



# Is predation of *Tuta absoluta* by three Neotropical mirid predators affected by tomato lines with different densities in glandular trichomes?

Vanda H. P. Bueno<sup>1</sup> · Juracy C. Lins Jr.<sup>2</sup> · Diego B. Silva<sup>3</sup> · Joop C. van Lenteren<sup>4</sup>

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## Abstract

Plants with glandular trichomes may provide protection against herbivores by impeding their movement, but may also hinder natural enemies. We investigated walking behavior and predation rates of the mirid predators *Campyloneuropsis infumatus*, *Engytatus varians*, and *Macrolophus basicornis* on two tomato lines with different densities of sticky trichomes. Also, the time spent by each predator species in various activities (immobile, walking, grooming, probing, and feeding) and the searching for and handling time of prey, eggs of *Tuta absoluta*, were observed. Tomato lines TOM 587 and TOM 687 were used, with TOM 687 having a 179% higher density of glandular trichomes. All three mirid predators easily climbed the sticky stems of both tomato lines and found eggs of *T. absoluta* on leaflets located on the top of the plants. Predation rates, grooming, probing, and feeding activities and the time spent by the three mirid predators until prey encounter were not influenced by a difference in density of trichomes on the two tomato lines. However, *E. varians* walked longer on TOM 584, and spent more time grooming than *M. basicornis*. *Macrolophus basicornis* walked longer on TOM 687. Our results show that the three mirid predators are apparently specialists of glandular plants, because differences in trichome density do not influence their activities, including their prey finding efficiency.

**Keywords** Biological control · Miridae · *Campyloneuropsis infumatus* · *Engytatus varians* · *Macrolophus basicornis* · Sticky trichome · *Solanum lycopersicum*

## Introduction

Plants deploy physical and chemical defenses against herbivores including structural traits such as surface waxes, spines and trichomes, and secondary metabolites that act

as repellents, toxins, and digestibility reducers (Price et al. 1980). Trichomes may provide both chemical and physical defense. They are morphologically very diverse and can be found in many plant species. Glandular trichomes possess a small membranous head containing toxins and/or adhesives (Glas et al. 2012) and can operate by irritating, trapping, or poisoning arthropods (Kennedy 2003). Non-glandular trichomes can act as a physical barrier to movement or prevent reaching nutritional tissue (Simmons and Gurr 2005).

Approximately 30% of all vascular plant species have glandular trichomes, including major crops such as tomato (*Solanum lycopersicum* L.) (Glas et al. 2012). On tomato, type I, IV, VI and VII glandular trichomes are found, of which type IV and VI are associated with high levels of resistance to arthropods (Kennedy 2003; Glas et al. 2012; Botega et al. 2017). Capitate type IV trichomes have a short multicellular stalk on a monocellular base and produce droplets of exudate at the tip. Globular type VI trichomes have a four-celled glandular head on a short multicellular stalk on a monocellular base (Glas et al. 2012). High densities of type

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✉ Vanda H. P. Bueno  
vhpbueno@den.ufla.br

<sup>1</sup> Department of Entomology, Federal University of Lavras, Lavras, Brazil

<sup>2</sup> Agricultural Research and Rural Extension Company of Santa Catarina, Experimental Station of Caçador, Caçador, Brazil

<sup>3</sup> Department of Entomology and Acarology, Luis de Queiroz College of Agriculture, University of São Paulo, Piracicaba, Brazil

<sup>4</sup> Laboratory of Entomology, Wageningen University, Wageningen, The Netherlands

IV or VI, have high levels of acylsugars in their exudate and play a major role in the resistance of *Solanum* spp. against several arthropods, including *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Maluf et al. 2010; Maciel et al. 2011). However, these hairs and their exudates can also negatively affect natural enemies of pests on tomato (Riddick and Simmons 2014).

Although trichomes are typically considered direct defenses against herbivory (Levin 1973), an increasing number of studies have shown indirect costs of high trichome densities as a result of suppressing top-down herbivore control by predators such as stink bugs (De Clercq et al. 2000; Lambert 2007), big-eyed bugs (Barbour et al. 1997), predatory mites (Krips et al. 1999), lacewings (Simmons and Gurr 2004), and coccinellids (Barbour et al. 1993; Riddick and Wu 2011). These indirect costs are caused by reducing the foraging efficacy, consumption rate, and survival of these predators (Riddick and Simmons 2014).

