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### Predator-prey interactions

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## Predator-prey interactions: How thrips avoid predation

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### HIGHLIGHTS

- We investigated the interaction between a predatory mite and three thrips species.
- *Frankliniella occidentalis* had complex antipredator behaviour but was preyed upon.
- *Thrips parvispinus* showed similar behaviour and was also preyed upon.
- *Echinothrips americanus* showed fewer defence types but often escaped predation.
- Suppressing the antipredator behaviour resulted in predation of all three species.

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### ABSTRACT

Biological pest control is successful in many agricultural systems, yet various pests can still not be controlled with natural enemies. Examples are invasive thrips species such as *Echinothrips americanus* Morgan and *Thrips parvispinus* (Karny) in Europe. The lack of biological control of these pests in several crops has been subscribed to their complex life cycle and cryptic behaviours, but their antipredator behaviours may prevent successful control and have not been studied extensively. One of these behaviours is the potential of thrips to kill the eggs of predatory mites, which we quantified. Furthermore, we observed the behaviour of first- and second-instar thrips larvae when attacked by starved predatory mites *Amblyseius swirskii* Athias-Henriot. For comparison, we included *Frankliniella occidentalis* (Pergande), which shows an array of defensive behaviours, but can be controlled successfully by several species of predatory mites. Second-instar larvae and adults of *F. occidentalis* and *T. parvispinus* killed predator eggs, but *E. americanus* did not. First- and second-instar larvae of all three species swung their abdomen to defend themselves, and *F. occidentalis* and *T. parvispinus* produced anal droplets, which are also involved in defence. Predators were not successful in attacking any second-instar larvae during 15-minute observations, which is sufficiently long for an attack. First-instar larvae of *F. occidentalis* and *T. parvispinus* were sometimes successfully attacked by the predatory mite before they could mount a defence, but first-instar *E. americanus* always defended themselves and were almost never preyed upon. Cooling thrips larvae to suppress antipredator behaviour increased predation for all species and stages, except for first instars of *F. occidentalis*. In conclusion, the lack of successful control of *E. americanus* is not caused by killing predator eggs, but by the efficient defensive behaviour of both larval instars. Our study furthermore suggests that *T. parvispinus* can potentially be controlled by *A. swirskii*.

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## 1. Introduction

Agriculture is slowly shifting towards more sustainable ways of controlling pests, due to environmental and health issues related to chemical pesticides, government regulations on such substances, the development of pest resistance, and consumer demands for products without pesticide residues (Ehlers, 1996; Matson et al., 1997; Storck et al., 2017; van Lenteren, 2012). Among these more sustainable ways of controlling pests, biocontrol practices play a big role (Ehlers, 1996; van Lenteren, 2012). Despite the increase of biocontrol practices and the intensive research behind it, not all biocontrol systems prove to be successful (Ehlers, 1996; van Lenteren, 2012). For example, certain thrips species, such as *Frankliniella occidentalis*, *Thrips tabaci* Lindeman, and *Scirtothrips dorsalis* Hood can be controlled with phytoseiids (Arthurs et al., 2009; Messelink et al., 2006; Ramakers and van Lieburg, 1982; Ramakers, 1980), whereas biocontrol is variable for others, such as *Echinothrips americanus* (Ghasemzadeh et al., 2017; Hoogerbrugge et al., 2014; Pijnakker et al., 2017). Anthocorid and mirid predators can efficiently prey on *E. americanus*, however with some limitations (Leman et al., 2020; Mouratidis et al., 2022; Opit et al., 1997). For example, food supplementation and oviposition sites are essential for *Orius* bugs, which rules out their use in several crops (Waite et al., 2014; Wong and Frank, 2013). For these crops, predatory mites could be used, but to date, no predatory mites have been found that can control *E. americanus*. The lack of success in controlling thrips in general is often attributed to their complex and cryptic life cycles (Berndt et al., 2004; Lewis, 1997), but is possibly also caused by the anti-predator behaviours of the thrips (Vangansbeke et al., 2023), which are potentially more effective against small predators such as mites than against larger predatory bugs.

Antipredator behaviours are generally thought of as prey defending themselves from predators in an array of ways, for example by physically fending off the attacker, by escaping or hiding, by tonic immobility, by chemical defence, or by avoiding areas with predators (Bakker and Sabelis, 1989; Choh et al., 2010; de Bruijn et al., 2006; Laurila et al., 1997; Lima and Dill, 1990; Magalhães et al., 2002; Montserrat et al., 2007; Sih, 1986; Teerling et al., 1993b). However, there are other interactions between thrips and predatory mites that may affect biological control. The concept of biological control is based on the dynamical interaction between a natural enemy and a pest species (prey) and assumes that each species has only one ecological role, either predator or prey. In practice, however, the ontogeny and the size of an individual often determine its ecological role (Beranek et al., 2023; Janssen et al., 2002; Polis, 1991; Saito, 1986a); larger individuals generally prey on smaller, more vulnerable individuals, thus, larger prey individuals can be invulnerable to predators. In contrast, small predator individuals may be killed and preyed by large prey individuals (Choh et al., 2012; Saito, 1986b, 1986a). This killing of small, vulnerable predator individuals by large prey can affect the behaviour of large predators, which avoid the presence of the counterattacking prey (Choh et al., 2012; de Almeida and Janssen, 2013; Faraji et al., 2001; Magalhães et al., 2005). As a consequence, the predation risk of vulnerable offspring of the adult prey may also be reduced (Choh et al., 2012; Janssen et al., 2002). In the specific case of thrips, their eggs and larval stages can be attacked by predatory mites, whereas adult thrips are commonly not attacked. In return, predator eggs can be attacked by several thrips stages, as was shown for larvae of *F. occidentalis* (Janssen et al., 2002; Magalhães et al., 2005; Vangansbeke et al., 2023).

