Contents lists available at ScienceDirect

Biological Control

Predator-prey interactions and life history of *Orius laevigatus* and *O. majusculus* feeding on flower and leaf-inhabiting thrips

A. Mouratidis [a,b,*], A.P. de Lima [a,c], M. Dicke [b], G.J. Messelink [a,b]

[a] *Wageningen University & Research, BU Greenhouse Horticulture, Bleiswijk, the Netherlands*
[b] *Wageningen University & Research, Laboratory of Entomology, Wageningen, the Netherlands*
[c] *Departamento de Biologia Animal, Centro de Estudos do Ambiente e do Mar (CESAM), Faculdade de Ciências da Universidade de Lisboa (FCUL), Lisbon, Portugal*

HIGHLIGHTS

- The sedentary leaf-inhabiting thrips *Echinothrips americanus* and *Thrips setosus* were easier to capture by *Orius* than the agile flower thrips *Frankliniella occidentalis*.
- *Orius laevigatus* was more successful in capturing the tested thrips species than *O. majusculus*.
- Both tested *Orius* species killed more sedentary leaf-inhabiting thrips than agile flower thrips in 24 h.
- Highest growth rates were found when the *Orius* predators fed on sedentary leaf-inhabiting thrips.

GRAPHICAL ABSTRACT
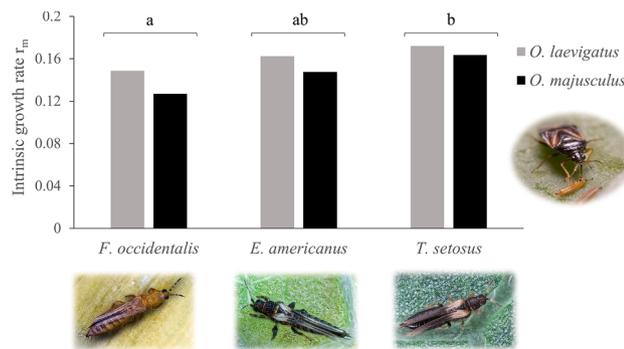
ABSTRACT

Thrips (Thysanoptera: Thripidae) are major pests in horticulture worldwide. Longstanding biological control strategies that have been developed for flower thrips such as *Frankliniella occidentalis* (Pergande) are being disrupted by the recent introduction of leaf-inhabiting thrips such as *Echinothrips americanus* Morgan and *Thrips setosus* Moulton in Northern Europe. In this study, we evaluated the predator–prey interactions, predation capacity, juvenile development and adult reproduction of the two commercial anthocorid predators *Orius laevigatus* (Fieber) and *Orius majusculus* (Reuter) (Hemiptera: Anthocoridae) on these thrips. In behavioral assays, predators were more successful in subduing and consuming sedentary leaf-inhabiting thrips adults compared to the highly mobile *F. occidentalis*. Furthermore, *O. laevigatus* was more successful in subduing prey compared to the bigger predator *O. majusculus*. Female adults of *O. laevigatus* and *O. majusculus* killed 18 and 20 *F. occidentalis* adults, respectively, in 24 h, while the kill rate was around two times higher when predators were offered *E. americanus* or *T. setosus* as prey. Developmental and reproductive parameters of both *Orius* predators were more favorable when feeding on the leaf-inhabiting thrips compared to *F. occidentalis*. This was further evident in the higher intrinsic rates of increase (r_m) we recorded on a diet of *E. americanus* compared to *F. occidentalis* (0.162 and 0.148 females/female/day for *O. laevigatus*, respectively; 0.148 and 0.127 for *O. majusculus*, respectively). Our findings

* Corresponding author at: Wageningen University & Research, BU Greenhouse Horticulture, Violierenweg 1, 2665 MV Bleiswijk, the Netherlands.
  E-mail address: angelos.mouratidis@wur.nl (A. Mouratidis).

show that *E. americanus* and *T. setosus* constitute high quality prey for anthocorid predators, highlighting the potential of these predators for effective pest control.

1. Introduction

Thrips (Thysanoptera: Thripidae) are one of the most important pests in agriculture and horticulture worldwide (Lewis, 1997). Due to their small size, cryptic behavior, ability to reproduce rapidly (in many cases through parthenogenesis) and polyphagy, many species have spread around the world through the trade of plant material, and have become key pests of various crops (Morse and Hoddle, 2005). Most thrips feed on plant and flower tissue, causing characteristic "silvering" damage, while they are also transmitting catastrophic pathogenic plant viruses (Riley et al., 2011). The western flower thrips *Frankliniella occidentalis* (Pergande) quickly became one of the world's most important and widespread invasive pests in the end of the 20th century (Kirk and Terry, 2003; Reitz, 2009), and still represents a major pest for horticulture today, partly due to the rapid development of resistance to chemical insecticides (Bielza, 2008; Gao et al., 2012). Biological control of thrips has proven a more successful and sustainable approach, and several natural enemies have been developed into commercial products and are being used around the world in augmentative biological control programs (van Lenteren, 2012).

As several thrips are preadapted to invasiveness due to their lifestyle, exotic species are continuously being intercepted in major hubs of horticultural trade (Morse and Hoddle, 2005). In the Netherlands, the poinsettia thrips *Echinothrips americanus* Morgan has established since 1993 and has been disrupting biological control practices of growers, especially in ornamental and sweet pepper crops (Ghasemzadeh et al., 2017; Vierbergen, 1998). Unlike *F. occidentalis* that preferably resides in narrow spaces in buds and flowering parts, the leaf-dwelling *E. americanus* is present on older leaves of the plant canopy, thus can be easily controlled using chemical insecticides (Shipp et al., 2001; Vierbergen, 1998). However, these practices inevitably cause negative effects on the already established biological control agents of other pests (Hoogerbrugge et al., 2014). Generalist predatory mites that are widely used in horticulture for the control of several pests including *F. occidentalis*, have not proven to be very effective against *E. americanus* (Ghasemzadeh et al., 2017; Hoogerbrugge et al., 2014; Pijnakker et al., 2017). Zoophytophagous predatory mirids (Hemiptera: Miridae) are more successful for the control of *E. americanus* (Ingegno et al., 2017; Leman et al., 2019), yet the plant damage they occasionally cause, limits their adoption in many crops, especially in floriculture (Castañé et al., 2011). Another invasive leaf-inhabiting thrips that is causing similar problems in Dutch horticulture is the Japanese flower thrips *Thrips setosus* Moulton. This species is native to Eastern Asia, and was first found in the Netherlands in a *Hydrangea* glasshouse in 2014 (Vierbergen and Loomans, 2016). Unlike its common name suggests, the Japanese flower thrips is not known to feed on pollen (Murai, 2001), and is commonly found feeding in the leaf canopy. *Thrips setosus* has a wide range of host plants including many ornamental and vegetable crops (Vierbergen and Loomans, 2016), while it is also an effective vector of the Tomato Spotted Wilt Virus (Tsuda, 1996), thus having the potential to become a major pest in horticulture.

Minute pirate bugs (Hemiptera: Anthocoridae) have proved successful predators of flower thrips (Disseelt et al., 1995; van der Meiracker and Ramakers, 1991). Several species of the genus *Orius* have been commercialized in recent years and met with great success (van Lenteren, 2012), while they may also spontaneously colonize field crops around the world (Funderburk et al., 2016; Nagai, 1990; Tommasini, 2004). The effectiveness of anthocorids lies in their ability to predate on both larval and adult stages of thrips, while they can also survive in crops on other plant-provided food sources, such as pollen when prey is scarce (Coll and Guershon, 2002). Due to their omnivorous feeding

habits, they induce plant defenses against important plant herbivores, further strengthening their role as biological control agents (Bouagga et al., 2018; De Puysseleyr et al., 2011). *Orius* are generalist predators, and while they are mainly used for the control of thrips, they are also predators of other key agricultural pests, such as whiteflies (Arnó et al., 2008), aphids (Harwood et al., 2007) and spider mites (Venzon et al., 2002). However, few studies have evaluated anthocorid predators for the biological control of the leaf-inhabiting thrips *E. americanus* (Opit et al., 1997; Pijnakker et al., 2017) and *T. setosus* (but see Nagai 1990; Pijnakker et al. 2019).

