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Feeding Preference and Foraging Behaviour of *Eriopsis connexa* on Two Aphid Species

Anna Mara Ferreira Maciel  | Lucas Ramos Vieira  | Rayana Mayara Rocha Carvalho  | Wesley Augusto Conde Godoy 

Department of Entomology and Acarology, "Luiz de Queiroz" College of Agriculture, University of São Paulo (USP), Piracicaba, São Paulo, Brazil

Correspondence: Anna Mara Ferreira Maciel (annamaramaci@gmail.com)

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ABSTRACT

Aphids are phloem-feeding insects that cause both direct and indirect damage to crops, reducing agricultural productivity. Among the available pest control strategies, biological control using natural enemies is a sustainable and effective approach. The ladybird *Eriopsis connexa* (Germar, 1824) is a generalist predator known for its voracity and ability to exploit aphid populations across diverse habitats. This study aimed to evaluate the foraging behaviour and prey preference of *E. connexa* when exposed to two aphid species, *Myzus persicae* (Sulzer, 1776) and *Aphis gossypii* Glover, 1877, under varying ecological contexts. We conducted three independent experiments to assess: (i) preference across developmental stages (2nd vs. 4th instars); (ii) functional response to increasing prey density; and (iii) prey choice in varying species proportions. Results indicate that *E. connexa* lacks an intrinsic preference for either aphid species. Instead, its predation behaviour is significantly influenced by prey characteristics such as instar stage and relative abundance. The predator tended to consume smaller instars and more abundant prey first, suggesting decisions based on prey profitability. These findings enhance our understanding of predator–prey dynamics and biological control strategies involving aphidophagous predators in agroecosystems.

1 | Introduction

The dynamics of predator–prey interactions are a fundamental aspect of ecology, as these relationships play a crucial role in shaping community structure and regulating insect populations. Among the various groups of insect predators, coccinellids stand out due to their vast species diversity, intense foraging activity and importance as natural enemies of agricultural pests (Ślipiński and Tomaszewska 2010; Michaud 2012; Pervez et al. 2020). The relationship between Coccinellidae and aphids has been recognised for centuries (Kirby and Spence 1826). Among the ladybird species, *Eriopsis connexa* (Germar, 1824) is widely distributed in South America and has demonstrated a high potential for reducing populations of multiple pest species, with a preference for aphids (Sarmiento et al. 2007; Dos Santos et al. 2020; Francesena et al. 2019; de Matos et al. 2022).

Globally, *E. connexa* plays an essential role in the natural control of aphids and mites, characterised by its polyphagy, voracity and widespread distribution across economically important crops (de Oliveira and Matos 2004; Nascimento et al. 2021). In addition to its foraging capacity and widespread presence, *E. connexa* has several traits valuable for integrated pest management (IPM), including populations selected for resistance to pyrethroid insecticides (Lira et al. 2019, 2023; D'Ávila et al. 2018; Rodrigues et al. 2020) and spinosyns (Costa et al. 2020), as well as its potential for mass rearing using alternative prey or artificial diets (Silva et al. 2009, 2013).

However, a detailed understanding of a natural enemy's interactions with prey under variable conditions is essential before recommending a natural enemy for biological control programmes. As generalist predators, ladybirds may exhibit prey preferences

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and shifts in foraging behaviour influenced by factors such as prey quality, size, distribution, density, starvation period, predator and prey developmental stages, and the presence of other predators (Zarghami et al. 2014; Rocca et al. 2017; Pervez and Yadav 2018).

Changes in prey abundance also influence predator strategies. Optimal foraging theory posits that predators adopt strategic choices to maximise their energy gain while minimising costs (Stephens and Krebs 1986). This theoretical framework enables researchers to explore scenarios in which the relationships among prey preference, attack rates and population stability can be analysed. An important tool for studying these dynamics is the functional response, which quantifies the number of prey consumed by a predator relative to prey density over a specific time period (Holling 1959). Key parameters in this model are the attack rate and handling time, and predators exhibiting Type II or Type III functional responses are often effective biological control agents (Sarmiento et al. 2007; Islam et al. 2021; Dami et al. 2023; Kulkarni and Evenden 2024).

Predator behaviour may shift as the relative density of prey species changes (Jaworski et al. 2013). These behavioural adjustments can promote prey population stability by increasing the consumption of more abundant prey while exerting less pressure on less abundant prey, preventing extinction or outbreaks (Murdoch 1969). This dynamic is valuable in pest management, as generalist predators can switch between prey species, helping to suppress pest populations in agricultural systems (Symondson et al. 2002).

Although several studies have explored the biology of *E. connexa* and its use in biological control (Almeida et al. 2021; Nascimento et al. 2021; de Matos et al. 2022), particularly regarding insecticide effects on behaviour and physiology (Lira et al. 2023; Nascimento et al. 2023; Rodrigues et al. 2024) knowledge of its ecological behaviours—such as foraging strategy, prey preference, functional response and switching behaviour—remains limited (Sarmiento et al. 2007; Francesena et al. 2019; Dos Santos et al. 2020; Nascimento et al. 2021).

