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Evaluating the biocontrol potential of lacewing larvae (*Mallada basalis*) against greenhouse thrips (*Heliothrips haemorrhoidalis*): predator functional responses to prey density at key life stages

JUNLIN CAO[1,2,3], KESHI ZHANG[1,2,4] & ZHI-QIANG ZHANG[1,2,5]*
[1]*School of Biological Sciences, 3A Symonds Street, University of Auckland, Auckland 1010, New Zealand.*
[2]*Bioeconomy Science Institute, Manaaki Whenua – Landcare Research Group, 231 Morrin Road, Auckland 1072, New Zealand.*
[3] *caoj@landcareresearch.co.nz; https://orcid.org/0009-0004-9133-1098*
[4] *zhangk@landcareresearch.co.nz; https://orcid.org/0000-0002-9731-078X*
[5] *zhangz@landcareresearch.co.nz; https://orcid.org/0000-0003-4172-0592*
**Corresponding author*

Abstract

Understanding predator-prey dynamics is crucial for assessing the biological control potential of generalist arthropod predators. The green lacewing (*Mallada basalis*) is a common natural predator in horticulture but has not yet been evaluated for its effects on greenhouse thrips (*Heliothrips haemorrhoidalis*) across different prey life stages. This study examined the functional responses of first and second instar *M. basalis* larvae to three life stages of thrips (second instar nymphs, pupae, and adults) under six initial prey densities (1, 2, 6, 10, 14, and 18 prey per cell) within a 24 h interval. The predation rate varied significantly ($p < 0.05$) overall with the instar of green lacewings and the life stage of thrips. Between the same prey densities, prey handling time of second instar lacewing larvae consistently exceeded (by c. 50%) that of first instar larvae. The quantity of prey that predators consumed appeared to vary with prey size, prey defence capabilities, and prey age. All functional responses were of type II but it shape varied at different prey developmental stages. Lacewing predation on pupal and adult thrips remained at low levels across varying densities, suggesting limited lacewing predation efficiency on these developmental stages. Our results indicate that lacewing larvae, particularly second instars, are effective predators of immature thrips and may contribute to biological control strategies targeting these early developmental stages. The stage-specific predation patterns we identified provide empirical insights for optimising the integration of lacewings into management programmes for greenhouse thrips.

Key words: insect predator; predator-prey dynamics; stage-specific predation; biological control; integrated pest management

Introduction

The avocado, *Persea americana* Mill. (1768), is one of the most economically valuable horticultural crops globally (Yahia 2023), primarily driven by the continuous growth of domestic and international market demand (Ayala Silva & Ledesma 2014). In 2023, global avocado production reached approximately 10.5 million tonnes, reflecting robust growth over the past few decades (Dixon & Pak 2008; Huang *et al.* 2023; Food and Agriculture Organisation of the United Nations 2025). New Zealand's avocado industry is also highly significant: the annual industry output value is about 150 million NZD, with exports accounting for around 100 million NZD and domestic sales totalling approximately 50 million NZD. In recent years, New Zealand's fresh avocado exports reached 112 million NZD in 2020 and 167 million NZD in 2021 (New Zealand Avocado 2023).

Avocados are highly valued for their rich nutritional content, particularly their high levels of monounsaturated fatty acids, dietary fibre, vitamins, and antioxidant compounds (Dreher & Davenport 2013; Araújo *et al.* 2018; Bhuyan *et al.* 2019). In New Zealand, avocado orchards are primarily located in the Bay of Plenty and Northland regions, supplying both the domestic market and high-end export markets. Maintaining avocado quality is crucial, as avocados are sold fresh and highly susceptible to physical damage—minor signs of pests or blemishes can degrade fruit quality,

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reduce market value, and hinder exports under stringent phytosanitary standards (Kassim *et al.* 2013; Karithi 2016). With global demand continuing to rise, sustaining avocado production and market competitiveness largely depends on effective integrated pest management strategies (Dara 2019), underscoring the need to incorporate biological control that in turn requires better understanding of predator-prey interactions within orchard ecosystems.

