



# Developmental time, potential food sources and predatory behaviour of the invasive pest species *Thrips parvispinus*

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**Abstract** Biological control of invasive thrips is a challenge in many agricultural systems, partly because of a lack of knowledge about their life cycle and interactions with their environment. *Thrips parvispinus* Karny (Thysanoptera: Thripidae) is an invasive species causing damage to many crops worldwide and on which our knowledge is still limited. We studied the developmental time of *T. parvispinus* under three different fluctuating temperature regimes, its predatory behaviour against the eggs of a phytoseiid predatory mite and the effect of different food sources on its oviposition rate. We showed that *T. parvispinus* adult females and L2 larvae can feed on a limited number of *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) eggs and that their predatory behaviour is significantly affected by

the nutritional quality of the host plant and the presence of pollen. Additionally, the oviposition rate of *T. parvispinus* females over six days was not positively affected by the presence of *Typha angustifolia* pollen, *Artemia* cysts or prey mites on bean leaves. Finally, we showed that the developmental time of *T. parvispinus* is relatively fast and comparable to that of the invasive thrips species *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). Our study provides further insight into the feeding behaviour of *T. parvispinus* as an omnivorous pest species and its interactions with its predators. *Thrips parvispinus* is unlikely to have a negative effect on phytoseiid mite populations and the use of supplementary food to support predatory mites in the crop does not seem to pose a risk of significantly increasing *T. parvispinus* populations.

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## Introduction

Biological pest control strategies are based on the use of living organisms (natural enemies) to suppress the population density or impact of a specific pest organism (Eilenberg et al. 2001). Understanding how arthropod pests and their natural enemies interact with their environment is essential to ensure the

efficacy of these strategies and move towards a more sustainable agriculture. This knowledge is often lacking in the case of invasive pest species, which arrive from other continents through international trade of plant material and represent a significant threat to agriculture worldwide (Paini et al. 2016).

In this study, we focused on an insect group particularly known for biological invasions around the world: thrips. Due to their small size, cryptic habits, short life cycle and polyphagous nature, many invasive thrips species have become a serious problem in agroecosystems (Morse and Hoddle 2006). A notorious invasive thrips is the western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), which has spread from North America to the rest of the world in the late 1970s and has since become a major crop pest (Kirk and Terry 2003). Many studies have focused on *F. occidentalis* over the last 50 years, resulting in significant progress in the use of sustainable solutions against thrips (Mouden et al. 2017). However, new invasive thrips species continue to expand beyond their original geographic areas and we still lack important basic knowledge about them. *Thrips parvispinus* Karny (Thysanoptera: Thripidae) is one of these species: originally from Southeast Asia, it has spread to Oceania, North America, Africa and Europe over the last 20 years (Palanisamy et al. 2023; EPPO Global Database). This polyphagous species causes serious damage to many greenhouse and field crops around the world, such as *Anthurium*, *Ficus*, sweet pepper, *Gardenia*, citrus, chili pepper and papaya (Mound and Collins 2000; Hulagappa et al. 2022). We still have limited knowledge about the life cycle of *T. parvispinus* under different climatic conditions and its behaviour and interactions with other arthropod species, which are critical factors affecting the efficacy of plant protection strategies. To advance knowledge on this topic, we studied three aspects of *T. parvispinus* physiology and behaviour: its developmental time, potential food sources and predatory behaviour.

In thrips species, the developmental time between each life stage can vary depending on several factors such as temperature, RH, diet, host plant or viruses (Teulon and Penman 1991; DeAngelis et al. 1993; Kumm and Moritz 2010; Park and Lee 2020). With temperature being one of the most physiologically dominant environmental factors and influencing every life history parameters in insects (Ullah and

Lim 2015), we chose to focus on the effect of temperature on *T. parvispinus* developmental time. A previous study on chili pepper leaves investigated the developmental time of *T. parvispinus* at an average temperature of 27 °C and 87% RH (Hutasoit et al. 2017). However, in field conditions, insects face temperature fluctuations which have a significant impact on their developmental time in comparison with constant temperatures (Manosathiyadevan et al. 2017). For *F. occidentalis*, the total developmental time from egg to adult was longer at fluctuating temperatures (23.8–31.5 °C) than at the corresponding constant temperature (27.3 °C): 10.4 and nine days, respectively (Ullah and Lim 2015). Moreover, studying developmental time of herbivorous insects at fluctuating temperatures gives growers a more realistic time frame for pesticide applications and allows them to better follow up on IRAC (Insecticide Resistance Action Committee) recommendations. In this study, we simulated realistic conditions (higher temperatures during the day and lower temperatures at night) and evaluated the developmental time of *T. parvispinus* under three different fluctuating temperature regimes on *Anthurium andreanum* leaves and flowers. *Thrips parvispinus* is a serious pest in *A. andreanum* greenhouses in the Netherlands, making it a relevant host plant to study the developmental time of this species.

