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RESEARCH ARTICLE

Life stage predatory performance and functional response of *Nesidiocoris tenuis* to *Phthorimaea absoluta*

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The tomato leaf miner *Phthorimaea* (*Tuta*) *absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is an important invasive pest native to South America that causes damage to solanaceous crops in many parts of the world. Under laboratory conditions, the predatory capacity of *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) was assessed on *P. absoluta* life stages. All *N. tenuis* life stages preferred eggs, 1st to 3rd instar larvae of *P. absoluta* over 4th instar and pupa. In addition, adult *N. tenuis* fed voraciously on eggs (4.78 ± 0.33 within 48h) and the 1st instar (4.12 ± 0.28 within 48h) of *P. absoluta*. Seven prey densities ranging from 5 to 110 eggs per leaf and 1st instar larva per individual petri dishes were exposed to adult female and the 5th nymphal stage of the predator for a functional response study. Adult and 5th nymphal *N. tenuis* females showed type III functional predatory response to varying densities of *P. absoluta*. The attack rate of adult female preying on 1st instar larva was the highest (0.025 h^{-1}). The highest handling time was recorded for the 5th nymphal stage that fed on 1st instar larva (0.030 h). Life stage-specific application of *N. tenuis* should be advocated to improve the biological control of *P. absoluta*. In tomato-based agroecosystems in Ghana, mature females and late nymphs of *N. tenuis* should be released during peak egg laying periods and early larval stages of the pest. Predation on vulnerable stages will increase thereby decreasing insect numbers before the larvae mine into the plant and are shielded by plant tissue. To sustainably manage *P. absoluta* in Ghana, pheromone monitoring, botanical insecticides and cultural practices should be used along with biological control using *N. tenuis* and other compatible biocontrol agents.

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INTRODUCTION

The tomato leaf miner, *Phthorimaea absoluta* (Meyrick) (Lepidoptera: Gelechiidae) causes severe damage to tomato and other solanaceous plant species. Adults lay eggs on the leaves, stem, flowers and fruits, and the larvae attack these parts of the tomato plant, causing fatal damage that can result in loss of the entire crop (Chermiti et al. 2009). As the larvae feed internally, they are thus protected from many insecticides, and, coupled with the absence of a threshold level and inadequate spraying technology, these pests are therefore very difficult to exterminate with chemicals (Tarusikirwa et al. 2020; Legwaila 2025). Furthermore, the continuous use of insecticides has driven the evolution of resistance in *P. absoluta* populations (Lietti et al. 2005; Campos et al. 2014). In efforts to control the pest, farmers in Ghana use different management options, including increasing the dose and frequency of insecticides to uneconomical and harmful levels to beneficial insects and other non-targeted organisms. An Integrated Pest Management (IPM) strategy that involves the use of indigenous predators such as *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) could offer a feasible way to manage *P. absoluta*, a pest whose larvae lives in a concealed environment due to its leaf mining and internal feeding behaviour, protecting it from many natural enemies.

Nesidiocoris tenuis is a zoophytophagous predator that is indigenous to the Mediterranean region (Schafer 1997; Esparza-Diaz et al. 2024). It is a generalist predator that feeds on *P. absoluta* and has been used as a biocontrol agent for insect pests, including numerous solanaceous crop pests like aphids, leaf miners, thrips, mites and lepidopterans (Desneux et al. 2007; Mollá et al. 2014). Prey availability is crucial for this species since *N. tenuis* cannot complete its life cycle without consuming prey (Urbaneja et al. 2005). Aside from its role of preying on several pests, it also feeds on vegetative and reproductive plant parts and causes damage such as necrotic rings on stems, flowers and small fruit abortion in the absence of prey (Sánchez & Lacasa 2008; Calvo et al. 2012). *Nesidiocoris tenuis* can prey on eggs and young larvae of other related lepidoptera species like *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae), and tomato fruit borer, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) (Devi et al. 2002; Pérez-Hedo & Urbaneja 2016). Furthermore, *N. tenuis* feeds by puncturing plant tissues, causing minor damage while simultaneously activating the plant's indirect defense mechanisms (Naselli et al. 2016; Pérez-Hedo & Urbaneja 2016); and, it has been shown to work together with parasitoids to reduce pest populations (Chailleux et al. 2013; Naselli et al. 2017). However, several biological and behavioural aspects of *N. tenuis* need to be assessed to improve our understanding of the predatory capabilities of the insect and the consequences this could have to pest management.

The number of prey an individual predator kills, as a function of prey density is known as the functional response (Holling 1965). Holling (1959) distinguished three categories of functional

responses, namely types I, II and III. The type I functional response curve is a straight line that shows density-independent prey killing. Type II is given as a hyperbolic curve that shows a negative density-dependent response, and a higher prey density means a lower percentage of prey is eaten. Type III is a sigmoidal curve with a positive density-dependent response at the initial level, and subsequently exhibiting negative density dependence as a result of satiation. A predator's feeding response to variations in prey density, or its functional response, is one of the measures used to assess its effectiveness. The functional response provides a quantitative explanation of a predator's behaviour in response to various prey densities (Farhadi et al. 2010). Attack rate and handling time are key parameters in studying functional response because they demonstrate how successfully a predator searches for its prey and consumes it. Handling time limits the highest feeding rate when prey is abundant, whereas the attack rate determines the initial slope of the response when prey density is low (Holling 1959; Juliano 2001; Fernández-Arhex & Corley 2003). Differences in feeding capacity and ecological interactions among pests and their natural predators and parasitoids make it important to study them across all life stages. These stage-specific traits improve predator–prey interactions by matching the most effective predator stage with the most vulnerable pest stage, improving establishment and control. For predator–prey models and pest control forecasts across prey densities, density-dependent functional response research with life-stage fluctuations enhances precision.

In the laboratory and greenhouses, scientists have shown that *N. tenuis* is an effective predator that eats the eggs and early instar larvae of *P. absoluta*, which lowers their numbers in tomato crops (Sánchez 2009; Anusha et al. 2025). Studies show that it works better when used together with other natural enemies and control strategies, making it a key component of integrated pest management (Chinchilla-Ramirez et al. 2020). The present study seeks to evaluate the effectiveness of *N. tenu*is in targeting the egg and early larval stages (1st to 3rd instar) of *P. absoluta* and to assess its potential for improving tomato pest management in Ghana through strategic, stage-specific release. Additionally, we aimed to assess the predator's efficacy across different pest population densities.

