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The Search Behavior of Omnivorous Thrips Larvae is Influenced by Spider Mite Cues

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Abstract The western flower thrips is an omnivorous insect that consumes both leaf tissue and spider mite eggs. For this reason, these thrips are often described as ‘opportunistic predators’ of spider mites. Several studies have shown that western flower thrips are often found in association with spider mites, and the development time of thrips decreases and their survivorship increases when they consume spider mite eggs. We tested the hypothesis that thrips larvae may respond to chemical cues from spider mites, and that they may modify their prey-searching behavior when these spider mite-induced cues are present. We prepared hexane extracts from: 1) webbing of spider mites isolated from maize leaves, 2) webbing produced by spider mites inside an empty glass tube to exclude any plant-derived cues from the extract, and 3) spider mite cuticle extracts. These three extracts were subsequently applied in droplets to one-half of filter papers, and hexane alone was applied in droplets to the other half. We showed that residence time of thrips larvae was higher on filter paper with spider mite webbing extract, especially when the extract originated from spider mites isolated in glass tubes. In the presence of webbing extracts, we also observed: 1) a decrease in velocity, 2) an increase of angular velocity and 3) an increase in time immobile. Extracts from spider mite cuticle only increased velocity and proportion of time immobile of the thrips larvae. Our results suggest that chemical cues from spider mite webbing induce an

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arrestment response and play an important role in the non-random search behavior of thrips larvae searching for eggs on spider mite infested plant leaves.

Keywords Prey-searching behavior · extensive search · foraging behavior · arrestant · *Frankliniella occidentalis* · carmine spider mite · *Tetranychus cinnabarinus*

Introduction

Omnivory, feeding on both animal prey and plant materials, is found in thousands of insect species (Coll and Guershon 2002). Whether omnivory is adaptive or a transitory stage towards specialization is a topic of debate (Dennis et al. 2011; Loxdale et al. 2011). Omnivorous insects, such as thrips (Thysanoptera: Thripidae), are sometimes considered ‘opportunistic’ predators because they do not rely on prey to survive and reproduce, and use plant tissue as their main food source (Trichilo and Leigh 1986; Mound 2005; Zhi et al. 2006). The term ‘opportunistic’ implies few specialized capabilities in detecting prey, and host searching behavior mainly based on host plant cues and on the relative availability of food items (Wilson et al. 1991).

Several species of thrips are omnivorous and feed on both living plant material and spider mite eggs (Acari: Tetranychidae) (Lincoln et al. 1953; Trichilo and Leigh 1986; Wilson et al. 1991). Thrips have a predator functional response that increases with density of spider mite eggs, and larval feeding is characterized by a shorter handling time of spider mite eggs than that of adult female thrips. Therefore thrips larvae are considered more efficient spider mite egg predators than conspecific adult female thrips (Trichilo and Leigh 1986). Consumption of spider mite eggs has been found to be beneficial to *Frankliniella schultzei* Trybom thrips, as it decreases their development time and increases survivorship (Milne and Walter 1997). In addition, the rate of spider mite egg predation by thrips is negatively correlated with the quality of the plant host. For instance, predation may increase if the host plant has poor nutritional quality (Magalhães et al. 2005) or if host plant defenses have already been induced by the damages of a former pest (Agrawal et al. 1999). There is evidence suggesting that the thrips *Scolothrips takahashii* Priesner, *F. schultzei* and *F. occidentalis* Pergande are attracted by plant volatiles induced by spider mite feeding (Shimoda et al. 1997; Silva et al. 2013), and spider mites and *F. occidentalis* thrips have been found in relative strong association in cotton fields (Pickett et al. 1988; Wilson et al. 1996; Martini et al. 2013) suggesting attraction of thrips toward spider mite infested plants (but see Pallini et al. (1999) who found attraction of *F. occidentalis* only toward spider mite infested leaves in the presence of thrips predators). Although the attraction of spider mite cues to thrips has been studied, there is no study of the behavioral responses of thrips larvae and other spider mite derived cues in locating spider mite eggs.