In tomato, high densities of glandular trichomes have been associated with negative effects on survival and density of nymphs and adults of heteropteran predators ((e.g., *Geocoris punctipes* (Say) (Hemiptera: Geocoridae) (Barbour et al. 1993), mobility (e.g., *Orius* spp. (Hemiptera: Anthocoridae), *Podisus maculiventris* Say (Hemiptera: Pentatomidae) (Coll et al. 1997; Lambert 2007), search capacity and prey consumption of nymphs and adults of *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) (Coll et al. 1997), *Podisus nigrispinus* (Say) (Hemiptera: Pentatomidae) (De Clercq et al. 2000), and nymphs of *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) (Economou et al. 2006).

Many species of predators lack morphological and/or behavioral adaptations to avoid trichomes or glandular exudates when walking on the plant surface while foraging for prey. However, several species possess features that permit them to survive and even thrive on sticky plants, like, for example, mirid predators (Cassis and Schuh 2012). These mirids inhabit pubescent, particularly glandular plant surfaces, which are avoided by many other entomophagous arthropods (Voigt et al. 2007; Wheeler and Krimmel 2015). According to Southwood and Juniper (1986) mirids have a small contact area with the plant surface, due their especially long hind tibiae, so that the hind femur is situated above body height. Moving one leg, the femur is raised and the tibia moves almost vertically, without contacting any trichomes. In addition, insects belonging to the tribe Dicyphini (Hemiptera: Miridae, Bryocorinae), like the three mirid predators of this study, possess specialized tarsi that enables them to walk on surfaces which contain sticky material from glandular trichomes. They also possess slender bodies with long legs and curved claws, which they use to grip onto trichomes and gain traction as they crawl over plant surfaces, but avoid contact with sticky compounds released from glandular trichomes (Schuh and Slater 1995; Voigt et al. 2007).

Adaptations by the avoidance strategy (Voigt and Gorb 2010), and by their body size (Wheeler and Krimmel 2015) make mirids specialists of glandular plants.

*Dicyphus errans* Wolff (Hemiptera: Miridae), for example, lives on a range of sticky plant species without experiencing any apparent negative effects (Voigt et al. 2007). Voigt and Gorb (2010) found that an avoidance strategy of mirids on sticky plants might interact with an early sensor defense strategy by rupturing fewer trichomes than other arthropods do. Also, insect body size plays an important role. Slender, lighter-bodied bugs, like *D. errans* (Voigt et al. 2007) use long legs to keep their bodies above the glandular exudates, whereas heavier, tough-bodied bugs, like *Pameridea* (Hemiptera: Miridae), often contact sticky exudates and are able to prevent contamination with exudates by using an anti-adhesive, epicuticular grease layer on the cuticle (Wheeler and Krimmel 2015). This makes mirids particularly interesting as potential biological control agents of prey on sticky plants, in addition to being generalists, preying on several important pests on tomato (Lange and Bronson 1981; Bueno et al. 2013).

During the past decades, interest in mirid predators did increase as several species have shown to be effective natural enemies of pests on tomato, including the invasive *T. absoluta*, in Europe (Calvo et al. 2012; van Lenteren et al. 2018a). In Brazil, three recently found Neotropical mirids (*Campyloneuropsis infumatus* (Carvalho), *Engytatus varians* (Distant), and *Macrolophus basicornis* (Say)) are considered promising candidates for biological control of *T. absoluta* and other pests on tomato (Bueno et al. 2013; van Lenteren et al. 2016, 2017). Under laboratory conditions, these predators are able to find their prey, survive, and reproduce on tomato (Bueno et al. 2012; Silva et al. 2018; van Lenteren et al. 2018b), prey on eggs and larvae of *T. absoluta* and show high fecundities (Silva et al. 2016a; van Lenteren et al. 2018b). Another approach to reduce *T. absoluta* damage is to select tomato lines with higher trichome densities (Maluf et al. 2010; Maciel et al. 2011), but these higher hair densities might interfere with predator efficiency. It is not yet known how tomato lines with different densities of glandular trichomes influence behavior and predation efficiency of the three recently found Neotropical mirids.

In this study, we hypothesize (1) that the three mirids are influenced in the same way by glandular trichomes in their searching and predation efficacy, and (2) that a tomato line with a high glandular trichome density results in a lower predation efficiency than a line with a lower trichome density. To test these two hypotheses, we evaluated (1) their climbing and walking activity on tomato stems, (2) their predation behavior (time spent on searching for and handling of the prey), predation rate of eggs of *T. absoluta* on leaflets, and their behavioral activities on two tomato lines with different densities of glandular trichomes.