MATERIALS AND METHODS

Source of *Phthorimaea absoluta*

The tomato leafminer larvae were initially obtained from a greenhouse (Hill Top) at Obosomase, in the Eastern Region, Ghana, in 2024. The larvae were raised on the pectomech tomato variety until they emerged as adults in the Biological Control Laboratory, Plant Protection and Regulatory Services Directorate (PPRSD) of the Ministry of Food and Agriculture in Pokuase, Accra, Ghana (5°41'48'' N, 0°17'09'' W). Field collected larvae and pupae were continuously added to the laboratory stock population. In order to standardise the predatory potential and functional response test, *P. absoluta* larvae were reared on the pectomech variety for two generations in improvised plastic containers (6 cm in diameter and 3 cm high); the tops covered with white organza mesh fabric (3 cm diameter). Adults were provided with 10% honey solution in moist cotton wool. The procedure for rearing followed Krechemer and Foerster (2017). Before the experiment, pupae of *P. absoluta* were sexed under a stereomicroscope by examining the ventral abdominal segments and position of the genital opening. The female pupae had a longitudinal suture or slit between the two small tubercles in the 8th abdominal segment. Mid-9th abdominal segment sutures were present in male pupae. Female pupae were larger and heavier than males (Genç 2016). Thirty mature pairs of adult *P. absoluta* moths (fully expanded wings and cuticle) were introduced into a rearing cage with the aid of an aspirator, and allowed to mate and the females lay eggs. The eggs were reared to different instars (1st, 2nd, 3rd and 4th larval instars) up to the second generation.

Source of *Nesidiocoris tenuis*

Nesidiocoris tenuis population was established by collecting populations from farmers' tomato fields early in the morning with the aid of an aspirator at Dome in the Greater Accra Region, Ghana (5°38'56'' N, 0°14'31'' W). The collected samples were placed in ventilated cages with fresh tomato leaves and transported to the laboratory in an insulated cooler within 45 minutes. The colony was maintained in Plexiglas cylinders (9 cm in diameter, 3.5 cm high) in the laboratory. Infested tomato leaves with *P. absoluta* and *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs served as a food source until the development of *N. tenuis* adults from the nymphal stages. Adults were later transferred into oviposition cages. Fresh tomato leaves were provided daily for egg laying. Eggs were monitored constantly for nymph emergence, thereby enabling the synchronisation of developmental stages for experimental purposes and ensuring the accuracy, reliability, and reproducibility of the rearing procedure. The colony was maintained at 27 ± 2 °C, 75 ± 2% RH.

Predation potential of nymphs and adults of *N. tenuis* against *P. absoluta* life stages

Nesidiocoris tenuis life stages used for the experiments were initially transferred to empty rearing cages. They were maintained in these cages for 24 h with access to water only, allowing them to acclimate before the start of the experiments. To determine the predatory potential of adult and nymphal stages of *N. tenuis* on *P. absoluta*, each of the five different immature stages of the leaf miner (eggs, 1st, 2nd, 3rd and 4th stage larval instars) were offered to each life stage of the predator separately. Each single nymph and adult stage of the predator, *N. tenuis*, were introduced to the tomato leaf miner, *P. absoluta*, life stages separately with the aid of an aspirator and allowed to feed for 48 hours (De Puysseleyr et al. 2013; Ettaib et al. 2016; Idemudia et al. 2024). Ten individuals of each of five different life stages of *P. absoluta* without *N. tenuis* were kept separately in individual petri dishes (9 cm diameter with a hole for ventilation covered by a fine mesh measuring 4.5 cm) as controls. Ten replicates were used in the treatments and controls. After 48 hours, the remaining host developmental stages (egg and larvae) were recorded under a stereomicroscope. The experiments were conducted in the laboratory at a temperature of 27 ± 2 °C, 75 ± 2% RH and 12:12 h (light: dark) photoperiod regime.

Functional response of *N. tenuis* adult and 5th nymphal stage preying on eggs and 1st instar larva of *P. absoluta*

The method used by Hassanpour et al. (2016), Gavkare et al. (2017), Michaelides et al. (2017) and Idemudia et al. (2024) was used to carry out the studies on functional response at a temperature of 27 ± 2 °C, 75 ± 2% RH. The functional response study was restricted to the egg and 1st instar larva of *P. absoluta* and adult and 5th nymphal stage of *N. tenuis*. The reason for using these life stages was that, from the predation potential study, adult and 5th nymphal *N. tenuis* stages preyed on more *P. absoluta* eggs and 1st instar larva than other life stages. Functional response studies require predatory stages that actively consume prey, making them the most appropriate stages for accurately assessing how predation changes with increasing prey density.

Before the experiments, the predators (48 h old) were maintained without prey for 12 h. The experiment was carried out in petri dishes (9 cm diameter) with a hole on the top (4.5 cm diameter) to allow for aeration. Day-old eggs and 1st instar larva of *P. absoluta* were handled as separate treatments and

introduced individually onto separate tomato leaves inside petri dishes at densities of 5, 10, 30, 50, 70, 90 and 110 individuals per leaf using a camel hairbrush. The 1st instar larvae were allowed to mine into the leaves before the predators were introduced, while the eggs remained unhatched during the experimental period.

These densities were selected based on initial observations indicating that the maximum number of prey consumed by young, mated females that fed on a number of prey for 24 hours was more than 80, hence ensuring that the highest density exceeded the ad libitum level. Prior to the experiment, *N. tenuis* specimens were examined under the microscope to distinguish adults from 5th instar nymphs based on wing development and reproductive characteristics. Fully grown adults had a slender, light green body with hemelytra covering the abdomen and developed genitalia. Unlike adults, the 5th nymphal stage had a smaller body size with conspicuous wing pads that did not cover the entire abdomen and a shorter, broader body (Sánchez et al. 2004; Urbaneja et al. 2012). There were ten replicates of treatments consisting of two separate prey stages, day-old eggs and 1st instar larvae of *P. absoluta*, placed individually on tomato leaves in petri dishes at each density and control treatment (prey without a predator). There was replacement of prey during the experiment. The number of eggs and larvae consumed by the predator life stages were recorded after 24 hours.