Spider mites produce dense webbing consisting of silk made of a keratin-like protein (Hazan et al. 1975). While this webbing is believed to provide effective protection against predatory mites (Sabelis and Bakker 1992), it also contains kairomones to which predators respond (Hislop and Prokopy 1981; Mayland et al. 2000; Roda et al. 2001). The presence of webbing also increases residency time of the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) on host plants (Mayland et al. 2000). Eggs and feces, which are deposited on spider mite webbing, could also attract

predatory mites (Hoffmann et al. 2011). Additionally, spider mite webbing has been described as a protection for thrips against predators (Pallini et al. 1998). However, the role of kairomones from spider mite webbing (and their associated elements such as eggs and feces) in the search behavior of thrips has never been studied.

Search behavior is influenced by two types of stimuli: attractants and arrestants (Kennedy 1978; Waage 1978). An attractant is a chemical that causes predators to orient movement toward its source, and an arrestant may involve stopping or slowing down locomotion (orthokinesis) and/or increase the rate of turning (klinokinesis) (Kennedy 1978). When the orthokinesis and klinokinesis reactions are combined, this behavior has often been given teleological names, such as, “intense search” or “extensive search”. For instance, Bond (1980) defined two types of searching behaviors for predators: “extensive search” is characterized by elevated velocity, low angular velocity (straight trajectories) and few immobile phases. It corresponds to a predator that superficially covers a large area to find a patch of prey. Conversely, “intensive search” is characterized by lower velocity, high angular velocity (more turns), and more immobile phases. It corresponds to a predator that forages intensively in a localized region in search for prey. We are unaware of any published studies describing arrestment responses or providing quantitative information on the search behavior of thrips larvae.

In this study, we hypothesized that chemical cues extracted from spider mite webbing may induce an arrested behavior of thrips larvae. We conducted behavioral assays to characterize the response by thrips larvae to the following hexane extracts from: 1) webbing of spider mites isolated from maize leaves, 2) webbing produced by spider mites inside an empty glass tube to exclude any plant-derived cues from the extract, and 3) spider mite cuticle extracts. These extracts were added in droplets to filter papers (denoted ‘zones’), and we recorded time spend in each zone. To determine if thrips larval behavior was impacted by spider mite webbing cues, we compared larval velocity, proportion of time immobile, and angular velocity across treatments. The findings from this study provide novel insight into the importance of chemical cues in the search behavior and omnivory of thrips larvae.

Material and Methods

Arthropod Cultures

Western flower thrips *F. occidentalis* were reared on organic cucumber at 24 ± 1 °C, 30–40 % relative humidity, and 16:8 L:D photoperiod, following the rearing protocol of DeGraaf and Glenys (2009). We used the red form of the two-spotted spider mite *Tetranychus urticae* [syn. *T. cinnabarinus* Boisduval, Auger et al. 2013)] reared on maize plants *Zea mays* L. (Poaceae). Care was taken to ensure that cucumbers used for thrips rearing were not infested with spider mites. To avoid contamination, each arthropod colony was maintained in separate facilities.

Preparation of Webbing and Cuticle Extracts

All extracts were hexane-based (98.5 % purity, Omnisolv® hexane HX0296, EMD Chemicals, Gibbstown, NJ). The first extract consisted of spider mite webbing directly

acquired from spider mite infested maize plants. For each extract a spider mite infested maize leaf was cut into 25 cm long pieces. Only pieces with continuous spider mite webbing along the mid vein were selected. With a fine paintbrush, spider mite webbing was collected from along the mid vein and directly immersed in a glass beaker with 5 ml of hexane. To remove all spider mites, eggs and webbing, the hexane was filtered through a sieve with stainless steel mesh (61 μm mesh opening, Geotech Environment Equipment, Denver, CO, USA) and then divided equally among five glass tubes with 1 ml in each.