The greenhouse thrips—*Heliothrips haemorrhoidalis* (Bouche, 1833), (Thysanoptera: Thripidae)—is an economically significant pest of ornamental plants and horticultural crops, such as ferns, avocados, rhododendrons, and various citrus fruits (Lima *et al.* 2012; Etienne *et al.* 2015; Larral *et al.* 2018). Although its origin is undetermined, it possibly originated in the Amazon River basin in Brazil. With global trade (Nakahara *et al.* 2015), greenhouse thrips have spread to nearly 80 countries and established themselves in different climate zones (de Souza *et al.* 2022; Logan *et al.* 2021; Nakahara *et al.* 2015). Under suitable conditions, eggs usually hatch in about 14 days, after which the species undergoes two feeding nymphal stages before entering a dormant pupal stage. The life cycle of thrips is as follows: egg stage, first instar nymph, second instar nymph, pre-pupa (characterized by 2 short wing buds and compact antennae), pupa (characterized by 4 long wing buds and curve back over the head antennae), adult (Mound & Walker. 1982; de Souza *et al.* 2022).

Several biological characteristics of this thrips species enabled its dispersal and establishment. 1) It reproduces through thelytokous parthenogenesis, so a single mother can initiate a population (Bene *et al.* 1998; Tang *et al.* 2015). 2) Females insert their eggs into the leaf using ovipositor, that protects them from predators and environmental disturbances (Ananthakrishnan 1984). 3) The species has a minimum number of known natural enemies or potential control agents. 4) These thrips can also survive on many different host species (de Souza *et al.* 2022). These factors collectively contribute to its tenacity, making it a difficult pest to control in integrated horticultural systems.

The harm caused to avocados by greenhouse thrips lies in their destructive feeding behaviour. Both nymphs and adults feed on the epidermal tissue of young leaves and fruits, leading leaf desiccation and death (Scott Brown & Simmonds 2006). The appearance of avocado fruit determines its market value; so even minor appearance damage can cause significant economic losses (Yahia 2023).

The green lacewing—*Mallada basalis* (Walker, 1853) (Neuroptera: Chrysopidae)—is a frequently used biocontrol agent (de Souza *et al.* 2022; Ye *et al.* 2017). Its larva stages are voracious omnivorous predators that can prey on a variety of soft arthropods, such as aphids, small caterpillars, mites, thrips, whiteflies (Boo *et al.* 1998; Cheng 2007; Cheng *et al.* 2010; Chen *et al.* 2014). The sickle-shaped jaws of the larva enable it to capture and pierce prey efficiently and digest it extra-orally. The lacewing larvae are effective at inhibiting pest populations on leaf and fruit surfaces (Early 2020). Its three larval instars can effectively control pests, but after cocooning and exclusion into adults, the diet changes to pollen and nectar (Ye *et al.* 2015).

Previous researchers have used parasitic wasps such as *Thripobius semiluteus* Boucek, 1977 and predatory thrips such as *Franklinothrips orizabensis* Johansen, 1974 to control greenhouse thrips (Bernardo *et al.* 2005) with limited success, mostly due to the high dispersal tendency of these predators. Therefore, we examined the suitability of green lacewing as alternative biocontrol agent against greenhouse thrips.

Functional response analysis provides a quantitative framework to characterise predator performance by examining how predation rates change with prey availability (Papanikolaou *et al.* 2021; Pritchard *et al.* 2017). Functional responses describe how predator consumption changes with prey density (Holling 1959). Type I shows a linear increase in consumption, assuming negligible handling time; Type II shows a decelerating intake rate due to handling time constraints; and Type III shows a sigmoid response, often reflecting learning or prey switching. Such information is crucial for predicting the capability of green lacewings to control the greenhouse thrips in orchard environments and for designing more targeted, stage-specific integrated pest management strategies. Therefore, we aimed to determine the functional responses of the first and second instar larvae of the green lacewing when exposed to three key life stages of the greenhouse thrips: second instar nymphs, pupae, and adults). By quantifying predation patterns across a range of prey densities, we aimed to assess differences in predation efficiency between lacewing instars and evaluate the relative vulnerability of different developmental stages of the thrips (Papanikolaou *et al.* 2021).