The development of thrips populations in agroecosystems also depends on their feeding behaviour and interactions with other arthropod species present in the crop. Biological control of thrips has long been based on the use of generalist phytoseiid predatory mites such as *Amblyseius swirskii* Athias-Henriot or *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) (van Houten et al. 1995; van Lenteren and Loomans 1999; Delisle et al. 2015). Besides their arthropod prey, generalist predatory mites can also develop and reproduce by feeding on non-prey food sources such as pollen (McMurtry and Croft 1997). Supplementary food sources like pollen or cysts of the brine shrimp *Artemia franciscana* Kellogg (Branchiopoda: Artemiidae) are therefore frequently used by growers to support the establishment of predatory mite populations in their crop before the pests are present or in case of prey scarcity (Messelink et al. 2014; Delisle et al. 2015; Pijnakker et al. 2020). However, several thrips species in the genera *Thrips* and *Frankliniella* are omnivorous and able to feed

on pollen and arthropod eggs additionally to their host plants, giving them the flexibility to adjust to variable resource supplies and regulate their nutrient intake to maximize their fitness (Trichilo and Leigh 1986; Wilson et al. 1996; Milne and Walter 1998; Murai 2000, 2001; Zhi et al. 2006; van Maanen et al. 2012; Martini et al. 2015). Several studies have therefore looked at the impact of different supplementary food types on thrips populations and biological thrips control (Skirvin et al. 2007; Leman and Messelink 2015; Vangansbeke et al. 2016; Deere et al. 2024). It has been shown, for example, that different types of pollen significantly increase the oviposition rate of *F. occidentalis* females on different host plants (Hulshof et al. 2003; Steinbach et al. 2012). Despite these observations, the application of pollen in a crop still seems to result in a better control of *F. occidentalis* by predatory mites in the long term (van Rijn et al. 2002; Leman and Messelink 2015). However, this positive finding should be approached with caution, as the outcome could be different for other thrips species. To test this hypothesis, we investigated the effect of three different supplementary food sources used in biological control on the oviposition rate of *T. parvispinus* females.

Finally, there is evidence that certain omnivorous thrips species such as *F. occidentalis* and *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) can feed on predatory and phytophagous mite eggs (Trichilo and Leigh 1986; Milne and Walter 1998; Faraji et al. 2002; Vangansbeke et al. 2014). Additionally, their egg consumption rate is influenced by the host plant nutritional quality, which refers to the levels of nitrogen and carbon, the presence or absence of defensive compounds (secondary metabolites), and the toughness or palatability of the plant (Nguyen-Dang et al. 2016). Omnivorous thrips consume more mite eggs on low-quality host plants than on high-quality host plants (Agrawal et al. 1999; Eubanks and Denno 2000; Janssen et al. 2003; Magalhães et al. 2005). A recent study showed that *T. parvispinus* can feed on eggs of the predatory mite *A. swirskii* on sweet pepper leaves (Beretta et al. 2024). Sweet pepper is known to be a low-quality host plant for several arthropod species, as part of the Solanaceae family in which plants are often rich in alkaloids and have a deterrent effect on insects (Thomas 1993; Lei et al. 2001; Janssen et al. 2003; Magalhães et al. 2005; Hori et al. 2011; Maharijaya et al. 2012). Bean, on the

other hand, has been described as a more attractive host plant for feeding and oviposition of *F. occidentalis*, in comparison with sweet pepper (Nyasani et al. 2013). The effects of host plant quality and alternative food sources on *T. parvispinus* predatory behaviour are still unknown, making it difficult to evaluate the possible negative effects of this behaviour on bio-control strategies. To explore this question further, we looked at the predation rate of *T. parvispinus* on *A. swirskii* eggs on two host plants of different nutritional quality: kidney bean (*Phaseolus vulgaris*, high quality) and sweet pepper (*Capsicum annuum* L., low quality), in the presence and absence of pollen.

## Materials and methods

Thrips and mite rearing: *Thrips parvispinus* and *Amblyseius swirskii*

*Thrips parvispinus* individuals were collected from an *Anthurium andreaeanum* production greenhouse and reared on pesticide-free bean pods (*Phaseolus vulgaris*) in plastic pots (diameter 7.5 × height 9 cm) with thrips-proof mesh (150 µm) lids and a vermiculite layer at the bottom. *Amblyseius swirskii* individuals were obtained from Koppert (Berkel & Rodenrijs, the Netherlands) and reared in plastic cups (diameter 8.5 × height 6 cm) with a water agar layer at the bottom and a cucumber (*Cucumis sativus*) leaf disk on top (abaxial side up). The mites were transferred weekly to new cups with fresh cucumber leaf disks. The rearing cups were closed with lids with a fine mite-proof mesh (150 µm) to allow ventilation. *Typha angustifolia* pollen (Nutrimite™, Biobest) was added weekly as food source for both species, which were maintained in a climate chamber at 25 °C, 70% RH and a L:D 16:8 photoperiod.

Developmental time of *Thrips parvispinus* on *Anthurium andreaeanum* at different temperatures