Statistical analysis

The mortality rate of *P. absoluta* life stages (eggs and larvae) in the replicated control treatment was minimal (~1%), so we did not account for control mortality. All data were analysed using R software (Version 4.4.3). The data on the predation potential of different life stages of *N. tenuis* on the different stages of *P. absoluta* was tested for normality using Shapiro-Wilk's test (Shapiro and Wilk, 1965). As a result of data violating the assumptions of parametric tests, a Generalized Linear Model (GLM) with a Poisson distribution and log-link function was used. The interaction between the predator and prey was not significant, whereas the single factors were significant. Therefore, the single factors were subjected to pairwise comparisons of estimated marginal means with Tukey adjustment.

The preference of the different life stages of *N. tenuis* to different life stages of *P. absoluta* was evaluated using Chesson's preference index (Chesson 1983). Chesson's preference index is given by:

$$\alpha_i = \frac{(r_i / n_i)}{\sum_{j=1}^{m}(r_i / n_i)}$$

where r_i is the number of prey of stage i consumed, n_i is the initial number of prey of stage i offered, and m is the total number of prey categories. Preference was interpreted relative to a neutral selection threshold, defined as $\alpha = 1/m$, where m is the number of prey life stages.

The type of functional response was ascertained using polynomial logistic regression of the proportion of prey consumed as a function of initial prey density. A type III functional response was determined, with the linear coefficients significantly positive and the quadratic coefficients significantly negative, revealing a sigmoidal relationship.

After the identification of a type III functional response, functional response parameters were estimated for each predator–prey combination using Hassell's Type III model with the *FRAIR* package in R software. Attack coefficients (b) and handling times (h) were estimated using maximum likelihood. Parameter uncertainty was quantified using non-parametric bootstrapping (900 iterations), and 95% confidence intervals were used to visually compare the functional response parameters among predator and prey life stages.

RESULTS

Predation potential of *N. tenuis* developmental stages on *P. absoluta* life stages

Predatory potential was significantly influenced by *N. tenuis* life stages ($\chi^2 = 245.34$, df = 5, $p < 0.001$) and *P. absoluta* life stages ($\chi^2 = 440.28$, df = 4, $p < 0.001$). However, the interaction between *N. tenuis* and *P. absoluta* life stages was not significant ($\chi^2 = 4.34$, df = 20, $p = 0.990$), indicating that *N. tenuis's* predatory potential across its life stages was consistent across *P. absoluta* life stages.

The predatory potential of *N. tenuis* against the different life stages of *P. absoluta* increased progressively through successive nymphal stages, with the adult stage recording the highest predatory potential against *P. absoluta* (5.14 ± 0.41 prey/predator) (Table 1). However, the predatory potential of the adult stage did not differ significantly from that of the 5th instar nymphal stages (Table 1).

Nesidiocoris tenuis predation increased as the developmental stages of *P. absoluta* increased. The predation of *N. tenuis* was highest at the egg stage of *P. absoluta* (4.78 ± 0.33 eggs/predator), followed by the 1st larval stage (4.12 ± 0.28 larvae/predator), which did not differ significantly from each other (Table 2). Although no predation was observed on 4th instar larva (0.00 ± 0.00 larva/predator), the predation rate for this stage was statistically similar to that of eggs and 1st instar larva, attributable to significant variability and zero variance (Table 2).

N. tenuis preference for *P. absoluta* life stages

The preference of the different life stages of *N. tenuis* to different life stages of *P. absoluta* is presented in Figure 1. Chesson's preference index showed clear stage-specific feeding preferences of *N. tenuis* on *P. absoluta*. Across the different life stages, preference index values varied among *N. tenuis* life stages, with values higher than the neutral line revealing positive selection and values below showing avoidance. The preference for the earlier life stages of *P. absoluta* was shown by *N. tenuis*, whereas there was a lower preference for the more developed

Table 1: Average predatory potential of the different life stages of *Nesidiocoris tenuis* against *Phthorimaea absoluta.*

Life stages of *Nesidiocoris tenuis*	Predatory potential (average +/– SE)
1st instar nymph	0.68 ± 0.10^{d}
2nd instar nymph	1.94 ± 0.18^{c}
3rd instar nymph	2.76 ± 0.24^{bc}
4th instar nymph	3.44 ± 0.28^{b}
5th instar nymph	4.34 ± 0.37^{ab}
Adult	5.14 ± 0.41^{a}

Average (± standard error [SE]) with different letters are significantly different from each other ($p < 0.05$) based on pairwise comparison of the estimated marginal means with Tukey's adjustment

Table 2: Average predatory potential of *Nesidiocoris tenuis* against different life stages of *Phthorimaea absoluta*

Life stages of *Phthorimaea absoluta*	Predatory potential (average +/– SE)
Egg	4.78 ± 0.33^{a}
1st instar larva	4.12 ± 0.28^{ab}
2nd instar larva	3.47 ± 0.23^{b}
3rd instar larva	2.88 ± 0.22^{c}
4th instar larva	0.00 ± 0.00^{ab}

Average (± standard error [SE]) with different letters are significantly different from each other ($p < 0.05$) based on pairwise comparison of the estimated marginal means with Tukey's adjustment