All these anti-predator behaviours, alone or combined, may contribute to the lack of biocontrol of certain pest species. The aim of this study was to study the anti-predator behaviours of three thrips species, *E. americanus*, *F. occidentalis*, and *T. parvispinus*, when faced with the predatory mite *Amblyseius swirskii*. Most research on anti-predator behaviour of thrips has focused on *T. tabaci* and *F. occidentalis*, and we included the latter in our study as a benchmark. Previous research has shown that adults and second-instar larvae of *F. occidentalis* prey on mite eggs (Faraji et al., 2002; Janssen et al., 2002; Magalhães et al., 2005;

Trichilo and Leigh, 1986; Vangansbeke et al., 2014). We investigated if this behaviour also occurs in *E. americanus* and *T. parvispinus*, and whether it could be a limiting factor for their biocontrol. Furthermore, *F. occidentalis* and *T. tabaci* are known to use several other defence mechanisms against their predators; they try to hit the predators with abdominal swings and produce anal droplets, which they attempt to deposit on the predators. When such an abdominal swing hits a predator, it often deters it from further predation attempts (Bakker and Sabelis, 1989), the more so when it is combined with the deposition of an anal droplet (Bakker and Sabelis, 1989; Teerling et al., 1993b). These droplets also contain a pheromone that acts as an alarm for conspecifics and promotes vigilance behaviour in thrips (de Bruijn et al., 2006; Teerling et al., 1993a; Teerling et al., 1993b). Because not much is known of the defensive behaviour of *E. americanus* and *T. parvispinus* show similar defensive behaviours as *F. occidentalis*, we recorded this behaviour of all three thrips species with adult *A. swirskii* as predator.

Lastly, we tested the effects of antipredator behaviours on predation by excluding them, similar to Bakker and Sabelis (1989). These authors showed how the capture success ratio of a predatory mite increased significantly when they were offered thrips larvae anesthetized with CO<sub>2</sub> and could thus not defend themselves. We investigated the effect of excluding antipredator behaviour of *F. occidentalis*, *E. americanus* and *T. parvispinus* larvae by cooling them and offering them to adult female *A. swirskii*.

## 2. Materials and methods

### 2.1. Plants, mites and thrips

Sweet pepper (*Capsicum annuum* L.) is one of the main host plants of the three thrips species studied here (He et al., 2020; Mound and Collins, 2000; Opit et al., 1997), and was used for experiments in this study. The plants were grown in a climate room (25 °C; 70 % RH; L16:D8) and leaf discs of these plants were used as experimental arenas. The predatory mite *A. swirskii* was reared on plastic arenas resting on sponges in water-containing trays and surrounded by a wet tissue barrier to avoid mite dispersal and to provide water (Nomikou et al., 2003). Small plastic roofs and cotton wool fibres were added on top of the plastic platforms to create a protected oviposition site. The arenas were kept in BugDorm cages (45 × 45 × 45 cm; 45 × 45 × 90 cm; Nylon mesh size 150 × 150, 160 µm aperture) to prevent contamination, and were kept in a climate room (25 °C; 67 % RH; L16:D8). The mites were fed with *Typha angustifolia* L. pollen twice per week.

Individuals of *E. americanus* were reared on common bean plants (*Phaseolus vulgaris* L.) in a BugDorm cage (as above) inside a climate room (conditions as above). Clean plants were added to the cultures twice per week. *Thrips parvispinus* and *F. occidentalis* originated from populations that were reared in an experimental greenhouse of the business unit Greenhouse Horticulture and Flower Bulbs of WUR in Bleiswijk, the Netherlands, and were subsequently cultured on fresh green bean pods in rearing cups (7.5 × 9 cm). The lids of the rearing cups contained a hole covered with fine gauze (mesh size 80 µm) to allow ventilation. The cultures were kept in a laboratory (21 ± 1 °C). Fresh green bean pods were washed with soap to remove any remains of pesticides and added to the cups three times per week. The bean pods served as oviposition substrate and food for the thrips. In addition, *Typha* pollen was added as extra food to these rearing units twice a week.

### 2.2. Egg-killing

Predatory mite eggs were obtained by allowing adult females of *A. swirskii* to lay eggs 24 h prior to the start of the experiment and were stored at a 5 °C until use. This storage did not affect their viability (GM Beretta, pers. obs). Egg-laying arenas consisted of sweet pepper leaves that were placed abaxial side up on agar (Duchefa Biochemie B.V., Daishin agar, Haarlem, The Netherlands; ratio 1 g:100 ml water) in cups

(7.5 × 9 cm) with a hole in the lid covered with fine gaze (mesh size 80 µm). Small plastic roofs, fine pieces of thread and pollen were added on top of the leaves as oviposition sites. Egg-killing experiments were conducted with first-instar larvae of *E. americanus* and *T. parvispinus* and second-instar larvae and adults of all three thrips species, obtained from their respective cultures.

Experimental arenas consisted of leaf discs (2.5 cm Ø), cut from c. three-week-old sweet pepper plants, placed abaxial side up on top of solidified agar inside small cups (2 × 3.5 cm). In every cup, one thrips was incubated for 24 h together with three mite eggs, clustered together at the centre of the leaf disk. Egg-killing experiments were conducted with 25 second-instar larvae and 25 adults of *E. americanus*, *T. parvispinus* and *F. occidentalis*. We also tested first-instar larvae of *E. americanus* and *T. parvispinus*, however we found no egg predation, and we therefore excluded these results. The species were tested simultaneously, together with 50 replicates with only mite eggs as control for natural mortality. All experiments were performed in a climate room (conditions as above). After 24 h, the number of killed predator eggs was assessed. Egg killing was assumed to have occurred when the number of eggs that hatched and the number of intact eggs did not add up to three per replicate.

Data on the incidence of egg killing were compared among the different species and life stages and with the control using a generalized linear model (GLM) with a binomial error distribution (logit link). Contrasts among treatments were assessed with the Tukey method (function `emmeans` of the package `emmeans`, Lenth, 2019). The numbers of killed eggs were compared for species and life stages that killed eggs with a GLM with a Poisson error distribution (logit link).

### 2.3. Antipredator behaviour

Behavioural observations were conducted with the first- and second-instar larvae of *E. americanus*, *T. parvispinus* and *F. occidentalis* and adult females of *A. swirskii*, the latter being the most voracious stage of this predatory mite. First- and second-instar larvae of *E. americanus* were gathered from egg cohorts as follows. Adult thrips, taken from the rearing units, were allowed to oviposit for 48–72 h in sweet pepper leaves, abaxial side up, on top of a layer of solidified agar (as above) in large Petri dishes (13 cm Ø) with a hole (7.5 cm Ø) covered with mesh (size 80 µm). First-instar larvae were selected based on their transparent-white colour and their head size, which is the same or bigger than their first abdominal segment. Second-instar larvae were selected based on their opaque, yellow colour, and their head being smaller than their first abdominal segment.