## Materials and methods

### Plants and insects

Two pre-commercial breeding lines of *Solanum lycopersicum* L. were used: TOM 687 with a high acylsugar content (31.27 nmol/cm<sup>2</sup>) and high density of glandular trichomes on leaves (340 hairs/cm<sup>2</sup>) and stems (2484/cm<sup>2</sup>), and TOM 584 with a low acylsugar content (21.13 nmol/cm<sup>2</sup>), and a lower density of trichomes on leaves (135/cm<sup>2</sup>) and stems (1384/cm<sup>2</sup>) (Lins Jr 2014). TOM 687, having a 2- to 2.5-fold higher trichome density than TOM 584, is mentioned to be both resistant to and less preferred for oviposition by the tomato borer *T. absoluta* (Maluf et al. 2010; Maciel et al. 2011). Seeds of these two tomato lines, supplied by HortiAgro Sementes Ltda, were sown in trays. After 20 days, the seedlings were planted in soil in plastic pots (1.5 L), and maintained in a greenhouse at natural conditions. Tomato plants of 45–60 days old of each tomato line were used in the experiments.

Adults of *T. absoluta* were collected from tomato plants at the Federal University of Lavras, Brazil, and maintained in mesh cages (90 × 70 × 70 cm) with tomato plants (cv Santa Clara) in the laboratory. New tomato plants were regularly placed into the cage to keep a stock colony of *T. absoluta* at 25 ± 2 °C, RH 70 ± 10% and 12 h photophase. Newly-emerged adults from this stock rearing were used in the experiments.

Stock colonies of the three mirid predators *C. infumatus*, *E. varians* and *M. basicornis* were maintained in the laboratory according to the methodology described in Bueno et al. (2013). Adults of each species collected from the field were identified (Ferreira and Henry 2011) and released individually in acrylic cages (60 × 30 × 30 cm) containing tobacco plants (*Nicotiana tabacum* L. cv. TNN) as an oviposition substrate and water source. *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) eggs were offered *ad libitum* as food. The stock colonies were kept at 24 ± 1 °C, RH 70 ± 10% and 12 h-photophase. Mirid females of 2–7 days old were used in the experiments, i.e., after their pre-oviposition period and when having reached their average daily predation rate.

### Predation rate of *Tuta absoluta* eggs by, and walking behavior of three mirid species on two tomato lines

Tomato plants of 45–60 days old of the two tomato lines were kept in cages (60 cm high, 30 cm in diameter) covered with organza tissue (40 mesh size) in a greenhouse. Five newly emerged couples of *T. absoluta* were introduced into the cages and allowed to lay eggs on the plants

for 72 h. After this period, the lower leaves of the plants were removed in order to be able to observe the predators walking on the tomato stem. Next, the total number of *T. absoluta* eggs on the remaining leaves on the apex of the plant was counted.

An individual female of each mirid predator was released on the lower part of the tomato stem inside the cage and observed until it reached the top of the plant. After 24 h, the number of *T. absoluta* eggs consumed by the female was counted. Eggs preyed on by the female were collapsed, empty, transparent and showed a ruptured chorion caused by the stylets of the mirid. Non-preyed eggs were yellow and not collapsed. Ten replicates were performed for each predator species and tomato line. A prey attack rate was estimated by dividing the number of eggs preyed by the total time that the female remained on the plant. This experiment was conducted in a greenhouse under natural conditions.

### Time allocation of activities by three mirid species on leaflets of two tomato lines

The time allocated to the activities immobile, grooming, walking, probing and feeding on the leaflets of two tomato lines was observed. The description of behavioral activities in Table 1 is based on Economou et al. (2006), and we also followed their experimental methods. Tests were performed in Petri dishes of 9 cm in diameter. Leaflets from each tomato line were placed with the abaxial surface upwards on a surface of water. A single female was released on the tomato leaflet, whereafter the Petri dish was sealed. Activities of the predator were observed with the naked eye and recorded during 40 min in a climate room at 25 ± 2 °C, RH 70 ± 10%. Ten replicates were performed for each combination of mirid predator species and tomato.