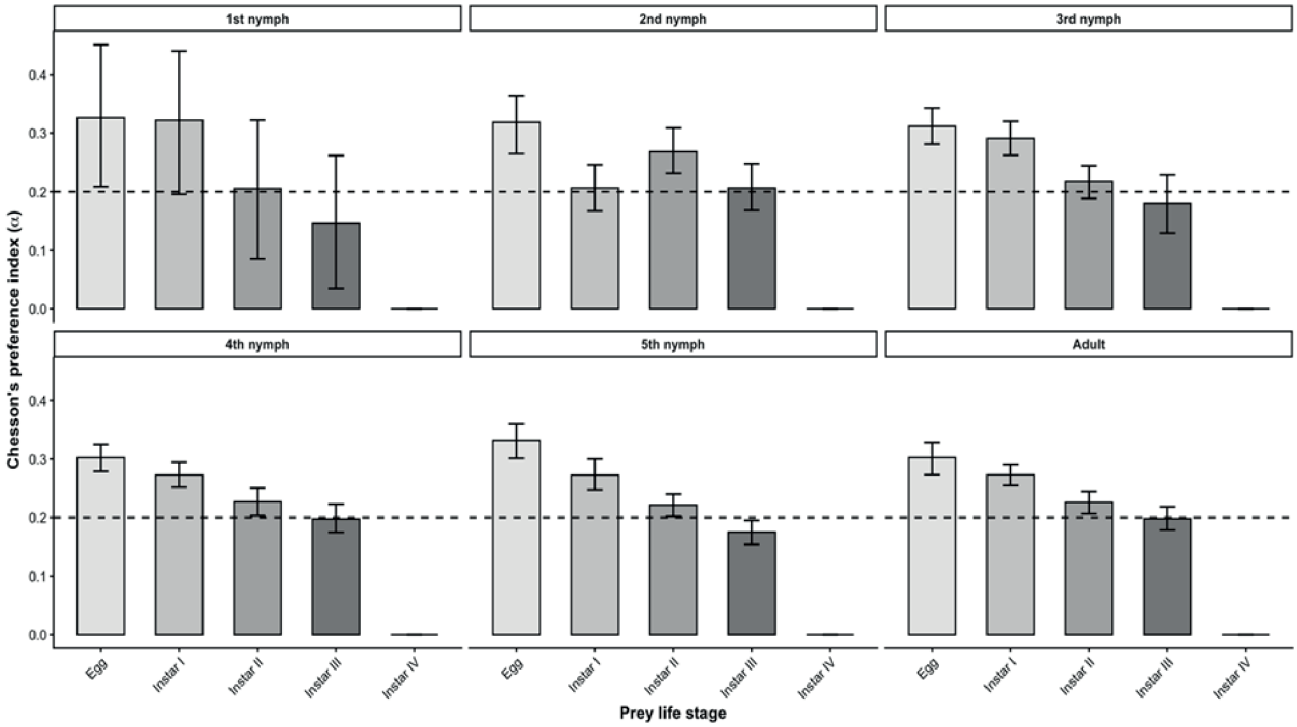

Figure 1: Preference of the different life stages of *N. tenuis* to different life stages of *P. absoluta*. Bars represent mean Chesson's preference index (α) for each prey stage, calculated separately for each life stage of *P. absoluta*. The dashed horizontal line (α = 0.2) indicates no preference; values above 0.2 indicate preference, while values below 0.2 indicate avoidance.

Table 3: Maximum likelihood estimates from logistic regression of proportion of prey number consumed as a function of initial prey densities by adult female and 5th nymphal stage of *P. absoluta*.

Predator life stage	Prey life stage	Parameter	Estimates	SE	Z-value	Pr (z)
Adult female	Egg	Linear	0.0631	0.0599	10.5	5.94×10^{-26}
		Quadratic	−0.000531	0.0000434	−12.3	1.58×10^{-34}
	1st instar	Linear	0.0628	0.00578	10.9	1.69×10^{-27}
		Quadratic	−0.000515	0.0000418	−12.3	5.54×10^{-35}
5th nymphal stage	Egg	Linear	0.0593	0.00571	10.4	2.80×10^{-25}
		Quadratic	−0.000471	0.0000414	−11.4	5.23×10^{-30}
	1st instar	Linear	0.0605	0.00555	10.9	1.28×10^{-27}
		Quadratic	−0.000463	0.0000397	−11.7	1.52×10^{-31}

stages, recording zero in the 4th instar larval stage of *P. absoluta* (Figure 1). The variation among *N. tenuis* life stages indicates an ontogenetic shift in *P. absoluta* selection.

Functional response of *N. tenuis*

Polynomial logistic regression of the proportion of prey consumed as a function of initial prey density indicated a type III functional response for both adult female and 5th instar nymphs of *N. tenuis* feeding on the eggs and 1st instar larva of *P. absoluta* (Table 3). The linear coefficient was significantly positive in all the predator-prey combinations, while the quadratic coefficient was significantly negative ($p < 0.001$) (Table 3), a pattern characteristic of a sigmoidal (type III) functional response. A low predation rate was observed in low prey densities and vice versa. Based on logistic regression results, the functional response parameters were estimated for each predator life stage and prey stage combination using Hassell's Type III model without prey replacement.

Prey consumption increased with prey density and reached an asymptote in all predator and prey combinations (Figure 2). Adult female *N. tenuis* showed higher consumption rates than 5th instar nymphs for both the egg and 1st instar larval stages of *P. absoluta*, especially at moderate to high prey densities. The consumption of the 1st instar larval stage of *P. absoluta* was slightly higher than egg consumption across *N. tenuis* life stages. The shaded confidence intervals around the fitted curves were narrow, revealing less overlap between *N. tenuis* life stages at higher prey densities. Therefore, these results show that the predation capacity of *N. tenuis* depends on its life stages.

Functional response analysis indicated a clear variation in the attack rate and handling time between the different life stages of *N. tenuis* and *P. absoluta* life stages (Figure 2). Attack rates differed between both *N. tenuis* and *P. absoluta* life stages. Adult female *N. tenuis* showed higher attack rates when feeding on *P. absoluta* eggs and the 1st instar larva as compared to the 5th nymphal stage. Adult *N. tenuis* females showed higher attack rates on the egg stage of *P. absoluta* (0.021 h^{-1}) as compared to the 5th nymphal stage (0.019 h^{-1}). Similarly, the attack rate of the female adult was higher on the 1st instar larva stage of *P. absoluta* (0.025 h^{-1}) relative to the 5th nymphal stage (0.015 h^{-1}). Also, among all the *N. tenuis* life stages, the attack rates were higher on the 1st instar larva stage compared to the egg stage of *P. absoluta* (Figure 3). However, confidence intervals overlapped between prey stages within predator groups, indicating moderate variability in the attack rates (Figure 3). Handling time varied between both *N. tenuis* and *P. absoluta* life stages. The handling

time of the 5th nymphal stage of *N. tenuis* was slightly higher when feeding on the 1st instar larva of *P. absoluta* (0.030 h) than for the egg stage (0.029 h). In contrast, adult female *N. tenuis* showed lower handling times when feeding on the 1st instar of *P. absoluta* (0.024 h) relative to the egg stage (0.03 h) (Figure 3). However, the confidence intervals overlapped between *P. absoluta* stages within *N. tenuis* life stages, indicating a moderate difference in their handling times (Figure 3).