Material and methods

Insect sources

Predators: Green lacewing (*M. basalis*) eggs (of unknown age) were purchased from BioForce Limited (Karaka, Auckland, New Zealand). Upon arrival, the eggs were individually reared in vials (15 mm in diameter, 50 mm in length) at room temperature (c. 23 °C), with uncontrolled relative humidity (RH) until hatching. First instar larvae were used immediately after hatching to ensure uniform larval age and hunger levels (< 12 h old).

To obtain second instar larvae, newly hatched larvae were individually reared and provided with frozen moth egg feed—*Ephestia kuehniella* Zeller, 1879 (Biobest, Belgium)—until they reached the second instar. Larvae were checked daily to confirm moulting and used within 12 h of reaching the second instar. All predators were starved for 24 h before placed in Munger cells for experiments to ensure a similar hunger level.

Prey: Greenhouse thrips, *H. haemorrhoidalis*, were obtained from a greenhouse-raised population at Bioeconomy Science Institute, Manaaki Whenua – Landcare Research Group, Auckland, New Zealand (uncontrolled temperature and RH). They were reared continuously on leaves in small avocado trees. The leaves served as both a food source and an oviposition substrate. Live second instar nymphs, pupae, and adults were collected from avocado trees in the greenhouse for experimentation using a fine brush (size 000).

Experimental set-up and assessments

We performed all our experiments under controlled laboratory conditions: 25 °C ± 1 °C, 80% ± 5% RH, and a 16:8 light–dark (L:D) photoperiod.

Predation experiments used a modified Munger cell as described by Wang *et al.* (2024). Each rearing cell consisted of two square plexiglass plates with an outer side length of 50 mm and a chamber height of 5 mm, forming the upper and lower surfaces of a flat microchamber. Inside the chamber, a fresh avocado leaf disc (c. 40 mm in diameter) rested on four layers of filter paper. The upper plexiglass plate contained a 30 mm diameter central opening, which was covered with a piece of plastic wrap; five small holes were punctured/pierced through the wrap using an insect pin (size 000) to allow air circulation. At the beginning of the 24-h predation period, filtered water was added to the filter paper to ensure that the leaf freshness.

During each experiment, prey (greenhouse thrips) of either second instar nymphs, pupae, or adults were added on the leaf discs at one of six initial prey densities (1, 2, 6, 10, 14, or 18 individuals per cell) using a fine brush. A predator lava (green lacewing) of either first or second instar stage was then gently transferred to a pre-prepared rearing cell. Each predator–prey combination was replicated 10 times (total of 360).

For prey consumption experiments, we recorded the total number of prey eaten at the end of the experiment (24 h)- predator individual/h. For determining functional response type, the number of remaining prey was counted at the end of the experiment, and the prey count for each replicate was calculated accordingly (N_ε). See *Statistical analysis* for further details of determination of predator attack rates and values for handling time (by predators of prey).

Statistical analysis

All statistical analyses were performed in R, version 4.5.2 (R Core team 2022). Prey consumption was summarised as mean ± standard error of the mean (SEM). First, Aligned Rank Transformed Analysis of Variance (ART ANOVA) was conducted to evaluate the effects of prey developmental stage, predator instar, and prey density on the number of prey consumed (Kay *et al.* 2021). An ART ANOVA was used due to a non-normal distribution of the prey consumption data. Before analysis, prey density was treated as a factor, and all variables were converted into categorical or numeric form as appropriate. The full factorial model included all main effects and their interactions. Significance thresholds followed conventional criteria ($p < 0.05$).

In addition to the logistic regression approach, a complementary mechanistic analysis was conducted by fitting a generalised functional response model incorporating a scaling exponent (q), in which a Type II response is parameterised as the special case $q = 0$, whereas values of $q > 0$ indicate deviation towards a Type III functional response. For each prey-predator combination, models allowing q to be estimated from the data were compared with nested Type II models with q fixed at zero using information criteria (AIC and BIC) (Pritchard *et al.* 2017).

$$N_\varepsilon = N_0\left[1 - \exp\left(a\left(hN_\varepsilon - T\right)\right)\right]$$

where a is the attack rate, h is the handling time, and T is the trial duration (24h). Each prey density (1, 2, 6, 10, 14, and 18 individuals) was considered an independent observation for each predator-prey combination (N_0). Variables included prey life stage, predator instar, initial prey density, and prey consumption over 24 h.