The goal of this study was to assess the behavioral interactions, predation capacity, juvenile development, reproduction, and growth rate of *Orius* predators on western flower thrips *F. occidentalis*, poinsettia thrips *E. americanus*, and Japanese flower thrips *T. setosus*. We focused on *Orius laevigatus* (Fieber) and *Orius majusculus* Reuter, as these predators are widely spread in Europe and commercially available (van Lenteren, 2012). With this study we aim to understand the effects of thrips species that differ in behavior on the fitness of generalist predators and provide insight on the potential control of leaf-inhabiting thrips by *Orius* predators.

2. Materials and methods

2.1. Insect cultures

Adults of *O. laevigatus* and *O. majusculus* were obtained in 2019 from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands) and EWH BioProduction (Tappernøje, Denmark), respectively. Predators were placed in plastic jars (Ø 11 cm × 13 cm) with lids covered with fine-mesh gauze (size 80 μm) for ventilation. In each jar, pesticide-free green bean pods (*Phaseolus vulgaris* L.) were placed as water source and oviposition substrate. Additionally, buckwheat hulls and a piece of tissue paper were added in the jars to provide hiding places for the predators and reduce cannibalism. Predators were fed *ad libitum* with a mixture of frozen *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs (Koppert Biological Systems) and *Artemia franciscana* Kellogg (Anostraca: Artemiidae) decapsulated cysts (BioBee Biological Systems, Sde Eliyahu, Israel). Food sources were offered on the adhesive surface of Post-it™ note strips (3 M, Kentucky, USA). Twice per week food sources were replenished, decaying bean pods were replaced and pods carrying predator eggs were placed into a new jar, starting a new rearing unit. Rearings were maintained in separate climatic cabinets (MLR – 350H®, Sanyo, Japan) at 25 ± 1 °C, 70 ± 10% RH and a photoperiod of 16:8 L:D.

Colonies of thrips were initiated from populations collected in greenhouses in the region of Bleiswijk (the Netherlands) and reared continuously on plants enclosed in insect rearing cages (75 × 75 × 115 cm, BugDorm-2400F, MegaView Science Co., Ltd., Taichung, Taiwan) in separate greenhouse compartments. Western flower thrips *F. occidentalis* were collected and continuously reared on flowering chrysanthemum plants (*Chrysanthemum indicum* Mount® Carmel, Syngenta Flowers North America, Gilroy, USA). *Echinothrips americanus* were collected from a gerbera greenhouse (*Gerbera jamesonii* L.) and reared on sweet pepper plants (*Capsicum annuum* L. Maranello F1; Enza Zaden Beheer, Enkhuizen, The Netherlands). Finally, *T. setosus* were collected from an hortensia greenhouse (*Hydrangea macrophylla* L.) and continuously reared on green bean plants (*Phaseolus vulgaris* L.). Plants were replenished in all thrips cultures twice per week, and all thrips were reared for at least 10 generations before being used in the experiments.

2.2. Experiments

All experiments were incubated in climatic cabinets at 25 ± 1 °C, $70 \pm 10\%$ RH and a photoperiod of 16:8 L:D. Two types of containers were used. Plastic medicine cups (Ø 2.5 × 4 cm, Vandeputte Medical Nederland, Nieuwegein, The Netherlands) were used for the nymphal development experiment of predators on different thrips species, and to deprive adult female predators of animal prey for the predation behavior and capacity trial. Plastic containers (Ø 8 × 5 cm, Paardekooper Verpakkingen, Oud-Beijerland, The Netherlands) were used to observe the predator behavior, evaluate the predation capacity, longevity and fecundity of *Orius* predators on the different thrips species. The aforementioned cups and containers were provided with a lid covered with fine mesh (80 × 80 μm) that ensured sufficient ventilation and no escape of insects. All predator–prey combinations involving the two predator species (*O. laevigatus* and *O. majusculus*) and the three thrips species (*F. occidentalis, E. americanus* and *T. setosus*) were investigated in no-choice experiments.

2.2.1. Predation behavior

Forty adult thrips of mixed-age and sex were released in the experimental arenas, consisting of a sweet pepper leaf disc (Ø 8 cm) with the adaxial side submerged in a layer of water agar (1% agar). Thrips were left to condition in the arena and start feeding for 1 h. Then, a single female predator was released. Predators were 1-week-old and deprived of animal prey individually in plastic cups for 24 h having only access to a 2 cm section of a bean pod. The behavior of the predator and its interactions with the thrips were observed under a stereomicroscope (Leica MZ95 Binocular Stereo Microscope) for 1 h. An encounter was noted as the predator's response to a thrips, by extending its rostrum and/or legs to capture it (Venzon et al., 2002). The encounter was successful when thrips was captured, and prey-feeding started. The time a predator spent feeding was recorded per prey captured. The successful encounter rate was calculated as the number of successful encounters divided by the total number of encounters. Predation rate (i.e. total number of thrips killed in 1 h) was also scored. All predator–prey combinations were replicated 6 times, except *O. laevigatus* with *E. americanus* and *T. setosus* that were replicated 5 times.

2.2.2. Predation capacity

We assessed the predation capacity of 1-week-old *Orius* predators deprived of animal prey 24 h prior. The same arenas as described in the predation behavior experiment were used. We offered 60 adult thrips to the predators to ensure ample prey availability throughout the duration of the experiment. Thrips were released in the experimental arenas 1 h before the female predator. Three control treatments without predators for each thrips species were included, to assess natural mortality. After 24 h, the predator was removed from the arena, and the number of dead thrips found was scored. All treatments were replicated 15 times.

2.2.3. Juvenile development

For all predator–prey combinations, 50–70 first nymphal instars of the predators (<24 h old) were randomly collected from the stock colonies and individualized in small containers (Ø 2.5 × 4 cm). In each container, a sweet pepper leaf disc (Ø 2.5 cm) was added on a 15 mm high moist gypsum layer. The leaf disc served as food for prey and a moisture source for the predators. Juvenile stages of the three thrips species were offered *ad libitum* to the *Orius* predators during their nymphal stage. Every other day, prey was replenished, leaf discs were replaced, and water was added to the gypsum layer. Development and survival of nymphs were recorded every other day for the first seven days, and subsequently daily. Newly emerged adults (<24 h old) were sexed and weighed using an analytical balance (Mettler Toledo AE100, Marshal Scientific, Hampton, USA).

2.2.4. Reproduction

Newly emerged adults (<24 h) from the developmental part of the study were paired, and each couple was transferred to a plastic container (Ø 8 cm × 5 cm). Adult predators were offered adult thrips *ad libitum* as a food source of the same species as in their juvenile stage. A piece of green bean pod cut between two seeds (*ca.* 6 cm) was fixed on the side of the container with an insect pin piercing the container from the outside and running through the core of the pod. This way, the bean pod remained in suspension inside the container, eliminating any possible hiding places for both prey and predators. Bean pods were replaced daily, and predator eggs were counted under a stereomicroscope. After the first egg was laid, bean pods were replaced every other day and prey was replenished until the predators died. Dead experimental individuals were replaced with similarly aged males or females from our stock culture, to ensure that every experimental individual was paired and under the same experimental conditions throughout its lifetime. When both experimental individuals were found dead, the replicate was terminated. Biological parameters of individuals introduced from the stock cultures were not scored. We followed this approach as *Orius* individuals exhibit higher longevity and female fecundity when kept without a pair, due to the mating costs involved in the traumatic insemination of *Orius* predators, and polygamous nature of *Orius* males (Arakawa et al., 2019; Leon-Beck and Coll, 2009). We monitored longevity, pre-oviposition period and fecundity. In addition, we evaluated predator egg hatch rate from at least five randomly selected experimental females that were 1-week-old. Bean pods bearing eggs that were <24 h old were placed in Petri dishes (Ø 8 cm × 1 cm). The status of the eggs was checked daily obtaining the developmental time and hatch rate of the eggs. Newly hatched nymphs were removed from the Petri dish to avoid cannibalism.