Prior to the behavioural observations, adult female mites were incubated on a clean rearing arena (described in section 2.1.) and starved for 24 h to increase their motivation to attack prey. They had access to water to prevent dehydration. Observation arenas consisted of a sweet pepper leaf disc (1.5 cm Ø), placed abaxial side up on top of a piece of cotton wool in water-filled Petri dishes (3.5 cm Ø). We released two thrips larvae (both first or both second instar) on each leaf disc to guarantee a high enough encounter rate of the predator with the thrips. They were released c. 18 h prior to the experiment to allow them to settle and to avoid changes in their activity due to the transfer. The Petri dishes were covered with a lid and kept in the laboratory (as above) until the start of the experiment. The experiment was started by transferring one starved adult female predatory mite to each arena, after which the behaviour and interactions with the thrips larvae were observed under a binocular microscope (Leica MZ 6, with Leica KL 1500 LCD light, 0.63 magnification), for 15 min, which was found to be sufficient time for at least one encounter of the starved predators with a thrips larva during preliminary observations.

The software package BORIS (8.0.9, Friard and Gamba, 2016, <https://www.boris.unito.it/>) was used to register the behaviour of thrips and mites while observing it through the microscope. Behaviours were regarded as state events or point events, depending on whether

they had a measurable duration (Table 1). Walking, grooming, sitting still, feeding and encounters were the registered behaviours of the mites; encounters, abdomen swings that were either hits or misses, and droplet production were those of the thrips larvae (Table 1). In total, 12 replicates were obtained for each instar of all three thrips species, each with a new predator and thrips larvae.

Matrices of the frequency of transitions between behaviours were constructed with BORIS and were used to create flow diagrams that show the succession of behaviours (Fig. S1). Frequencies were calculated by dividing the numbers of transitions from behaviour A to behaviour B by the total numbers of occurrence of behaviour A. The encounter rate was calculated as the total number of encounters of the predator with a thrips larva divided by the total walking time, with the assumption that the predators only searched for prey when walking. Encounter rates were compared for the different species and life stages using a GLM with a Gaussian error distribution (identity link). Encounter success ratios were calculated as the total number of killing events divided by the total number of encounters. A maximum of two killing events could occur in one replicate. Log (x + 1) transformed numbers of thrips abdomen swings that hit the predator per encounter were compared for different species and life stages with a GLM with a Gaussian error distribution (identity link). The occurrence of droplet production during an encounter was compared among each species and between life stages per species with a GLM with a binomial error distribution (logit link). Other data analysed consisted of proportions, such as the proportions of encounters with a defence, proportions of swings that were hits, proportions of abdomen swings that were either a hit or a miss followed by the mite giving up, proportions of hits followed by a feeding event, proportions of droplet production followed by the mite giving up and the encounter success ratios. These data were compared among larval stages and thrips species with a GLM with a binomial error distribution (logit link). Overdispersion was tested with the dispersion test of the package DHARMA (Hartig, 2022), and quasi-binomial GLMs (logit link) were used in case of overdispersion. All models were checked with normal error plots and plots of residuals against fitted values. The significance of factors and interactions was determined with likelihood ratio (L.R.) tests. Contrasts among treatments were assessed with the Tukey method (function `emmeans` of the package `emmeans`, Lenth, 2019).

**Table 1**

The behaviours observed during the observations of the interactions between the predatory mite *A. swirskii* and larvae of the three thrips species *F. occidentalis*, *E. americanus* and *T. parvispinus*.

Behaviour	Type <sup>a</sup>	Category	Description
Walk <sup>b</sup>	State	Mite behaviour	The mite is walking.
Grooming <sup>b,c</sup>	State	Mite behaviour	The mite is cleaning itself, rubbing its legs along its body or cleaning its forelegs
Still <sup>b</sup>	State	Mite behaviour	The mite sits still.
Feeding <sup>b</sup>	State	Mite behaviour	The mite feeds on a larva.
Encounter <sup>b</sup>	State	Encounter	The mite encounters one of the thrips larvae.
Miss	Point	Thrips APB	Thrips larva swings its abdomen, missing the mite.
Hit	Point	Thrips APB	The thrips larva swings its abdomen, hitting the mite.
Droplet	Point	Thrips APB	The thrips larva produces a droplet of anal fluid.

The behaviours were divided into three categories: mite behaviour, thrips anti-predator behaviour (APB), and encounter. <sup>a</sup> Behaviours were regarded as state events, which had a duration, or point events, of which the duration could not be measured; <sup>b</sup>: these behaviours were also scored in the experiment with cooled thrips larvae; <sup>c</sup>: grooming was combined with sitting still in the experiment with cooled thrips larvae.



## 2.4. Suppressing antipredator behaviour

Experiments where the antipredator behaviours of thrips larvae were prevented were performed with the same species and instars as in the previous experiment. Initially, we tried to anaesthetise thrips larvae with CO<sub>2</sub> following the method of Bakker and Sabelis (1989), but this method proved unsuccessful. We therefore put two thrips larvae, either first- or second instar, were on a sweet pepper leaf disk and cooled them in a freezer at -28 °C for 60 min prior to the start of the observations. Some larvae started moving during the observation time and were omitted from further analysis. All other larvae recovered soon after the 15 min. observation time.

Because the movement speed of *A. swirskii* would be lower on a cooled leaf disc, the cooled thrips larvae were placed on a new leaf disk at room temperature straight after being taken from the freezer. Because the cooled thrips were not showing any activity, this transfer immediately before the observations did not affect their behaviour. The non-cooled first- or second-instar thrips larvae used for the control were added to a leaf disk c. 6 h before the start of the observations to prevent effects of handling them. Owing to logistical constraints, observations and registration of behaviours were as above, except that behaviours of replicates with *T. parvispinus* and *F. occidentalis* were scored with a digital timer. We recorded the same behaviours as in section 2.3, however, grooming and sitting still of the predators were combined (Table 1) because we were interested in the active searching time and not in the behaviours while the mites were not moving or interacting with thrips larvae. Since the cold treatment effectively eliminated any thrips movement, abdominal swings and droplet production were observed only for the thrips in the control group. The number of replicates used in this experiment are displayed in legend of Fig. 4 and data were analysed as in Section 2.3, but focused on the comparisons between control vs cooled thrips.