Adult females and the 5th nymphal stage of *N. tenuis* exhibited a preference for feeding on *P. absoluta* eggs and 1st instar larval stages (Figure 4). The Chesson's preference index shows a slight variation between predator and prey life stages. The adult female and 5th nymphal stages feeding on *P. absoluta* eggs and 1st instar larval stages recorded a preference index closer to the neutral preference line (α = 0.5), indicating no strong preference for either life stage of *P. absoluta*. However, the preference index recorded in

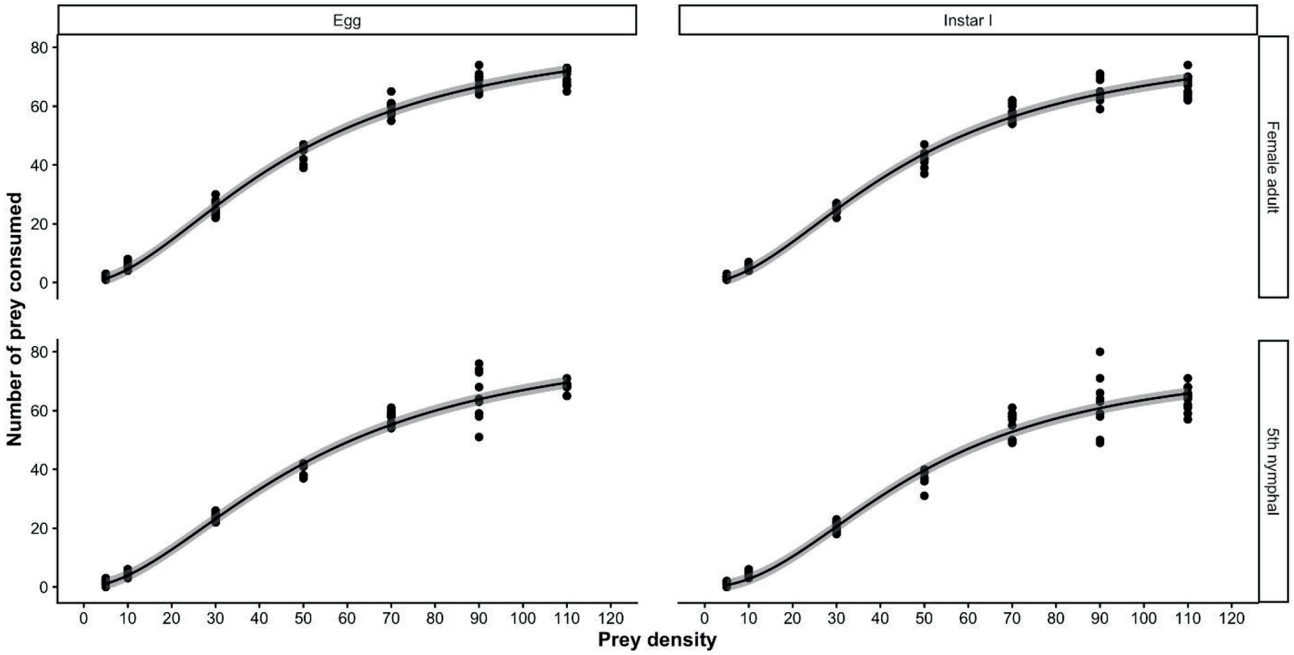

Figure 2: Type III functional response of *N. tenuis* across *P. absoluta* life stages. Points represent observed prey consumption, solid lines indicate fitted functional response curves, and shaded areas represent 95% confidence intervals.