**Table 1** Description of observed activities of the three mirid predators on two tomato lines with different trichome densities according to Economou et al. (2006)

Activities	Description
Immobile	Standing immobile without probing, feeding, grooming
Moving	Forward motion
Grooming	Rubbing the tarsi over each other, or over other parts of the body (rostrum, antennae, abdomen)
Probing	Moving the rostrum on the plant surface, while standing immobile or showing small movements
Feeding	Piercing the rostrum in the plant and sucking fluid

## Searching for and handling time of prey by three mirid species on leaflets of two tomato lines

Three newly emerged males and females of *T. absoluta* were released and kept for 24 h in small plastic containers (200 mL) containing leaflets of two tomato lines as an oviposition substrate. In order to keep the leaflets turgid, the petioles were placed inside Eppendorf tubes (2 ml) filled with distilled water. Next, *T. absoluta* adults were removed and excess eggs were carefully taken away until 15 eggs were present on the abaxial surface of each leaflet. The leaflets with eggs were placed with their abaxial surface upwards on a surface of water in Petri dishes (9 cm diameter). A single mirid female was released on the leaflet and then the Petri dish was sealed with parafilm. The time spent searching for prey and handling it was observed with the naked eye for 20 min in a climate room at  $25 \pm 2$  °C, RH  $70 \pm 10\%$ . Searching time is defined as the time spent by the female predator between two activities, e.g., when it finishes preying on the first *T. absoluta* egg until it starts preying on the second egg. Handling time is the total time spent by predators to consume one egg of *T. absoluta*.

### Data analysis

Before analysis, the raw data were tested for normality (Shapiro–Wilk test) and homogeneity of variances (Bartlett's test). The percentage of time spent by each predator species on walking, remaining immobile, grooming, probing, and feeding on the two the tomato lines was analyzed by a two-way ANOVA. Means were separated by pair-wise post hoc comparisons (Fisher's LSD test) ( $\alpha = 0.05$ ) among the two treatments for each parameter. Numbers of preyed eggs and times spent by females searching for and handling of prey were not normally distributed, so we could not use a standard parametric test. Instead, we used the non-parametric Mann–Whitney U-test for comparison of these variables for the three mirid predators on the two tomato lines. All the statistical procedures were made using the statistical package SPSS v.21.

### Results

Females of the three mirid predators were able to walk on the stems without being caught by the sticky trichomes, and preyed on *T. absoluta* eggs deposited on the apical part of leaves of both tomato lines. The number of eggs laid by *T. absoluta* during 72 h on leaves in the apical part of the plant was  $149.0 \pm 8.64$  (sd) on TOM 584 and  $112.2 \pm 7.34$  (sd) on

TOM 687, so significantly higher on the less hairy tomato line. The total number of consumed eggs by the three mirids during 24 h on tomato lines TOM 584 or TOM 687 was not significantly different (Mann–Whitney U-test; *C. infumatus*:  $Z = -0.53$ ,  $P = 0.596$ ; *E. varians*:  $Z = -0.833$ ,  $P = 0.405$ ; *M. basicornis*:  $Z = -0.947$ ,  $P = 0.344$ ) (Fig. 1). The attack rates of *C. infumatus*, *E. varians*, and *M. basicornis* on *T. absoluta* eggs were, respectively, 1.04, 0.81, and 1.25 eggs  $\text{h}^{-1}$  on TOM 584, and 0.80, 1.21, and 1.06 eggs  $\text{h}^{-1}$ , respectively, on TOM 687.

Also, the percentages of total time spent on each activity (walking, grooming, probing, immobile, and feeding) by female predators on leaflets of the two tomato lines were similar (Fig. 2). However, the time spent on grooming, probing and feeding on the leaflets of the two tomato lines were different when averaged across species (Table 2). *Macrolophus basicornis* spent more time on feeding and probing on leaflets than *E. varians* regardless of the tomato line (Fig. 3). A significant interaction was found between mirid species and tomato lines for the time spent on walking (Table 3). *Engytatus varians* walked longer on the line TOM 584 than TOM 687. Contrary, *M. basicornis* walked longer on TOM 687, while there was no difference in time walked on the two tomato lines for *C. infumatus* (Table 3).

Finally, the time spent by females of the three mirid species on searching for and handling of prey did not significantly differ on both tomato lines (Fig. 4).

