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Functional responses and diet-dependent fecundity of *Stratiolaelaps scimitus* (Acari: Laelapidae) preying on western flower thrips pupae (Thysanoptera: Thripidae)

HAIYU CHI[1,5], LIXIA XIE[2,3,6]* & ZHI-QIANG ZHANG[1,4,7]*
[1]*School of Biological Sciences, University of Auckland, 3A Symonds Street, Auckland 1010, New Zealand*
[2]*Department of Entomology, College of Plant Protection, Shandong Agricultural University, Taian 271018, Shandong, People's Republic of China*
[3]*Shandong Province Higher Education Collaborative Innovation Centre for Comprehensive Management of Agricultural and Forestry Crop Diseases and Pests in the Yellow River Basin, Taian 271018, Shandong, People's Republic of China*
[4]*Bioeconomy Science Institute, 231 Morrin Road, Auckland 1072, New Zealand*
[5] *Chihaiyu007@gmail.com; https://orcid.org/0009-0001-8959-1606*
[6] *xielixia2006@163.com; https://orcid.org/0000-0003-1029-3575*
[7] *zhangz@landcareresearch.co.nz; https://orcid.org/0000-0003-4172-0592*
**Corresponding author*

Abstract

Western flower thrips, *Frankliniella occidentalis,* remains difficult to manage in crops because their non-feeding pupal stage is largely concealed in the soil, making it unreachable by foliar insecticides and canopy-dwelling natural enemies. The soil-dwelling laelapid mite *Stratiolaelaps scimitus* is widely used against edaphic pests, but its performance on thrips pupae relative to factitious prey, and the contribution of different life stages to thrips suppression, are still poorly quantified. We first compared no-choice predation and fecundity of adult females offered either thrips pupae or the dried fruit mite *Carpoglyphus lactis* (male adults), with a starvation treatment as control. *S. scimitus* females readily attacked both prey types and produced significantly more eggs when food was available than under starvation, but 48 h oviposition did not differ significantly between the two diets, indicating that thrips pupae and *C. lactis* provided comparable short-term nutritional support. Next, we quantified the functional responses of *S. scimitus* deutonymphs, adult males and adult females, to thrips pupae across six prey densities (1, 3, 5, 8, 12 or 15 pupae per arena) over 24 h. All tested stages of *S. scimitus* exhibited a Type II functional response. Adult females had the shortest handling time and highest asymptotic consumption (≈7.6 pupae per day), adult males were intermediate (≈5.8 pupae day^{-1}), and deutonymphs the lowest (≈3.9 pupae day^{-1}). These results confirm *S. scimitus* as an effective predator of thrips pupae, with mixed-stage populations contributing to pupal mortality, and support current mass-rearing practices on factitious prey for subsequent deployment against this pest in crops.

Key words: Biological control, thrips pests, strawberries, diet, predation, reproduction

Introduction

The western flower thrips, *Frankliniella occidentalis* (Pergande, 1895), is among the most destructive pests of greenhouse ornamentals and vegetables worldwide (Pergande 1895; Reitz *et al.* 2020; Wu *et al.* 2025). Thrips larvae and adults feed on leaves, flowers, and fruits, causing extensive scarring, distortion, and discoloration, and adults also vector important tospoviruses such as tomato spotted wilt virus, causing significant feeding damage and posing continued risks (Shalileh *et al.* 2016; Wu *et al.* 2025). Heavy reliance on pesticides for thrips management has led to severe resistance and widespread control failures, and broad-spectrum chemistries can further destabilize management by suppressing natural enemies and competitor thrips species that normally help limit *F. occidentalis* populations (Srivastava *et al.* 2014; Gao *et al.* 2023).

Western flower thrips are also well established in New Zealand, where they have been recorded from a wide range of horticultural crops and ornamentals since the mid-1990s (Teulon & Nielsen 2005). A key challenge to control

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F. occidentalis is its cryptic soil-dwelling pupal stage. After feeding, second-instar nymphs typically drop from plants into the soil or growth medium to pupate (Whittaker & Lewis 1975; Ebssa *et al.* 2006). On crops that do not flower or have simpler flowers, over 90% of western flower thrips second-instar nymphs have been observed to leave plants and pupate in the soil (Buitenhuis & Shipp 2008). For example, 92–93% of thrips associated with non-flowering chrysanthemums and roses pupated in the soil (Buitenhuis & Shipp 2008), and nearly 98% of thrips on bean plants dropped to pupate in soil (Berndt *et al.* 2004a). The non-feeding prepupal and pupal stages temporarily dwell in the upper soil layer, often 0–5 mm deep, where conventional foliar insecticides and foliar predators cannot easily reach them (Whittaker & Lewis 1975).

This behavior protects the thrips during pupation from foliar natural enemies like *Neoseiulus cucumeris* (Oudemans, 1930), *Amblyseius swirskii* Athias-Henriot, 1962, or *Orius* spp., which do not forage in soil (Saito & Brownbridge 2018; Funderburk *et al.* 2019; Murunde *et al.* 2019; Amarathunga *et al.* 2024). Field studies have further demonstrated that combining multiple foliar predators does not necessarily improve the control of *F. occidentalis* when the soil-dwelling pupal stage remains unaddressed (Albendín *et al.* 2015). Moreover, even microbial biopesticides such as *Beauveria bassiana* can provide only partial suppression of *F. occidentalis* in greenhouse crops, and their efficacy is highly dependent on environmental conditions and application strategy (Zhang *et al.* 2019). Effective control of *F. occidentalis* therefore requires tactics targeting the below-ground pupal stage, in conjunction with above-ground controls.

Pupation in soil exposes thrips prepupae and pupae to edaphic predators, making the soil a critical zone for intervention (Berndt *et al.* 2004a). Soil-dwelling predatory mites such as members of the Laelapidae can prey on these otherwise protected stages during their brief 2–5 day developmental period in soil (Murunde *et al.* 2019; Wu *et al.* 2014). The use of such natural enemies offers an opportunity to suppress the thrips population in its soil refuge.

Stratiolaelaps scimitus (Womersley, 1956) (Acari: Laelapidae), formerly known as *Hypoaspis miles* (Berlese, 1892), is a soil-dwelling predatory mite that has been widely adopted for the biological control of edaphic pests. *S. scimitus* is a generalist mesostigmatid mite that feeds on a range of small soil organisms (Womersley 1956; Park *et al.* 2021a). Notably, it has recently been increasingly demonstrated that it is an effective predator of thrips in their soil stages (prepupae and pupae) (Wu *et al.* 2014; Zhu *et al.* 2023). *S. scimitus* will also readily consume fungus gnat larvae, shore fly eggs, springtails, bulb mites, and other soil pests (Wu *et al.* 2014; Yang *et al.* 2020; Mazzutti *et al.* 2023), and has been shown to effectively suppress fungus gnats of the genus *Lycoriella* in horticultural and mushroom-production systems (Lan *et al.* 2025)