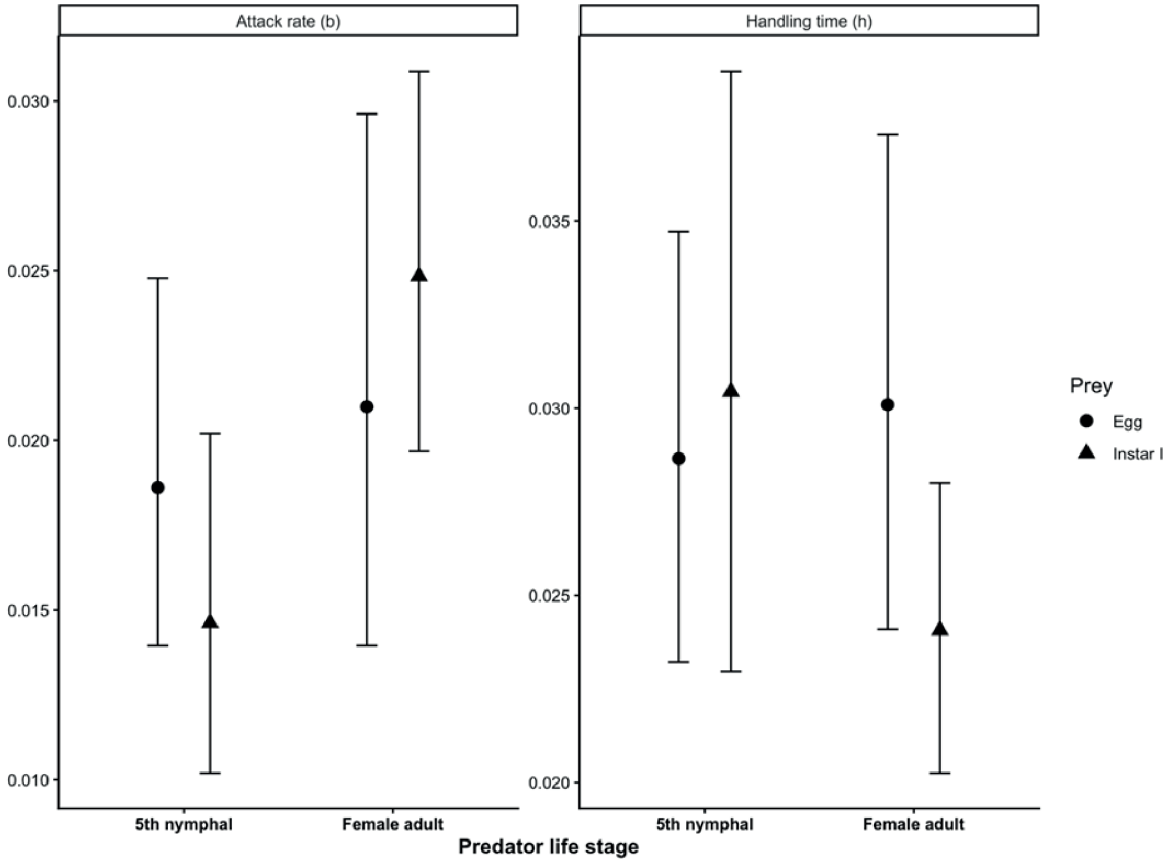

Figure 3: Functional response estimates of attack rate (h^{-1}) and handling time (h) during the considered time interval (24 hours) of the 5th nymphal stage and adult female of *N. tenuis*.

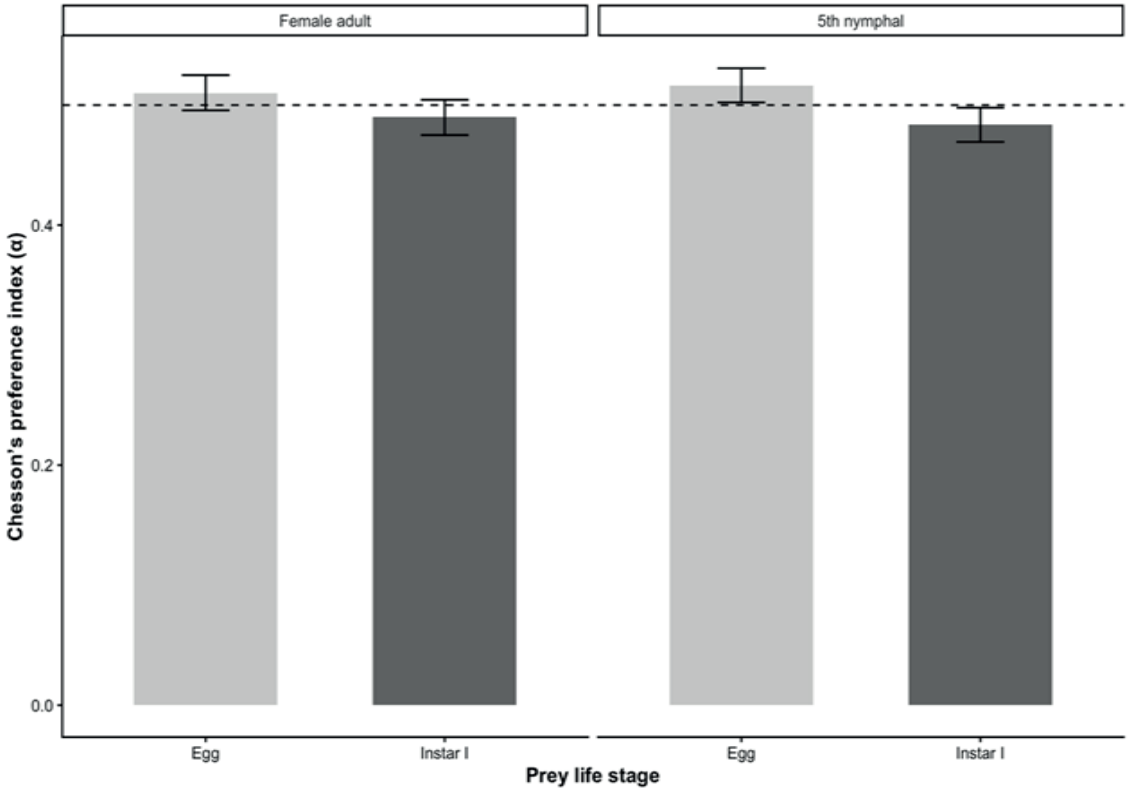

Figure 4: Preference of the 5th nymphal and adult female stages of *N. tenuis* to the egg and 1st instar larval stages of *P. absoluta*. Bars represent mean Chesson's preference index (α) for each prey stage, calculated separately for each life stage of *P. absoluta*. The dashed horizontal line (α = 0.5) indicates no preference; values above 0.5 indicate preference, while values below 0.5 indicate avoidance.

both adult female and 5th nymphal stages of *N. tenius* was higher in the egg stages of *P. absoluta* as compared to the 1st instar larval stage (Figure 4). The confidence interval of adult female *N. tenuis* overlapped with the neutral line, showing no statistical difference in their preference to *P. absoluta* life stages (Figure 4). These results indicate ontogenetic differences in prey selection and are consistent with functional response analyses showing higher predation efficiency on the egg stages of *P. absoluta*.

DISCUSSION

A crucial factor in limiting the growth and invasion of an exotic pest is the efficiency of local natural enemies in controlling its population (Naselli et al. 2016). One such natural enemy is *N. tenuis* whose population density in tomato fields or greenhouses depends on agricultural practices, prey availability, and pest control. In open-field environments, populations are typically low and fluctuate with the availability of prey, such as eggs and larvae of pests, beginning at a few individuals per plant during the early crop stages and increasing as pest populations grow. Greenhouses have consistent temperatures and abundant host plants, making predator populations more stable and often higher, especially when introduced for biological control (Calvo et al. 2012). Effective greenhouse biological control methods can reduce pest populations like tomato leaf miners and whiteflies with dose concentrations of 0.5 *N. tenuis* per plant, with *E. kuehniella* eggs as an alternative prey (Urbaneja et al. 2012). *Nesidiocoris tenuis* is zoophytophagous and may perforate plant tissues when food is scarce; hence, high population density numbers of the agent may lead to increased plant damage (Sánchez 2009). Thus, pest control in field and greenhouse tomato production requires monitoring and releasing predator populations to maintain equilibrium.