To eliminate the potential effect of plant chemical cues that could have been collected along with spider mite webbing from maize leaves in the previous experiment, we isolated five female spider mites in 10 cm glass tubes. Tubes were sealed with a small cotton plug and placed bottom up in an incubator (16:8 L:D, 23 °C). After 48 h, the spider mites were still alive and had produced webbing inside the glass tubes. Each glass tube was rinsed with 1 ml hexane, and thereafter pooled into a single tube. This extract was filtered through a sieve with stainless steel mesh as above. To extract chemicals from spider mite cuticle, we isolated 25 spider mites on white filter paper and immersed them for 30 s directly into 1 ml hexane. This extract was filtered through a sieve with stainless steel mesh as mentioned above.

Behavioral Assays

We conducted behavioral assays in circular arenas that consisted of a single 90 mm diameter filter paper (1 Qualitative, Whatman, Maidstone, UK). A single second instar thrips larva was used in each arena and was used only once. A perimeter of Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) was established on the edge of each filter paper to contain individual thrips larvae within the arena. The filter papers were divided in two equal-sized zones, and each zone received a different treatment. Preliminary tests ($N=7$) confirmed that in the absence of any treatment (plain filter paper), thrips larvae spent equal amounts of time in each zone of the arena (see results). For each treatment, about 1 ml extract was applied with a Pasteur pipette as small droplets to a given zone at least 1 cm away from the separation of the two zones to obtain uniform coverage within the zone but without cross-contamination across zones. The hexane was allowed to evaporate for 5 min before a thrips larva was transferred into the arena. At the onset of each trial, a thrips larva was placed in the center of the filter paper and its subsequent movement was recorded for 15 min. Arenas were placed on a platform 20 cm below a Panasonic® CCD video camera (RWV-CP484, Panasonic Corporation of North America, Secaucus, NJ, USA) and illuminated with two tabletop lamps each with a 35 cm 13 W white cool light bulb at a height of 18 cm above either side of the arena with the bulbs parallel to the platform. These lamps were the sole light source in the room. Room conditions were 23 °C and 35 % RH. Thrips behavior was analyzed and quantified with video tracking software (Ethovision®, Noldus, Wageningen, the Netherlands). We recorded: time spent in each zone (denoted “residence time”) average larval velocity, angular velocity and proportion of time immobile in each zone.

In the first experiment ($N=10$), behavioral responses of thrips larvae to negative controls (clean filter paper) versus positive controls (hexane only) were observed to confirm that the hexane solvent itself did not influence their behavior. To test the behavioral response of thrips larvae to spider mite webbing, a second experiment ($N=25$) was conducted with spider mite webbing extract from maize leaves versus a

positive control (hexane only). To eliminate the potential effect of plant chemical cues that could have been collected along with spider mite webbing from maize leaves in the previous experiment, we conducted a third experiment ($N=21$): the response to spider mite webbing extract from isolated spider mites versus a positive control (hexane only). Finally we tested the behavioral responses of thrips larvae to spider mite cuticular extract ($N=16$) versus a positive control (hexane only).

Statistical Analysis

Statistical analysis of the behavioral responses by individual thrips larvae relative to the extract was performed using the R statistical package version 2.14.0 (The R Development Core Team, Vienna, Austria). For each experiment, comparisons of average thrips larval velocity (denoted “velocity”), proportion of time immobile, and angular velocity in a given zone (denoted “angular velocity”) between the control and treatments were performed using paired t-tests because the data were normally distributed with homogenous variance. We excluded from these analyses cases where thrips larvae spent all their time in a single zone (three in webbing extract from tubes treatment and five in cuticle extract treatment). Residence time in a given zone was compared using a Wilcoxon signed-ranked test on differences due to the non-normal distribution of these data. To determine a potential arrestment response of thrips larvae to spider mite extracts, velocity, proportion of time immobile, and angular velocity were compared between the four behavioral assays with analysis of variance (ANOVA). If ANOVA showed a significant difference among treatments we applied a Tukey’s significant difference test to determine which treatment differed significantly from the others. Additionally, we used Pearson correlation coefficients to study correlations between average velocity, proportion of time immobile, and angular velocity of individual thrips larvae. To investigate if the movement parameters contributed to the correct classification of individuals among treatments we performed linear discriminant analysis (function `lda`, library `MASS`). We compared the predictions from the discriminant analysis with the distribution of thrips among treatments. Then, based on the accuracy of the discriminant analysis we determined if classification using movement parameters matches distribution of thrips among treatments.