We assessed the developmental time of *T. parvispinus* under three different temperature treatments on *A. andreaeanum* leaves and flowers. The temperature treatments tested were: average 17.6 °C (16 h at 19 °C/8 h at 15 °C), average 21.6 °C (16 h at 23 °C/8 h at 19 °C) and average 25.6 °C (16 h at 27 °C/8 h at 23 °C). Plastic cups (diameter 8.5 × height 6 cm) containing a

water agar layer at the bottom (to keep a high humidity inside the cups) covered with a filter paper disk (to allow thrips to walk on the agar without drowning) were prepared. One young *Anthurium andreaeanum* (Elido cultivar) leaf and flower were placed together in each cup. The stem of each leaf and flower was placed in an Eppendorf tube (1.5 ml) filled with agar to prevent the flowers and leaves from drying out. On the first day of the experiment, five adult thrips females were placed in each cup for 24 h to lay eggs. During these 24 h the cups were stored in a climate chamber at the desired temperature treatment, 70% RH and a L:D 16:8 photoperiod. For the 17.6 °C treatment, the cups were placed at 25 °C for the first 24 h to ensure that the females would lay eggs. After 24 h, all adult females were removed from the cups and the cups were stored at the temperature corresponding to their treatment. The cups were checked every 24 h until the first instar (L1) larvae emerged. For each temperature treatment, the L1 larvae that emerged on the same day were gently transferred with a thin brush together into a new cup (with a fresh *Anthurium* leaf and flower), with a maximum of 5 L1 larvae per cup. A total of 95, 61 and 176 L1 larvae were collected for the treatments 17.6 °C, 21.6 °C and 25.6 °C, respectively. The new cups containing the L1 larvae were checked again every 24 h until the first prepupae appeared. Since many prepupae were hidden in the agar and difficult to reach, they were not transferred into new cups. Fresh leaves and flowers were added weekly throughout the experiment to replace the old ones. After the first prepupae appeared, the cups were continuously checked every 24 h until all adults had emerged.

#### Predatory behaviour of *Thrips parvispinus* against *Amblyseius swirskii* eggs

We tested whether *T. parvispinus* adult females and second instar (L2) larvae prey on *A. swirskii* eggs and if this predatory behaviour is influenced by the host plant quality or the presence of an alternative food source like pollen. Plastic cups (diameter 4 × height 4 cm) containing a layer of water agar at the bottom and a leaf disk (sweet pepper or bean) on top (abaxial side up) were prepared. In each cup, we placed three *A. swirskii* eggs (0–24 h old) and one *T. parvispinus* adult female or L2 larva with a thin brush. To test the effect of pollen on the predatory behaviour of *T.*

*parvispinus*, we added approximately 5 mg of *Typha angustifolia* pollen (Nutrimite™, Biobest) to half of the cups. We made sure that the *A. swirskii* eggs were on one side of the cup, and the pollen on the other, so that the eggs would not come into contact with the pollen. Cups containing only *A. swirskii* eggs with and without pollen were used as a control treatment for both host plants. All the cups were closed with thrips- and mite-proof mesh lids (150 µm) and stored in a climate chamber at 25 °C, 70% RH and a L:D 16:8 photoperiod. The status (intact, hatched, dead) of the *A. swirskii* eggs in each cup was assessed after 48 h. Mite eggs that remained in the cups after 48 h were observed for two more days to confirm their status (hatched or dead) by checking for the emergence of mite larvae. Each combination of thrips life stage, host plant and pollen treatment was tested with 14–18 replicates.

#### Effect of different supplementary food treatments on the oviposition rate of *Thrips parvispinus*

We assessed the effect of different supplementary food treatments, commonly used to support predatory mite populations, on the oviposition rate of *T. parvispinus* females: *Typha angustifolia* pollen (Nutrimite™, Biobest), *Artemia franciscana* cysts (Bioartfeed, BioBee) and *Thyreophagus entomophagus* (Mitefood II, Bionline). A treatment with the host plant only (without supplemental food) was added as a control. Plastic cups (diameter 4 × height 4 cm) containing a layer of water agar at the bottom with a kidney bean leaf disk on top (abaxial side up) were prepared. The food treatments pollen and Artemia were added to the cups on sticky notes (3 M, 1.3 × 1.3 cm). Each sticky note was fully covered with either pollen or Artemia, which corresponded to approximately 20 mg of pollen and 90 mg of Artemia per cup. The *T. entomophagus* food treatment was added in the cups by filling the lid of a 0.5 ml Eppendorf tube with approximately 12 mg of Mitefood II material (with bran), which corresponded to approximately 500 *T. entomophagus* mites (a mix of all life stages) per cup. The control treatment contained no supplementary food. One three-week-old *T. parvispinus* adult female was added to each cup. The cups were closed with thrips-proof mesh lids and stored for three days in a climate chamber at 25 °C, 70% RH and a L:D 16:8 photoperiod. After the first three days (oviposition

days [0–3]), all *T. parvispinus* females were transferred into new cups with the same food treatment and stored in the climate chamber for another three days (oviposition days [3–6]). The cups from which the females were removed were returned to the climate chamber for five more days to allow the eggs to hatch. After three days in the new cups, the females were removed and the empty cups were placed in the climate chamber again for five more days to allow the eggs to hatch. The number of larvae was then counted in all cups to assess the oviposition rates from days [0–3] and days [3–6]. Each food treatment was tested with 15 replicates.

### Statistical analysis

The statistical analyses and graphics were made in R, version 4.0.2 (R Core Team 2020).

#### *Developmental time of Thrips parvispinus on Anthurium andreanum at different temperatures*

We first calculated the mean developmental time of the different life stages (egg to L1, L1 to prepupa, prepupa to adult) for each replicate (plastic cup) of each temperature treatment. We then calculated the weighted mean developmental time, weighted SD and SE for each life stage per temperature treatment by taking into account the number of thrips individuals in each replicate. Regarding the SD, we took into account the uncertainty in the measurements caused by the fact that the adult females laid eggs in the cups for the first 24 h and that we only checked the cups at 24 h intervals (law of uncertainty propagation). For this, we used the following correction factor (JCGM 100:2008, 2008):

Corrected weighted SD:

$$SD_{corrected} = \sqrt{SD^2 + \left(\frac{48}{2\sqrt{3}}\right)^2}$$

Finally, to obtain the average developmental time from egg to adult for each temperature, we summed the weighted average developmental times of the different life stages. We then calculated the pooled SD and SE of the egg-to-adult average developmental time for each temperature.