Investigating foraging behaviour is crucial, as it reflects the predators' adaptive capacities to exploit diverse prey types in response to varying prey availability (Heit et al. 2008; Hodek and Evans 2012). Such behaviour enhances the efficiency of natural enemies by enabling them to target the most abundant prey species, thereby improving population regulation. Understanding a predator's prey preferences and behavioural responses is critical to evaluating its predatory potential and effectiveness in biological control programmes.

In this study, we investigated the foraging behaviour of *E. connexa* in response to two aphid species, *Myzus persicae* (Sulzer, 1776) and *Aphis gossypii* Glover, 1877, under varying conditions. These aphids are highly polyphagous pests. The species *M. persicae*, the green peach aphid, feeds on over 40 plant families (Blackman and Eastop 2000), while *A. gossypii*, a major pest of cotton, also infests cucurbits, citrus, potato, peach and pepper (Blackman and Eastop 2000). The primary damage caused by these aphids stems from their ability to transmit plant viruses: *M. persicae* transmits more than 100 plant viruses, and *A. gossypii* is a vector for at least 76 viral diseases in a wide range of crops (Chan et al. 1995; CABI 2021).

This study aimed to investigate *E. connexa*'s prey preference for varying aphid species and instars, analyse its foraging behaviour in mixed-prey environments with different species densities and proportions, and evaluate its functional response to each aphid species.

2 | Materials and Methods

2.1 | Insect Rearing

Eriopsis connexa and the aphids *M. persicae* and *A. gossypii* were reared in the Ecology and Forest Entomology Laboratory, Department of Entomology and Acarology, University of São Paulo (USP)/Luiz de Queiroz College of Agriculture (ESALQ), Piracicaba, São Paulo, Brazil. The aphids of *M. persicae* were maintained in 15 cm diameter Petri dishes, containing a cabbage (*Brassica oleracea*) leaf disk on 10% agar. The dishes were sealed with a white paper towel secured by a rubber band to prevent aphid escape while allowing aeration inside the Petri dish. The cabbage leaves were sourced from plants grown in a greenhouse. The dishes were kept under controlled conditions (20°C ± 1°C, 70% ± 10% RH, and a L:D 14:10 photoperiod). *A. gossypii* was reared using a similar method, using cotton (*Gossypium hirsutum*) leaf disks under specific conditions (25°C ± 1°C, 70% ± 10% RH, and a L:D 12:12 photoperiod). Maintenance was performed twice weekly.

Adults of *E. connexa* were maintained in transparent polyethylene containers (350 mL) with perforated lids to allow gas exchange and humidity control. The pots were housed under controlled conditions (25°C ± 1°C, 70% ± 10% RH, and a L:D 12:12 photoperiod). The diet provided consisted of an artificial diet mixture of brewer's yeast, water and honey (1:1:1 ratio), along with *Ephestia kuehniella* (Lepidoptera: Pyralidae) eggs. A 0.5-mL microtube filled with water and sealed with moistened cotton was also included. Paper towels were used as obstacles to prevent cannibalism and serve as an oviposition substrate. The ladybird's containers were maintained every 48 h, and *E. kuehniella* eggs were offered daily.

Eggs were collected daily and stored in plastic Petri dishes (9 cm diameter) inside a BOD incubator until larval hatching. When larvae reached the second instar, they were transferred at a density of two per flat-bottom glass tubes (8 × 2.5 cm). These tubes were sealed with PVC plastic film perforated to allow gas exchange and humidity control. They were maintained in the BOD incubator under the same conditions described previously for ladybirds, and larvae were fed *E. kuehniella* eggs until adult emergence. Upon reaching adulthood, ladybirds were separated into transparent polyethylene containers (as mentioned in the previous paragraph) to maintain subsequent generations.

2.2 | Bioassay 1: Foraging Behaviour of *Eriopsis connexa* in Different Prey Instars

Adult *E. connexa* were subjected to predation choice tests, using second- and fourth-instar *M. persicae* and *A. gossypii* as prey. A completely randomised design (CRD) with six treatments was implemented to encompass three predation

categories: (i) predation only on *M. persicae* instars, (ii) predation only on *A. gossypii* instars, and (iii) predation on both species and different instars of aphids. The six treatments were: (a) predation on second- and fourth-instar *M. persicae* (M2M4), (b) predation on second- and fourth-instar *A. gossypii* (A2A4), (c) predation on second instar of both species, *A. gossypii* and *M. persicae* (M2A2), (d) predation on fourth instar of both species, *A. gossypii* and *M. persicae* (M4A4), (e) predation on fourth-instar *M. persicae* and second-instar *A. gossypii* (M4A2), (f) predation on second-instar *M. persicae* and fourth-instar *A. gossypii* (M2A4).

Each treatment was replicated 10 times in plastic Petri dishes (9 cm diameter) under controlled conditions ($25^{\circ}\text{C} \pm 2^{\circ}\text{C}$; $70\% \pm 10\%$ RH). Ten nymphs (five per instar and species combination) were provided per dish. Predation events were recorded at 15-min intervals over a 2-h observation period. A predation event was defined as the successful capture and subsequent killing of prey. Before the trials, all *E. connexa* adults were starved for 24 h and had no prior exposure to aphids. Figure 1 shows the six treatments. Treatments (a) and (b) assessed whether older instars were preferred by the predator regardless of the species offered. Options (c) and (d) were used to analyse whether one species was preferred over another according to the instar provided. Treatment choices (e) and (f) tested the interaction between species and instars.