## 3. Results

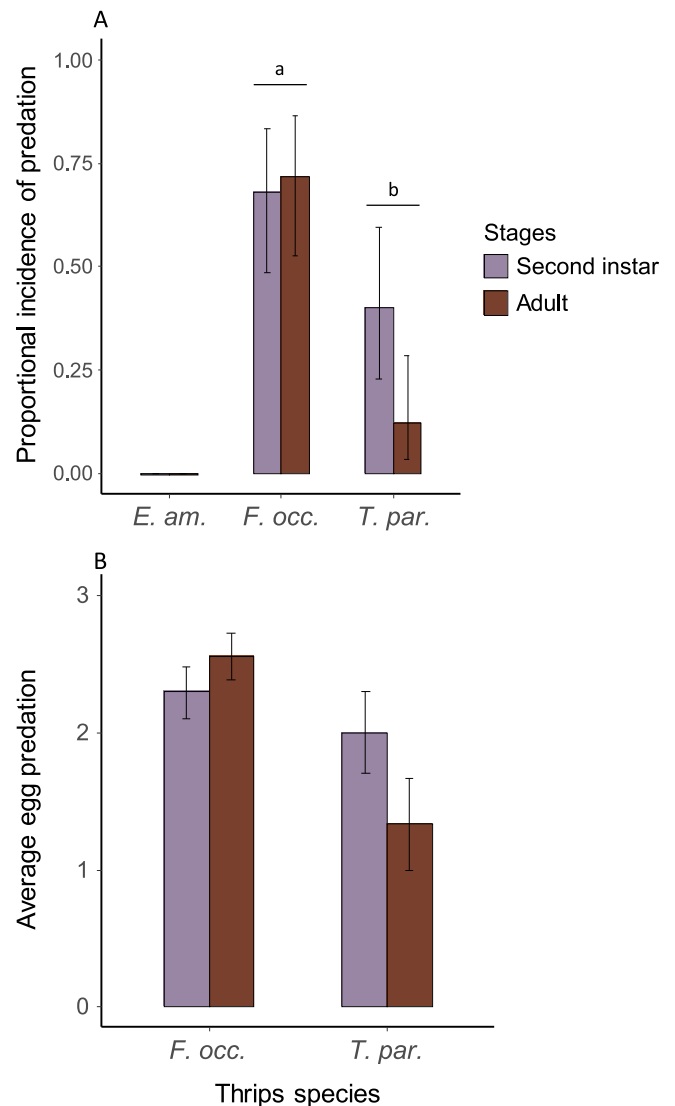
### 3.1. Egg-killing

The tendency of second instars and adults of the three thrips species to kill eggs of the predatory mite differed significantly among species (Fig. 1A, glm, Deviance = 69.7, d.f. = 2,  $p < 0.0001$ ), but not between second instars and adults within the same species (Fig. 1A, glm, Deviance = 1.80, d.f. = 1,  $p = 0.18$ ). None of the stages of *E. americanus* killed any eggs, and they were therefore excluded from further analysis. Second-instar larvae and adults of *F. occidentalis* had a higher propensity to kill eggs of *A. swirskii* than did *T. parvispinus* (Fig. 1A). Comparing only those individuals of *T. parvispinus* and *F. occidentalis* that killed eggs showed that there were no significant differences in the numbers of eggs killed between stages or species (Fig. 1B, glm, species: Deviance = 1.48, d.f. = 1,  $p = 0.22$ ; stages: Deviance = 0.022, d.f. = 1,  $p = 0.88$ ). Thus, the main difference between the two species is that more individuals of *F. occidentalis* than of *T. parvispinus* killed predator eggs.

### 3.2. Antipredator behaviour

The first behaviour observed was always the predators walking (Fig. S1). They then changed to grooming, sitting still or encountering a thrips larva. Rarely, predators would encounter a thrips larva when grooming or sitting still (Fig. S1). Encounters resulted in defence by the thrips larva and ended in attacking and feeding on the thrips or in the predators walking away, grooming or sitting still (Fig. S1).

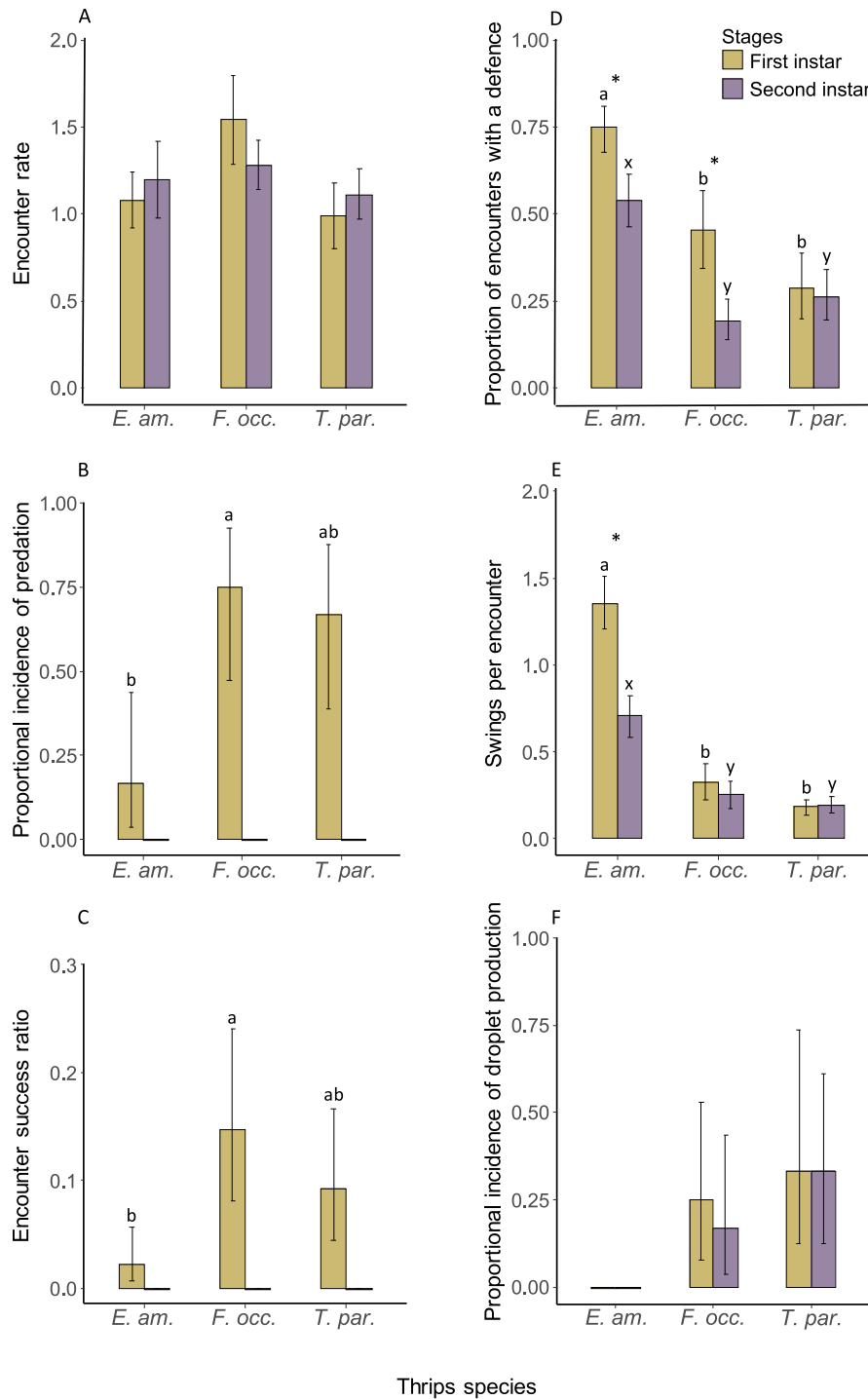
In most cases, the mite found a thrips larva, and the encounter rates (e.g. the number of encounters per total time spent walking) did not differ among thrips species and larval stages (Fig. 2A, glm, species:  $F_{2,69} = 1.96$ ,  $p = 0.15$ ; stage:  $F_{1,68} = 0.002$ ,  $p = 0.96$ ). Predators did not succeed in preying on second-instar larvae of any of the thrips species (Fig. 2B, and S1), and predation on first-instar larvae differed