Intrinsic rates of increase (r_m) were calculated with the formula of Birch (1948): $\sum l_x m_x e^{-rmx} = 1$, where x equals the age class of the female in days, l_x is the age specific survival at age class x, and m_x is the number of female offspring produced per female at each age class interval x. Intrinsic rates of increase and their pseudo-values were calculated following the procedure described by Maia et al., (2014), using the jackknife procedure to obtain standard error estimates (Meyer et al., 1986).

2.3. Data analysis

Continuous and count data that fulfilled the normality and homoscedasticity assumptions were analyzed with an ANOVA. When these requirements were not met, count data were analyzed with a generalized linear model (GLM) with Poisson error distribution. Binary data were analyzed through GLM with binomial error distribution and probit link. To account for under- or overdispersion in the GLMs when necessary, we changed the error distributions to quasipoisson for count data and quasibinomial for binary data (McCullagh and Nelder, 1989). To account for pseudo-replication in the observation experiment where a single predator had multiple encounters within the studied timeframe, we included the experimental individual as random effect in a Generalized linear mixed model (GLMM) analysis. For the GLMM, negative binomial error distribution with linear parameterization was chosen as the best fitting, based on AICc criteria (Hardin and Hilbe, 2018). For all studied parameters, two-way factorial analyses were initially applied. When interaction between factors was not significant, we performed post hoc analysis using Tukey's HSD to separate means on significant main effects. When a significant interaction between factors was found, means were compared pairwise. Sex ratios were compared to an equal distribution (1:1) using Chi-square tests. All statistical analyses were performed using the statistical software R 4.0.2 (R Core Team, 2021). We used the 'multcomp' package to perform post hoc analyses (Hothorn et al., 2008), the 'glmmTMB' package to fit GLMM (Brooks et al., 2017), and the 'DHARMa' package to perform residual diagnostics for all models (Hartig, 2022).

3. Results

3.1. Predation behavior

Predation rate during 1 h was affected by thrips species ($\chi^2 = 5.251$, df = 2, $P = 0.005$), but not by predator species ($\chi^2 = 0.879$, df = 1, $P = 0.185$), while their interaction was also not significant ($\chi^2 = 0.221$, df = 2, $P = 0.811$). *Orius* predators killed fewer *F. occidentalis* than *T. setosus* and *E. americanus* in 1 h of observation (Fig. 1A).

Total number of encounters was similarly influenced by thrips species ($\chi^2 = 36.318$, df = 2, $P < 0.001$), whereas predator species ($\chi^2 = 4.588$, df = 1, $P = 0.17$) and their interaction ($\chi^2 = 6.729$, df = 2, $P = 0.238$) were not significant. *Orius majusculus* encountered on average twice as many *F. occidentalis* individuals in 1 h, in comparison with *E. americanus* and *T. setosus* (Fig. 1B).

Both predator and prey influenced the percentage of successful encounters ($\chi^2 = 8.513$, df = 1, $P = 0.048$ and $\chi^2 = 50.881$, df = 2, $P < 0.001$, respectively) whereas the interaction was not significant ($\chi^2 = 5.924$, df = 2, $P = 0.275$). Overall, *O. laevigatus* was more successful in subduing and killing prey than *O. majusculus*, while *F. occidentalis* was the more difficult to successfully subdue and kill for both predators (Fig. 1C).

Prey handling time was influenced by thrips species ($\chi^2 = 6.791$, df = 2, $P = 0.033$), but not by predator species ($\chi^2 = 0.008$, df = 1, $P = 0.928$) and neither from their interaction ($\chi^2 = 0.137$, df = 2, $P = 0.933$). *Orius* predators exhibited a significantly longer handling time when preying upon *F. occidentalis* compared to the other thrips species (Fig. 1D).

3.2. Predation capacity

The number of thrips killed in 24 h by the predators is shown in Fig. 2. Natural thrips mortality was insignificant (never exceeded 5%, data not shown) and therefore not included in the analysis. No signification interaction effect was found between thrips and predator ($F = 2.793$, df = 2, $P = 0.067$). *Orius majusculus* was overall more voracious
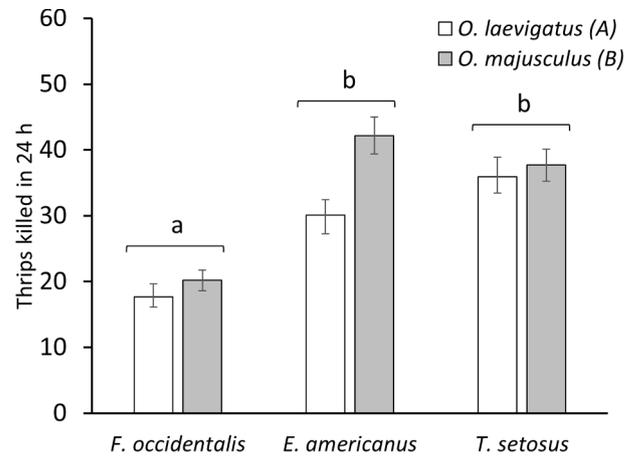

Fig. 2. Predation capacities (means ± SE) of adult females *O. laevigatus* and *O. majusculus* on adult thrips, expressed as the number of prey killed in 24 h. Bars with different lowercase letters within predator denote significant differences between prey species, different uppercase letters denote overall differences between predator species ($P < 0.05$): ANOVA followed by Tukey's HSD pairwise comparisons.
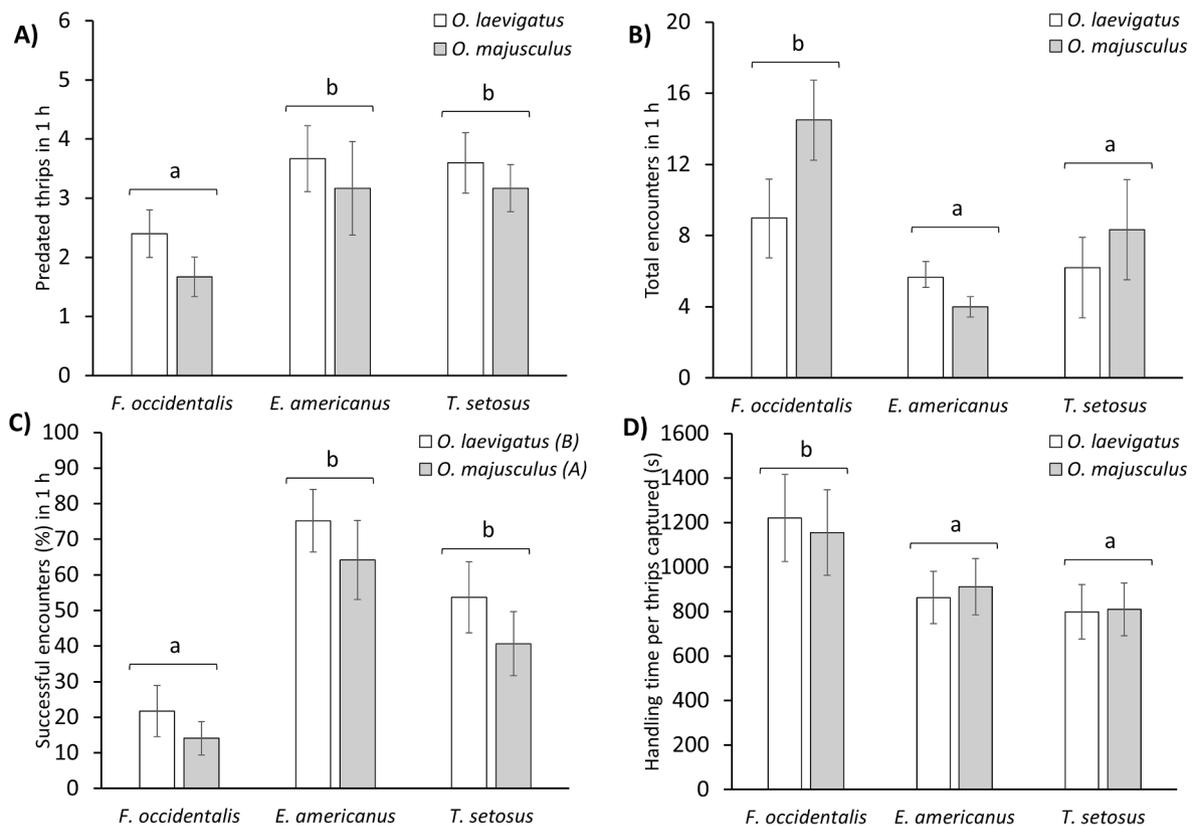