Results

Residence Time

There was no significant difference during preliminary tests between time spent by thrips larvae in the right (353.10 ± 60.28 s) or the left side of the filter paper (541.15 ± 58.50 s) (Wilcoxon signed-ranked test: $W=16$, $N=7$, $P=0.219$). Similarly, there was no significant difference between time spent by thrips larvae in the top (536.01 ± 63.88 s) or the bottom side of the filter paper (358.24 ± 67.99 s) (Wilcoxon signed-ranked test: $W=10$, $N=7$, $P=0.469$). There was no significant difference in the amount of time thrips larvae spent in each of the two zones when contrasting positive and negative controls (Wilcoxon signed-ranked test: $W=53$, $N=10$, $P=0.853$, Fig. 1a). The residence time of thrips larvae was marginally higher in zones contaminated with webbing on maize leaves (Wilcoxon signed-ranked test: $W=413$, $N=25$, $P=0.052$, Fig. 1b),

whereas thrips larvae spent significantly more time in zones with extract from webbing produced by females isolated in glass tubes (Wilcoxon signed-ranked test: $W=351$, $N=21$, $P=0.001$, Fig. 1c). Finally, extracts from spider mite cuticle did not elicit a significant response by thrips larvae in terms of residence time (Wilcoxon signed-ranked test: $W=131$, $N=16$, $P=0.925$, Fig. 1d).

Analyses of Movement Parameters

Firstly, we compared movement parameters between the control and each of the treatment zones. Velocity was not significantly different between the control and: 1) hexane only ($t=0.353$, d.f. = 9, $P=0.732$), 2) webbing extract from leaves ($t=0.396$, d.f. = 24, $P=0.696$), 3) webbing extract from tubes ($t=0.950$, d.f. = 17, $P=0.362$) or 4) cuticle extract ($t=1.258$, d.f. = 10, $P=0.237$). The proportion of time immobile was not significantly different between the control and 1) hexane ($t=0.694$, d.f. = 9, $P=0.505$), 2) webbing extract from leaves ($t=0.864$, d.f. = 24, $P=0.396$), 3) webbing extract from tube ($t=1.531$, d.f. = 17, $P=0.144$) or 4) cuticle extract ($t=2.037$, d.f. = 10, $P=0.069$). The angular velocity was not significantly different between control and: 1) hexane ($t=0.167$, d.f. = 9, $P=0.871$), 2) webbing extract from leaves ($t=1.033$, d.f. = 24, $P=0.312$), 3) webbing extract from tube ($t=0.621$, d.f. = 17, $P=0.543$), or 4) cuticle extract ($t=579$, d.f. = 10, $P=0.575$).