2.3 | Bioassay 2: Foraging Behaviour in *Eriopis connexa* in Different Proportions of Aphid Species

To investigate the influence of prey density on switching behaviour in *E. connexa*, a completely randomised design (CRD) was implemented with four treatments (A–D) and 12 replicates.

Prey ratios of *A. gossypii* (A) to *Myzus persicae* (M) were manipulated inversely across treatments: (A) 10A:40M, (B) 20A:30M, (C) 30A:20M, and (D) 40A:10M, maintaining a constant total of 50 aphids per Petri dish. Adult *E. connexa* were starved for 24 h before the trials. Each experimental arena (plastic Petri dish, 9 cm diameter) contained one *E. connexa* adult and the designated prey mixture. After 24 h, each predator was removed, and the number of preys consumed was recorded.

2.4 | Bioassay 3: Functional Response of *Eriopis connexa* Preying on *Aphis gossypii* and *Myzus persicae*

The functional response of *E. connexa* to the aphids *M. persicae* and *A. gossypii* was investigated using a completely randomised design (CRD) with two treatments: (a) single-species arena with *M. persicae* and (b) single-species arena with *A. gossypii*. Six prey density levels (10, 25, 40, 55, 70 and 85 aphids per Petri dish) were tested for each species, with 10 replicates per density. Each Petri dish (15 cm diameter) contained a cotton leaf (*G. hirsutum*). Adult *E. connexa* were starved for 24 h before trials to standardise hunger levels. Prey density levels were determined based on preliminary tests of daily consumption rates. In each trial, one *E. connexa* was introduced into a dish, and the number of unconsumed aphids was recorded after 24 h. No prey replenishment occurred during the experiment.

2.5 | Statistical Analysis

To analyse the prey instar preference experiment, Kaplan-Meier survival analysis was conducted using the *survfit* function, in software R (R Core Team 2024), to evaluate predation

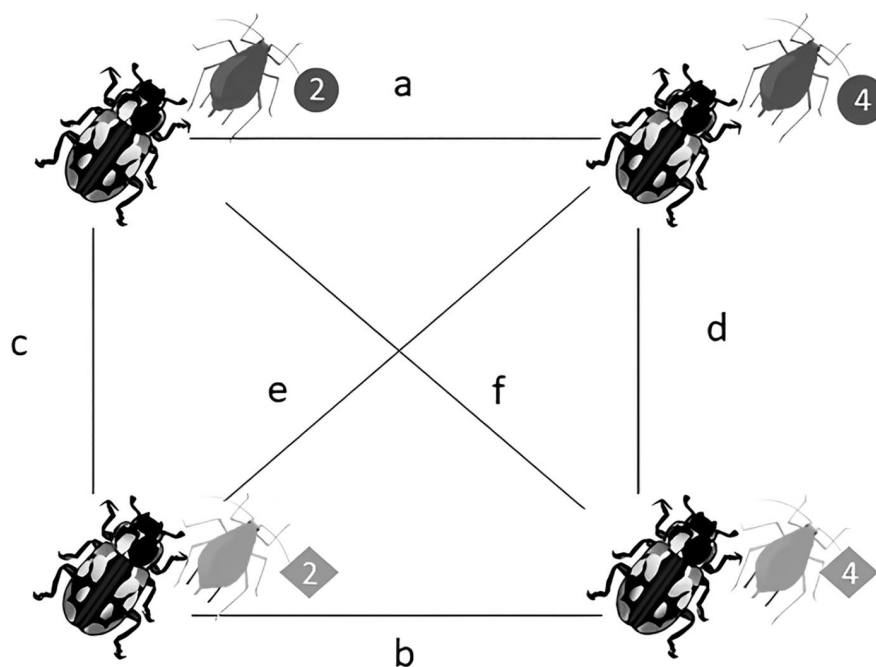


FIGURE 1 | Experimental design for the foraging behaviour of *Eriopis connexa* on different instars of *Myzus persicae* and *Aphis gossypii*. The circle shape represents individuals of the species *M. persicae*, while the diamond represents individuals of the species *A. gossypii*. The numbers indicate the instars of the aphids used in each treatment.

events across treatments, with observations recorded at 15-min intervals. Mean survival times were calculated for each treatment. Survival curves were compared using the log-rank (LR) test (*survdif* function), and pairwise comparisons between treatments were conducted with the *pairwise_survdif* function. We also adjusted *p*-values for multiple comparisons using the Bonferroni correction to control type I error. All functions are available in the *survival* package. In the risk table below the survival curves, the value outside parentheses represents the number of aphids at risk at the beginning of each interval, that is, those still alive and not censored immediately before that time point. The value inside parentheses shows the percentage of individuals at risk relative to the total number of aphids included in that treatment at time zero. All analyses were carried out using software R 4.4.1 (R Core Team 2024).