Fig. 1. (A) Predated thrips, (B) total number of encounters, (C) successful encounters (%), and (D) handling time (means ± SE) of adult females of *O. laevigatus* and *O. majusculus* on adult thrips during the 1 h observation experiments. Bars with different lowercase letters within predator denote significant differences between prey species, different uppercase letters note overall differences between predator species ($P < 0.05$): GLM quasipoisson (Predation rate and Number of encounters); GLM quasibinomial (Success ratio); GLMM negative binomial (Handling time). Tukey's HSD pairwise comparisons.

than *O. laevigatus* ($F = 7.443$, df $= 1$, $P = 0.008$). Thrips identity was also significant ($F = 33.849$, df $= 2$, $P < 0.001$), with both predators killing fewer *F. occidentalis* than *T. setosus* and *E. americanus*.

3.3. Juvenile development

Nymphal survival to adulthood was influenced by prey species ($\chi^2 = 13.731$, df $= 2$, $P = 0.001$), while predator species and their interaction did not cause a change in survival ($\chi^2 = 0.006$, df $= 1$, $P = 0.939$ and $\chi^2 = 2.199$, df $= 2$, $P = 0.333$, respectively) (Table 1). Feeding on *T. setosus* led to an overall higher survival rate for predators compared to *F. occidentalis*.

Egg hatching rate ranged from 87 to 97% (Table 1). Predator species ($\chi^2 = 0.345$, df $= 1$, $P = 0.557$), thrips species ($\chi^2 = 3.366$, df $= 2$, $P = 0.189$) and their interaction ($\chi^2 = 2.912$, df $= 2$, $P = 0.233$) did not affect the egg hatching rate. The egg stage lasted *ca.* 4.5–4.9 days, and its duration was not affected by predator ($\chi^2 = 0.007$, df $= 1$, $P = 0.935$), prey species ($\chi^2 = 1.723$, df $= 2$, $P = 0.423$), or their interaction ($\chi^2 = 0.026$, df $= 2$, $P = 0.987$).

Development times of males and females were pooled together as no significant effect of sex was found ($\chi^2 < 0.001$, df $= 1$, $P = 0.996$). Nymphal development lasted *ca.* 10.5 days, with no significant effects found for predator species ($\chi^2 = 0.014$, df $= 1$, $P = 0.907$), thrips species ($\chi^2 = 0.042$, df $= 2$, $P = 0.979$), and their interaction ($\chi^2 = 0.037$, df $= 2$, $P = 0.982$).

Sex ratios of both *Orius* species were female biased when presented with *E. americanus* as prey during their juvenile development ($\chi^2 = 5.769$, $P = 0.016$ for *O. laevigatus*; $\chi^2 = 4.568$, $P = 0.033$ for *O. majusculus*). In all other treatments, sex ratio did not differ significantly from a 1:1 sex ratio (Table 1).

Adult female weight was affected by predator species, thrips species and their interaction ($F = 275.045$, df $= 1$, $P < 0.001$; $F = 18.144$, df $= 2$, $P < 0.001$ and $F = 5.226$, df $= 2$, $P = 0.007$, respectively) (Table 1). Female predators reached the lowest weight on a nymphal diet consisting of *F. occidentalis* larvae. *Orius majusculus* females reached the highest weight on a diet of *E. americanus*, whereas *O. laevigatus* females gained the most weight on a diet of *T. setosus* and *E. americanus*.

Male adults of *O. majusculus* were heavier than males of *O. laevigatus* ($F = 77.694$, df $= 1$, $P < 0.001$). Thrips species significantly affected adult male weight ($F = 9.246$, df $= 2$, $P < 0.001$); the interaction of predator species and thrips species was not significant ($F = 0.151$, df $= 2$, $P = 0.860$). Feeding on *F. occidentalis* during juvenile development resulted in the lowest weight for predators, while no significant

differences were noted between *E. americanus* and *T. setosus* (Table 1).

3.4. Reproduction

Longevities of both female and male predators were different for the two species ($\chi^2 = 6.054$, df $= 1$, $P = 0.044$ for females; $\chi^2 = 51.561$, df $= 1$, $P < 0.001$ for males) and were affected by thrips species ($\chi^2 = 42.676$, df $= 2$, $P < 0.001$ for females; $\chi^2 = 26.98$, df $= 2$, $P < 0.001$ for males), but they were differentially affected by the predator–prey combinations ($\chi^2 = 18.055$, df $= 2$, $P = 0.002$ for females; $\chi^2 = 40.75$, df $= 2$, $P < 0.001$ for males). Both males and females *O. laevigatus* lived longer than *O. majusculus* when feeding on *E. americanus* and *F. occidentalis*; such an effect was not recorded when offering *T. setosus* as prey (Table 2).

Lifetime oviposition was affected by predator species ($\chi^2 = 492.6$, df $= 1$, $P < 0.001$) with *O. laevigatus* laying more eggs than *O. majusculus*, and by thrips species ($\chi^2 = 474.1$, df $= 2$, $P < 0.001$) with predators feeding on *E. americanus* resulting in a higher lifetime fecundity compared to *F. occidentalis*. The interaction between these factors was not significant ($\chi^2 = 143.55$, df $= 2$, $P = 0.052$). *O. majusculus* feeding on *F. occidentalis* registered the lowest lifetime fecundity (49.8 eggs), approximately half the number of eggs laid when feeding on *E. americanus* or *T. setosus*. Similarly, *O. laevigatus* recorded a higher lifetime fecundity when feeding on *E. americanus* (169 eggs), while feeding on *F. occidentalis* or *T. setosus* led to *ca.* 35% lower lifetime fecundity (Table 2). Pre-oviposition period of the *Orius* species lasted for 3–4 days, and it was not affected by predator species ($\chi^2 = 0.775$, df $= 1$, $P = 0.177$), thrips species ($\chi^2 = 0.016$, df $= 2$, $P = 0.982$), or their interaction ($\chi^2 = 1.327$, df $= 2$, $P = 0.209$).

Intrinsic rate of population increase was found higher for *O. laevigatus* compared to *O. majusculus* ($F = 20.769$, df $= 1$, $P < 0.001$). Furthermore, prey species significantly affected the intrinsic growth rate of both predators ($F = 51.579$, df $= 2$, $P < 0.001$), while the interaction between predator and prey was not significant ($F = 1.093$, df $= 2$, $P < 0.340$). Feeding on *T. setosus* led to the highest intrinsic rate of population increase values, followed by *E. americanus*, while feeding on *F. occidentalis* led to the lowest values (Table 2).

4. Discussion

Orius species are generalist predators feeding on a plethora of arthropod prey, yet the type of prey they consume has a great impact on their fitness and predation capacity (Aragón-Sánchez et al., 2018; Bonte et al., 2015; Toft et al., 2020). In this study, we showed for the first time

Table 1

Developmental parameters (means ± SE) of *O. laevigatus* and *O. majusculus* feeding on juvenile stages of different thrips species at 25 °C.