Results

Prey consumption

Prey developmental stage, predator instar, and prey density all had significant main effects on predation (Table 1). The predator consumed more prey pupae compared to second instars (Fig. 1). Second instar predators consumed more prey than the first instar ones. At higher prey densities, more prey was consumed by predators.

Significant interactions exist between prey and predator life stages, indicating that second instar lacewing larvae prey on more thrips than first instar larvae when the prey stage was a pupa or adult (Table 1, Fig. 1). The significant interactions between prey and predator density, as well as between different predator densities, further demonstrate that predation rates varied with density for different predator-prey combinations. Also, significant interactions were observed between prey developmental stage, predator age, and prey density.

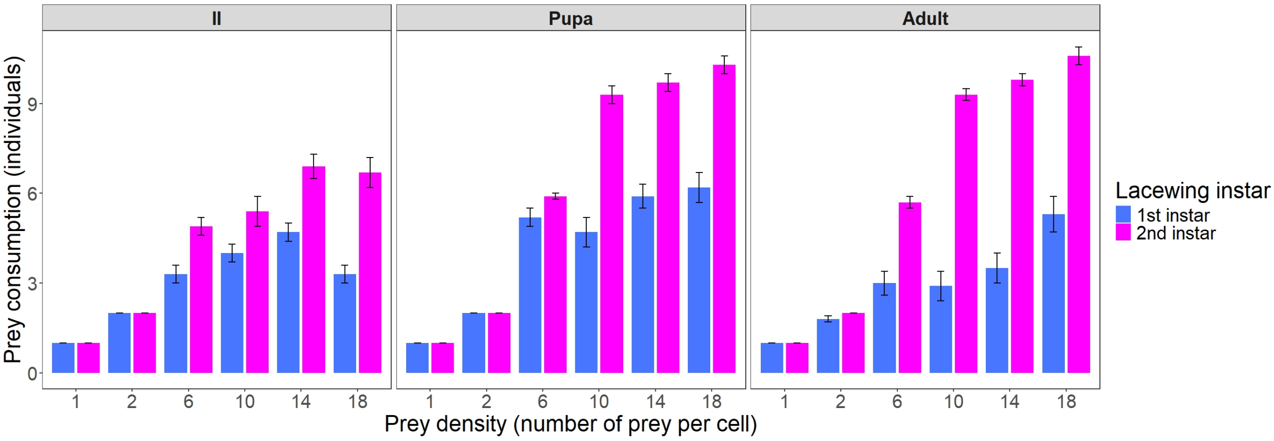

Figure 1. Number of greenhouse thrips *Heliothrips haemorrhoidalis* consumed by larvae of the green lacewing *Mallada basalis* (first and second instars) at varying prey densities (number of prey per cell) across three different developmental stages of the prey (second instar nymph or II, pupa, adult).

Table 1. Test statistics from ART ANOVA testing the effects of predator (*Mallada basalis*) developmental stage (first or second instar), prey (*Heliothrips haemorrhoidalis*) stage (second instar, pupa, or adult), and prey density (six different densities) on prey consumption.

Effect	***df* (numerator)**	***df* (denominator)**	***F***	***p***
Prey stage	2	324	74.437	< 0.001
Predator instar	1	324	551.955	< 0.001
Prey density	5	324	423.401	< 0.001
Prey × Predator	2	324	35.077	< 0.001
Prey × Density	10	324	12.056	< 0.001
Predator × Density	5	324	69.039	< 0.001
Prey × Predator × Density	10	324	6.742	< 0.001

Functional response

Logistic regression analysis of the proportion of prey consumed indicated a consistent functional response pattern across all prey stages and predator instars (Table 2). In all prey-predator combinations, the linear coefficient of prey density in the logistic model was significantly negative, whereas no significant quadratic term was detected. These results demonstrate a declining proportion of prey consumed with increasing prey density and provide no evidence for a sigmoidal (Type III) functional response.