#### *Predatory behaviour of Thrips parvispinus against Amblyseius swirskii eggs*

We looked at the effect of the factors “Host plant” (bean, sweet pepper), “Life stage” (*T. parvispinus* adult, *T. parvispinus* larva), “Food” (pollen, no pollen) and their interaction on the mortality rate of *A. swirskii* eggs. We used a Generalized Linear Model (GLM) with Binomial error distributions and a logit link function. The response variable was expressed as a proportion (number of eggs dead after 48 h/number of eggs tested) for each replicate. The categorical variables Host plant, Life stage and Food were expressed as fixed effects in the model. Since one of the variable levels (control) had only “0” values, there was a quasi-complete separation issue in our data which caused convergence failures in our model. To solve this issue, we used the Firth method (Firth 1993) and the brglm2 package. We used the model-fitting method of the maximum likelihood (Laplace approximation) and used likelihood ratio tests to select the most parsimonious model. We then carried out pairwise comparisons of estimated marginal means (emmeans package, Tukey test) to assess differences within Host plant, Life stage and Food levels.

#### *Effect of different supplementary food treatments on the oviposition rate of Thrips parvispinus*

We looked at the effect of the factors “Food treatment” (Artemia, Control, Pollen, Prey mite) and “Time period” (0–3 days, 3–6 days) as well as the interaction between these two factors on the number of *T. parvispinus* larvae produced by each female. We used a GLM with Negative Binomial distributions and a log link function. The response variable was expressed as the number of *T. parvispinus* larvae counted for each replicate. The categorical variable Food treatment and the continuous variable Time period were expressed as fixed effects in the model. After selecting the most parsimonious model, we carried out multiple comparisons of means (multcomp package, Tukey test) to assess differences between Food treatments.

## Results

### Developmental time of *Thrips parvispinus* on *Anthurium andreaeanum* at different temperatures

The developmental time of *T. parvispinus* was directly influenced by the average temperature: the higher the temperature the shorter the developmental time (Fig. 1 and Supplementary Table S1). The average developmental time from egg to adult was  $14.4 \pm 0.63$  days at  $25.6^\circ\text{C}$ ,  $18.51 \pm 0.82$  days at  $21.6^\circ\text{C}$  and  $28.58 \pm 0.86$  days at  $17.6^\circ\text{C}$ .

### Predatory behaviour of *Thrips parvispinus* against *Amblyseius swirskii* eggs

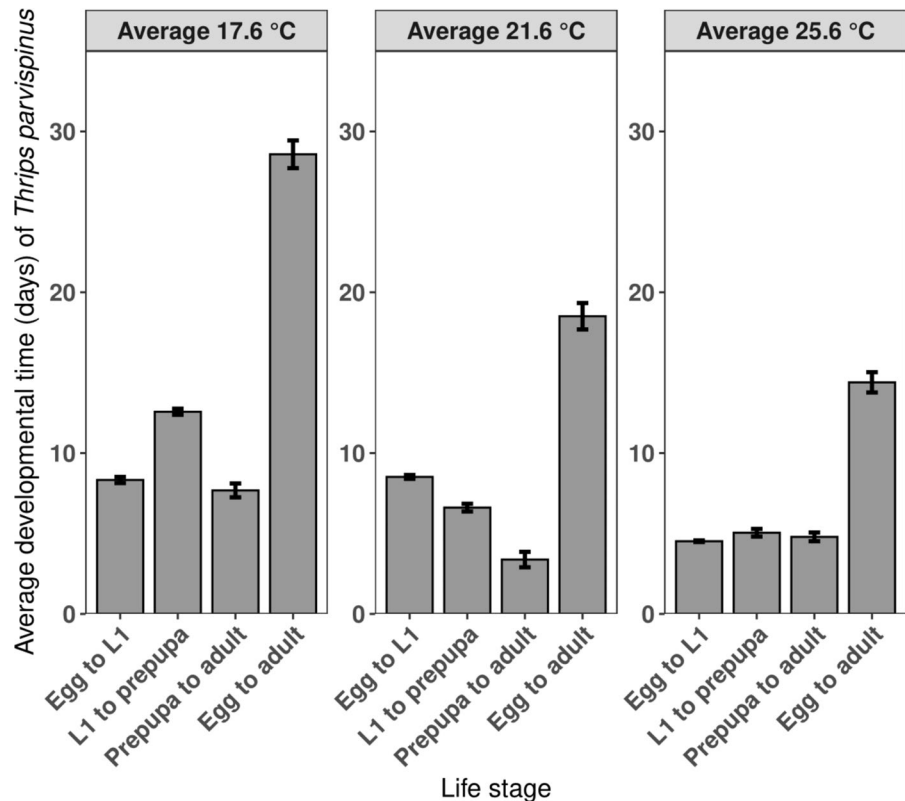
The presence of *T. parvispinus* had a statistically significant effect on the mortality of *A. swirskii* eggs: significantly more *A. swirskii* eggs died in the presence of *T. parvispinus* adult females and L2 larvae than in the controls without thrips ( $\chi^2 = 104.3$ ;  $df = 2$ ;  $P < 0.0001$ ; Fig. 2). There was also a statistically significant interaction between the factors host plant

