroptera Tingidae). However, paralysis might be more common than realized until now. In addition to the observations by Neal *et al*. (1991), Broekhuizen (2017) and the authors of this paper, He *et al*. (2024) mention in a recent paper for another zoophytophagous mirid species: "We speculate that the hyaluronidase in *Cyrtorhinus lividipennis* functions to enhance the efficient infiltration of other salivary secretions, thereby accelerating the paralysis and digestion of prey tissues".

Duration of encounters and feeding events with spider mites and whitefly

Encounters of *M. basicornis* with prey not followed by feeding last only a few seconds and is similar for contacts with juvenile and adult spider mites, and whitefly nymphs. Feeding events are shortest on juvenile spider mites, intermediate on adult spider mites and longest on whitefly nymphs. When adult spider mites are offered together with whitefly nymphs, feeding events on spider mites are significantly shorter than when juvenile and adult spider mites are offered in a choice test. This change in feeding time may suggests a preference for whitefly nymphs.

Prey acceptance

All three mirid species showed higher and similar percentages acceptance of adult spider mites (39-45%) than juvenile mites (24-31%) in the choice tests. In the no-choice tests acceptance of adult spider mites was similar (36-46%), but varied among species when juvenile spider mites were offered (15-34%). Juvenile spider mites were significantly less accepted than adult spider mites by *M. basicornis* and *E. varians*, but not by *C. infumatus*. The above data show a preference for adult spider mites by *M. basicornis* and *E. varians*.

In choice tests with adult spider mites and whitefly nymphs acceptance of spider mites was similar for the three mirid species (20-34%), but lower than in the tests were only spider mites were offered. Acceptance of whitefly nymphs also did not differ among the mirid species, but acceptance was significantly higher (53-65%) than that of spider mites, showing a preference for whitefly prey above spider mites.

Predation rates, percentages acceptance and prey preference

Above, we used the term prey acceptance and based on the percentages acceptance, we conclude that the three mirid predators we studied prefer adult spider mites above juvenile ones and prefer whitefly nymphs over adult spider mites. In our opinion, in most situations it is not possible to conclude whether a predator prefers one prey type over another by experiments where two or more prey types are exposed to a predator for a certain amount of time after which the number of preys consumed is counted. Observation of the predation behaviour is essential to find out if different predation rates are based on preference or on other factors like impossibility to penetrate the cuticle or defensive behaviour of a prey. This explains why we have not used the Manly index (Manley *et al.*, 1972) for the analysis of prey preference of the mirids study reported in this paper. Often the word preference is used while the authors actually studied predation rates (see e.g. Soares *et al.*, 2024).

Conclusions

1- The data presented in this paper clearly show that three Neotropical mirid predators (*M. basicornis*, *E. varians* and *C. infumatus*) attack and feed on nymphs and adults of the spider mite *T. urticae* on tomato, which was hitherto unknown.
2- The predators continue to do so even in the presence of a preferred prey, *B. tabaci*, although acceptance of adult spider mites is lower when presented together with whitefly nymphs than when offered alone or in combination with juvenile mites.
3- The predators might, thus, be used for the control of spider mites on tomato, a plant on which predatory mites that are very successful predators in other crops are limited in their foraging behaviour by the high density of sticky trichomes.
4- *M. basicornis* apparently paralyses spider mite prey, because attempts of mites to escape quickly vanished after they were pierced by the stylets of the mirid.

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