Its broad diet and ability to survive periods of prey scarcity make *S. scimitus* amenable to mass-rearing and commercial use (Park *et al.* 2021a). Indeed, this mite is commercially produced by multiple biocontrol suppliers and widely used in integrated pest management programs in greenhouses (Knapp *et al.* 2018). *S. scimitus* is commercially available in New Zealand (*e.g.*, Hyper-Mite™ Bioforce) and increasingly applied for soil-dwelling pest management in protected-crop production (Nielsen *et al.* 2025). Growers primarily release *S. scimitus* (as *"H. miles"*) to target fungus gnat infestations, and it has now also shown value in controlling thrips pupae in soil (Cloyd 2019; Zhu *et al.* 2023). Early studies confirmed that releasing *S. scimitus* (as *"H. miles"*) into potted crops could significantly reduce thrips emergence from pupae (Berndt *et al.* 2004a; Cloyd 2019). For instance, Berndt *et al.* (2004b) showed that soil applications of *H. miles* or a related mite "*Hypoaspis aculeifer* (G. Canestrini, 1884)" (now known as *Gaeolaelaps aculeifer*) achieved up to 45–81% reduction in adult thrips emergence (Berndt *et al.* 2004b). This highlights the value of *S. scimitus* as a biocontrol agent targeting the soil-dwelling thrips stages. Park *et al.* (2021b) compared *S. scimitus* and *G. aculeifer* in laboratory arenas and found both mites actively preyed on thrips prepupae and pupae (Park *et al.* 2021b). *S. scimitus* was observed to consume roughly two to three thrips pupae per day at specific thrips densities (Berndt *et al.* 2004b; Park *et al.* 2021b).

More recent work has started to investigate how *S. scimitus* responds to the density of thrips as prey. For example, Zhu *et al.* (2023) measured the predation rates of *S. scimitus* on the pupae of the thrips *Megalurothrips usitatus* (Bagnall, 1914) across varying densities, and recorded a maximum consumption of approximately seven thrips per female mite per day at high prey availability (Zhu *et al.* 2023). This suggests *S. scimitus* has substantial capacity to suppress thrips when pupae are abundant. In greenhouse experiments *S. scimitus* has also been proven effective in combination with other biocontrol tactics. Zhang *et al.* (2021) demonstrated that simultaneous releases of *S. scimitus* and entomopathogenic fungal granules (*Beauveria bassiana*) significantly reduced western flower thrips populations in potted plants (Zhang *et al.* 2021). Ebssa *et al.* (2006) showed that combined applications of predatory mites and entomopathogenic nematodes achieved substantially higher suppression of western flower thrips than either agent used alone, under both growth-chamber and greenhouse conditions (Ebssa *et al.* 2006). Such use of *S. scimitus* can also complement above-ground natural enemies like *Orius* bugs or *Neoseiulus* mites to provide more complete thrips suppression across all life stages (Wu *et al.* 2014; Funderburk *et al.* 2019; Amarathunga *et al.* 2024). These findings underscore the importance and timeliness of evaluating *S. scimitus* as a thrips pupal predator under various conditions and highlight the applied value of *S. scimitus* as a biocontrol agent targeting the soil-dwelling thrips stages.

Although *S. scimitus* is a well-known generalist predator, important gaps remain regarding how different prey types and predator life stages influence its performance. In commercial mass-rearing, factitious prey mites such as *Tyrophagus putrescentiae* (Schrank, 1781) and *Carpoglyphus lactis* (Linnaeus, 1758) are commonly used to sustain cultures of predatory mites (Prado Freire & De Moraes 2007; Park *et al.* 2021a). These astigmatids are easy to produce, but their nutritional value may differ from natural prey like thrips, and it is unclear whether feeding on thrips pupae versus factitious prey alters *S. scimitus* reproduction or population growth. Here, we distinguish prey nutritional value (the per-capita nutritional support a prey provides to an individual predator, reflected by short-term oviposition under standardized conditions) from predator population performance (the longer-term capacity for population increase, which is typically captured by demographic parameters such as survival, development, and age-specific fecundity). Previous diet studies have shown that laelapid predators vary in their development and fecundity depending on prey types (Navarro-Campos *et al.* 2016; Meehan *et al.* 2022); for example, *S. scimitus* could reproduce on *Ephestia kuehniella* (Zeller, 1879) eggs and grain mites such as *C. lactis*, but with different reproductive outputs (Xie *et al.* 2018; Meehan *et al.* 2022). However, no study has directly compared *S. scimitus* performance on thrips pupae versus a factitious mite prey.

Another unresolved issue concerns the relative contributions of females, males, and nymphs to predation. Most research has focused on adult females (Castro-López *et al.* 2021; Zhang *et al.* 2022), the most voracious stage, while the predatory roles of males and juveniles remain insufficiently quantified, despite their collective relevance to overall biocontrol impact. Quantifying the contribution of each predator stage is important, because an effective biocontrol agent relies on the collective impact of its entire population, not just females.

Understanding the functional response of *S. scimitus* to thrips pupae is also essential for predicting field efficacy. Functional response models describe how prey density affects consumption and are typically classified as Type I, II or III (Holling 1959). Type II responses indicate saturation at high prey densities, whereas Type III responses can enhance pest regulation through density-dependent increases in predation (Holling 1959). Fitting *S. scimitus* predation data to these models yields parameters such as attack rate and handling time, which are valuable for optimizing release strategies and forecasting predator-prey dynamics (Zhu *et al.* 2023). Functional response analysis has been widely applied to other thrips predators to compare their efficiency and to guide biological control programs (Zhu *et al.* 2023), and applying it to *S. scimitus* will similarly clarify its potential to suppress thrips pupae across varying pest densities. Given these considerations, this study (1) compares *S. scimitus* predation and reproduction on *F. occidentalis* pupae versus *C. lactis*, and (2) determines the functional response type and parameters for *S. scimitus* females, males, and nymphs feeding on *F. occidentalis* pupae at different densities. By addressing the prey nutritional value and predator stage-specific predation, and characterizing functional responses, this study aims to fill key knowledge gaps and refine predictions of *S. scimitus* biocontrol performance against western flower thrips.

Material and methods

Experimental organisms and rearing conditions

Predatory mite: *Stratiolaelaps scimitus* (Acari: Laelapidae): The initial colony of *S. scimitus* was obtained from a commercial supplier (Bioforce Limited, South Auckland, New Zealand). Mites were maintained in a climate-controlled incubator at 25 ± 1 °C, 80% relative humidity (RH), and a 16:8 h light:dark photoperiod. A water-pan rearing method was employed to prevent escape: Petri dishes containing the mite culture (with a moist organic soil substrate) were placed in larger trays of water, creating a water moat barrier around each dish (Zhang *et al.* 2024). The tray base contained a sponge layer, over which a sheet of black plastic film was laid, and filter paper was inserted along the junction between the sponge and the plastic to maintain moisture and prevent mold from forming at the junction. This set-up ensured the mites had access to moisture but could not leave the culture arena (following the methods of Wang *et al.* 2024). The mites were fed *ad libitum* frozen eggs of the flour moth *E. kuehniella* as a staple diet prior to experiments, because these eggs are widely used as a nutritionally rich and standardized food for predatory mites and support normal development and reproduction of *S. scimitus* (Xie *et al.* 2018). Using *E. kuehniella* eggs as a neutral basal diet allowed the establishment of a healthy stock population without pre-conditioning the predators to either thrips pupae or factitious mite prey, thereby minimizing potential carry-over effects on subsequent feeding and reproduction assays.