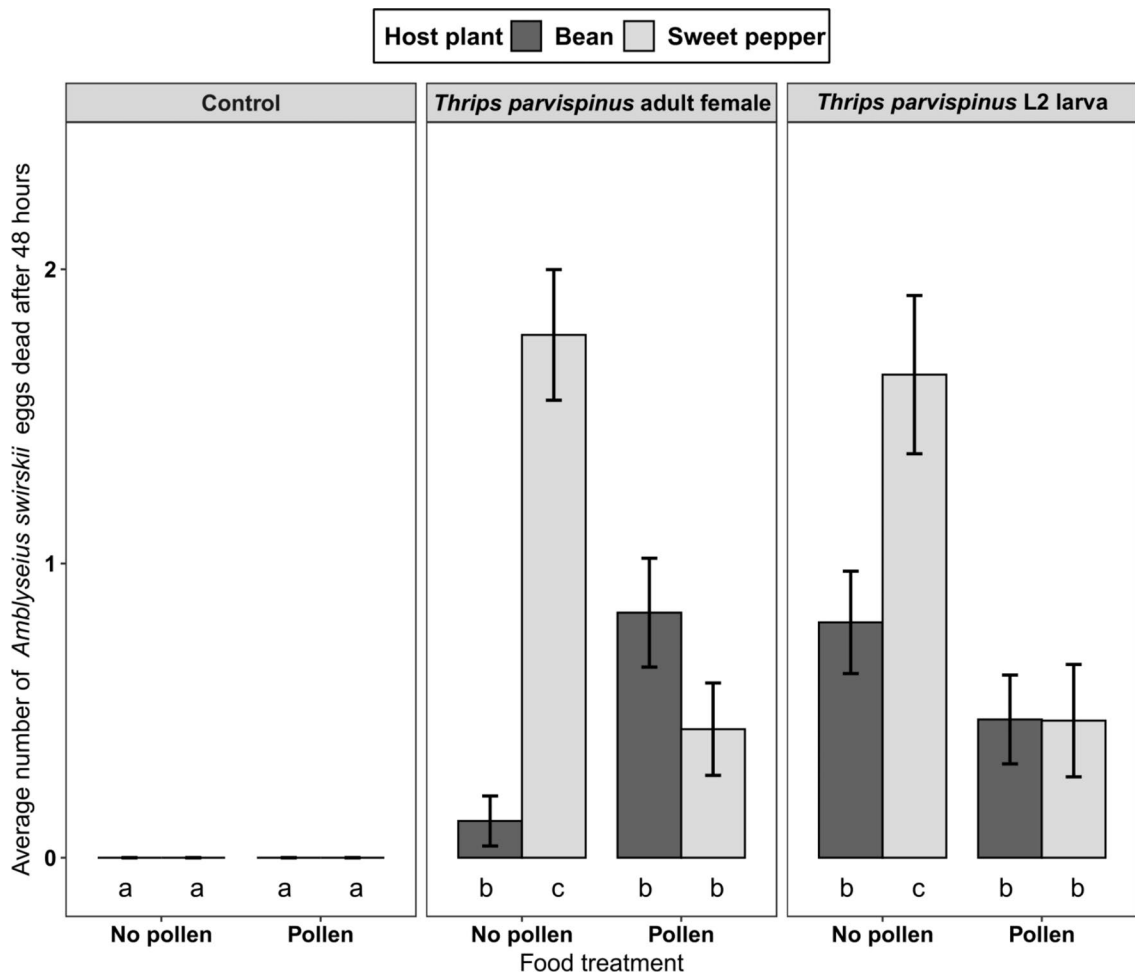
and food ( $\chi^2 = 26.3$ ;  $df = 1$ ;  $P < 0.0001$ ). On sweet pepper leaves, the mortality of *A. swirskii* eggs was significantly higher without pollen than with pollen, for both *T. parvispinus* adult females and L2 larvae ( $P < 0.0001$ ). However, on bean leaves, there was no significant difference in the mortality of *A. swirskii* eggs with or without pollen for both *T. parvispinus* adult females and L2 larvae ( $P = 0.2$ ). On sweet pepper without pollen, *T. parvispinus* adult females and L2 larvae killed an average of  $1.7 \pm 0.2$  and  $1.6 \pm 0.3$  *A. swirskii* eggs in 48 h, respectively. On sweet pepper with pollen,  $0.43 \pm 0.1$  and  $0.46 \pm 0.2$  *A. swirskii* eggs were killed by *T. parvispinus* adult females and L2 larvae, respectively.