Predator	Prey species	Nymphal survival (%)	Developmental time (days)	Adult weight (mg)		Egg hatch rate (%)	Egg duration (days)	Sex ratio (male: female)
				Males	Females			
O. laevigatus	*F. occidentalis*	67.2 ± 6.0Aa (61)	10.85 ± 0.12Aa (41)	0.325 ± 0.019Aa (15)	0.386 ± 0.012a (26)	88 ± 3.75Aa (75)	4.55 ± 0.07Aa (66)	1:1.73
	E. americanus	88.9 ± 4.7Aab (45)	10.71 ± 0.12Aa (39)	0.391 ± 0.018Ab (12)	0.448 ± 0.011b (27)	97.2 ± 1.94Aa (72)	4.93 ± 0.05Aa (70)	1:2.25*
	T. setosus	92.6 ± 5Ab (27)	10.64 ± 0.16Aa (25)	0.401 ± 0.015Ab (10)	0.468 ± 0.013b (15)	91.8 ± 3.91Aa (49)	4.91 ± 0.08Aa (45)	1:1.5
O. majusculus	*F. occidentalis*	73.5 ± 5.4Aa (68)	10.7 ± 0.13Aa (50)	0.465 ± 0.013Ba (28)	0.609 ± 0.024c (22)	87.1 ± 6.02Aa (31)	4.52 ± 0.1Aa (27)	1:0.78
	E. americanus	79.6 ± 5.8Aab (49)	10.73 ± 0.13Aa (37)	0.531 ± 0.028Bb (12)	0.723 ± 0.013d (25)	89.5 ± 4.06Aa (57)	4.88 ± 0.08Aa (51)	1:2.08*
	T. setosus	90.9 ± 5Ab (33)	10.67 ± 0.15Aa (30)	0.522 ± 0.019Bb (16)	0.634 ± 0.022c (14)	94.7 ± 3.62Aa (38)	4.78 ± 0.09Aa (36)	1:0.86

Means within a column followed by different upper case letters denote significant main effect of predator; means within a column followed by different lower case letter denote significant main effect of thrips ($P < 0.05$). When the interaction between predator and thrips is significant, means are compared pairwise within columns. GLM binomial (nymphal survival, egg hatch rate); GLM Poisson (developmental time; egg duration); ANOVA (male and female weights); Tukey's HSD. Number of individuals tested in each parameter is noted in parentheses. Values followed by an asterisk differ significantly from a 1:1 sex ratio (Chi-square test).

Table 2

Reproductive parameters, longevity, and intrinsic rate of increase (means ± SE) of *O. laevigatus* and *O. majusculus* feeding on adult stages of different thrips species at 25 °C.

Predator species	Prey species	Pre-oviposition period	Lifetime fecundity	Longevity		r_m
				Males	Females	
O. laevigatus	*F. occidentalis*	3.47 ± 0.17Aa (17)	109 ± 8.4Ba (17)	16.7 ± 1.3 cd (12)	16.7 ± 0.9ab (17)	0.1485 ± 0.0029Ba
	E. americanus	3.94 ± 0.36Aa (18)	169 ± 14.6Bb (18)	22.9 ± 1.6d (10)	23.8 ± 1.5c (18)	0.1624 ± 0.0036Bab
	T. setosus	3.86 ± 0.25Aa (14)	115 ± 12.8Bab (14)	10.7 ± 1.6ab (11)	16.1 ± 1.1ab (14)	0.1719 ± 0.0039Bb
O. majusculus	*F. occidentalis*	3.79 ± 0.21Aa (14)	49.8 ± 5.4Aa (14)	8.05 ± 0.66a (19)	12.1 ± 0.8a (14)	0.1269 ± 0.0043Aa
	E. americanus	3.3 ± 0.15Aa (23)	99.7 ± 13.8Ab (23)	11.9 ± 1.5abc (11)	18.7 ± 1.5bc (23)	0.1476 ± 0.0044Aab
	T. setosus	3.23 ± 0.6Aa (13)	102 ± 15.3Aab (13)	13.1 ± 1.2bc (15)	19.4 ± 1.3bc (13)	0.1634 ± 0.0058Ab

Means within a column followed by different upper case letters denote significant main effect of predator; means within a column followed by different lower case letter denote significant main effect of thrips ($P < 0.05$). When the interaction between predator and thrips is significant, means are compared pairwise within columns. GLM quasipoisson (pre-oviposition period; lifetime fecundity; longevity males and females); ANOVA (intrinsic growth rate r_m); Tukey's HSD. Number of individuals tested in each parameter is noted in parentheses.

that both *O. laevigatus* and *O. majusculus* can successfully feed and reproduce on the leaf-inhabiting thrips *E. americanus* and *T. setosus*, and that their reproduction potential was higher when compared to the common prey of these predators, *F. occidentalis*. This finding may be explained by the sedentary nature of the leaf-inhabiting thrips used in our study, rendering them an easy to capture prey as shown in the behavioral experiments. However potential differences in the nutritional value of thrips may have also mediated the differential fitness benefits for the predators.

Predator-prey interactions were assessed in detail for combinations of adult female *Orius* predators and adult thrips prey. Encounters lasted usually a few seconds, followed by the capture or escape of the prey. *Frankliniella occidentalis* was by far the most difficult prey to subdue for both predators tested, with predation occurring in only 21.7 % and 14.5 % of total encounters for *O. laevigatus* and *O. majusculus*, respectively. In contrast, both predators were more successful in subduing the more sedentary leaf-inhabiting thrips *E. americanus* and *T. setosus*. A similar capture to encounter rate of *ca.* 20 % has been reported between adult *Orius insidiosus* (Say) and *Frankliniella* species in structurally complex arenas consisting of sweet pepper inflorescences (Reitz et al., 2006), while much higher *ca.* 50 % successful rate were reported when leaf-inhabiting soyabean thrips were offered as prey (Isenhour and Yeargan, 1981a). The difference in mobility between thrips may be due to their dietary habits, as only *F. occidentalis* feeds on high quality plant pollen leading to higher energy reserves (Kirk, 1995). Our findings are in agreement with previous studies performed with anthocorid predators and prey of the same guild that differ in mobility (Fritsche and Tamò, 2000; Meyling et al., 2003; Reitz et al., 2006). Furthermore, we found that *O. laevigatus* was overall more successful in subduing prey than *O. majusculus*. This was likely due to the difference in size of both predators. *Orius majusculus* is *ca.* 30% bigger than *O. laevigatus* (Pericart, 1972), and while increased predator size may lead to higher predation rates (Mendoza et al., 2020), it can also limit the success of a predator in subduing small and agile prey (Gergs and Ratte, 2009).

Both *Orius* predators killed a higher number of sedentary leaf-inhabiting thrips compared to *F. occidentalis*. Predation rates during 24 h of adult female predators on *F. occidentalis* (17.7 ± 1.9 for *O. laevigatus* and 20.2 ± 1.6 for *O. majusculus*) are similar to those reported before for these predators (Cocuzza et al., 1997a; Tommasini et al., 2004). Interestingly, we found that predation rates on leaf-inhabiting thrips were almost two times higher compared to *F. occidentalis*. All thrips species used as prey were of similar size, with the exception of *E. americanus* being slightly bigger, thus prey size alone cannot explain the different predation rates reported here. While high predation rates may occur as an attempt to fulfil a nutritional gap caused by feeding on low quality prey (Mendes et al., 2002), feeding on *E. americanus* and *T. setosus* led to the highest reproductive characteristics in our study, suggesting that these thrips are an excellent food source for *Orius* predators. Anthocorids often kill more prey than they consume when confronted with prey of reduced mobility (Isenhour and Yeargan, 1981b; Meyling et al., 2003). On the other hand, attacking highly mobile prey such as *F. occidentalis* adults uses more energy and has an increased foraging cost, thus predators may cease hunting before being fully satiated (Meiracker and Sabelis, 1999). We therefore hypothesize that the lower predation rate observed in our study on *F. occidentalis* was due to the increased mobility of this prey. Furthermore, feeding time on *F. occidentalis* was longer than on the leaf-inhabiting thrips, suggesting that predators may have only partially consumed sessile prey, and fully depleted their prey when it was more difficult to subdue. *Orius* predators employ extra-oral digestion, which yields higher protein levels earlier during feeding of captured prey (Cohen, 1995). This may lead to partial consumption of prey, ingesting only the high-quality nutrients, when prey is abundant and easy to subdue according to optimal foraging theory (Sih, 1980).