### Discussion

In this study the number of prey eggs available to the predators was well above the average number that adult females of the three mirids eat, i.e. 39 for *C. infumatus*, 49 for *E. varians* and 35 for *M. basicornis*, during a 24 h predation period (van Lenteren et al. 2018c). The fact that ample prey was available is also expressed by the average number of

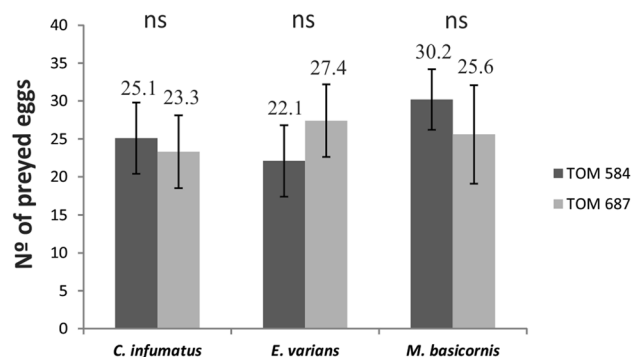
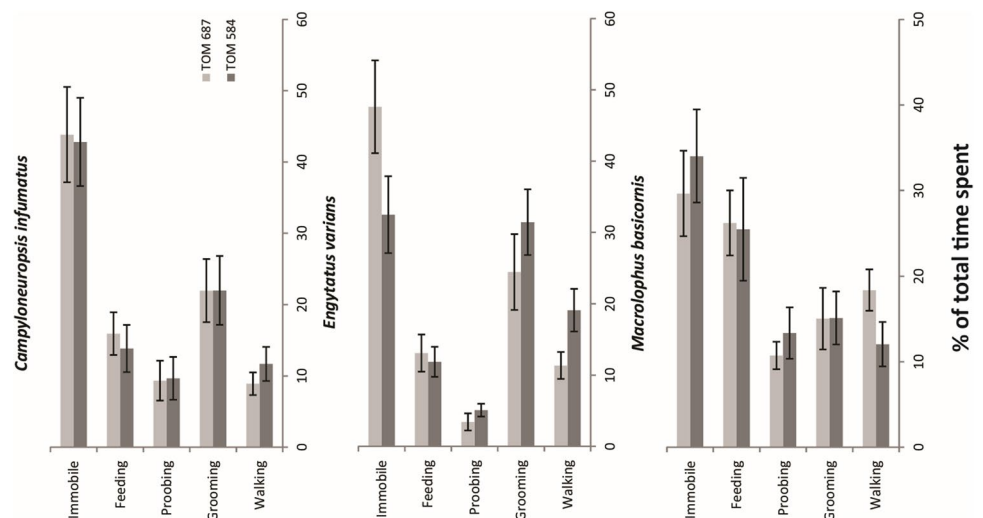


Fig. 1 Number of *Tuta absoluta* eggs consumed during 24 h by *Campyloneurospis infumatus*, *Engytatus varians*, and *Macrolophus basicornis* on tomato lines TOM 584 and TOM 687

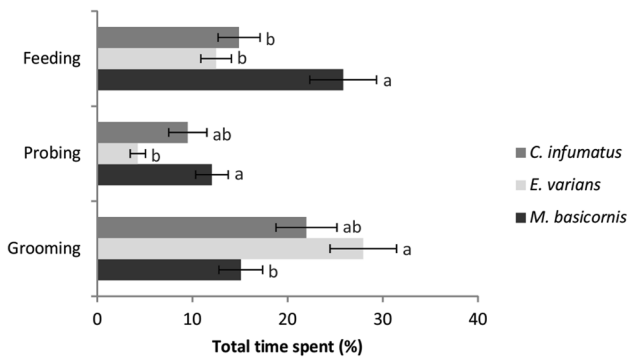
**Fig. 2** Time spent (% ± SE) during 40 min by *Campyloneuropsis infumatus*, *Engytatus varians* and *Macrolophus basicornis* on standing immobile, walking, grooming, probing, and feeding on tomato lines TOM 584 and TOM 687



**Table 2** *F* and *P*-values of averages across tomato lines and predator species for each activity of the mirid predators *Campyloneuropsis infumatus*, *Engytatus varians*, and *Macrolophus basicornis* (ANOVA two-way analyses)