### Effect of different supplementary food treatments on the oviposition rate of *Thrips parvispinus*

The factor Food treatment had a statistically significant effect on the oviposition rate of *T. parvispinus* females ( $\chi^2 = 21.1$ ;  $df = 3$ ;  $P < 0.0001$ ; Fig. 3). The Time period factor did not have any significant effect on the oviposition rate ( $\chi^2 = 0.001$ ;  $df = 1$ ;

**Fig. 1** Average developmental time (days)  $\pm$  SE of different life stages of *Thrips parvispinus* at three different temperatures: Average  $17.6^\circ\text{C}$  (16 h at  $19^\circ\text{C}$ /8 h at  $15^\circ\text{C}$ ), Average  $21.6^\circ\text{C}$  (16 h at  $23^\circ\text{C}$ /8 h at  $19^\circ\text{C}$ ), Average  $25.6^\circ\text{C}$  (16 h at  $27^\circ\text{C}$ /8 h at  $23^\circ\text{C}$ )





**Fig. 2** Average number  $\pm$  SE of *Amblyseius swirskii* eggs dead after 48 h for a combination of three treatments: “Life stage” (control without thrips, *Thrips parvispinus* adult female or *T. parvispinus* L2 larva), “Host plant” (bean or sweet pepper

leaf disk) and “Food” (with or without *Typha angustifolia* pollen). Different letters report statistically significant differences between each level of all three treatments ( $P < 0.05$ )

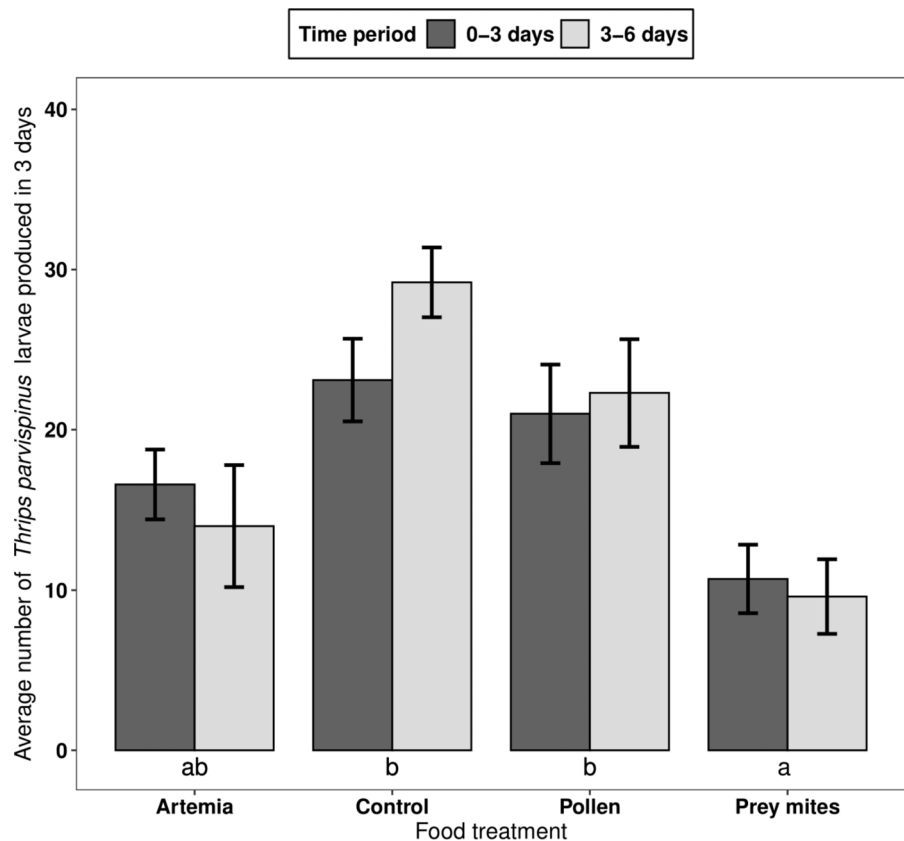
$P = 0.97$ ) and there was no significant interaction between Food Treatment and Time period ( $\chi^2 = 0.9$ ;  $df = 3$ ;  $P = 0.8$ ). For both time periods (0–3 days and 3–6 days), *Thrips parvispinus* females laid significantly more eggs in the food treatments Pollen and Control ( $22.3 \pm 3.3$  and  $29.2 \pm 2.2$  eggs for time period 3–6 days) than in the Prey mites treatment ( $9.6 \pm 2.3$  eggs for time period 3–6 days;  $P = 0.001$  and  $P < 0.0001$  respectively). There was no significant difference in oviposition rates between the Control, Pollen and Artemia treatments ( $P > 0.09$ ), nor between the treatments Artemia and Prey mites ( $P = 0.2$ ).

## Discussion

The aim of this study was to better understand the interactions between the invasive pest *T. parvispinus* and its environment in agroecosystems, and how this can affect biological control strategies. We studied the developmental time of this species under three fluctuating temperature regimes, its predatory behaviour on *A. swirskii* eggs and its oviposition rate when fed with different supplementary food sources.