Prey mite: *Carpoglyphus lactis* (Acari: Carpoglyphidae): The dried fruit mite *C. lactis* was originally sourced from Bioforce. The mites were reared in plastic containers (≈250 mL) with screw-cap lids that had mesh-covered holes for ventilation, on a mixture of wheat bran (approximately 96%), dry yeast (approximately 3%), and sugar (approximately 1%).. Cultures were kept at 25 °C,80% RH, 16:8 h L:D, similar to the conditions reported by Zhang and Zhang (2021). This prey mite serves as a standard laboratory diet for many predatory mite species (Liu *et al.* 2025) and was provided to *S. scimitus* in one of the feeding treatments (see below).

Prey insect: western flower thrips (*Frankliniella occidentalis*): The western flower thrips colony was established from individuals collected on strawberry flowers and foliage at Good Planet, Riverhead, Auckland, New Zealand. Thrips were mass-reared in the laboratory at 25 ± 1 °C,80% RH, and 16:8 h L:D in a ventilated plastic box system (approx. 25 × 15 × 8 cm). The thrips were provided with fresh snow pea pods (*Pisum sativum* L.) as food and oviposition substrate, following a rearing method modified from Price *et al.* (2022). The boxes had mesh-covered openings to allow airflow while preventing thrips from escaping. New pea pods were added or replaced as needed to maintain the colony and support continuous thrips development. This set-up yielded abundant thrips of all life stages for use in experiments. Only the pupal stage of *F. occidentalis* was used as prey in the assays. To standardize prey quality, late-stage female thrips larvae were isolated and allowed to pupate (<24 h into the pupal stage) for use in experiments.

Experimental arena preparation

All predator–prey interactions were conducted in enclosed acrylic micro-arenas to confine the mites and prey and to maintain humidity. A total of 75 identical arenas (modified Munger cells) were constructed, each consisting of two transparent plexiglass (acrylic) slides clamped together. A circular cavity (arena space) of 15 mm diameter and 2 mm height was drilled into the center of the slides to serve as the observation chamber. This arena size follows commonly used modified Munger cell designs for predatory mite functional response assays and were chosen to provide sufficient space for predator-prey encounters and active searching, while remaining small enough to ensure frequent contact between predators and prey without unduly restricting their natural movement. The bottom of each chamber was lined with a piece of black plastic film (for contrast and visibility) that had been perforated with a 3 × 3 grid of evenly spaced pinholes, forming a nine-point dot matrix. Four layers of water-moistened filter paper were placed directly beneath this plastic lining so that moisture could seep through the pinholes, keeping the arena humid. The top of the chamber was covered with a layer of transparent food wrap (clingfilm), which was also perforated with fine holes using a grade-0 minuten insect pin to allow adequate air exchange. (Zhang & Zhang 2021). Once the top and bottom slides were assembled, metal clips were used to securely hold the chamber together. This design (adapted from Zhang & Zhang 2021) provided a confined, humid environment for the mites and prevented both predators and prey from escaping during the trials. All prepared modified Munger cells (hereafter referred to as cells) were equilibrated at the experimental temperature and humidity before introducing any insects or mites.

Experiment 1: No-choice predation assay

Objective: This experiment evaluated the predation performance of *S. scimitus* on two different prey types and the consequent effects on predator fecundity, in a no-choice setting. Predatory mites were offered either the astigmatid prey mites (*C. lactis*) or thrips pupae (*F. occidentalis*), or given no prey (starvation), and their 24 h consumption and egg production were recorded.

Predator preparation: Adult female *S. scimitus* mites were used as predators. To ensure uniform physiological status, cohorts of synchronized first-instar nymphs were initially selected and reared under identical conditions until maturity. Synchronization was achieved by collecting first-instar nymphs that had molted within the same calendar day from the stock culture; these newly molted nymphs were then reared together to adulthood, resulting in age-synchronized adult females. From these, unmated young females that had just completed the pre-oviposition period were collected. Each female was then individually placed into an empty experimental arena and starved for 24 h (with access to moisture from filter paper only) to standardize hunger before the trial.

Treatments: After the 24 h starvation period, each female predator was assigned to one of three prey treatments (25 replicates per treatment): (i) *C. lactis* prey—the predator was provided with 12 live *C. lactis* (male adult mites or non-pregnant female adult mites) per day; (ii) thrips pupae prey—the predator was provided with four fresh *F. occidentalis* pupae (female, <24 h into pupation) per day; (iii) starvation control—no prey were provided. The numbers of prey offered in treatments (i) and (ii) were selected based on previous studies and preliminary observations, and were intended to exceed the typical daily consumption of a single adult female *S. scimitus* under similar laboratory conditions and prey densities. Specifically, preliminary trials indicated that offering 12 adult *C. lactis* individuals was sufficient to ensure ad libitum prey availability and that prey supply did not become limiting over a 24 h period. For treatments (i) and (ii) the specified prey items were introduced into the arena at the start of the trial and again 24 h later (day 2), so that each predator had continuous access to prey for a total of 48 h. This design ensured that prey availability was not limiting and that observed differences in oviposition reflected prey nutritional value rather than prey quantity. Any prey remaining from the first day were removed before adding fresh prey on the second day. All cells were kept randomly distributed in the incubator (25 °C, 80% RH, 16:8 h L:D) during the experiment to avoid positional bias.

Data collection: The cells were inspected after 24 h and again after 48 h. At each observation (conducted in the same order as set-up to minimize time-of-day effects) the following data were recorded for each replicate:

(1) Number of prey consumed by the predator
Counting missing or damaged prey. For *C. lactis* consumption was inferred by counting the number of individuals remaining; for thrips pupae a prey individual was counted as consumed if it was either entirely gone or only very few remains, such as exuviae or collapsed husks, were present. In cases where pupae were clearly attacked—such as shriveled, or partially deflated—but not fully consumed, partial consumption was recorded as 0.5.

(2) Number of eggs laid by the *S. scimitus* female
Egg counts were made by carefully scanning the black arena surface for newly deposited mite eggs. After the 48-h period the predator was removed and final data recorded. From these observations we compared the predation efficiency of *S. scimitus* on the two prey types (mites vs. thrips) and assessed how each diet affected the predator's reproductive output (as an indicator of prey nutritional value).

Experiment 2: Functional response assay

Objective: This experiment examined how prey density influences the predation rate of *S. scimitus* and whether the predator's life stage or sex alters its functional response to thrips pupae. We tested three categories of *S. scimitus* (adult females, adult males, and deutonymphs) against a range of thrips pupal densities to characterize their functional response type (II or III) and estimate key parameters (attack rate and handling time).

Predator stage preparation: Predatory mites of three different stages/sexes were obtained from the colony: (a) adult females—virgin female mites that had just reached adulthood and completed their pre-ovipositional maturation (age 3 d as adults, ready to lay eggs); (b) adult males—young adult males (3 d post-emergence); (c) deutonymphs—second-instar nymphs of synchronized age, selected 2 d after molting from the protonymph and used in the experiment after a subsequent 24 h starvation period (*i.e.* at approximately 3 d post-molt), before the onset of adult emergence. To ensure uniform hunger, individuals of all groups were isolated and starved (water only) for 24 h prior to use, similar to Experiment 1. Each predator was then placed alone into an experimental arena just before the prey were introduced.