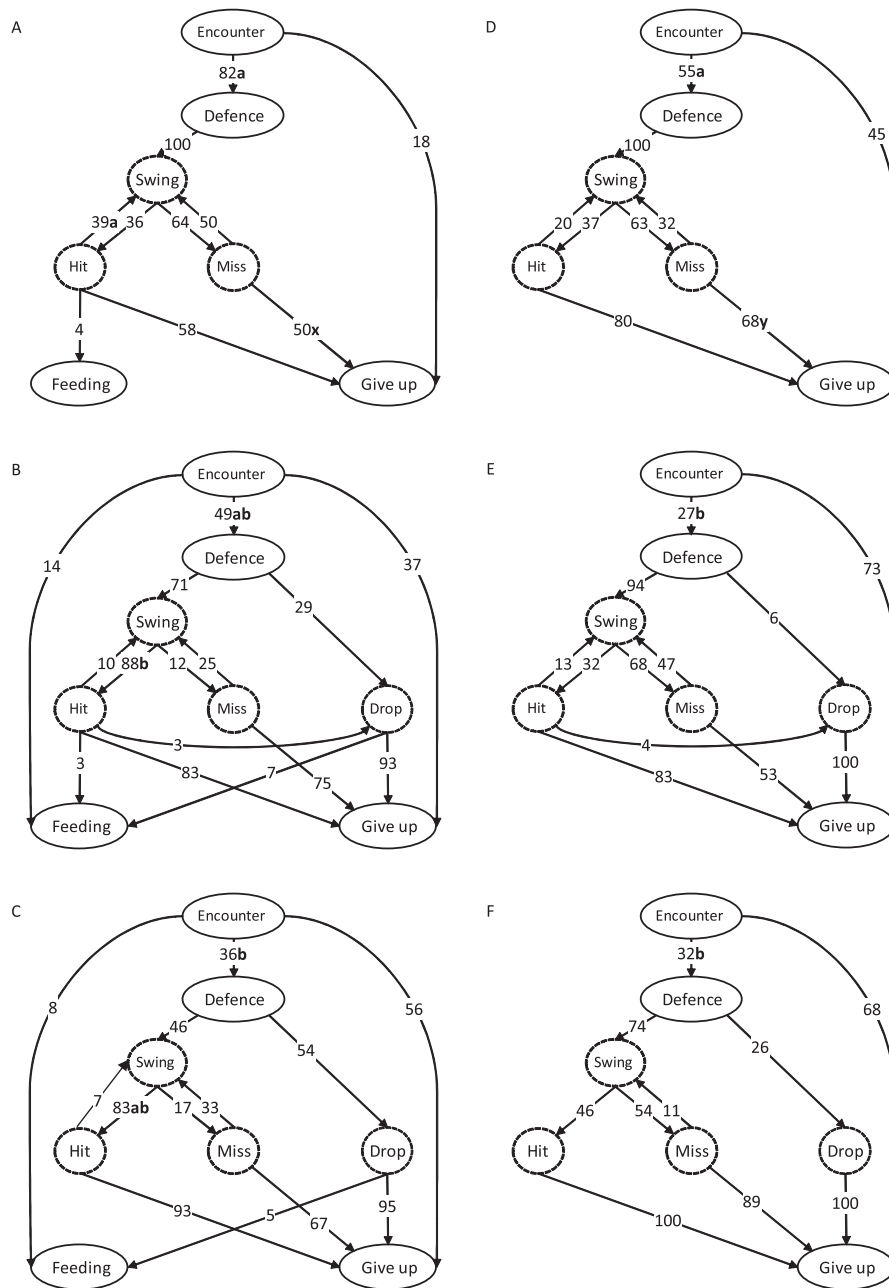
**Fig. 1.** The killing of eggs of the predatory mite *Amblyseius swirskii* by three species of thrips. A. The proportion ( $\pm 95\%$  c.i.) of thrips (out of 25) that killed predator eggs. Each replicate consisted of three eggs of the predatory mite *A. swirskii* and one second-instar larva (light, lilac) or one adult (dark, bordeaux) of one of three thrips species (*E. am.* = *Echinothrips americanus*, *F. occ.* = *Frankliniella occidentalis*, *T. par.* = *Thrips parvispinus*). B. The number of killed eggs averaged over those thrips individuals that killed eggs ( $\pm$ s.e.) in the same experiment. Different letters above the bars indicate significant difference between species.

significantly among species (Fig. 2B, glm, Deviance = 10.21, d.f. = 2,  $p = 0.0061$ ). Predation of first-instar *E. americanus* was significantly lower than of first-instar *F. occidentalis* and predation of first-instar *T. parvispinus* was intermediate (Fig. 2B). Together with the lack of significant differences in encounter rates (Fig. 2A), this suggests that the interaction during an encounter with a predator differed among first-instar larvae of the three thrips species, and between first- and second-instars of each species. We therefore analysed the behaviour of thrips and predators during these encounters in more detail.