The switching behaviour in the prey ratio experiment was assessed using Manly's preference index (β) log-scaled (Moradi et al. 2020) within the framework of Manly (1974), calculated as:

$$\beta_1 = \frac{\log\left(\frac{e_1}{A_1}\right)}{\log\left(\frac{e_1}{A_1}\right) + \log\left(\frac{e_2}{A_2}\right)}$$

where β_1 (Beta = Manly preference index) is the preference for a particular prey, e_1 and e_2 are the number of type 1 and 2 prey remaining at the end of the experiment, respectively, and A_1 and A_2 are the number of type 1 and 2 prey offered, respectively. In this study, the species *A. gossypii* was considered species one, and *M. persicae* was considered species two. Index values range from 0 to 1, where an index close to 1 indicates strong preference for *A. gossypii* while values closer to 0 indicate a preference for *M. persicae*. A value around 0.5 suggests no strong preference (random predation). Manly's indices were compared across treatments using analysis of variance (ANOVA), followed by the Tukey test for group-level comparisons, using software R (R Core Team 2024).

The type of functional response (Type II or III) was determined using the *frair_test* function from the *frair* package (Pritchard et al. 2017), based on the number of preys consumed. After identifying the functional response type, data were fitted to Rogers' equation (Rogers 1972) corresponding to the identified response type. Initial parameter estimates and fixed values were provided, and the model was optimised using the *frair_fit* function, which employs maximum likelihood estimation to derive functional response parameters (attack rate *a* and handling time *h*). To formally compare these parameters between species, the *frair_compare* function was applied, performing a likelihood-ratio test on models fitted separately for each species. Statistical significance of differences in *a* and *h* was evaluated based on the resulting *z*-values and *p*-values.

Parameter uncertainty was also assessed using non-parametric bootstrapping via the *frair_boot* function, which operates on the output of *frair_fit*. Bootstrap results generated 95% BCa (bias-corrected and accelerated) confidence intervals for the fitted

curves, visualised using the *drawpoly* function. The overlap of these bootstrap confidence intervals between species was used to assess potential differences in predation parameters. These intervals provided a representation of uncertainty but were not used as a formal test of differences. All analyses were carried out using R (R Core Team 2024).

3 | Results

3.1 | Bioassay 1: Foraging Behaviour of *Eriopsis connexa* on Different Prey Instars

Regarding the aphid instars provided, the survival curves in Figure 2 depict the predation dynamics of *E. connexa* across treatments, with predation events recorded at 15-min intervals. Complete prey consumption by *E. connexa* was observed in two treatments: both aphid species in the second instar (M2A2) and the treatment where *M. persicae* was in the fourth instar and *A. gossypii* in the second instar (M4A2). In contrast, no complete predation occurred in the remaining treatments (Figure 2).

To statistically validate these differences, a log-rank test was used to compare the mean survival times across observed intervals (Table 1). The analysis revealed significant differences among treatments (log-rank test: $\chi^2 = 310$, $df = 5$, $p < 0.0001$), supporting the survival curve patterns (Figure 2).

Survival analysis revealed significant differences in predation rates among treatments. Predation was fastest when both species were offered in the second instar (M2A2) with a mean survival time of aphids of 19.5 min, followed by the mixed-instar treatment with 69.2 (M4A2), while treatments involving fourth-instar aphids (e.g., M4A4) exhibited markedly slower predation (Table 1). This indicates that predation by *E. connexa* was significantly faster when both species were offered in the second instar (M2A2) compared to the other treatments, indicating that instar stage, rather than species identity, strongly influenced predation dynamics.

Post hoc statistical comparisons revealed no significant differences in mean predation times among the treatments M4A2, A2A4, M2M4 or M2A4 (Table 1), suggesting similar predation efficiency across these groups.

In contrast, the lowest predation rate was observed in the M4A4 treatment (both species in the fourth instar), with a mean survival time of 93.7 min. This stark contrast highlights that *E. connexa* consumed prey more rapidly and completely when the prey items were small (M2A2), and the predation number declined markedly when both species were large (M4A4).

3.2 | Bioassay 2: Foraging Behaviour in *Eriopsis connexa* in Different Proportions of Aphid Species

The mean preference index (β_1) varied across aphid proportion treatments (Table 2). In treatment A (10 *A. gossypii*