Prey density treatments: *F. occidentalis* pupae were used as the prey in all functional response trials. Six levels of initial prey density were tested: 1, 3, 5, 8, 12 or 15 thrips pupae per arena. For each predator group (female, male, deutonymph), 10 replicates were set up at each prey density (for a total of 3 × 6 × 10 = 180 cells). Predators were randomly assigned to density treatments. To begin a trial, the designated number of thrips pupae (mixed sex, <24 h old pupae) were gently transferred into a random location of the arena with the starved predator. The cells were then sealed and placed in the incubator under the same conditions as above. Predation was allowed to proceed for 24 h undisturbed.

Data collection: After 24 h each arena was examined and the number of thrips pupae consumed by the predator was recorded. Prey were scored as being consumed using the same criteria described earlier, including the 0.5 value assigned to partially consumed individuals. Any pupae that had molted into adults during the test (which was rare within 24 h at 25 °C) were noted and counted as "not consumed." These data (prey density offered vs. number consumed) for each predator type were used to fit functional response models. The primary objective of this experiment was to compare stage- and sex-specific predatory capacity across life stages of *S. scimitus*, independent of reproductive output. Although adult females are capable of oviposition, reproductive output was not recorded in this experiment because the objective was to compare the predation capacity among adult females, adult males, and deutonymphs—stages for which egg production is not universally applicable. Therefore, fecundity data were excluded for all stages. Each arena/replicate was treated independently for analysis.

Statistical analysis

All statistical analyses were performed using R software (Version 4.4.0; R Core Team 2024). Summary data are presented as mean values ± standard error of the mean (SEM). For all statistical tests the significance level was set at $\alpha = 0.05$.

No-choice predation data: In Experiment 1 we examined how prey treatment affected oviposition of *S. scimitus*. Two response variables were analyzed: the number of eggs laid during the first 24 h (day 1 eggs) and the cumulative number of eggs laid over 48 h (total eggs). Because preliminary diagnostics indicated that these count data were not normally distributed and that variances were heterogeneous among treatments, a non-parametric approach was adopted. We applied an aligned rank transform for non-parametric factorial analysis of variance (ART ANOVA) using the ARTool package in R to test for differences among the three treatment groups (Kay *et al.* 2014; Yang *et al.* 2025). This procedure aligns and ranks the data, enabling factorial ANOVA on non-normal data while retaining interaction effects (Kay *et al.* 2014). Separate ART ANOVAs were conducted for day 1 eggs and total eggs. When a significant overall effect of treatment was found ($P < 0.05$), pairwise comparisons between groups were performed using Wilcoxon rank-sum tests with a Bonferroni-adjusted α.

Functional response modeling: In Experiment 2 we used a two-step procedure to characterize the functional response of each predator group (female, male, and deutonymph). First, we determined the functional response type (Type II vs. Type III) by examining how the proportion of prey consumed (Ne/N0) changed with initial prey density (N0). This was done using the logistic regression approach of Juliano (2001), implemented via the frair_test function in the package FRAIR in R (Juliano 2001; Pritchard *et al.* 2017). A significantly negative linear coefficient of N0 in the logistic model indicates a declining proportion of prey eaten with increasing density and is diagnostic of a Type II response, whereas a significant positive linear term (with a significant quadratic term) is consistent with a sigmoidal Type III response (Holling 1959). Within a generalised functional response framework, a Type II response is defined by a scaling exponent (q) equal to zero, whereas positive values of q indicate a transition toward a Type III response (Pritchard e*t al.* 2017). Based on this formulation, we evaluated predator-prey interactions using a mechanistic modelling approach in which q was either estimated from the data or constrained to zero. For each predator group, the support for these alternative formulations was assessed by comparing models with free versus fixed q values using Akaike and Bayesian information criteria (AIC and BIC). Both approaches yielded consistent results, with all predator stages showing evidence of a Type II functional response; therefore, subsequent analyses assumed a Type II functional response.

Because prey were not replaced during the 24 h assay and prey density therefore declined as they were consumed, we fitted Rogers' random predator form of the Type II functional response, which is a depletion-corrected variant of Holling's disc equation (Rogers 1972). For illustration, the standard Holling Type II and Type III equations are shown in Eq. (1) $N_e=\frac{aN_0T}{1+ahN_0}$ and Eq. (2) $N_e=\frac{aN_0^2T}{1+ahN_0^2}$. The explicit form of the Rogers' random predator type II model used in this study is given in Eq. (3) $N_e = N_0\left(1 - e^{-a(T-hN_e)}\right)$, where *N*e is the number of prey eaten in time T ($T = 1$ day in this study), and N0 is the initial prey density. Prior to analysis, partially consumed pupae were treated as killed and rounded up to the nearest whole prey. Model parameters—attack rate (a) and handling time (h)—were estimated for each predator group by maximum likelihood using the frair_fit function (response = "rogersII") in FRAIR (Pritchard *et al.* 2017). Uncertainty in a and h was quantified by non-parametric bootstrap resampling (frair_boot), and 95% confidence intervals for both parameters and fitted curves were derived from the bootstrap distributions. Functional response curves with their 95% confidence bands for the three predator stages were plotted based on the fitted Rogers II models.

Results

Experiment 1: No-choice feeding and fecundity

In the no-choice assay, adult female *S. scimitus* readily attacked both prey types (Table 1). When offered 12 *C. lactis* per day, females consumed on average 17.0 ± 0.33 individuals over the 48 h assay, whereas those given four *F. occidentalis* pupae per day consumed 4.48 ± 0.13 pupae. Because the two prey types differed markedly in body size and in the number of individuals supplied, we did not statistically compare prey consumption between diets and instead used these data simply to confirm active feeding in the two prey treatments.

Egg production showed clear differences among the three treatments (Table 1; Figure 1). Over 48 h females fed on thrips pupae laid on average 1.88 ± 0.12 eggs per female, compared with 1.60 ± 0.10 eggs on *C. lactis*, whereas starved females produced only 0.80 ± 0.10 eggs. When all three treatments (thrips, *C. lactis*, and starvation) were included in the analysis, prey treatment had a highly significant effect on total egg production (ART ANOVA : $F_{2,\ 72} = 28.23$, $P < 0.001$), whereas first-day oviposition did not differ significantly among treatments ($F_{2,\ 72} = 2.64$, $P = 0.078$). *Post hoc* Wilcoxon pairwise comparisons revealed that this overall significance for total eggs was driven almost entirely by the strong contrast between starved females and those provided with either prey type: both prey treatments produced significantly more eggs than the starvation control (adjusted $P < 0.001$), whereas total egg production did not differ significantly between the thrips and *C. lactis* diets (adjusted $P = 0.305$). To more directly evaluate the relative nutritional value of the two prey types, we therefore fitted a reduced model, including only the two prey diets and excluding the starvation treatment.