Consistent with the logistic regression analysis, results from the generalised functional response model incorporating a scaling exponent (q) also supported the same functional response pattern (Table 2). For most prey-predator combinations, allowing q to vary did not improve model performance relative to the nested model with q fixed at zero, as indicated by small or negative ΔAIC values. Although the adult prey-first instar predator combination showed a slightly positive ΔAIC when q was estimated, this difference was minimal and did not alter the overall functional response classification. Collectively, these results confirm that lacewing predation on thrips across all prey stages and predator instars is best described by a Type II functional response.

Parameter estimations based on the Holling II response revealed significant differences between prey developmental stages and predator instars (Table 3). The overall predation efficiency of second instar predator (*M. basalis*) larvae was higher than that of first instar larvae, as evidenced by their shorter handling times and attack rates comparable to or higher than those of first instar larvae. Among the three developmental stages of the *H. haemorrhoidalis* thrips prey, the pupae suffered the highest attack rates. The handling time for second instar lacewing larvae predating the thrips was consistently shorter than that for first instar larvae, with the shortest handling times for prey pupae and adults.

Table 2. Logistic regression analysis for determining functional response type of the predator (*Mallada basalis*) lacewing for it thrip prey (*Heliothrips haemorrhoidalis*) at different life stages of predator and prey.

Prey stage (thrip)	**Predator instar (lacewing)**	**Logistic coefficient b ± SE**	**z value**	**p value**	**q estimate**	**ΔAIC (q free − q= 0)**	**Functional response**
adult	I	–0.111 ± 0.020	–5.67	< 0.001	–0.827	+0.99	Type II
adult	II	–0.233 ± 0.032	–7.20	< 0.001	0.186	–1.81	Type II
II	I	–0.177 ± 0.021	–8.24	< 0.001	–0.798	–1.79	Type II
II	II	–0.159 ± 0.022	–7.36	< 0.001	–0.865	–0.84	Type II
pupa	I	–0.171 ± 0.022	–7.89	< 0.001	–0.573	–1.93	Type II
pupa	II	–0.260 ± 0.034	–7.63	< 0.001	0.345	–1.64	Type II

Table 3. Functional response test statistics for different life stages or prey and predator. Attack rate (a) represents the ability of the predator (*Mallada basalis*) to encounter and successfully attack prey (*Heliothrips haemorrhoidalis*) per unit of time (h); Handling time (h) represents the time (24 h or 1 day) required for a predator to process a single prey.[a]

Prey (thrip) life stage	Predator (lacewing) instar	a (individual prey/h)	h (time in 24h)
2nd instar	1st instar	1.704	0.208
Pupa	1st instar	1.584	0.126
Adult	1st instar	0.922	0.167
2nd instar	2nd instar	1.408	0.104
Pupa	2nd instar	1.526	0.056
Adult	2nd instar	1.447	0.052

[a] The greater the value of a, the higher the predator's search and capture efficiency. The smaller the value of h, the faster the predator can complete a predation event, obtaining more prey in the same amount of time.

Discussion

Functional response analysis in this study revealed that *M. basalis* larvae exhibited a Holling type II response to *H. haemorrhoidalis* at all developmental stages. This pattern was also reflected in our functional response curves. The fitted parameters further support this. For species exhibiting a Holling type II response, handling time is a key limiting factor for the predator's maximum predation rate (Pritchard *et* al. 2017). Type II response curves are among the most common in arthropod predators, typically associated with predators highly dependent on extra-oral digestion, such as the predatory mite *Neoseiulus cucumeris* (Oudemans, 1930) (Dalir *et al.* 2021) and harlequin ladybird *Harmonia axyridis* (Pallas, 1773) (Li *et al.* 2024). From a biocontrol perspective, this implies that lacewings can exert strong predation pressure even in conditions of prey scarcity, making them suitable for suppressing early pest outbreaks.

We found that when first instar lacewing larvae faced high densities (14–18) of second instar thrips, consumption of prey by the predators decreased. This trend is consistent with the functional response parameters. Second instar thrips experienced one of the highest attack rates among the thrips prey life stages, despite this prey type having the longest handling time. This combination—high a but long h—accelerated the onset of prey consumption saturation, causing predators to reach their time-processing limit quickly, which resulted in lower total consumption at the highest prey densities, as also shown by the flattening of the response curve (Fig. 2).