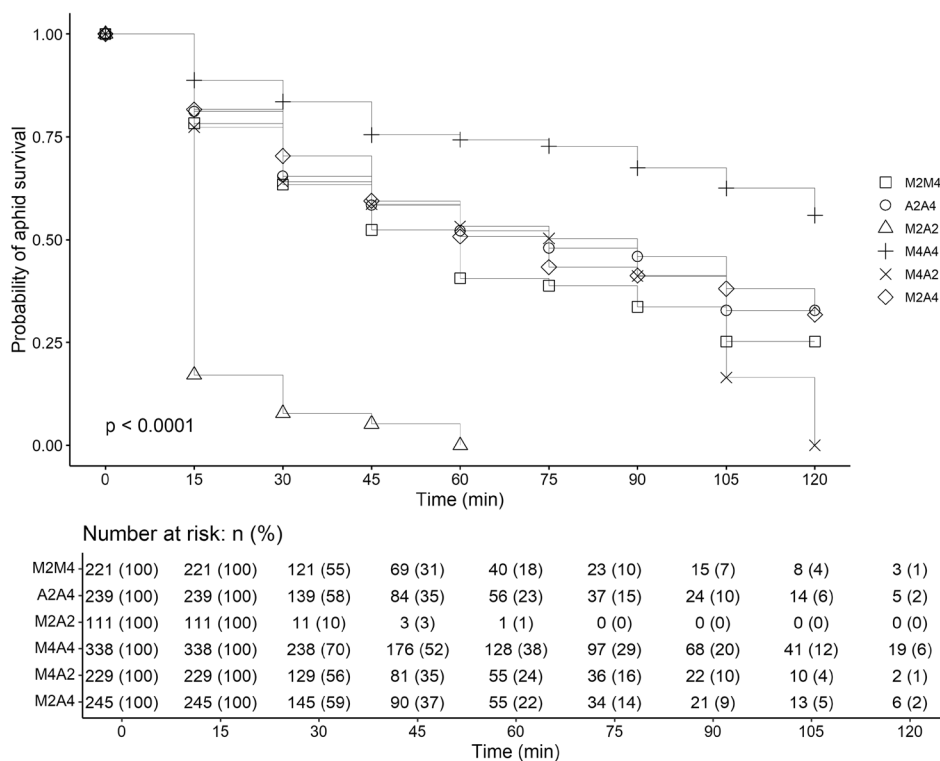


FIGURE 2 | Survival of *Eriopsis connexa* consumption under different treatments containing *Aphis gossypii* and *Myzus persicae* in different instars. In the risk table, values outside parentheses indicate aphids at risk; values in parentheses show the percentage relative to the initial number. A2, *A. gossypii* 2nd instar; A4, *A. gossypii* 4th instar; M2, *M. persicae* 2nd instar; M4, *M. persicae* 4th instar.

TABLE 1 | Mean survival times in minutes (\pm SEM) of *Eriopsis connexa* under different treatments with the aphid species *Aphis gossypii* and *Myzus persicae* at different instars. Different letters in the column indicate significant differences among treatments (the log-rank test adjusted by the Bonferroni method, $p < 0.05$).

Treatment	Aphid total consumed	Aphid average survival times
M2M4	97	64.85 \pm 3.66b
A2A4	95	72.56 \pm 3.45b
M2A2	100	19.51 \pm 1.18a
M4A4	83	93.70 \pm 2.48c
M4A2	100	69.17 \pm 3.33b
M2A4	95	72.73 \pm 3.49b

and 40 *M. persicae*), *E. connexa* showed no clear preference ($\beta_{1\text{mean}} = 0.53$). In contrast, under the inverse condition in treatment D (40 *A. gossypii*, 10 *M. persicae*), the predator showed a stronger preference for *A. gossypii* ($\beta_{1\text{mean}} = 0.70$). A similar pattern was observed between treatments B (20 *A. gossypii*, 30 *M. persicae*) and D, where the preference index was 0.52 and 0.70, respectively. These results suggest that *E. connexa*'s predatory behaviour varies depending on the proportion of aphid species available.

Statistical analysis using ANOVA confirmed a significant effect of treatments ($df = 3$, $F = 3.68$, $p < 0.02$). Tukey's multiple comparison test indicated significant differences between

TABLE 2 | Mean preference index of each treatment (\pm SD) of *Eriopsis connexa* under different densities in the same experimental area of the aphid species *Aphis gossypii* and *Myzus persicae*. Different letters in the column indicate significant differences among treatments (Tukey multiple comparison test, $p < 0.05$).

Treatment	Aphid proportions (<i>A. gossypii</i> : <i>M. persicae</i>)	$\beta_{1\text{mean}}$
A	10:40	0.534 \pm 0.13a
B	20:30	0.521 \pm 0.14a
C	30:20	0.598 \pm 0.16ab
D	40:10	0.705 \pm 0.17b

treatments A and D ($p = 0.041$) and between B and D ($p = 0.024$), demonstrating that *E. connexa* exhibited a change in behaviour depending on the density of each offered aphid species.

3.3 | Bioassay 3: Functional Response of *Eriopsis connexa* Preying on *Aphis gossypii* and *Myzus persicae*

Adult *E. connexa* exhibited a type II functional response, with average prey consumption increasing as the density of *M. persicae* and *A. gossypii* went up (Figures 3 and 4). This conclusion is supported by a logistic regression analysis performed by the *frair_test* function, which revealed a significant negative relationship between the initial prey density and the proportion