Table 1. Mean (± SE) prey consumption and egg production of adult female *Stratiolaelaps scimitus* over 48 h in the no-choice assay under three prey treatments: factitious prey mite *Carpoglyphus lactis* (adult males), *Frankliniella occidentalis* pupae, and starvation ($n = 25$ replicates per treatment).

Treatment	**Prey consumed (48 h)**	**Predatory eggs laid (48 h)**
C. lactis adults	16.96 ± 0.33	1.60 ± 0.10
F. occidentalis pupae	4.48 ± 0.13	1.88 ± 0.12
Starvation	0 ± 0	0.80 ± 0.10

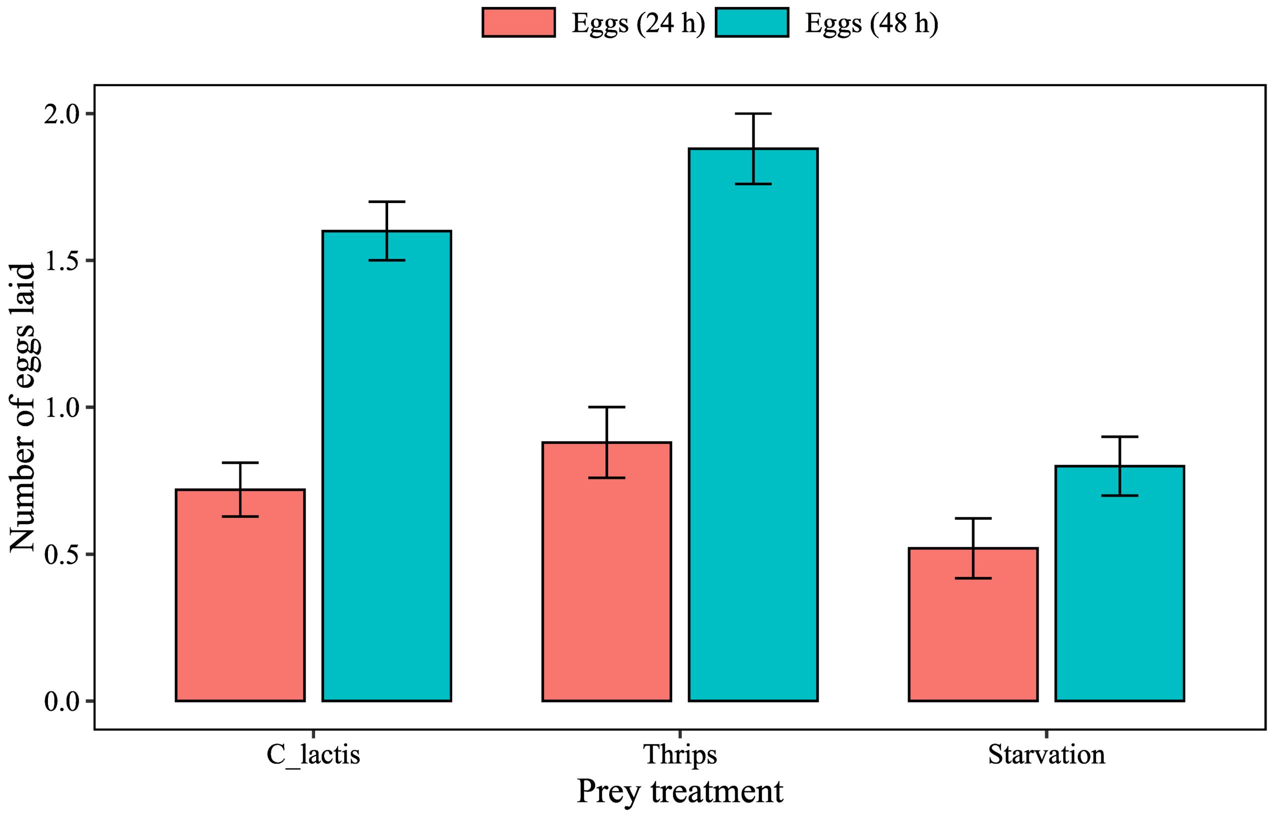

Figure 1. Egg production (mean ± SE) of adult female *Stratiolaelaps scimitus* over 24 h and 48 h under three prey treatments (*Carpoglyphus lactis* male adults, *Frankliniella occidentalis* pupae, and starvation) in the no-choice assay ($n = 25$ per treatment).

In this reduced two-diet model, treatment had no effect on first-day egg production (ART ANOVA: $F_{1,\ 48} = 0.88$, $P = 0.354$), indicating that short-term (0–24 h) oviposition was similar for both prey types. For total egg production over 48 h, females fed on thrips pupae tended to lay more eggs than those fed on *C. lactis*, but this difference was not significant ($F_{1,\ 48} = 2.82$, $P = 0.100$).

Taken together, these results show that prey availability strongly enhances *S. scimitus* fecundity compared with starvation, whereas under our experimental conditions, both *C. lactis* and thrips pupae supported comparable fecundity of *S. scimitus* over a 48-h period, and any nutritional advantage of thrips pupae over the factitious prey diet was statistically weak (Figure 1).

Experiment 2: Functional response of Stratiolaelaps scimitus *to* Frankliniella occidentalis *pupae*

Across all predator stages, the number of *F. occidentalis* pupae consumed over 24 h increased with initial prey density and then tended to plateau at higher densities (Table 2). At the lowest density (one pupa), adult females and males consumed on average 1.0 pupa (*i.e.* all available prey), while deutonymphs consumed 0.75 ± 0.13 pupae. As density increased from 3 to 15 pupae, mean consumption rose for all stages, but at different rates. At the highest density (15 pupae), females consumed 6.1 ± 0.21 pupae, males 5.1 ± 0.22 pupae, and deutonymphs 3.05 ± 0.20 pupae (Table 2), indicating that adult females consistently exhibited the highest prey intake, followed by males and then deutonymphs.

Table 2. Descriptive statistics for the functional response of *Stratiolaelaps scimitus* to *Frankliniella occidentalis* pupae. Shown are the mean (± SE) numbers of pupae consumed in 24 h by deutonymphs, adult females, and adult males at six initial prey densities (1, 3, 5, 8, 12, and 15 pupae) in the arena (n = 10 replicates per stage-density combination).

Density	Deutonymph	Female adult	Male adult
1	0.75 ± 0.13	1.00 ± 0.00	1.00 ± 0.00
3	1.40 ± 0.15	2.4 ± 0.18	2.35 ± 0.20
5	2.15 ± 0.18	3.25 ± 0.11	3.00 ± 0.21
8	2.80 ± 0.15	4.40 ± 0.16	4.15 ± 0.22
12	3.00 ± 0.21	5.65 ± 0.17	4.90 ± 0.16
15	3.05 ± 0.20	6.10 ± 0.21	5.10 ± 0.22

ART ANOVA confirmed that both predator stage and prey density significantly affected thrips consumption, and that their interaction was significant as well (Table 3). Predator life stage had a highly significant main effect on the number of pupae consumed ($F_{2,162} = 138.75$, $P < 0.001$), reflecting the strong differences among deutonymphs, males, and females observed in the descriptive statistics. Prey density also had a highly significant main effect ($F_{5,162} = 206.47$, $P < 0.001$), with consumption increasing as more pupae were offered. The stage × density interaction was likewise significant ($F_{10,162} = 9.45$, $P < 0.001$), indicating that the effect of increasing prey density on consumption differed among predator stages. In particular, differences between females, males, and deutonymphs were small at low densities (e.g. one pupa), but became progressively larger at higher densities (12–15 pupae), where females consumed almost twice as many pupae as deutonymphs. Consistent with the functional response curves, adult females consumed more pupae than males and deutonymphs across all densities, and the between-stage differences became more pronounced at higher prey densities.