An encounter could end in a successful attack (e.g. feeding) or in the predator giving up (i.e. walking, sitting still, grooming; Fig. 3). A striking difference between the first-instars of *E. americanus*-larvae and those of the two other species was that the former always defended themselves during an interaction (Fig. 3A), whereas the first-instar larvae of the other two species were sometimes subdued without having defended (Fig. 3B, C). The larvae of all three species swung their



**Fig. 2.** The interaction of the predatory mite *A. swirskii* with larvae of three thrips species during 15 min. A. The average encounter rates ( $\pm$ s.e.) of adult female predatory mites with thrips larvae. Encounter rates are expressed as number of encounters divided by total walking time of the predator. B. The proportion ( $\pm$ 95 % c. i.) of individual predatory mites (out of 12) that killed at least one thrips larva. C. The average encounter success ratio ( $\pm$ c.i.) of adult female predatory mites with thrips larvae. The ratio is given as the proportion of encounters that resulted in a successful attack. D. The proportion ( $\pm$ 95 % c.i.) of encounters with predators in which the thrips larvae defended themselves; E. the number of swings ( $\pm$ se) per encounter; F. The proportion ( $\pm$ 95 % c.i.) of replicates in which thrips larvae produced droplets when defending themselves against a predator. Light (green) bars show first-instar larvae, dark (ilac) bars are second-instar larvae. Different letters above the bars indicate significance among first instar (a, b) and second instar (x, y) larvae of the three species. Asterisks above pairs of bars indicate significant differences between the two stages of the same species. See legend to Fig. 1 for further explanation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** The interaction of the predatory mite *A. swirskii* with larvae of three thrips species during 15 min (same experiment as in Fig. 2). Flow diagrams show the sequence of behaviours of the predatory mite *A. swirskii* and first (A – C) and second-instar larvae (D – F) of the species *E. americanus* (top row), *F. occidentalis* (middle row), or *T. parvispinus* (bottom row) during their encounters. Numbers in the flow diagrams represent the percentage of a behaviour followed by another behaviour. Letters a and b after some numbers indicate significant differences among the same stage of the three species and letters x and y indicate significant differences between the two stages of the same species. Defensive behaviours of thrips are shown in dashed circles. See Table 1 for a description of the behaviours. An encounter ended when the mite started feeding on the larva or when giving up (i.e. walking away, sitting still, or grooming). See Fig. S1 for flow diagrams of further behaviour and explanation.

abdomen in attempts to hit the predator, and such hits often resulted in the predator giving up (Fig. 3). Larvae of *E. americanus* did not produce droplets during interactions with the predator, and droplet production by larvae of the other two species often resulted in the predator giving up (Fig. 3).

There were significant differences in the proportions of encounters with first-instar thrips larvae that resulted in successful attacks among thrips species and instars (Fig. 2C, glm, Deviance = 12.7, d.f. = 2,  $p = 0.0018$ ). More first-instar larvae of *F. occidentalis* were killed than of *E. americanus*, whereas the predation rate of first-instar larvae of *T. parvispinus* was intermediate (Fig. 2C).

To further investigate the causes of the differences in encounter success ratios among species and instars, we compared the defensive behaviour of the thrips larvae. There were significant differences in the proportion of encounters in which the thrips larvae defended themselves (i.e. producing droplets and swinging their abdomen) (Fig. 2D glm, interaction of species with instar: Deviance = 7.49, d.f. = 2,  $p = 0.024$ ). The first- and second-instar larvae of *E. americanus* defended themselves significantly more frequently than the respective instars of the other two species (Fig. 2D), and first-instar larvae of *E. americanus* and *F. occidentalis* defended themselves more frequently than their respective second-instar larvae (Fig. 2D). Furthermore, the number of

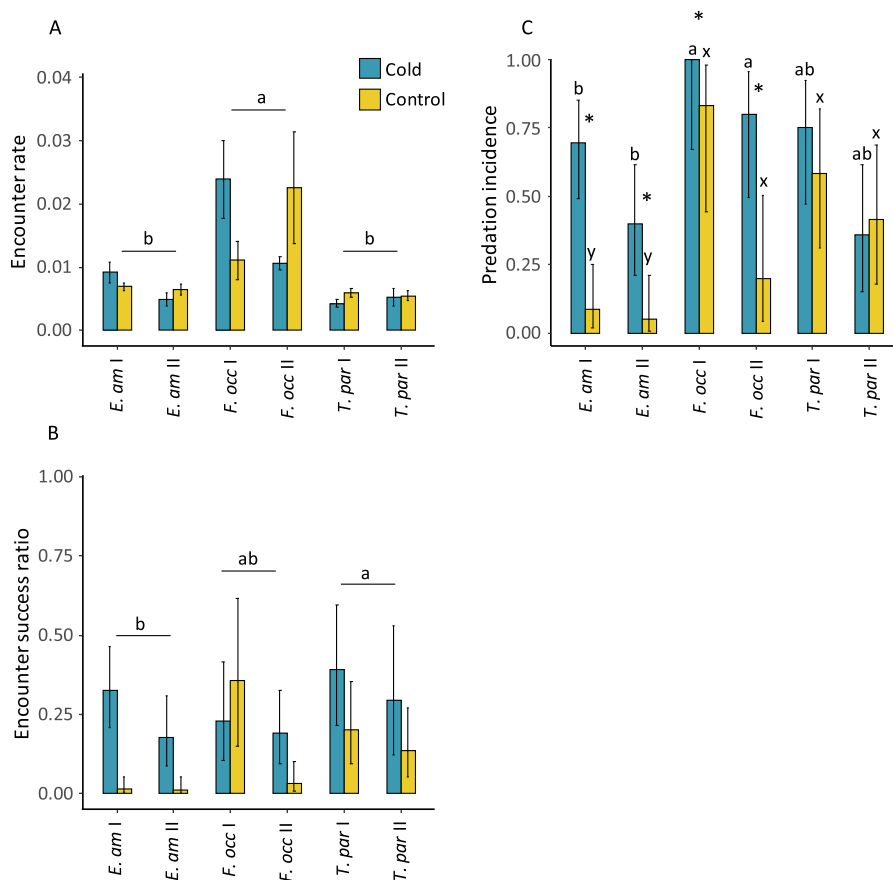
abdomen swings (hits plus misses) during the encounters differed significantly among species and larval stages (Fig. 2E, interaction of species with instar: glm,  $F_{2,66} = 4.47$ ,  $p = 0.015$ ). First- and second-instar larvae of *E. americanus* swung their abdomen significantly more during an encounter with the predator than the corresponding instars of the other two species, and first instars of *E. americanus* swung their abdomen more than second instars of the same species (Fig. 2E). In general, the hits of all species were effective since they almost always led to the mites giving up (Fig. 3). However, the proportions of hits that were followed by the predator giving up differed significantly between instars (glm, Deviance = 4.58, d.f. = 1,  $p = 0.032$ ) and among species (glm, Deviance = 17.7, d.f. = 2,  $p < 0.001$ ). Predators gave up the least after a hit by first-instar *E. americanus*, and the most after hits by first- and second instars of *T. parvispinus* (Fig. 3).