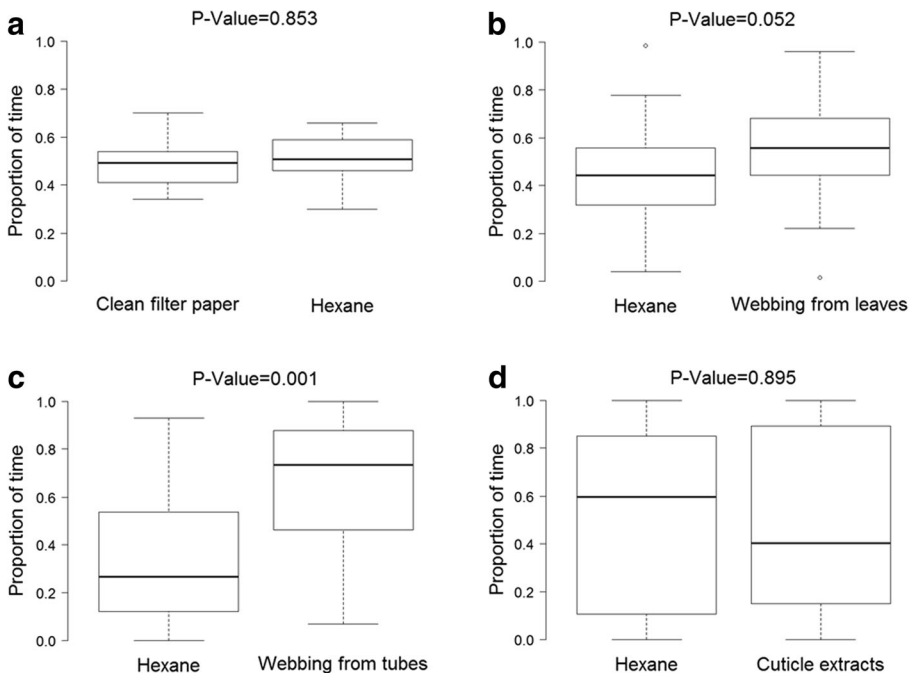


Fig. 1 The proportion of time spent by second instar thrips larvae in behavioral assays in 15 min (900 s) trials: **a** positive control (hexane only) versus negative control (clean filter paper), **b** compounds extracted directly from spider mite webbing on maize leaf versus positive control, **c** compounds extracted from webbing in glass tubes versus positive control, and **d** compounds extracted from adult spider mites versus positive control

As these comparisons within each behavioral assay were not significant, we compared velocity, the proportion of time immobile and the angular velocity between the different behavioral assays. The velocity of thrips larvae was significantly higher in arenas without spider mite extracts than in the presence of the hexane and negative controls (clean filter paper) (ANOVA: $F = 38.55$, d.f. = 3, 68, $P < 0.001$, Fig. 2a). Likewise, larvae had a lower proportion of time immobile in the presence of the hexane and negative controls (clean filter paper) than with any other extracts (ANOVA: $F = 8.03$, d.f. = 3, 68, $P < 0.001$, Fig. 2b). However, only the larvae on extracts from webbing from maize leaves or from glass tubes had a higher angular velocity than the larvae on hexane only (ANOVA: $F = 52.69$, d.f. = 3, 68, $P < 0.001$, Fig. 2c). We found a negative correlation between velocity and the proportion of time immobile (Pearson's coefficient of correlation: $r = -0.53$, $N = 72$, $P < 0.001$), a strong positive correlation between proportion of time immobile and angular velocity (Pearson's coefficient of correlation: $r = 0.72$, $N = 72$, $P < 0.001$), and finally a negative correlation between angular velocity and velocity (Pearson's coefficient of correlation: $r = -0.36$, $N = 72$, $P = 0.002$). Linear discriminant analysis classified 59 out of 72 individuals within the correct treatment, with no errors for the hexane group and only one inaccurate classification for thrips exposed to cuticle extract. We subsequently pooled thrips exposed to webbing from leaves and tubes in the same group, and rerun the discriminant analysis. In this case, the discriminant analysis correctly classified 70 out of 72 individuals, a significant improvement over the previous case ($\chi^2 = 9.00$, d.f. = 1, $P = 0.003$). Altogether, the results of the discriminant analysis and Pearson's correlations demonstrated that we observe three distinct movement patterns: (1) high velocity, little time immobile, with straight trajectories, (2) lower velocity, more time immobile, and with curved trajectories (orthokinesis and klinokinesis reactions), and (3) low velocity, high proportion of time immobile but with straighter trajectories (orthokinesis reactions only). The first movement pattern was associated with larvae in the hexane control, and the second was associated with larvae in the presence of webbing extract from leaves or from glass tubes. Finally the third movement pattern was associated with larvae in the presence of cuticle extracts (Fig. 3).