Logistic regression analysis of the proportion of prey consumed (Ne/N_0) as a function of initial prey density (N_0) showed that all three predator stages exhibited a Type II functional response (Table 4). For adult females, the linear coefficient of density in the logistic model was significantly negative ($b = –0.391 ± 0.144$ SE, $z = –2.71$, $P = 0.0067$), and adult males showed a similarly negative and significant coefficient ($b = –0.420 ± 0.144$ SE, $z = –2.92$, $P = 0.0035$). Deutonymphs also had a negative linear term ($b = –0.232 ± 0.127$ SE, $z = –1.83$, $P = 0.0672$), consistent with a Type II pattern, albeit with weaker statistical support. Consistent with the logistic regression results, analysis using a generalised functional response model incorporating a scaling exponent (q) provided no evidence for a Type III response in any predator stage. In all cases, the flexible models converged to $q = 0$, and models allowing q to vary were not supported over the nested Type II models (q fixed at 0) based on information criteria ($\Delta AIC = 2$; $\Delta BIC \approx 4$; Table 5). In all cases, the declining proportion of prey consumed with increasing density and the absence of evidence for a sigmoidal (Type III) response justified fitting a Type II functional response model for each stage.

Subsequent fitting of Rogers' random predator Type II model to the consumption data quantified the functional response parameters for each predator group (Table 6). Attack rate (a) tended to be higher in adults than in deutonymphs, with the highest point estimate in males ($a = 3.06$, 95% CI: 1.84–5.42), followed by females ($a = 2.53$, 95% CI: 1.63–4.06) and deutonymphs ($a = 1.44$, 95% CI: 0.80–2.86). Handling time (h) differed clearly among stages: females had the shortest handling time ($h = 0.132$ d, 95% CI: 0.096–0.168 d), males had an intermediate value ($h = 0.172$ d, 95% CI: 0.132–0.214 d), and deutonymphs had the longest handling time ($h = 0.255$ d, 95% CI: 0.169–0.343 d). These differences in h translated into substantial variation in the theoretical maximum daily consumption ($1/h$): approximately 7.58 pupae day^{-1} for females, 5.81 pupae day^{-1} for males, and 3.92 pupae day^{-1} for deutonymphs. These parameter estimates indicate that adult females are the most efficient predators overall, while deutonymphs contribute less to thrips suppression, particularly at higher prey densities.

The fitted Rogers Type II curves for the three predator stages, together with their 95% confidence bands, are shown in Figure 2. For all stages, the number of pupae consumed increased rapidly at low prey densities and then gradually approached an asymptote as density increased, with no low-density shoulder, confirming the Type II functional response identified by the logistic regression. Across the entire range of prey densities the female curve lay above those of males and deutonymphs, while the deutonymph curve consistently remained lowest. The increasing separation among curves at higher densities visually reflects the significant stage × density interaction detected by ART-ANOVA, and is consistent with the parameter estimates of handling time and maximum consumption in Table 4. The separation of the female's curve from those of the males and deutonymphs reflects the significantly higher predation by females, especially at higher prey densities.

Table 3. Results of aligned rank transform ANOVA testing the effects of predator stage (deutonymph, adult female, adult male), prey density (treated as a factor with six levels: 1, 3, 5, 8, 12, and 15 pupae), and their interaction on the number of *Frankliniella occidentalis* pupae consumed by *Stratiolaelaps scimitus* in 24 h (n = 10 replicates per stage-density combination).

Treatment	*df*	*df*__**res**	*F*	***p***
Stage	2	162	138.757	<0.001
Density	5	162	206.475	<0.001
Stage × density	10	162	9.451	<0.001

Table 4. Results of logistic regression of the proportion of *Frankliniella occidentalis* pupae consumed by *Stratiolaelaps scimitus* as a function of initial prey density, used to determine functional response type for each predator stage. The linear coefficient *b* represents the first-order term in the logistic model; a significantly negative *b* indicates a Type II functional response.

Stage	**Type**	*b*	**SE**	*z*	***p***
Deutonymph	II	-0.232	0.127	-1.830	0.067
Female	II	-0.391	0.144	-2.712	0.007
Male	II	-0.420	0.144	-2.918	0.004

Table 5. Model comparison results for determining functional response type of *Stratiolaelaps scimitus* females, males, and deutonymphs feeding on *Frankliniella occidentalis* pupae, based on a generalised functional response model incorporating a scaling exponent (q). ΔAIC and ΔBIC represent differences between the flexible model (with q estimated) and the nested Type II model ($q = 0$). Positive ΔAIC and ΔBIC values indicate support for the Type II functional response.

Stage	*q*	**ΔAIC**	**ΔBIC**
Female	0	2	4.1
Male	0	2	4.1
Deutonymph	0	2	4.1

Table 6. Estimated parameters of the Rogers' type II functional response of *Stratiolaelaps scimitus* deutonymphs, adult females, and adult males to *Frankliniella occidentalis* pupae over 24 h. *a* is the attack rate and *h* is the handling time; *a_low* and *a_high* and *h_low* and *h_high* denote the 95% bootstrap confidence limits for *a* and *h*, respectively. *max_attack_rate* represents the asymptotic maximum number of pupae that can be attacked per predator in 24 h (1/*h*).

Stage	*a*	*a_low*	*a_high*	*h*	*h_low*	*h_high*	*max_a*
Deutonymph	1.442	0.798	2.859	0.255	0.169	0.343	3.923
Female	2.533	1.634	4.060	0.132	0.096	0.168	7.577
Male	3.062	1.844	5.419	0.172	0.132	0.214	5.806