There was no significant difference in droplet production between instars of *F. occidentalis* or *T. parvispinus* (Fig. 2F, glm, Deviance = 0.96, d.f. = 1,  $p = 0.33$ ) or between species (Fig. 2F, glm, Deviance = 0.11, d.f. = 1,  $p = 0.74$ ). Droplet production was an effective defence mechanism: the mites gave up in over 90 % of the cases when a droplet was produced (Fig. 3B, C, E, F). There were no significant differences in the proportions of encounters with droplet production followed by the mites giving up between *F. occidentalis* and *T. parvispinus* (Fig. 3, glm, Deviance = 0.30, d.f. = 1,  $p = 0.59$ ) or between larval stages (Fig. 3, glm,

Deviance = 2.21, d.f. = 1,  $p = 0.14$ ), but only 12 individuals out of 72 produced droplets during the experiments.

### 3.3. Suppressing antipredator behaviour

The cooling treatment was effective in suppressing thrips movements and defensive behaviours such as abdomen swings and droplet production. Cooling the thrips larvae did not result in significant differences in encounter rates (Fig. 4A, effect of cooling: glm,  $F_{1,165} = 0.064$ ,  $p = 0.80$ ). There was also no significant difference in encounter rates between stages (glm,  $F_{1,164} = 0.43$ ,  $p = 0.51$ ), but there was a significant difference among species (glm,  $F_{2,165} = 9.29$ ,  $p < 0.001$ ), caused by the predators having a higher encounter rate with *F. occidentalis* than with the other two species (Fig. 4A). Except for first-instar larvae *F. occidentalis*, the cooling treatment resulted in a significantly higher proportion of successful encounters: cooled larvae that were encountered were killed more often than control ones (Fig. 4B, glm,  $F_{1,149} = 19.8$ ,  $p < 0.001$ ). The lack of difference in first-instar *F. occidentalis* was perhaps caused by the low number of replicates (six). Furthermore, there was a significant difference in the encounter success ratio among species (glm,  $F_{2,147} = 3.09$ ,  $p = 0.048$ ), caused by predators being less successful in attacking *E. americanus* than *T. parvispinus* (Fig. 4B). Cooling the thrips larvae significantly increased the predation rate of



**Fig. 4.** The interaction of *A. swirskii* with larvae of three thrips species during 15 min. Dark (blue) bars show interactions with larvae that were cooled to prevent defensive behaviour, light (yellow) bars with control larvae that were not cooled. A. The encounter rate ( $\pm$ s.e.) of adult female predatory mites with cooled and non-cooled thrips larvae. B. The encounter success ratio ( $\pm$ 95 % c.i.). C. The proportion ( $\pm$ 95 % ci) of predatory mites that killed thrips larvae. Numbers of replicates varied among treatments due to limitations of the numbers in the rearing units (*E. americanus*, first instars (*E. am I*): 23 replicates for control and cooled, second instars (*E. am II*): 20 replicates for both; *F. occidentalis*, first instars (*F. occ I*): 6, second instars (*F. occ II*): 10; *T. parvispinus*, first instars (*T. par I*): 12; second instars (*T. par II*): 14 for cooled, 12 for control). In panel A and B, different letters above the bars indicate significance among species. In panel C, different letters (a, b) above the dark (blue) bars indicate significance among cooled larvae of the three species, different letters (x, y) above the light (yellow) bars indicate significance among uncooled larvae of the three species. Asterisks above pairs of bars give significance of difference between cooled and not cooled larvae per stage within species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



larvae of *E. americanus* and *F. occidentalis*, but not of *T. parvispinus* (Fig. 4C, interaction of treatment with thrips species: glm, Deviance = 10.98, d.f. = 2,  $p = 0.0041$ ). When the larvae were not cooled, the larvae of *E. americanus* were attacked much less than those of the other two species (Fig. 4C), as was found before (Fig. 2B, 3).

#### 4. Discussion

The aim of this study was to investigate the antipredator behaviours of larvae of the thrips species *E. americanus*, *F. occidentalis*, and *T. parvispinus* when faced with the predatory mite *A. swirskii* to ultimately assess the implications of these prey-predator interactions on biocontrol. The first antipredator behaviour we evaluated was the killing of predator eggs by thrips (Janssen et al., 2002). Second-instar larvae and adults of *T. parvispinus* and *F. occidentalis* killed eggs of *A. swirskii*, but none of the life stages of *E. americanus* killed such eggs. Similar conclusions were reached also by Vangansbeke and colleagues (2023) when performing comparable experiments with the predatory mite *Amblydromalus limonicus* (Garman and McGregor). Hence, the question remains why *E. americanus* did not kill predator eggs? One reason may have been the quality of the host plant for this species. Several thrips species are polyphagous and their diet choice depends on the quality of the host plant present (Agrawal et al., 1999; Agrawal and Klein, 2000; Janssen et al., 2003). For example, *F. occidentalis* kills and consumes more eggs of mites when the quality of their host plant is low (Agrawal and Klein, 2000; Janssen et al., 2003). An exception to this is when the eggs are of a predator that is dangerous to the thrips, in which case the thrips kill and consume the eggs regardless of plant quality (Janssen et al., 2003). Hence, thrips do not solely kill eggs for food but also as a form of antipredator behaviour (Janssen et al., 2003, 2002). In the case of *E. americanus* in our experiments, none of these two conditions were fulfilled: the predators were not dangerous to *E. americanus* and the sweet pepper leaf discs used in the egg killing experiment are of high quality for this thrips species (Hoogerbrugge et al., 2014). An earlier study showed that *E. americanus* did not benefit from the supply of pollen, suggesting that this species is less omnivorous than other thrips species such as *F. occidentalis*, and therefore possibly also do not feed on mite eggs (Ghasemzadeh et al., 2017). An alternative explanation is that *E. americanus* might have not recognized *A. swirskii* eggs as food. Most larvae of *F. occidentalis* also ignored predator eggs initially, but once one egg was killed by a larva, all larvae started killing and feeding on the eggs (A. Janssen, pers. obs.). We therefore suggest investigating if larvae and adults of *E. americanus* are capable of feeding on predator eggs on different quality host plants, whether they kill eggs of different predators, and whether they can learn that the eggs are a potential food source.