Nymphal development of *O. laevigatus* and *O. majusculus* feeding on larvae of the different thrips lasted about 11 days, similar to previous studies performed with these predators (Riudavets and Castañé, 1998; Tommasini et al., 2004). Similarly, egg stage duration and egg hatching rate did not differ between the different diets for both *Orius* predators. However, nymphal survival was found to be lower for *O. laevigatus* predators feeding on *F. occidentalis* larvae compared with the leaf-inhabiting thrips. Larvae of *F. occidentalis* exhibit effective defensive mechanisms against predators, including counterattacking and the production of anal droplets that may deter potential predators such as predatory mites (de Bruijn et al., 2016; Faraji et al., 2001). We did not observe such strong defensive behaviors from *T. setosus* and *E. americanus* larvae. Neonate *O. laevigatus* nymphs are of similar size as thrips larvae and may have failed to consistently subdue *F. occidentalis* larvae early in their nymphal development, leading to a high mortality rate (data not shown). Furthermore, predators that reached the adult stage gained about 15% less body weight when feeding on *F. occidentalis* larvae compared to larvae of the leaf-inhabiting thrips. Body size is positively related with reproduction in insects (Honěk, 1993), and the results of our study support this principle. Body weights of female predators feeding on leaf-inhabiting thrips larvae approached values reported for high quality diets such as *E. kuehniella* eggs (Bonte and De Clercq, 2008; Toft et al., 2020), highlighting the high nutritional value of these thrips for anthocorid predators.

Remarkably, when *Orius* predators were offered *E. americanus* larvae as nymphal diet, we found a female-skewed sex ratio. However, we do not attribute this finding to the nymphal diet, as neonate predators used in our study originated from long-standing stock cultures produced on factitious prey (*E. kuehniella* eggs and *Artemia* cysts). Strongly female biased sex ratios have been reported for the African anthocorid *Orius naivashae* (Poppius) and were attributed to the effects of *Wolbachia* endosymbiotic bacteria (van de Walle, 2014). However, results of this

study do not report such strong and consistent skewed ratios to suggest such an effect. Furthermore, molecular analyses from our *Orius* populations did not reveal the presence of *Wolbachia* endosymbionts. We thus assumed that the sex ratios recorded here were due to sample error and relatively low number of replicates, and calculated the growth rates on the basis of a 1:1 sex ratio, commonly reported for *O. laevigatus* and *O. majusculus* (Bahşi and Tunç, 2012; Sanchez and Lacasa, 2002; Tommasini et al., 2004).

Adult predators feeding on *E. americanus* and *T. setosus* adults showed higher reproductive potential compared to a *F. occidentalis* adult diet. While pre-oviposition period was similar among all diets, lifetime fecundity, longevity and intrinsic growth rate were higher on a diet consisting of sedentary leaf-inhabiting thrips. This may have been due to the different diet of the thrips used as prey in this study (bean plants for *T. setosus*, sweet pepper plants for *E. americanus*, and ripe Chrysanthemum flowers with pollen for *F. occidentalis*), as prey diet influences its nutritional value for predators (Strohmeyer et al., 1998). For example, *O. majusculus* reproductive fitness when fed on fruit flies is higher when the flies were reared on a protein-rich diet (Montoro et al., 2021). Nevertheless, increased mobility of prey may also lead to lower fitness for a predator regardless of its nutritional value, as the predator's energy cost to pursue, subdue and handle the prey increases (Griffiths, 1980). Results of the present study support this hypothesis, as *F. occidentalis* individuals were much harder to subdue by *Orius* predators, ultimately leading to lower reproductive success.

Nevertheless, *Orius* predators are very successful in controlling flower thrips such as *F. occidentalis* (Dissevelt et al., 1995; Riudavets and Castañé, 1998; van der Meiracker and Ramakers, 1991). Their success is most likely facilitated by habitat overlap (Northfield et al., 2017), as anthocorid predators occupy the same niche as flower thrips and positively respond to the semiochemicals of their prey (Teerling et al., 1993; Traczyk et al., 2020; Vaello et al., 2017). Structural complexity of flowers may further limit the ability of thrips residing in narrow spaces to escape predation. Thus, anthocorids may aggregate on flowering tissues where they do not need to cover long distances across the plant to locate suitable prey, minimizing their foraging costs and risk of higher-order predation (Griffiths, 1980). Furthermore, in periods of prey scarcity anthocorids may remain on flowering tissues, as feeding on pollen and nectar may partially substitute animal prey (Cocuzza et al., 1997b). Consequently, suppression of leaf-inhabiting herbivores such as *E. americanus* and *T. setosus* by anthophilous *Orius* predators may not be as successful as the high reproductive traits suggest in our study. Further research on foraging of *Orius* predators and their control of leaf-inhabiting herbivores in field trials is needed to evaluate their biological control potential.

Availability of data and materials

The datasets supporting this article can be obtained from Mendeley Data: https://doi.org/10.17632/nj9pkvjvrg.1.

CRediT authorship contribution statement

A. Mouratidis: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft. **A.P. de Lima:** Methodology, Investigation, Data curation, Writing – review & editing. **M. Dicke:** Supervision, Writing – review & editing. **G.J. Messelink:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

Acknowledgements

References

Aragón-Sánchez, M., Román-Fernández, L.R., Martínez-García, H., Aragón-García, A., Pérez-Moreno, I., Marco-Mancebón, V.S., 2018. Rate of consumption, biological parameters, and population growth capacity of *Orius laevigatus* fed on *Spodoptera exigua*. BioControl 63 (6), 785–794. https://doi.org/10.1007/s10526-018-9906-4.

Arakawa, T., Taniai, K., Maeda, T., 2019. The mating systems of three species of minute pirate bug, *Orius sauteri*, *O. minutus*, and *O. strigicollis*. Entomol. Exp. Appl. 167 (2), 141–151. https://doi.org/10.1111/eea.12740.

Arnó, J., Roig, J., Riudavets, J., 2008. Evaluation of *Orius majusculus* and *O. laevigatus* as predators of *Bemisa tabaci* and estimation of their prey preference. Biol. Control 44 (1), 1–6. https://doi.org/10.1016/j.biocontrol.2007.10.009.

Bahşi, Ş.Ü., Tunç, İ., 2012. The response of a southern strain of *Orius majusculus* (Reuter) (Hemiptera: Anthocoridae) to photoperiod and light intensity: Biological effects and diapause induction. Biol. Control 63 (2), 157–163. https://doi.org/10.1016/j.biocontrol.2012.06.007.

Bielza, P., 2008. Insecticide resistance management strategies against the western flower thrips, *Frankliniella occidentalis*. Pest Manag. Sci. 64 (11), 1131–1138. https://doi.org/10.1002/ps.1620.

Birch, L.C., 1948. The Intrinsic Rate of Natural Increase of an Insect Population. J. Anim. Ecol. 17 (1), 15. https://doi.org/10.2307/1605.

Bonte, M., De Clercq, P., 2008. Developmental and reproductive fitness of *Orius laevigatus* (Hemiptera: Anthocoridae) reared on factitious and artificial diets. J. Econ. Entomol. 101, 1127–1133. https://doi.org/10.1093/jee/101.4.1127.

Bonte, J., De Hauwere, L., Conlong, D., De Clercq, P., 2015. Predation capacity, development and reproduction of the southern African flower bugs *Orius thripoborus* and *Orius naivashae* (Hemiptera: Anthocoridae) on various prey. Biol. Control 86, 52–59. https://doi.org/10.1016/j.biocontrol.2015.04.007.

Bouagga, S., Urbaneja, A., Rambla, J.L., Granell, A., Pérez-Hedo, M., 2018. *Orius laevigatus* strengthens its role as a biological control agent by inducing plant defenses. J Pest Sci 91 (1), 55–64. https://doi.org/10.1007/s10340-017-0886-4.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400. https://doi.org/10.32614/rj-2017-066.

Castañé, C., Arnó, J., Gabarra, R., Alomar, O., 2011. Plant damage to vegetable crops by zoophytophagous mirid predators. Biol. Control 59 (1), 22–29. https://doi.org/10.1016/j.biocontrol.2011.03.007.

Cocuzza, G.E., De Clercq, P., Lizzio, S., Van De Veire, M., Tirry, L., Degheele, D., Vacante, V., 1997a. Life tables and predation activity of *Orius laevigatus* and *O. albidipennis* at three constant temperatures. Entomol. Exp. Appl. 85, 189–198. https://doi.org/10.1023/A:1003127310860.