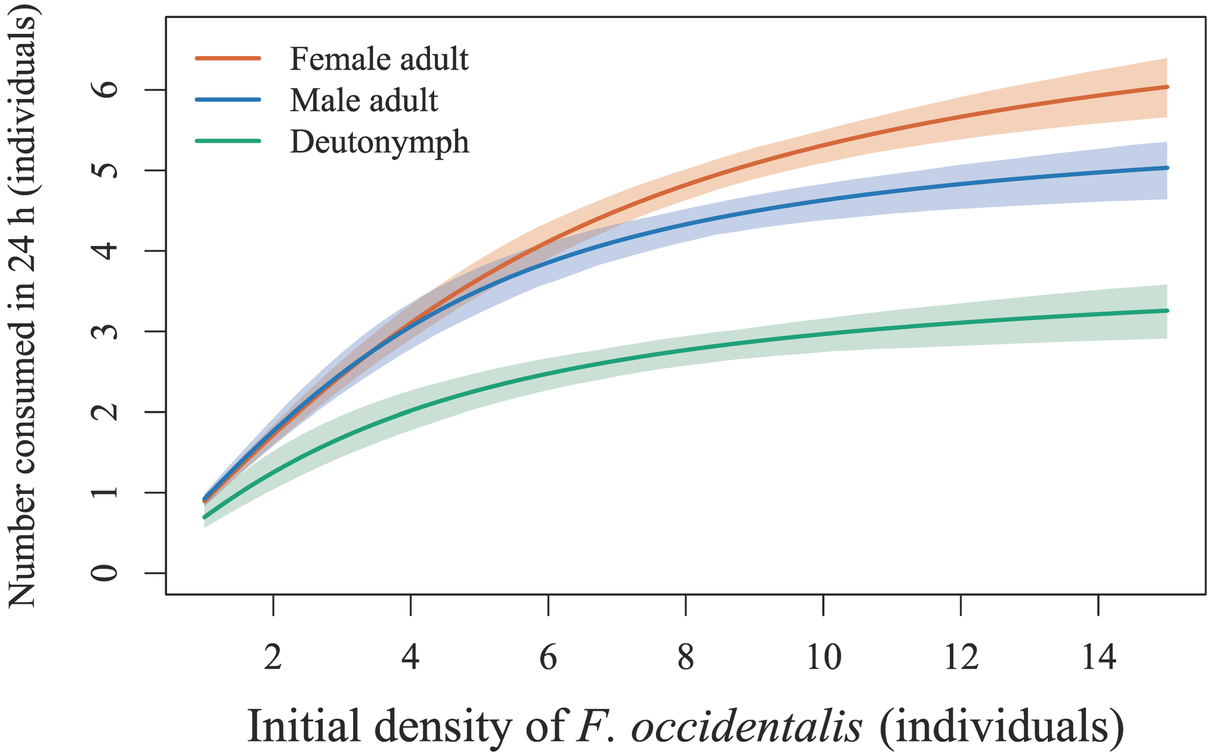

Figure 2. Rogers' type II functional response curves of *Stratiolaelaps scimitus* deutonymphs, adult females, and adult males to *Frankliniella occidentalis* pupae over 24 h. Solid lines show the fitted number of pupae consumed as a function of initial pupal density for each predator stage, and shaded bands represent 95% bootstrap confidence intervals ($n = 10$ replicates per stage-density combination).

Discussion

This study provides new insights into how prey type and predator life stage shape the performance of the soil-dwelling predatory mite *S. scimitus* as a biological control agent of western flower thrips. Overall, our results showed that (i) adult females could reproduce on a diet consisting solely of *F. occidentalis* pupae, and although their short-term fecundity is slightly higher than when feeding on the factitious prey mite *C. lactis*, the difference is not statistically significant; and (ii) females, males, and deutonymphs all exhibited a Type II functional response to thrips pupae, with adult females having the shortest handling time and highest potential daily consumption.

These findings refine our understanding of the trophic ecology of *S. scimitus* and help place its role in integrated thrips management alongside other predatory mites and microbial or above-ground natural enemies (Berndt *et al.* 2004b; Messelink *et al.* 2006; Pozzebon *et al.* 2015; Zhang *et al.* 2019).

Prey quality and fecundity of S. scimitus

In the no-choice assay, females produced significantly more eggs when prey were available than under starvation, confirming the dependence of short-term oviposition on current food intake (Navarro-Campos *et al.* 2016; Park *et al.* 2021a). However, fecundity over 48 h did not differ statistically between the two prey diets, and thrips pupae only showed a weak tendency to support higher egg production than *C. lactis*. This suggests that both prey types provided adequate nutrition for egg maturation over short time scales, despite clear differences in prey size and handling requirements. Early studies have shown that *S. scimitus* is a broadly polyphagous predator, so its reproductive performance is unlikely to depend on a single prey type. Other diet studies have likewise shown that *S. scimitus* and other laelapid mites can maintain reproduction on a range of factitious foods, including astigmatid mites and *E. kuehniella* egg (Prado Freire & De Moraes 2007; Xie *et al.* 2018; Meehan *et al.* 2022; Wang *et al.* 2024).

The modest egg production observed in our 48-h assay (1.6–1.9 eggs per female) is consistent with the previously reported fecundity of *S. scimitus* under comparable conditions. Females in our experiment had been reared on *E. kuehniella* eggs and then starved for 24 h before being exposed to the test diets, so part of their oviposition in all treatments was probably supported by reserves accumulated on this high-quality food rather than by the new prey alone (Meehan *et al.* 2022). The fact that starved females still laid approximately 0.8 eggs per day indicates that short-term egg production can be buffered by stored resources and that diet effects may become more obvious over longer periods spanning multiple gonotrophic cycles. Life-table work by Park *et al.* (2021a) shows that mated *S. scimitus* females maintained continuously on abundant *T. putrescentiae* laid on average 1.5 eggs per day, which essentially matches the daily rates implied by our 48 h totals (Park *et al.* 2021a). In our study, fecundity in the *C. lactis* treatment was slightly lower than the maximum values reported by Xie *et al.* (2025), who supplied *S. scimitus* with 20 *Tyrophagus curvipenis* Fain, 1993 per day. Although both *T. curvipenis* and *C. lactis* are storage mites, the higher fecundity observed by Xie *et al.* is probably attributable to differences in prey biomass and handling difficulty. In Xie *et al.* 2025, mated females exhibited feeding rates comparable to those in our study yet achieved higher oviposition, whereas unmated females showed both slightly lower feeding and lower fecundity. Taken together, this suggests that the primary driver is prey intake, with *T. curvipenis* – being larger (and somewhat more mobile and difficult to subdue) – probably yielding greater energetic returns per prey item than *C. lactis*, thereby supporting higher egg production under comparable feeding rates (Xie *et al.* 2025). By contrast, fecundity in the thrips treatment was somewhat higher than the averages reported by Navarro-Campos *et al.* (2016) for laelapid mites fed exclusively on second-instar thrips larvae, possibly because *F. occidentalis* pupae are easier to subdue and/or provide higher nutritional value than mobile larvae (Navarro-Campos *et al.* 2016). Overall, these comparisons indicate that our 48-h assay captured an early phase of the reproductive response to diet, but that the absolute oviposition rates we observed are well within the expected range for *S. scimitus* given its moderate intrinsic fecundity and the short observation window.

From an applied perspective, the similarity in fecundity on thrips pupae and *C. lactis* supports current rearing practices in which *S. scimitus* is produced on factitious prey and then released into crops, where it must switch to a diverse array of soil organisms, including thrips pupae, fungus gnat larvae, leek maggots, and other micro-arthropods (Castilho *et al.* 2009; Knapp *et al.* 2018; Zhou *et al.* 2018; Mazzutti *et al.* 2023). Studies on other predatory mites have shown that factitious foods can sustain populations between outbreaks of the target pest, thereby stabilizing biological control (Zhang & Zhang 2021; Zhang *et al.* 2025). Our findings indicate that thrips pupae do not impose a major nutritional penalty relative to *C. lactis*, so that mass-reared *S. scimitus* released into thrips-infested substrates should be able to maintain reproduction while contributing to pest suppression.