Although the abdominal swings of first-instar *E. americanus* were less effective per swing than those of the other two thrips species (Fig. 3), they swung their abdomen at the predator more often than the other species (Fig. 2E), finally resulting in fewer successful attacks (Fig. 2C). Moreover, *E. americanus* larvae always defended themselves, whereas larvae of the other two species did not. Perhaps *E. americanus* is capable of better defence because it is better at perceiving a predator early during an encounter, which agrees with this last observation (Fig. 3A, B, C). First-instar *E. americanus* larvae have longer and thicker hairs than the larvae of the other two species (Vangansbeke et al., 2023), and these hairs could serve as mechanoreceptors, helping the larvae in detecting the predator early on, before it contacts the actual body of the larva. Indeed, carefully touching these hairs with a brush always resulted in an abdominal swing or the thrips running away (A. Janssen, pers. obs.). Given that the abdominal swings seems to ultimately lead to prevention of predation, it is likely that biocontrol of *E. americanus* is highly affected by this antipredator behaviour. However, younger first-instar *E. americanus* larvae are still likely to be vulnerable to predation: although the predation of c. 18 h old first-instar larvae in the experiment on antipredator behaviour was low (Fig. 2C), we found higher predation

rates on 6 h old first-instar larvae (Fig. 4B). Thus, we might have missed a short period of vulnerability during the experiments on antipredator behaviour. Moreover, our conclusions are based on short observations (15 min), and perhaps longer exposure of thrips larvae to the predator would have resulted in higher predation rates. Indeed, Ghasemzadeh and colleagues (2017) found higher predation rates over a period of three days than we observed here. Perhaps predators become more experienced in attacking thrips over time, and consequently more successful. Nevertheless, this period of vulnerability may be too short for effective control of *E. americanus* by predatory mites.

In addition to the mechanical defence, thrips often use chemical defence mechanisms that influence its interaction with *A. swirskii*. Certain thrips species, among which *F. occidentalis*, produce anal droplets and predators give up their attack when hit by such a droplet (de Bruijn et al., 2006; Teerling et al., 1993b). We also observed droplet production by *T. parvispinus* during their encounters with *A. swirskii*, which frequently resulted in the predator giving up (Fig. 3C, F). In contrast, the larvae of *E. americanus* did not produce droplets during their encounters with predatory mites (Fig. 3A, D), yet, when they were gently poked with a brush, they did so (G.M. Beretta and L. Zandbergen, pers. obs.). This suggests that they might use this defense when attacked by other predators than *A. swirskii*, and/or that they produce them as an alarm signal, as has also been described for other thrips species (de Bruijn et al., 2006; Teerling et al., 1993b).

Although *F. occidentalis* and *T. parvispinus* exhibit various defensive behaviours, the former can still be controlled effectively by predatory mites (e.g. Buitenhuis et al., 2015; Manners et al., 2013; Messelink and Holstein-saj, 2008; Messelink et al., 2006; Shipp and Wang, 2003). More experiments are needed to assess whether *T. parvispinus* can also be controlled successfully by *A. swirskii*, but the fact that their first-instar larvae are vulnerable to predation is promising. The antipredator behaviour of *E. americanus*, in contrast, proved to successfully prevent most predation by *A. swirskii*, which was confirmed with the experiments in which defensive behaviours were excluded, which resulted in higher predation rates. This might be even more true on plants where predators may encounter other, more easily obtainable food types.

*Thrips parvispinus* is a new invasive species in Europe (Mound and Collins, 2000) and not much is known about it, let alone the possibilities to control it with natural enemies. *Amblyseius swirskii* proved to be able to prey on the first-instar larvae of this species, suggesting that it is a promising species to control *T. parvispinus*. The fact that it does kill predatory mite eggs may hamper biological control, but given that more *F. occidentalis* kill eggs (Fig. 1a) and can still be controlled by the predatory mite suggests that control of *T. parvispinus* by *A. swirskii* is also possible. *Echinothrips americanus* did not prey on predator eggs, in agreement with the observations of Vangansbeke et al. (2023), thus we conclude that such counterattacks cannot be the reason for the failing biocontrol of this species. We suggest that the ability of *E. americanus* larvae to persistently fend off the predator is the main cause for lack of control by predatory mites, which was confirmed with experiments in which these defensive behaviours were suppressed.

#### 5. Conclusions

We show that the success of predators to control pest species partially depends on the defensive behaviour of the pest. This is particularly true for the control of *E. americanus* with predatory mites, which has been reported as unsuccessful. Larvae of *E. americanus* defend themselves so well that even the first-instar larvae, which are vulnerable to predation in other thrips species, are almost invulnerable to mite predation. To achieve biocontrol of *E. americanus*, there is therefore the urgent need to find a predator species that is less affected by the antipredator behaviours of this thrips and can establish well in the crops.

## CRedit authorship contribution statement

**Giuditta M. Beretta:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Lotte Zandbergen:** Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Jacques A. Deere:** Investigation, Writing – review & editing. **Gerben J. Messelink:** Investigation, Writing – review & editing, Conceptualization, Formal analysis, Methodology, Writing – original draft. **Karen Muñoz Cárdenas:** Investigation, Writing – review & editing. **Arne Janssen:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing, Funding acquisition.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2023.105437>.

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