Discussion

We found that thrips larvae spent more time in areas contaminated with spider mite webbing extracts compared to areas contaminated with solvent alone, especially when webbing extracts did not include plant chemical cues. On the other hand, residence time of thrips larvae was not significantly different between areas contaminated with spider mite cuticle extract compared to areas contaminated with solvent. Comparisons of movement parameters within each behavioral assay (i.e., control vs treatment zone) were not significantly different, however comparisons of movement parameters between the different assays showed a significant change in thrips' foraging behavior in response to spider mite extracts. Webbing extract induced both orthokinesis and klinokinesis reactions, whereas cuticle extract induced only orthokinesis reactions. The reasons why such differences in movement patterns only appeared between behavioral assays but not between treatments and control zones within each assay warrant further investigation. Attractant compounds are possibly influencing thrips larval behavior

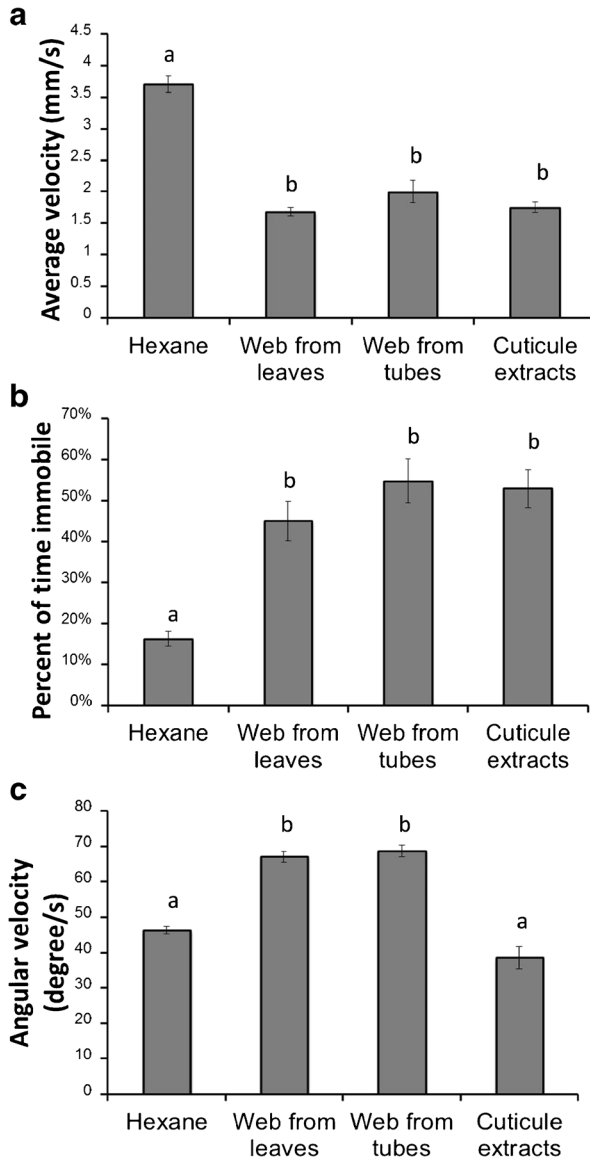


Fig. 2 **a** Average velocity (mm/s), **b** percentage of time immobile, **c** angular velocity (degree/s) of second instar thrips larvae in behavioral assays under the different treatments. Different letters indicate significant differences at the $\alpha < 0.05$ level

and induce orientation of the larvae toward the webbing extract contaminated area, as suggested by the increase of residence time in zones contaminated by webbing extract. Alternatively, thrips larvae might be influenced by volatile cues that pervade the entire arena, and not only by contact chemicals from the webbing extracts. Additional experiments with olfactometers are needed to account for the presence of volatile attractants in spider mite extracts.