Stage-specific functional responses

All three predator categories—deutonymphs, males, and females—exhibited a Holling Type II functional response to *F. occidentalis* pupae, characterized by a rapid increase in consumption at low densities followed by saturation at higher densities (Holling 1959; Hassell & Comins 1978). Type II responses are widely reported for predatory mites attacking thrips or other small arthropods and reflect constraints imposed by handling time and digestive physiology (Zhou *et al.* 2018; Zhu *et al.* 2023; Amini *et al.* 2025). Our logistic regression results and Rogers' random predator fits agree with previous analyses of *S. scimitus* preying on *M. usitatus* pupae, where both predators also showed a clear Type II response (Zhu *et al.* 2023). The estimated maximum daily consumption by female *S. scimitus* in our study (≈ 7.6 pupae) is very similar to the 7.1 *M. usitatus* pupae reported for females in Zhu *et al.* (2023), despite differences in prey species, arena design, and temperature, suggesting that this value may represent an approximate upper bound on per-capita predation by female *S. scimitus* under optimal laboratory conditions.

Our stage-specific parameters revealed substantial differences among predator categories. Adult females had the shortest handling time and therefore the highest asymptotic predation rate, whereas deutonymphs had the longest handling time and lowest maximum consumption, with males occupying an intermediate position. Similar rank orders have been reported for other laelapids and soil predators, where reproductive females are typically the most voracious stage (Berndt *et al.* 2004b; Castro-López *et al.* 2021). Interestingly, our attack-rate estimates were highest for males, while females outperformed them in overall consumption due to shorter handling times. This pattern may reflect differences in searching versus processing behavior: males might be more active in locating pupae but invest less time per prey item, while females invest heavily in consuming each pupa to support egg production. Zhou *et al.* (2018) similarly reported short handling times and high maximum consumption (≈ 15 first-instar *Bradysia odoriphaga* Yang & Zhang, 1985 larvae per day) for female *S. scimitus*, emphasizing their efficiency as predators of edaphic pests (Zhou *et al.* 2018).

Importantly, our work quantifies predation by males and deutonymphs, stages that are often ignored in thrips biocontrol studies (Zhang *et al.* 2022). Although these stages cannot contribute directly to reproduction (males) or may not yet be reproductive (deutonymphs), they nonetheless kill substantial numbers of thrips pupae, especially at moderate densities. In our assays, males consumed up to ≈5 pupae day^{-1} at the highest density and deutonymphs nearly 4 pupae day^{-1} theoretically at the infinite density. Comparable contributions of non-female stages have been documented for other predator-thrips systems, such as *Neoseiulus cucumeris* and *Macrocheles mammifer* (Berlese, 1918*)* feeding on thrips (Zhu *et al.* 2023; Dalir *et al.* 2025). These results support the view that the entire age-structured population of *S. scimitus* should be considered when estimating field impact and designing release strategies.

Implications for thrips management and integration with other natural enemies

The predominance of a Type II functional response has important implications for the use of *S. scimitus* in thrips management programs. Type II predators tend to exploit prey efficiently at low to intermediate densities but can become saturated at high densities, leading to a declining proportion of prey removed as density increases (Juliano 2001). This means that *S. scimitus* may be most effective when thrips populations are still moderate and before massive accumulation of pupae in the soil. Nevertheless, when deployed at realistic release densities, these per-capita rates can translate into substantial mortality of the soil-dwelling thrips stage (Ebssa *et al.* 2006; Wu *et al.* 2014; Zhang *et al.* 2021).

Our findings complement previous work demonstrating that soil-dwelling predators can substantially reduce adult thrips emergence when combined with above-ground enemies and microbial control agents. Studies in Europe and China have shown that *S. scimitus* and related laelapids suppressed *F. occidentalis* or other thrips in potted plants, chrysanthemums, and cyclamens, especially when releases were coordinated with entomopathogenic fungi, nematodes or foliar predatory mites (Ebssa *et al.* 2006; Messelink *et al.* 2006; Buitenhuis & Shipp 2008; Wu *et al.* 2014; Zhang *et al.* 2021). Soil predators can also contribute to the control of multiple pests simultaneously—such as as fungus gnats, shore flies, and root-feeding nematodes—thereby increasing the overall economic value of biological control for protected crops (Yang *et al.* 2020; Castro-López *et al.* 2021; Mazzutti *et al.* 2023). In this context, our stage-specific functional response estimates provide parameters that can be incorporated into population models and simulation tools for designing integrated strategies that combine *S. scimitus* with foliar predators such as *Orius* spp. or *Neoseiulus* spp., and with entomopathogens such as *Beauveria bassiana*.

The comparable reproductive output by *S. scimitus* when feeding on thrips pupae and *C. lactis* is also relevant for commercial deployment. Because *S. scimitus* is typically mass-produced on factitious prey and sold as mixed-stage populations (Prado Freire & De Moraes 2007; Knapp *et al.* 2018; Nielsen *et al.* 2025), there has been concern that a long history of culture on non-target food might reduce performance on the target pest. Our data suggest that, at least over short time scales, mites reared on artificially provided food are capable of switching to thrips pupae without suffering a fecundity deficit, consistent with the high dietary plasticity reported for laelapid predators (Xie *et al.* 2018, 2025). Maintaining alternative prey in the soil (*e.g.,* supplemental factitious food) may therefore help sustain predator populations between thrips outbreaks and buffer against the saturation of predation inherent in Type II responses (Messelink *et al.* 2006; Navarro-Campos *et al.* 2016).

Limitations and future research

Several limitations of our study should be acknowledged. First, both experiments were conducted under constant laboratory conditions at 25 °C with single predator individuals in small cells. Field and greenhouse environments are more heterogeneous, and temperature, humidity, soil structure, and the presence of alternative prey can all modify predation rates and functional response parameters (Meehan *et al.* 2022). Second, our no-choice assay used only female pupae of *F. occidentalis*, whereas the functional response experiment did not distinguish the sex of pupae, treating all pupae as a single prey category. Sex- or stage-specific differences in pupal vulnerability may occur in thrips, and predation rates on prepupae, male pupae or other thrips species could differ from the patterns observed here, as suggested by previous comparative studies (Berndt *et al.* 2004b; Castro-López *et al.* 2021; Park *et al.* 2021b). Third, our no-choice design does not capture potential prey preferences when multiple soil prey coexist, which could influence the share of predation directed at thrips versus other organisms.

Future research should therefore extend the present work by (i) quantifying longer-term reproduction and population growth on mixed diets, combining thrips pupae with factitious prey *C. lactis*; (ii) assessing how temperature and soil moisture influence the functional response of each life stage; and (iii) integrating our parameter estimates into spatially explicit models that include above-ground predators, plant architecture, and grower release strategies (Amarathunga *et al.* 2024). Greenhouse or semi-field trials in New Zealand crops will be particularly valuable to validate whether the per-capita predation rates reported here translate into meaningful reductions in thrips populations when *S. scimitus* is released at realistic densities and combined with other components of integrated pest management. Such work will help refine recommendations for release timing, dosage, and compatibility with other biological control agents, thereby improving the reliability of thrips control in protected cropping systems.

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