Myzus persicae

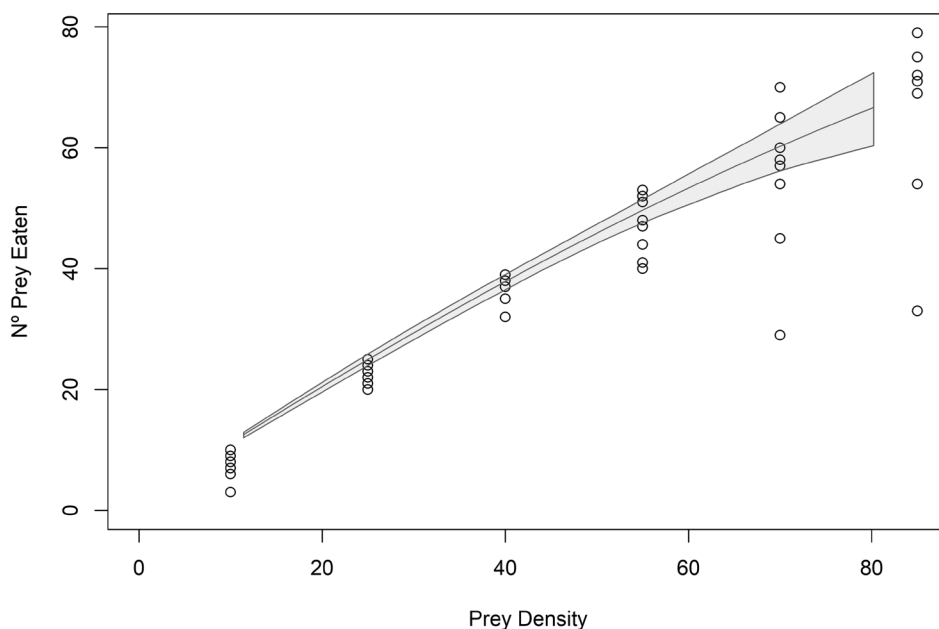


FIGURE 3 | Functional response of *Eriopis connexa* consuming different densities of *Myzus persicae*.

Aphis gossypii

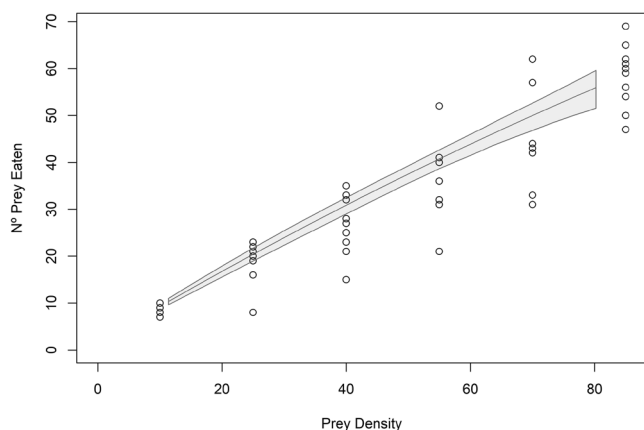


FIGURE 4 | Functional response of *Eriopis connexa* consuming different densities of *Aphis gossypii*.

of prey consumed for both *A.gossypii* (coefficient = -0.005 , $z = -2.84$, $p = 0.004$) and *M.persicae* (coefficient = -0.017 , $z = -6.43$, $p < 0.001$).

Eriopis connexa exhibited a higher attack rate on *M.persicae* (2.80 h^{-1}) than on *A.gossypii* (1.43 h^{-1}), while handling times

were similar between species (0.007 h vs. 0.004 h , respectively) (Table 3). Bootstrap 95% BCa confidence intervals for attack rate (a) and handling time (h) indicated variation in parameter estimates between species, with $a = 1.122\text{--}1.807$ and $h = 0\text{--}0.009 \text{ h}$ for *A.gossypii*, and $a = 2.091\text{--}3.765$ and $h = 0.002\text{--}0.011$ for *M.persicae*. Formal comparison using *frair_compare* showed that the attack rate was significantly higher for *M.persicae* than for *A.gossypii* ($\Delta a = -1.38$, $p < 0.001$), whereas handling time did not differ significantly between species ($\Delta h = -0.002$, $p = 0.156$).

4 | Discussion

The results from the three bioassays demonstrate that the foraging behaviour of the ladybird *E. connexa* in response to different aphid species and proportions is not driven by an inherent preference for a specific species, but is strongly influenced by the developmental stage of the aphids and their relative abundance in the environment. Prey selection can be influenced by several characteristics, including prey size, mobility and nutritional quality (Bilde and Toft 1994; Xue et al. 2025).

The survival analysis provides compelling evidence that aphid instar plays a more critical role than species identity in shaping

TABLE 3 | Estimates (\pm SE) of attack rate (a , aphids per predator per hour, h^{-1}) and handling time (h , hours per aphid, Th) plus 95% confidence limits (CL) of aphid consumption by *Eriopis connexa*.

Treatment	a (h^{-1})	95% CL		h (T_h)	95% CL	
		Lower	Upper		Lower	Upper
<i>Myzus persicae</i>	2.805 ± 0.19	2.033	3.857	0.007 ± 0.001	0.002	0.011
<i>Aphis gossypii</i>	1.431 ± 0.11	1.222	1.828	0.004 ± 0.001	0	0.009

the predation patterns of *E. connexa*. Complete prey consumption occurred in treatments where both species were offered in the second instar (M2A2) or in a mixed-instar treatment with *M. persicae* in the fourth instar and *A. gossypii* in the second instar (M4A2). However, the mean survival time was significantly shorter in M2A2 (19.5 min) than in M4A2 (69.2 min), indicating faster and more efficient predation when both prey types were in early instars.

The trend of higher predation on early instar aphids is not unique to *E. connexa* but has also been observed in other generalist predators. For example, *Orius albidipennis* showed a preference for first- and second-instar aphid nymphs over older stages (Rashedi et al. 2020). Similarly, although *Coccinella septempunctata* adults exhibited the highest consumption rate on fourth-instar aphids, Yang et al. (2022) reported that the highest attack rates and shortest handling times occurred when predators fed on early instars. Despite involving different predator species, these findings support our results, particularly when considering the survival time data, and reinforce the notion that early instars are more accessible and efficiently consumed by predators like *E. connexa*.