The determination of the quantity of prey killed by predators is essential for assessing the impact of predators on prey population dynamics (Messina & Sorenson 2001). The feeding potential of *N. tenuis* in the current study was observed only on eggs, 1st, 2nd and 3rd instar larvae of *P. absoluta*. Additionally, adult and the 5th nymphal stage exhibited great preference to the eggs of *P. absoluta*. The current research findings reaffirms the earlier observations made by Ettaib et al. (2016), Sireesha et al. (2018) and Dhanapal et al. (2021), who discovered that *N. tenuis* adults and nymphs consumed *P. absoluta* larvae in all stages, with the exception of the 4th instar larva and pupa. It was also observed that as the predator grows in size, it devours more prey and that the size of the prey affects how quickly the predator will consume its prey (Urbaneja et al. 2010).

In terms of its efficient use as a biocontrol agent, *N. tenuis* adult and 5th nymphal stage preference for *P. absoluta* eggs is considered advantageous due to their capacity to provide adequate pest suppression at the egg stage of the pest, which is a non-feeding stage, and prevents their further development and population build-up into the active feeding stages. This observation may be linked to various factors, including the immobile nature of the eggs and the propensity of the mirid bug to consume smaller developmental stages.

The functional response is an important indicator of a predator's potential efficacy against a particular prey since it depicts the relationship between the predator's rate of consumption and the density of its prey (Gavkare et al. 2017). In the present study, laboratory experiments showed that *N. tenuis* exhibited a type III functional response. The number of *P. absoluta* eggs and 1st instar larva eaten by *N. tenuis* increased with increasing prey density. A type III functional response indicates a low-density natural refuge for prey, as predation rates decline when prey availability is limited, often due to decreased encounter rates, prey switching, or limits related to predator learning. This density-dependent phenomenon enables a proportion of the prey population to evade predation, hence diminishing the risk of extinction at low densities. As prey abundance escalates, predation pressure intensifies swiftly, augmenting control, whereas it diminishes as prey populations wane. As a result, prey populations are maintained at low levels instead of being eradicated, fostering stable predator–prey

interactions and facilitating sustained biological control (Holling 1959; Murdoch & Oaten 1975; Hassell 2000).

A study by Michaelides et al. (2017) on the impacts of two generalist predators preying on *P. absoluta* eggs, showed that *N. tenuis* and *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) displayed a type III functional response. The results of the present study also confirm this pattern, as *N. tenuis* exhibited a type III functional response similar to that reported. Two predatory mirid bugs *Macrolophus caliginosus* Wagner (Heteroptera: Miridae) and *N. tenuis* that were found to be effective against *P. absoluta* showed a type III functional response when they preyed on *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Alerodidae) in an experiment carried out in the laboratory to determine their predatory potential (Enkegaard et al. 2001; Hamdan 2006; Madbouni et al. 2017). According to Queiroz et al. (2015), when *Amphiareus constrictus* (Stal) (Hemiptera: Anthocoridae) and *Blaptostethus pallescens* (Poppius) (Hemiptera: Anthocoridae) preyed on different densities of *P. absoluta* eggs, they displayed a type III functional response. Enkegaard et al. (2001) discovered that when the predator *M. pygmaeus* fed on different densities of *T. vaporariorum* 1st instar nymphs, it exhibited a type III functional response. Predators exhibiting a Type III functional response can effectively regulate pest populations in the field and green house at moderate to high concentrations, rendering them valuable as biological control agents (Michaelides et al. 2017; Kalinkat et al. 2023). The efficacy of the management depends on operational parameters like the timing and frequency of releases, the quality and number of parasitoids or predators, and meteorological occurrences (Fernández-Arhex & Corley 2003).

The findings of the present study reveal that the adult female of *N. tenuis* demonstrated a reduced attack rate of 0.021 h^{-1} when preying on *P. absoluta* eggs, in contrast to an attack rate of 0.025 h^{-1} on 1st instar larva. This indicates that eggs were comparatively more challenging for the predator to perceive, especially at low densities, perhaps due to their tiny size, immobility, and reduced visibility on the leaf surface. At low egg densities, the predator seemed to underutilise eggs and instead prioritised 1st instar larva, which may be more easily detectable due to minimal movement or feeding activity on the leaf tissue. As egg concentrations increased, predation on eggs escalated, possibly indicating behavioural adaptation and enhanced foraging efficiency by the predator. This pattern exemplifies a type III functional response, wherein predators demonstrate learning behaviour, prey switching, or enhanced searching efficiency as prey density increases. The predator may initially need time to identify eggs as a viable food source; however, as egg density rises, it modifies its foraging technique and escalates egg intake.

This study demonstrated that *N. tenuis* exhibited a higher overall predation rate on *P. absoluta* eggs, perhaps due to the reduced handling time involved in egg ingestion. Eggs typically necessitate less time to capture and ingest than larval stages, enabling the predator to feed on more prey within the same timeframe. Thus, while eggs may initially be more challenging to identify, once discovered, they constitute an effective and lucrative food supply for the predator, resulting in heightened predation at elevated egg density.

It has been observed that predators with longer handling time cause the functional response to "saturate" more quickly (Kisdi & Liu 2006). *Nesidiocoris tenuis* was found to be a more competitive predator than *M. pygmaeus* for *P. absoluta* eggs in an experiment carried out to test the multiple predatory response of two predators. This was due to its shorter handling time and saturation levels at larger prey densities (Michaelides et al. 2017).