Cocuzza, G.E., De Clercq, P., Van De Veire, M., De Cock, A., Degheele, D., Vacante, V., 1997b. Reproduction of *Orius laevigatus* and *Orius albidipennis* on pollen and *Ephestia kuehniella* eggs. Entomol. Exp. Appl. 82, 101–104. https://doi.org/10.1023/A:1002931622011.

Cohen, A.C., 1995. Extra-oral digestion in predaceous terrestrial Arthropoda. Annu. Rev. Entomol. 40 (1), 85–103. https://doi.org/10.1146/annurev.en.40.010195.000505.

Coll, M., Guershon, M., 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. Annu. Rev. Entomol. 47 (1), 267–297. https://doi.org/10.1146/annurev.ento.47.091201.145209.

de Bruijn, P.J.A., Egas, M., Sabelis, M.W., Groot, A.T., 2016. Context-dependent alarm signalling in an insect. J. Evol. Biol. 29 (3), 665–671. https://doi.org/10.1111/jeb.12813.

De Puysseleyr, V., Höfte, M., De Clercq, P., 2011. Ovipositing *Orius laevigatus* increase tomato resistance against *Frankliniella occidentalis* feeding by inducing the wound response. Arthropod. Plant. Interact. 5 (1), 71–80. https://doi.org/10.1007/s11829-010-9117-0.

Dissevelt, M., Altena, K., Ravensberg, W.J., 1995. Comparison of different *Orius* species for control of *Frankliniella occidentalis* in glasshouse vegetable crops in the Netherlands. Meded. Fac. Landbouwkd. en Toegepaste Biol. Wet. Univ. Gent 60, 839–845.

Faraji, F., Janssen, A., Sabelis, M.W., 2001. Predatory mites avoid ovipositing near counterattacking prey. Exp. Appl. Acarol. 25, 613–623. https://doi.org/10.1023/A:1016100212909.

Fritsche, M.E., Tamò, M., 2000. Influence of thrips prey species on the life-history and behaviour of *Orius albidipennis*. Entomol. Exp. Appl. 96, 111–118. https://doi.org/10.1023/A:1004015216361.

Funderburk, J., Frantz, G., Mellinger, C., Tyler-Julian, K., Srivastava, M., 2016. Biotic resistance limits the invasiveness of the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), in Florida. Insect Sci. 23 (2), 175–182. https://doi.org/10.1111/1744-7917.12250.

Gao, Y., Lei, Z., Reitz, S.R., 2012. Western flower thrips resistance to insecticides: detection, mechanisms and management strategies. Pest Manag. Sci. 68 (8), 1111–1121. https://doi.org/10.1002/ps.3305.

Gergs, A., Ratte, H.T., 2009. Predicting functional response and size selectivity of juvenile *Notonecta maculata* foraging on *Daphnia magna*. Ecol. Modell. 220 (23), 3331–3341. https://doi.org/10.1016/j.ecolmodel.2009.08.012.

Ghasemzadeh, S., Leman, A., Messelink, G.J., 2017. Biological control of *Echinothrips americanus* by phytoseiid predatory mites and the effect of pollen as supplemental food. Exp. Appl. Acarol. 73 (2), 209–221. https://doi.org/10.1007/s10493-017-0191-1.

Griffiths, D., 1980. Foraging costs and relative prey size. Am. Nat. 116 (5), 743–752. https://doi.org/10.1086/283666.

Hardin, J., Hilbe, J., 2018. Generalized linear models and extensions. J. Qual. Technol. https://doi.org/10.1080/00224065.2008.11917728.

Hartig, F., 2022. Residual diagnostics for hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.5. http://florianhartig.github.io/DHARMa/. https://doi.org/https://cran.r-project.org/package=DHARMa.

Harwood, J.D., Desneux, N., Yoo, H.J.S., Rowley, D.L., Greenstone, M.H., Obrycki, J.J., O'Neil, R.J., 2007. Tracking the role of alternative prey in soybean aphid predation by *Orius insidiosus*: A molecular approach. Mol. Ecol. 16, 4390–4400. https://doi.org/10.1111/j.1365-294X.2007.03482.x.

Honěk, A., 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66 (3), 483. https://doi.org/10.2307/3544943.

Hoogerbrugge, H., Lenferink, K.O., van Houten, Y., Bolckmans, K., 2014. Screening of three phytoseiid mite species as biocontrol agents of *Echinothrips americanus*. IOBC/WPRS Bull. 102, 97–101.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical J. 50 (3), 346–363. https://doi.org/10.1002/bimj.200810425.

Ingegno, B.L., Bodino, N., Leman, A., Messelink, G.J., Tavella, L., 2017. Predatory efficacy of *Dicyphus errans* on different prey. Acta Hortic. 1164, 425–430. https://doi.org/10.17660/ActaHortic.2017.1164.55.

Isenhour, D.J., Yeargan, K.V., 1981a. Interactive behavior of *Orius insidiosus* [Hem.: Anthocoridae] and *Sericothrips variabilis* [Thys.: Thripidae]: Predator searching strategies and prey escape tactics. Entomophaga 26 (2), 213–219. https://doi.org/10.1007/BF02375034.

Isenhour, D.J., Yeargan, K.V., 1981b. Predation by *Orius insidiosus* on the soybean thrips, *Sericothrips variabilis*: Effect of prey stage and density. Environ. Entomol. 10, 496–500. https://doi.org/10.1093/ee/10.4.496.

Kirk, W.D.J., 1995. Feeding behavior and nutritional requirements. In: Parker, B.L., Skinner, M., Lewis, T. (Eds.), Thrips Biology and Management. Springer US, Boston, MA, pp. 21–29. https://doi.org/10.1007/978-1-4899-1409-5_2.

Kirk, W.D.J., Terry, L.I., 2003. The spread of the western flower thrips *Frankliniella occidentalis* (Pergande). Agric. For. Entomol. 5 (4), 301–310. https://doi.org/10.1046/j.1461-9563.2003.00192.x.

Leman, A., Ingegno, B.L., Tavella, L., Janssen, A., Messelink, G.J., 2019. The omnivorous predator *Macrolophus pygmaeus*, a good candidate for the control of both greenhouse whitefly and poinsettia thrips on gerbera plants. Insect Sci. 27 (3), 510–518. https://doi.org/10.1111/1744-7917.12655.

Leon-Beck, M., Coll, M., 2009. The mating system of the flower bug *Orius laevigatus*. Biol. Control 50 (2), 199–203. https://doi.org/10.1016/j.biocontrol.2009.03.016.

Lewis, T., 1997. Thrips as Crop Pests. CABI, Wallingford, UK.

Maia, A.D.H.N., Pazianotto, R.A.D.A., Luiz, A.J.B., Marinho-Prado, J.S., Pervez, A., 2014. Inference on arthropod demographic parameters: Computational advances using R. J. Econ. Entomol. 107 (1), 432–439. https://doi.org/10.1603/EC13222.

McCullagh, P., Nelder, J.A., 1990. Generalized Linear Models. Appl. Statistics 39 (3), 385. https://doi.org/10.2307/2347392.

Meiracker, R.A.F., Sabelis, M.W., 1999. Do functional responses of predatory arthropods reach a plateau? A case study of *Orius insidiosus* with western flower thrips as prey. Entomol. Exp. Appl. 90 (3), 323–329. https://doi.org/10.1046/j.1570-7458.1999.00452.x.

Mendes, S.M., Bueno, V.H.P., Argolo, V.M., Silveira, L.C.P., 2002. Type of prey influences biology and consumption rate of *Orius insidiosus* (Say) (Hemiptera, Anthocoridae). Rev. Bras. Entomol. 46, 99–103. https://doi.org/10.1590/S0085-56262002000100012.

Mendoza, J.E., Balanza, V., Cifuentes, D., Bielza, P., 2020. Selection for larger body size in *Orius laevigatus*: Intraspecific variability and effects on reproductive parameters. Biol. Control 148, 104310. https://doi.org/10.1016/j.biocontrol.2020.104310.