In the M4A2 treatment, where *M. persicae* was offered fourth instar and *A. gossypii* in the second instar, complete prey consumption was still achieved. This suggests that when a more accessible prey (second-instar *A. gossypii*) is available, *E. connexa* initiates feeding on it and subsequently invests time in handling the more challenging prey (fourth-instar *M. persicae*). This sequential feeding pattern was not observed in treatments involving different instars of the same species (e.g., A2A4), possibly due to similarity in prey recognition or a reduced motivation to engage with more difficult prey when the expected reward is lower.

In contrast, the treatment where both species were offered in the fourth instar (M4A4) resulted in the lowest predation rate, with a mean survival time of 93.7 min. These findings support the idea that *E. connexa* preys more efficiently on early and smaller aphids, regardless of species, optimising energy intake by prioritising easier-to-handle prey (Crawley and Krebs 1992; Roger et al. 2000).

From a biological control perspective, the ability of *E. connexa* to efficiently consume early aphid instars suggests potential overlap with parasitoid activity, as many parasitoids prefer younger or smaller hosts for oviposition (Lykouressis et al. 2009; Perdikis et al. 2004; Martinou and Wright 2007; Soni and Kumar 2021; Sengonca et al. 2008). However, our results demonstrate that *E. connexa* is also capable of preying on later instars, particularly when early instars are less available. As older aphids are often less suitable or unsuitable for successful parasitism, due to continued reproduction by the host (Khatri et al. 2017; Perdikis et al. 2004) or enhanced defensive behaviours (He et al. 2011), the consumption of these stages by *E. connexa* may enhance biological control by targeting individuals that would otherwise escape parasitism. Furthermore, in systems where parasitoids prefer older instars (e.g., He et al. 2011), *E. connexa* can complement parasitoid activity by suppressing younger stages. This complementary predation–parasitism dynamic broadens the scope of aphid suppression across developmental stages and

reinforces the value of integrating both natural enemies in IPM programmes.

In our study, when evaluating predatory behaviour in response to varying prey proportions, we observed that *E. connexa* exhibited a preference for *A. gossypii* when it was more abundant. When *M. persicae* dominated the mixture, *E. connexa* showed no clear preference; however, as the proportion of *A. gossypii* increased, *E. connexa* consistently preferred this species. The pattern suggests that the ladybird's preference is not fixed but context-dependent, influenced by the relative abundance of prey species and potentially by their morphological or nutritional characteristics. The study reported by Messelink et al. (2008) noted that whitefly control improved by the presence of thrips, but the thrips control was not affected by the presence of whiteflies. Also, a similar pattern of context-dependent selectivity was reported for four instar larvae of *Scymnus syriacus*, where the Maily preference index for the 50:30 ratio was higher for *Aphis spiraeicola*, and for the 30:50 ratio, there was no significant preference for either of the two species of aphid (Moradi et al. 2020). Such asymmetric effects of prey species on each other via a shared predator have been documented and are known to influence prey dynamics in predator–prey systems (Van Maanen et al. 2012; Desneux et al. 2019; Messelink et al. 2008).

This asymmetric interaction between *M. persicae* and *A. gossypii* may be attributed to behavioural or morphological differences between the aphid species. *A. gossypii* is smaller bodied than *M. persicae* (Maciel A.M.F, personal observation), which could in principle facilitate quicker handling and consumption. However, our functional response analyses showed no significant difference in handling time between the two species, suggesting that size alone does not explain the observed preference. Instead, the consistent selection of *A. gossypii* when more abundant may reflect a combination of prey availability and morphological or behavioural traits that make it a more readily exploited resource. Farhoudi et al. (2014) showed that aphid size is a more important factor than colour in contributing to the predation preference of *Aphidoletes aphidimyza* (Rondani). Nevertheless, *M. persicae* was readily consumed by *E. connexa*, with no evidence of avoidance or reduced foraging efficiency. Indeed, de Matos et al. (2022) reported that *M. persicae* is a suitable prey for this predator, supporting the notion that while prey size may influence preference in certain contexts, *E. connexa* maintains high foraging efficiency across different aphid species.

The functional response parameters revealed that *E. connexa* exhibited a significantly higher attack rate (2.80 h^{-1}) on *M. persicae* compared to *A. gossypii* (1.43 h^{-1}), whereas handling times did not differ between the two species (0.007 and 0.004 h, respectively). While the estimated handling time was numerically greater for *M. persicae*, this difference was not statistically supported. These results indicate that prey accessibility and relative abundance are more important drivers of predation dynamics than species identity per se. In the experiment under mixed-prey conditions, when *A. gossypii* was more abundant, *E. connexa* showed a preference for *A. gossypii*. These findings reinforce the hypothesis that smaller-bodied prey may be easier to exploit when available in sufficient numbers.