Our results showed that *T. parvispinus* adult females and L2 larvae can both eat at least three *A. swirskii* eggs in 48 h and that their predatory

**Fig. 3** Average number  $\pm$  SE of larvae produced by *Thrips parvispinus* females in three days for two time periods (0–3 days, 3–6 days) and four food treatments (*Artemia franciscana* cysts on bean leaf, Control bean leaf only, *Typha angustifolia* pollen on bean leaf, *Thyreophagus entomophagus* prey mites on bean leaf). Different letters report statistically significant differences between food treatments ( $P < 0.05$ )



behaviour is significantly influenced by the nutritional quality of the host plant and the presence of pollen. In the absence of pollen, *T. parvispinus* ate significantly more *A. swirskii* eggs on sweet pepper than on bean leaves: adult females and L2 larvae ate an average of 1.7 and 1.6 *A. swirskii* eggs on sweet pepper leaf disks, respectively, and only 0.1 and 0.8 eggs on bean leaves. The predation rate we observed on sweet pepper corresponds to what has been observed in a recent study, where *T. parvispinus* adults and larvae ate an average of one to two *A. swirskii* eggs per day on sweet pepper leaf disks (Beretta et al. 2024). We expected this difference in predation rate between the two host plants, because sweet pepper is a lower quality host plant than bean and previous studies with the omnivorous thrips *F. occidentalis* showed that more prey is consumed on low-quality host plants than on high-quality host plants (Trichilo and Leigh 1986; Milne and Walter 1998; Agrawal et al. 1999; Eubanks and Denno 2000; Faraji et al. 2002; Janssen et al. 2003; Magalhães et al. 2005; Vangansbeke et al. 2014). *Thrips parvispinus* might consume less

plant material on sweet pepper leaves than on bean leaves and compensate this lower plant intake by feeding on available alternative food sources such as mite eggs. The difference we observed in predation rates between the two host plants could also be due to the diet previously experienced by the thrips. The *T. parvispinus* individuals used in our study were reared on bean pods before the start of the experiment, potentially making them better adapted to bean leaves than to sweet pepper leaves. Hopkins' host selection principle states that insects should prefer foliage from their rearing host plant over that of an alternative host (Hopkins 1916). However, there is no real consensus on the veracity of this theory (Barron 2001; Mader et al. 2012) and this higher thrips predation rate on sweet pepper leaves has also been observed in studies where the thrips individuals were exposed to a sweet pepper diet before the start of the experiment (Janssen et al. 2003; Magalhães et al. 2005). It is therefore not completely clear whether *T. parvispinus* adult females or larvae would have behaved differently if they had been reared on sweet pepper instead of bean pods, but



we can reasonably assume that this factor alone is not enough to explain the higher predation rate on sweet pepper than on bean.

Interestingly, there was no significant difference between the predation rates of *T. parvispinus* on *A. swirskii* eggs on sweet pepper and bean leaves when pollen was available. *Thrips parvispinus* adult females and L2 larvae ate between 0.43 and 0.83 *A. swirskii* eggs on both host plants when pollen was available, similar to their predation rate on bean leaves without pollen. The presence of pollen therefore significantly affected the predatory behaviour of *T. parvispinus* on sweet pepper leaves only. Similar results have been observed with other thrips species and seem to indicate that omnivorous thrips prefer to eat pollen rather than mite eggs when given a choice between the two food sources. For example, it has been shown that *F. occidentalis* larvae kill the same number of *Iphiseius degenerans* (Berlese) (Acari: Phytoseiidae) eggs on sweet pepper and cucumber. However, when Typha pollen was added next to the *I. degenerans* eggs, the predation rate of *F. occidentalis* larvae on both host plants decreased significantly: from 2.5 to 3 eggs per day without pollen to less than 0.5 eggs per day with pollen (Janssen et al. 2003). These results suggest that pollen is a higher quality food source for thrips than phytoseiid mite eggs. In particular, pollen has a significant effect on developmental time in certain thrips species: *F. occidentalis* larvae develop faster when they feed on leaf tissue and pollen than when they feed on leaf tissue only (Hulshof et al. 2003; Zhi et al. 2005). Besides the regulation of their nutritional intake, omnivorous thrips can also decide to switch their diet from plants to arthropods to reduce competition from other herbivores (van Maanen et al. 2012) or to reduce the risk of predation by predators (Janssen et al. 2002). Previous studies showed that thrips larvae can pierce the eggs of their phytoseiid predators as a mechanism to reduce the future risk of predation (Janssen et al. 2002; Walzer and Schausberger 2009). *Frankliniella occidentalis* larvae, for example, can discriminate between eggs of harmless predatory mite species and eggs of a dangerous predatory mite species and will kill more eggs of the latter. In addition, adult predatory mites avoid ovipositing near killed eggs and thrips larvae living near killed predatory mite eggs experience an almost fourfold reduction of predation (Janssen et al. 2002). In our study, *A. swirskii*

is a predator of *T. parvispinus* larvae. Interestingly, however, phytoseiid predatory mites such as *A. swirskii* have a strong preference for L1 thrips larvae. L2 larvae, which are bigger and stronger, are more difficult to kill (Bakker and Sabelis 1989; Wimmer et al. 2008; Jandricic et al. 2016). Could *T. parvispinus* adult females and L2 larvae be actively involved in the protection of L1 larvae by killing predatory mite eggs? So far, maternal care in thrips has only been observed in very few species (Crespi 1990; Gilbert 2014). In the absence of parental care, siblings sometimes evolve to cooperate (Rebar et al. 2020). Since *T. parvispinus* adult females and L2 larvae killed significantly less *A. swirskii* eggs on bean than on sweet pepper leaves and in the presence of pollen, their priority seems to lie in the optimization of their nutritional intake rather than in the protection of their offspring or their younger siblings from predatory mites.