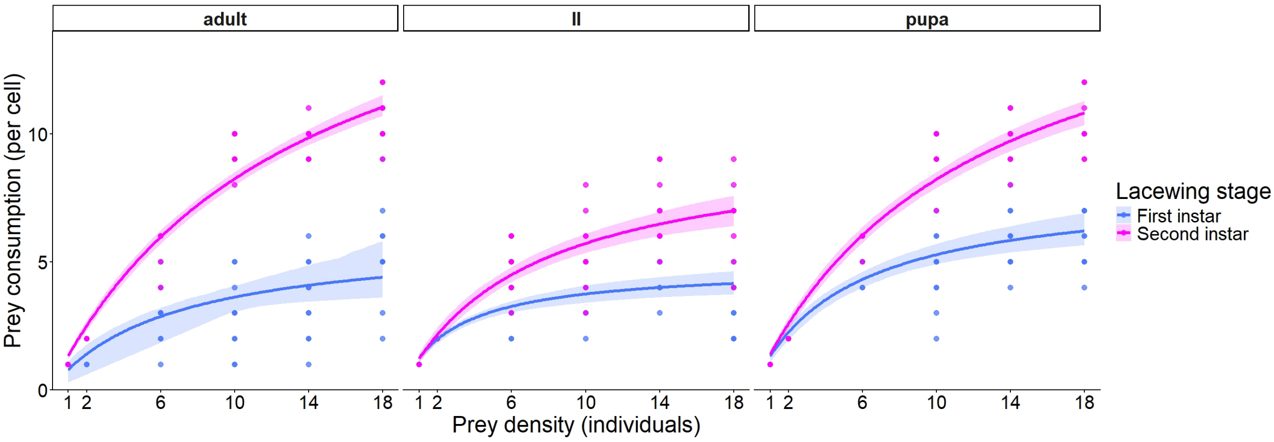

Figure 2. Functional response of predatory green lacewing *Mallada basalis* larvae (first and second instars) feeding on greenhouse thrips prey (*Heliothrips haemorrhoidalis*) at varying prey densities (number of prey per cell) and across different developmental stages of the prey (second-instar nymph or II, pupa, and adult).

The first and second instar nymphs of *H. haemorrhoidalis* secrete a viscous substance that accumulates on leaf surfaces as thrips density increases (Fig. 3). We suggested that this secretion may contaminate or hinder the movement of smaller first-instar lacewing larvae, reducing their ability to effectively capture prey, or it may serve a defensive purpose. Previous studies have documented that this liquid can entangle and kill predatory mites such as *Neoseiulus californicus* (McGregor, 1954) (Sazo *et al.* 2006). We found that the accumulation of secretions (per unit area of leaf surface) was greater under high-density conditions (Cao J.'s pers. obs.). This could explain the unexpected decrease in predation that we observed in our experiments. Second instar lacewings, being larger and stronger, and having more developed mouthparts, were less affected by these secretions, and had higher prey consumption across all densities. Further studies should avoid small, enclosed arenas with high thrips density.