The handling time for *N. tenuis* life stages varied a little depending on the stage of the prey that was being handled. The 5th nymphal stage took a bit longer to handle the 1st instar larva of *P. absoluta* than the eggs. This suggests that juvenile predators may take a longer time to prey on larval instars. On the other hand, adult female *N. tenuis* handled 1st instar larva better than eggs. This could mean that they were better at preying, have greater experience, morphologically well developed, and have high feeding capacity (Urbaneja et al. 2012; Biondi et al. 2013). The overlap of confidence intervals between prey stages within each predator life stage indicates that these differences were minor and not notably evident, suggesting that both eggs and early instar larvae of *P. absoluta* are similarly exploitable prey for *N. tenuis* (Murdoch & Oaten 1975). The present study revealed that the attack rate and handling time of *N. tenuis* varied depending on the stage of the predator and prey. This information is crucial for exploiting the full potential of *N. tenuis* alongside other candidate biological control agents as integral part of developing country-specific IPM strategy for *P. absoluta* in tomato cropping systems in Ghana. However, feeding during the acclimation period on *P. absoluta* and *E. kuehniella* eggs may have affected the observed prey preferences of *N. tenuis* due to consumer learning, indicating a possible experimental artefact. Generalist predators can develop search images, whereby repeated exposure improves prey detection, attack efficiency and handling success, regardless of inherent preference (Holling 1959; Murdoch & Oaten 1975). Adult females with prior experience may, exhibit improved foraging efficiency and develop a bias toward egg prey in subsequent feeding trials consistent with principles of optimal foraging theory (Stephens & Krebs 1986). Learning-induced changes in prey selection and functional responses in other mirid predators demonstrate the need of integrating learning effects in laboratory predation research (Schenk & Bacher 2002; Jaworski et al. 2013).

The predictive power of determining functional responses in the laboratory with a single prey species and basic settings may be restricted when predicting predator behaviour in the field or in a greenhouse. Arthropod predators face complicated surroundings and a variety of prey circumstances in the wild or in greenhouse conditions (Mahdian et al. 2007). Furthermore, if prey is few or nonexistent, *N. tenuis*'s feeding habit on tomato plants may cause serious damage (Arnó et al. 2010; Castañé et al. 2011). When the prey density is low, it will lead to the enhanced search ability of the predator. In this context, these dynamics highlight the importance of well-timed releases and predator-prey balance, underscoring the role of augmentative biological control as an environmentally sustainable approach for managing pests, particularly invasive species such as the fall armyworm in Ghana. Consistent with this approach, the findings of the present study show that *N. tenuis* exhibits effective predation on the vulnerable stages of *P. absoluta*, supporting its potential use as a candidate predator for augmentative biological control in tomato agroecosystems. A study on the augmentative control of fall armyworm using *Telenomus remus* (Nixon) (Hymenoptera: Scelionidae) indicated that this natural enemy parasitises egg masses in maize farming systems under natural conditions (Agboyi et al. 2021). The diversity of parasitoids and predators in Ghana, with species including *T. remus*, *Trichogramma* spp., *Chelonus bifoveolatus* (Szépligeti) (Braconidae: Hymenoptera), *Coccygidium luteum* (Brullé) (Hymenoptera: Braconidae), *Rhynocoris segmentarius* (Germar) (Hemiptera: Reduviidae), *Zelus obscuridorsis* (Stål) (Hemiptera: Reduviidae), *Necremnus* spp., *N. tenuis* and *M. pygmaeus,* establishes a robust ecological basis for augmentative biological control and facilitates their integration with cultural and selective chemical methods to preserve natural enemy populations (Mansour et al. 2019; CABI 2020; Idemudia et al. 2024). A study conducted to determine the insect diversity and abundance of tomato accessions in Ghana reported that, ladybird beetles, lacewings, spiders, predatory

ants, and parasitoids such as *Trichogramma* spp. found in tomato fields help to suppress pests such as aphids, whiteflies, and several lepidopteran pests (Ofori et al. 2014). *Nesidiocoris tenuis* can synergistically interact with these natural enemies by preying on pest eggs and early instars that evade parasitism; however, competition with other predators may arise under conditions of low prey availability (Calvo et al. 2012; Messelink et al. 2014).

Poorly coordinated augmentative or conservation measures may hinder early pest suppression due to intraguild predation and competition (Sylla et al. 2017; Kinyanjui 2021). *Nesidiocoris tenuis* prey effectively on early developmental stages of *P. absoluta* but may also consume alternative prey and plant tissues, influencing crop performance and interactions with other natural enemies (Desneux et al. 2010; Mirhosseini et al. 2019). Laboratory experiments cannot completely replicate the intricate dynamics in the field resulting from environmental variability, diversity of prey, and competing natural adversaries (Sylla et al. 2017). Consequently, a representative multi-site greenhouse and field investigations throughout the major tomato growing regions and agroecological zones in Ghana are essential to further evaluate and understand predator-prey dynamics, intraguild interactions, predator learning, plant-feeding behaviour, and the ecological compatibility and significance of local species (Mirhosseini et al. 2019). Site-specific experiments will optimise predator release densities, timing, and complementary crop management approaches, thereby resulting in lower pesticide usage and fostering sustainable tomato production under the umbrella of IPM in Ghana (Sylla et al. 2017; Kinyanjui et al. 2021; Tham-Agyekum et al. 2025).

CONCLUSION

This study has demonstrated that *N. tenuis* is an effective life stage-dependent predator of *P. absoluta*, with adult females and 5th-instar nymphs preying most on eggs and 1st instar larva and stabilising type III responses. Predation by *N. tenuis* was reduced in the late larval instars of the prey indicating that *N. tenuis* can be used as a biological control agent for the eggs, especially during the peak laying period of *P. absoluta* and early instar larvae. For effective and sustainable field releases of the predator, one must consider other potential biocontrol agents (*T. remus*, *C. bifoveolatus*, *C. luteum, R. segmentarius*, *Z. obscuridorsis*, *N. tenuis* and *M. pygmaeus)* that have preference for the adult and late nymphal stages of *P. absoluta* in combination with other IPM methods such as surveillance, botanical pesticides, and cultural practices for sustainable pest management.

RECOMMENDATIONS

Follow up greenhouse and field studies at different agroecological zones or locations within the country are needed to confirm these laboratory findings, evaluate prey relationships, study predator learning and plant-feeding behaviour and predator preference towards the target pest among other prey species.

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AUTHOR'S CONTRIBUTIONS

All authors designed the research methodology, read and approved the manuscript. Hannah Serwaa Nuamah conducted the laboratory experiment, analysed some part of the data and wrote the manuscript. Maxwell Kelvin Billah, Ken Okwae Fening, and Lakpo Koku B. A. Agboyi offered insight into data analysis, presentation, and read the manuscript as Supervisors. Clinton Gyabeng analysed some part of the data and read the manuscript.

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