Our results also showed that alternative food sources (other than plant tissue) had no positive effect on the oviposition rate of *T. parvispinus* females on bean leaves. We tested the effects of three different food sources (Typha pollen, Artemia cysts and prey mites) on the oviposition rate of *T. parvispinus* females over six days. The oviposition rate was significantly lower when prey mites were added to the bean leaf, compared to a bean leaf alone. The leaf damage generated by the alive prey mites in the cups probably decreased the leaf quality for the thrips, explaining why the oviposition rate was lower in this treatment. What is surprising, however, is that the presence of pollen on the bean leaf did not result in an increase in the oviposition rate of *T. parvispinus* females. Many studies have shown that different types of pollen significantly increase the oviposition rate of *F. occidentalis* females on different host plants (Trichilo and Leigh 1986; Hulshof et al. 2003; Steinbach et al. 2012; Leman and Messelink 2015; Vangansbeke et al. 2016). In our study, we used bean leaf disks which we described earlier as a high-quality host plant on which *T. parvispinus* females ate few predatory mite eggs. Similar to our predation experiment, *T. parvispinus* females might have been “satisfied” with the quality of the bean leaf disk and may not have needed to eat pollen to compensate for a poor-quality host plant. However, this hypothesis is contradicted by the results of two studies showing that the oviposition rate of *F. occidentalis* females was significantly higher on bean and cucumber leaves when pollen

was available (Hulshof et al. 2003; Vangansbeke et al. 2016). Bean and cucumber are also considered high quality host plants for *F. occidentalis*, which did not stop the females from consuming pollen. Alternatively, we could hypothesize that the effect of pollen on the oviposition rate of *T. parvispinus* females is visible only after a period longer than six days. However, in previous studies on *F. occidentalis* females, the positive effect of Typha pollen was already visible after 3–4 days (Leman and Messelink 2015; Vangansbeke et al. 2016). If there was a positive effect of pollen on the oviposition rate of *T. parvispinus* females, we can therefore reasonably assume that six days would be enough to see it. Another reason for these different results between *F. occidentalis* and *T. parvispinus* could be that *F. occidentalis* is better adapted to eating pollen than *T. parvispinus*. Even though they are part of the same family (Thripidae), *F. occidentalis* and *T. parvispinus* do not share the same genus. However, closely related thrips species from the *Thrips* genus such as *T. tabaci* and *T. hawaiiensis* also have a higher egg production when they feed on pollen (Murai 2000, 2001). It is therefore still difficult to explain why the oviposition rate of *T. parvispinus* females did not increase when Typha pollen was available. We might have to test different pollen types and different host plants to see an effect of pollen on *T. parvispinus* females.

Finally, we showed that the developmental time of *Thrips parvispinus* is influenced by temperature, as with most arthropods: the higher the temperature, the shorter its developmental time (up to a certain thermal limit). On Anthurium leaves and flowers, *T. parvispinus* eggs become adults in  $14.4 \pm 0.63$  days,  $18.5 \pm 0.82$  days and  $28.5 \pm 0.86$  days at an average temperature of 25.6 °C, 21.6 °C and 17.6 °C, respectively. These results are coherent with the results of a previous study on chili leaves at 27 °C, where *T. parvispinus* eggs became adults in 12.57 days for the females and 12.97 days for the males (Hutasoit et al. 2017). The developmental time of *Thrips parvispinus* is comparable to that of two other well-known pest thrips species: *F. occidentalis* and *T. tabaci*. Eggs have been shown to develop into adults in 15.9 and 13.9 days at a constant temperature of 25 °C for *F. occidentalis* and *T. tabaci* respectively (Murai 2000; McDonald et al. 2013). *Thrips parvispinus*, *F. occidentalis* and *T. tabaci* are part of the largely phytophagous

family Thripidae, in which generation times of 12 to 15 days are not uncommon. A few taxa of insects can complete a whole life cycle in 15 days or less under favourable conditions: among them are thrips, aphids and parasitic wasp species (Danks 2006). This rapid developmental time is one of the reasons why phytophagous thrips like *T. parvispinus* are difficult to control, especially at high temperatures. In this study, we carried out our experiment on Anthurium leaves. However, it is important to keep in mind that our results might have been different on other host plants, since thrips developmental time is also influenced by the host plant they feed on (Zhang et al. 2007).

In conclusion, our study showed that *T. parvispinus* L2 larvae and adult females can predate on phytoseiid mite eggs and that this predatory behaviour is significantly affected by the nutritional quality of the host plant and the presence of higher quality food sources like pollen. *Thrips parvispinus* adult females and L2 larvae eat fewer *A. swirskii* eggs on high-quality host plants and when pollen is available. Furthermore, the oviposition rate of *T. parvispinus* females on bean leaf disks was not positively affected by Typha pollen, Artemia cysts or prey mites. These results are rather positive for current biological control strategies against thrips: *T. parvispinus* is unlikely to have a negative effect on phytoseiid mite populations on high-quality host plants and might only have a limited effect on low-quality host plants. Moreover, the presence of a supplementary food source like pollen, frequently used by growers to support phytoseiid mite populations in the crop, helps mitigate *T. parvispinus* predatory behaviour without increasing the fecundity of *T. parvispinus* adult females in the short term.

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**Data availability** The data of this study is available from the corresponding author upon reasonable request.

## Declarations

**Competing interests** The authors have no competing interests to declare that are relevant to the content of this article.

**Research involving human participants and/or animals** This study does not contain any results involving human participants or vertebrate animals.

**Informed consent** All authors reviewed and approved the final version of this manuscript and consent for its publication.

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