Factor	df	Walking		Grooming		Probing		Feeding		Immobile	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Tomato lines	1	0.506	0.480 <sup>NS</sup>	0.432	0.514 <sup>NS</sup>	0.685	0.150 <sup>NS</sup>	0.198	0.659 <sup>NS</sup>	0.664	0.419 <sup>NS</sup>
Mirid species	2	2.752	0.073 <sup>NS</sup>	4.292	0.019*	5.911	0.005*	7.311	0.002*	1.998	0.145 <sup>NS</sup>
Tomato lines × mirid species	2	4.332	0.018*	0.414	0.663 <sup>NS</sup>	0.127	0.881 <sup>NS</sup>	0.017	0.983 <sup>NS</sup>	1.443	0.245 <sup>NS</sup>

\*Significant (*P* < 0.05)



**Fig. 3** Time spent (% ± SE) during 40 min by *Campyloneuropsis infumatus*, *Engytatus varians*, and *Macrolophus basicornis* on feeding, probing, and grooming, regardless of effect of tomato line. Columns followed by different letters differ significantly (Fisher’s LSD test, *P* < 0.05)

eggs eaten by the three predators during our experiment, which ranged between averages of 22 and 30 eggs per 24 h and was not significantly different on the two tomato lines, while the number of prey eggs was significantly lower on the hairy tomato line (112) than on the less hairy line (149).

We found that females of *E. varians* spent less time walking on the tomato line with higher densities of glandular

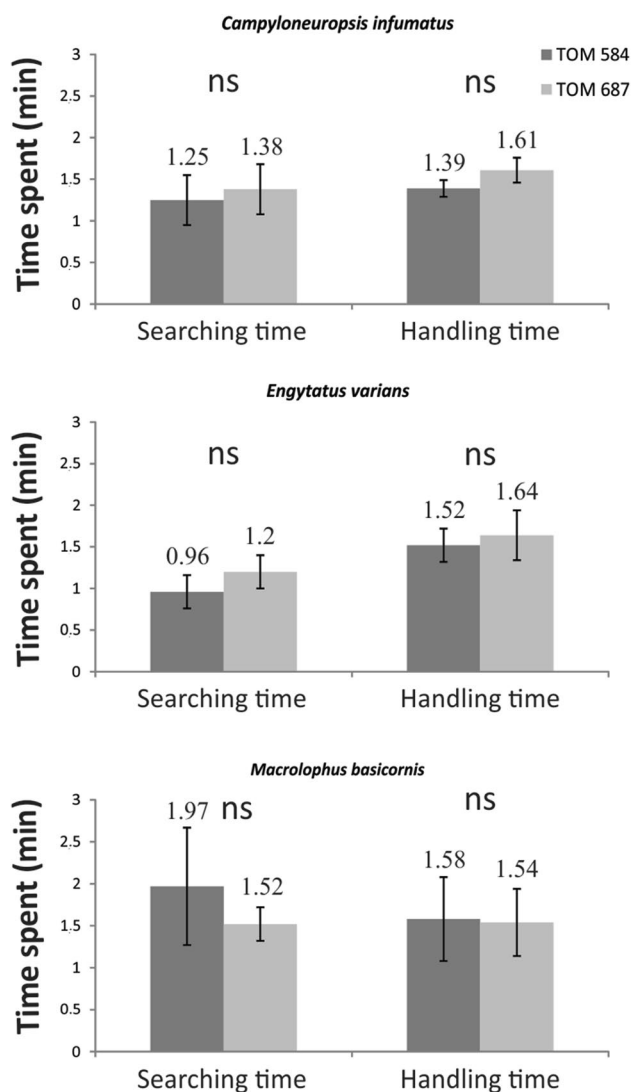
**Table 3** Percentage of total time spent on walking activity by the mirid predators *Campyloneuropsis infumatus*, *Engytatus varians*, and *Macrolophus basicornis* on two tomato lines

Tomato lines	Mirid species		
	<i>C. infumatus</i>	<i>E. varians</i>	<i>M. basicornis</i>
TOM 584	11.69bA	19.12aA	12.05bB
TOM 687	8.91bA	13.36bB	18.37aA

Mean followed by the same lower case letter in the rows and capital letters in the columns do not differ by Fisher’s LSD test (*P* < 0.05)

trichomes, contrary to *M. basicornis*. This might be attributed to the body size and weight, as *E. varians* females are heavier than those of *M. basicornis* (Bueno et al. 2018). *Macrolophus basicornis* and *E. varians* were not influenced by a difference in hair density, which Economou et al. (2006) also found for nymphs of *M. pygmaeus* when exposed to different densities of glandular trichomes on tomato. Walking on sticky stems is more challenging than walking on leaves and entrapments caused by exudates of glandular trichomes may occur mostly in this part of the plant (Kennedy 2003; Lambert 2007). In our study, the densities of glandular trichomes on stems of both tomato lines were much higher than the densities on the leaves. However, no difficulties or