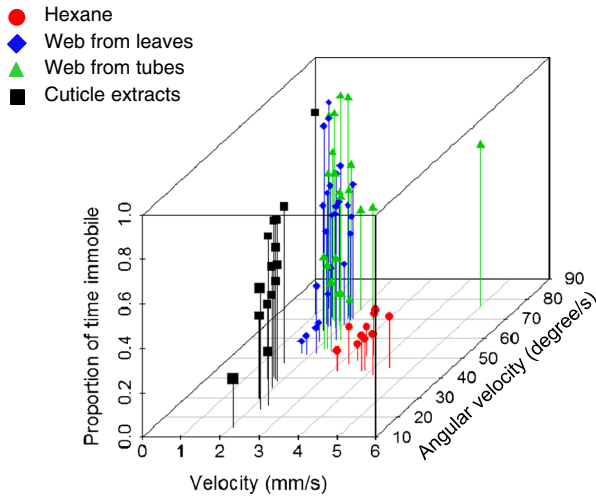


Fig. 3 Three dimensional scatter plot showing velocity, proportion of time immobile and angular velocity of second instars thrips larvae during bioassays

Despite the fact that spider mites and thrips are often sympatric under field conditions (Pickett et al. 1988; Wilson et al. 1996; Martini et al. 2013), and that thrips are considered important predators of spider mite eggs in the field (Lincoln et al. 1953; Trichilo and Leigh 1986; Wilson et al. 1991), the potential attraction of thrips toward spider mites infested plants remains controversial (Pallini et al. 1998, 1999). However, a recent study by Silva et al. (2013), showed that *F. occidentalis* was attracted to volatiles released by plants subjected to spider mite feeding. The attractiveness of spider mite-induced volatiles to thrips has been demonstrated in other species (Shimoda et al. 1997; Agrawal et al. 1999). Regarding webbing cues, Shimoda et al. (1997) found webbing, faeces or eggs of the two-spotted spider mites were not attractive to the predatory thrips, *Scolothrips takahashii* Priesner in olfactometer experiments. It is possible that spider mite induced volatiles are used by thrips as long-range cues for prey detection (at the plant level), when chemical cues from the webbing might serve as short-range cues to induce arrestment responses by thrips larvae.

The extracts that elicited arrestment responses by thrips larvae must contain chemicals that have an important role for spider mites, otherwise their production would have been eliminated by natural selection. The chemicals present in spider mite webbing may have a role during spider mite mating. Indeed, Penman and Cone (1974) showed that the presence of webbing produced by a female prior to quiescence increased male attraction. The webbing is also used by spider mites to locate conspecifics, and larvae are more responsive to the presence of conspecific webbing than adults (Clotuche et al. 2013).

Many species of thrips are considered facultative and opportunistic predators of spider mite eggs (Wilson et al. 1991, 1996; Mound 2005; Zhi et al. 2006), which implies that they do not specifically forage for spider mite eggs, but will consume them when they are encountered. In this study, we demonstrated that thrips larvae are able to adapt their search behavior in the presence of semiochemicals found in spider mite webbing, where eggs are usually laid. These movement patterns tend to localize their

movement in a smaller area and would be particularly efficient in helping them in the localization of spider mite eggs that are randomly distributed on spider mite webbing.

Optimal foraging theory predicts that facing two preys, a predator should choose the one that optimizes its net energetic gain (Stephen and Krebs 1986). Consequently, in the case of an omnivorous insect, predatory behavior should be privileged rather than herbivory when the nutritional quality of the host plant is poor. This positive relationship between predation and poor host plant value has been described in thrips (Agrawal et al. 1999; Magalhães et al. 2005). We now need to know if the thrips responses to spider mite cues change with the nutritional quality of the host plant. Theory would predict that omnivorous thrips should be more sensitive to spider mite cues while present on a nutritionally deficient plant.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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