Meyer, J.S., Ingersoll, C.G., McDonald, L.L., Boyce, M.S., 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. Ecology 67, 1156–1166. https://doi.org/10.2307/1938671.

Meyling, N.V., Enkegaard, A., Brødsgaard, H., 2003. Two *Anthocoris* bugs as predators of glasshouse aphids - voracity and prey preference. Entomol. Exp. Appl. 108, 59–70. https://doi.org/10.1046/j.1570-7458.2003.00071.x.

Montoro, M., De Fine Licht, H.H., Sigsgaard, L., 2021. Nutritional quality of *Drosophila melanogaster* as factitious prey for rearing the predatory bug *Orius majusculus*. Insect Sci. 28 (1), 191–202. https://doi.org/10.1111/1744-7917.12758.

Morse, J.G., Hoddle, M.S., 2005. Invasion Biology of Thrips. Annu. Rev. Entomol. 51 (1), 67–89. https://doi.org/10.1146/annurev.ento.51.110104.151044.

Murai, T., 2001. Life history study of *Thrips setosus*. Entomol. Exp. Appl. 100, 245–251. https://doi.org/10.1023/A:1019236726421.

Nagai, K., 1990. Suppressive effect of *Orius* sp. (Hemiptera: Anthocoridae) on the population density of *Thrips palmi* Karny (Thysanoptera: Thripidae) in eggplant in an open field. Japanese J. Appl. Entomol. Zool. 34 (2), 109–114. https://doi.org/10.1303/jjaez.34.109.

Northfield, T.D., Barton, B.T., Schmitz, O.J., 2017. A spatial theory for emergent multiple predator–prey interactions in food webs. Ecol. Evol. 7 (17), 6935–6948. https://doi.org/10.1002/ece3.3250.

Opit, G.P., Peterson, B., Gillespie, D.R., Costello, R.A., 1997. The life cycle and management of *Echinothrips americanus* (Thysanoptera: Thripidae). J. Entomol. Soc. Br. Columbia 94, 3–6.

Pericart, 1972. Hémiptères : Anthocoridae, Cimicidae et Microphysidae : de l'ouest-paléarctique. Masson et Cié. París, France. https://doi.org/10.1038/158078b0.

Pijnakker, J., Leman, A., Vangansbeke, D., Wäckers, F.L., 2017. *Echinothrips americanus*: A bottleneck for integrated pest management in ornamentals?. In: Comm. Appl. Biol. Sci. Ghent University, Ghent, pp. 105–111.

Pijnakker, J., Overgaag, D., Guilbaud, M., Vangansbeke, D., Duarte, M., Wackers, F., 2019. Biological control of the Japanese flower thrips *Thrips setosus* Moulton (Thysanoptera: Thripidae) in greenhouse ornamentals. IOBC/WPRS Bull. 147, 107–112.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria https://www.r-project.org/.

Reitz, S.R., 2009. Biology and ecology of the western flower thrips (Thysanoptera: Thripidae): The making of a pest. Florida Entomol. 92 (1), 7–13. https://doi.org/10.1653/024.092.0102.

Reitz, S.R., Funderburk, J.E., Waring, S.M., 2006. Differential predation by the generalist predator *Orius insidiosus* on congeneric species of thrips that vary in size and behavior. Entomol. Exp. Appl. 119 (3), 179–188. https://doi.org/10.1111/j.1570-7458.2006.00408.x.

Riley, D.G., Joseph, S.V., Srinivasan, R., Diffie, S., 2011. Thrips Vectors of Tospoviruses. J. Integr. Pest Manag. 2, 1–10. https://doi.org/10.1603/IPM10020.

Riudavets, J., Castañé, C., 1998. Identification and evaluation of native predators of *Frankliniella occidentalis* (Thysanoptera: Thripidae) in the Mediterranean. Environ. Entomol. 27, 86–93. https://doi.org/10.1093/ee/27.1.86.

Sanchez, J.A., Lacasa, A., 2002. Modelling population dynamics of *Orius laevigatus* and *O. albidipennis* (Hemiptera: Anthocoridae) to optimize their use as biological control agents of *Frankliniella occidentalis* (Thysanoptera: Thripidae). Bull. Entomol. Res. 92, 77–88. https://doi.org/10.1079/BER2001136.

Shipp, J.L., Gillespie, D.R., Fry, K.M., Ferguson, G.M., 2001. In: Biological Control Programmes in Canada, 1981-2000. CABI, Wallingford, pp. 115–119. https://doi.org/10.1079/9780851995274.0115.

Sih, A., 1980. Optimal foraging: Partial consumption of prey. Am. Nat. 116 (2), 281–290.

Strohmeyer, H.H., Stamp, N.E., Jarzomski, C.M., Bowers, M.D., 1998. Prey species and prey diet affect growth of invertebrate predators. Ecol. Entomol. 23, 68–79. https://doi.org/10.1046/j.1365-2311.1998.00101.x.

Teerling, C.R., Gillespie, D.R., Borden, J.H., 1993. Utilization of western flower thrips alarm pheromone as a prey-finding kairomone by predators. Can. Entomol. 125 (3), 431–437. https://doi.org/10.4039/Ent125431-3.

Toft, S., Jensen, K., Sørensen, J.G., Sigsgaard, L., Holmstrup, M., 2020. Food quality of *Ephestia* eggs, the aphid *Rhopalosiphum padi* and mixed diet for *Orius majusculus*. J. Appl. Entomol. 144 (4), 251–262. https://doi.org/10.1111/jen.12739.

Tommasini, M.G., 2004. Collection of *Orius* species in Italy. Bull. Insectology 57, 65–72.

Tommasini, M.G., Van Lenteren, J.C., Burgio, G., 2004. Biological traits and predation capacity of four *Orius* species on two prey species. Bull. Insectology 57, 79–93.

Traczyk, E., Funderburk, J., Martini, X., 2020. Foraging behavior responses of *Orius insidiosus* to thrips cues. Entomol. Exp. Appl. 168 (10), 716–722. https://doi.org/10.1111/eea.12955.

Tsuda, S., 1996. Localization of Tomato Spotted Wilt Tospovirus in Larvae and Pupae of the Insect Vector *Thrips setosus*. Phytopathology 86 (11), 1199. https://doi.org/10.1094/Phyto-86-1199.

Vaello, T., Casas, J.L., Pineda, A., De Alfonso, I., Marcos-García, M.Á., 2017. Olfactory response of the Predatory Bug *Orius laevigatus* (Hemiptera: Anthocoridae) to the Aggregation Pheromone of Its Prey, *Frankliniella occidentalis* (Thysanoptera: Thripidae). Environ. Entomol. 46, 1115–1119. https://doi.org/10.1093/ee/nvx141.

van de Walle, A., 2014. Alternatieve voedingsbronnen voor de kweek van *Orius thripoborus* en *Orius naivashae*. Univ, Gent, Gent, Belgium [In Dutch].

van der Meiracker, R., Ramakers, P.M.J., 1991. Biological control of the western flower thrips *Frankliniella occidentalis* in sweet pepper, with the anthocorid predator *Orius insidiosus*. Meded. Fac. Landbouwkd. en Toegepaste Biol. Wet. Univ. Gent 56, 241–249.

van Lenteren, J.C., 2012. The state of commercial augmentative biological control: Plenty of natural enemies, but a frustrating lack of uptake. BioControl 57 (1), 1–20. https://doi.org/10.1007/s10526-011-9395-1.

Venzon, M., Janssen, A., Sabelis, M.W., 2002. Prey preference and reproductive success of the generalist predator *Orius laevigatus*. Oikos 97 (1), 116–124. https://doi.org/10.1034/j.1600-0706.2002.970112.x.

Vierbergen, G.B., 1998. *Echinothrips americanus* Morgan, a new thrips in Dutch greenhouses (Thysanoptera: Thripidae). Proc. Sect. Exp. Appl. Entomol. Netherlands Entomol. Soc. 9, 155–160.

Vierbergen, G.B., Loomans, A.J.M., 2016. *Thrips setosus* (Thysanoptera: Thripidae), the Japanese flower thrips, in cultivation of *Hydrangea* in the Netherlands. Entomol. Ber. 76, 103–108.