**Fig. 4** Time spent (in minutes,  $\pm$  SE) by *Campyloneuropsis infumatus*, *Engytatus varians*, and *Macrolophus basicornis* on searching for and handling of *Tuta absoluta* eggs on tomato lines TOM 584 and TOM 687 (ns not significant, Mann–Whitney *U* test)

effects on locomotion on tomato stems by adults of the three mirids were found. Our experiments lasted 24 h and we do not expect that longer exposure will result in negative effects on mirid survival and predation, as rearings in cages on the tomato lines did not indicate obvious decreases in mirid populations over time.

Predators clean themselves to remove dirt, and in this study, the time spent by the *C. infumatus*, *E. varians* and *M. basicornis* on grooming was not different between the two tomato lines despite differences in glandular trichome densities. However, among species, *E. varians* spent more time grooming (27.9% or 11.1 min) than *C. infumatus* (21.9% or 8.7 min) and *M. basicornis* (15.0% or 6.0 min). Nevertheless, time spent on grooming did not make a difference in

their time spent in searching for eggs of *T. absoluta*. Economou et al. (2006) found that nymphs of the mirid predator *M. pygmaeus* groomed significantly longer on the tomato cultivar H30 with a high leaf trichome density (43.6 trichomes/mm<sup>2</sup>), than on the cultivars Elxis (13.3 trichomes/mm<sup>2</sup>), and Dombito (19.0 trichomes/mm<sup>2</sup>).

Nymphs of *Orius niger* Wolff (Hemiptera: Anthocoridae) spent most of the time grooming their tarsi and rostrum on tomato (Economou et al. 2006) and *O. insidiosus* walked less and showed a reduced searching efficiency on tomatoes with a high trichome density (Coll et al. 1997). Long periods of grooming could be an attempt to remove the sticky exudates released from the tips of glandular trichomes, and high densities of these trichomes on tomato would result in more exudate released on the leaf surface, which then traps small arthropods (Fancelli and Vendramim 2002; Muigai et al. 2002; Maluf et al. 2007).

In our study, *M. basicornis* fed longer from leaves than *C. infumatus* and *E. varians*. It is well known that mirid predators show zoophytophagy, i.e., they feed on both prey and plant material, and plant feeding may result in damage (Gabarra et al. 1988; Castané et al. 2011). However, we earlier demonstrated that feeding by nymphs and adults of the three mirids we studied did not result in plant and fruit damage, either in the presence or absence of prey (Silva et al. 2016b; van Lenteren et al. 2018b).

Times searching for and handling of prey by the three mirid predators in this study were not affected by trichome densities. Different densities of trichomes also did not interfere the searching efficiency of *Orthothylus marginalis* L. (Hemiptera: Miridae) (Björkman and Ahrné 2005). However, non-mirid heteropterans belonging of other families showed reduced foraging efficiency on plants with glandular trichomes, as e.g., *Nabis americanoferus* Carayon (Hemiptera: Nabidae) and *Geocoris pallens* Stal (Hemiptera: Geocoridae) (Gassmann and Hare 2005).

The negative impact of glandular trichomes on many natural enemies suggests that herbivores, including *T. absoluta*, utilize glandular plants as a result of natural selection, because they provide enemy-free space (Jeffries and Lawton 1984), even if egg laying and development of the herbivore itself is influenced negatively by a higher hair density and concurrent changes in plant chemistry (our results presented above, and Maluf et al. 2010; Maciel et al. 2011). However, mirid predators, including the three species we studied, apparently have evolved morphological and behavioral characteristics to overcome and even profit from the enemy-free space created by glandular trichomes.

With regard to the hypotheses formulated in the introduction, we found support for the first hypothesis in that predators were influenced in the same way by the tomato trichomes in their walking and predation efficacy. However, we did not find support for the second hypothesis,

as higher glandular trichome densities did not result in a lower searching and predation efficacy than at lower trichome densities. The results of these experiments once more suggest the potential of *C. infumatus*, *E. varians* and *M. basicornis* for control of *T. absoluta* and other pests on tomato.

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