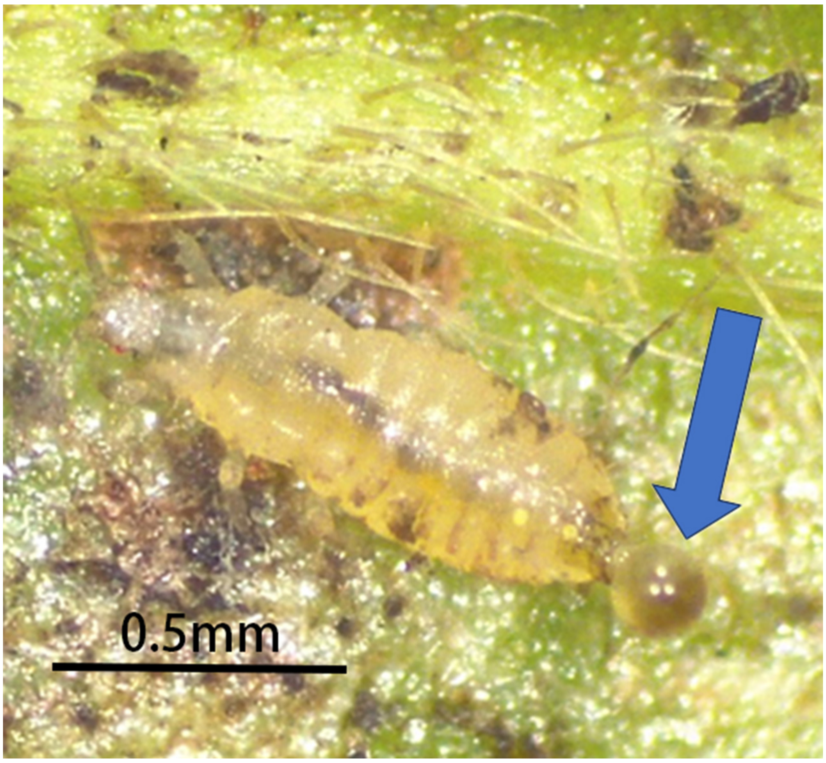

Figure 3. Secretions from the tail of a second-instar nymph thrips (*Heliothrips haemorrhoidalis*). The arrow points to the sticky excretions produced by the thrips.

The differences we found in this study between predation on the three developmental stages are consistent with previous findings that pupae and early nymphs are generally more susceptible to predation than adults due to limited mobility and weaker defence mechanisms (Lima *et al.* 2012). The body size difference between the first and second instar lacewings is consistent with existing reports that predation efficiency in lacewing larvae increases significantly with larval instar (Ye *et al.* 2015). Predation rates can serve as fundamental input parameters for a functional response model framework (Holling 1959). Predation rates can serve as fundamental input parameters for a functional response model framework (Holling 1959). High predator life stage has high prey consumption. Predation rates quantify population-level predation dynamics in the functional response model and ultimately guide the design of biocontrol strategies by determining the optimal predator developmental stage and the most readily available prey developmental stage (Early 2020).

Our results demonstrate that *M. basilis*, the green lacewing, is a promising biocontrol agent for greenhouse thrips, *H. haemorrhoidalis*. The life stage-specific vulnerability of thrips observed in our results suggests that lacewing releases would be most effective when targeting periods dominated by pupae and early nymphs, due to the most favourable predator attack-rate and handling-time profiles. While the parasitic wasp *T. semiluteus* and predatory thrips *F. orizabensis* have been used in previous greenhouse thrips control programmes (Dennill 1992; Froud & Stevens 2002), their high dispersal rate/ability prevents them from sustaining effective control in open orchards. In another greenhouse experiment (Cao J.'s unpubl. data), at a lacewing: thrips ratio of 1:20, larval lacewings remained on avocado leaves until almost all thrips were consumed. In contrast to the parasitic wasp and predatory thrips, lacewing larvae are less mobile, and can exert sustained, stage-specific predation pressure on thrips populations. Considering all these advantages, we believe *M. basali* provides a practical and effective alternative for the biocontrol of greenhouse thrips, *H. haemorrhoidalis*.

Limitations

This study still had some limitations. The experiment was conducted in a laboratory environment, which cannot fully simulate the spatial complexity of the natural environment. As noted, in our *Materials and methods* section, we could not conduct experiments involving third instar lacewing larvae and first instar thrips nymphs because of resource limitations.

Conclusions

This study evaluated the predation performance of the first and second instar lacewing larvae on greenhouse thrips prey at three developmental stages of the prey (second-instar nymphs, pupae, and adults), and at various prey densities. The results showed that both the predator's instar and the prey's life stage influenced predation dynamics.

Our findings indicate that lacewings, especially their second-instar larvae, possess significant potential as an effective biocontrol agent for greenhouse thrips. Targeting the early developmental stages of thrips can significantly improve the effectiveness of lacewing biocontrol strategies. Future tests and validation in greenhouses and fields—as well as research on predator-prey behavioural interactions—will further refine the application of lacewings in sustainable pest management programmes.

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