The observed behaviour suggests that *E. connexa* may adopt an optimal foraging strategy in the presence of both species, initially consuming the smaller and more abundant *A. gossypii*, and subsequently shifting to *M. persicae*, which, despite requiring similar handling effort according to our results, may still impose higher energetic costs due to its larger body size and mobility. This behaviour aligns with optimal foraging theory, which predicts that predators will adjust their feeding strategies to maximise net energy gain depending on prey availability and characteristics (Stephens and Krebs 1986). In this study, *E. connexa* exhibited a type II functional response, consistent with findings by other authors (Lira et al. 2019; Dos Santos et al. 2020). This type of foraging is particularly relevant under type II functional response dynamics, where predator saturation and prey handling time are critical decision-making factors (DeLong and Uiterwaal 2022).

In addition to varying prey proportions, with *E. connexa* displaying a consistent preference for *A. gossypii* as its proportion increased, the second experiment further supports the hypothesis that prey size and ease of handling influence foraging behaviour. In the M4A2 treatment, with *M. persicae* in the fourth instar and *A. gossypii* in the second instar, complete consumption was observed, suggesting again that *E. connexa* initiates predation on the more accessible prey and subsequently shifts to those requiring greater energetic investment cost. In this sense, the apparent preference for *A. gossypii* when it is more abundant reflects a strategic foraging decision rather than an inherent preference. When *M. persicae* was dominant, no clear preference emerged, likely due to the energy cost associated with this species, even if it offers higher nutritional reward, leading to an initially balanced attack rate across species.

Our results demonstrate that *E. connexa* can prey on both aphid species but exhibits behavioural flexibility by adjusting its predation strategy based on ecological context. Moreover, in cropping systems where both *A. gossypii* and *M. persicae* co-occur, such as cotton-vegetable or pepper-brassica intercropping systems, *E. connexa* may act as an effective agent by initially reducing *A. gossypii* populations and subsequently shifting to *M. persicae*, offering broad suppression across prey stages.

Author Contributions

Anna Mara Ferreira Maciel: conceptualization, data curation, formal analysis, investigation, funding acquisition, methodology, writing – original draft, writing – review and editing. **Lucas Ramos Vieira:** investigation, methodology, writing – review and editing. **Rayana Mayara Rocha Carvalho:** investigation, methodology, writing – review and editing. **Wesley Augusto Conde Godoy:** conceptualization, methodology, supervision, funding acquisition, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting the findings of this study are available in the Zenodo Repository at: <https://doi.org/10.5281/zenodo.17516770>.

References

- Almeida, D. P., G. C. M. Berber, E. L. Aguiar-Menezes, and A. L. S. Resende. 2021. "Evaluation of Biological Parameters of *Eriopis connexa* (Germar, 1824) and *Coleomegilla maculata* (DeGeer, 1775) (Coleoptera: Coccinellidae) Fed With Alternative Prey Developed at the Integrated Center for Pest Management-UFRRJ." *Scientific Electronic Archives* 14: 8–16. <https://doi.org/10.36560/14120211193>.
- Bilde, T., and S. Toft. 1994. "Prey Preference and Egg Production of the Carabid Beetle *Agonum dorsale*." *Entomologia Experimentalis et Applicata* 73: 151–156. <https://doi.org/10.1111/j.1570-7458.1994.tb01850.x>.
- Blackman, R. L., and V. F. Eastop. 2000. *Aphids on the World's Crops: An Identification and Information Guide*. 2nd ed, x + 466 pp. John Wiley & Sons Ltd.
- CABI. 2021. "*Myzus persicae* (Green Peach Aphid)." CABI Compendium. <https://doi.org/10.1079/cabicompendium.3564>.
- Chan, C. K., A. R. Forbes, and D. A. Raworth. 1995. *Aphid-Transmitted Viruses and Their Vectors of the World*. Research Branch, Agriculture Canada.
- Costa, P. M. G., R. L. dos Santos, D. V. do Nascimento, and J. B. Torres. 2020. "Does Spinetoram Pose Low Risk to the Neotropical Lady Beetle *Eriopis connexa* (Coleoptera: Coccinellidae)?" *Phytoparasitica* 48: 491–499. <https://doi.org/10.1007/s12600-020-00802-x>.
- Crawley, M. J., and J. R. Krebs. 1992. "Foraging Theory." In *Natural Enemies*, edited by M. J. Crawley, 90–114. Blackwell Scientific Publications.
- Dami, B. G., J. A. Dos Santos, E. P. Barbosa, C. Rodriguez-Saona, and A. M. Vacari. 2023. "Functional Response of 3 Green Lacewing Species (Neuroptera: Chrysopidae) to *Leucoptera coffeella* (Lepidoptera: Lyonetiidae)." *Journal of Insect Science* 23: 15. <https://doi.org/10.1093/jisesa/iead038>.
- D'Ávila, V. A., W. F. Barbosa, L. C. Reis, B. S. Gallardo, J. B. Torres, and R. N. C. Guedes. 2018. "Lambda-Cyhalothrin Exposure, Mating Behavior and Reproductive Output of Pyrethroid-Susceptible and Resistant Lady Beetles (*Eriopis connexa*)." *Crop Protection* 107: 41–47. <https://doi.org/10.1016/j.cropro.2018.01.009>.
- de Matos, S. T. S., P. J. Savi, C. C. Melville, T. M. dos Santos Cividanes, F. J. Cividanes, and D. J. de Andrade. 2022. "Suitability of Spider Mites and Green Peach Aphids as Prey for *Eriopis connexa* (Germar) (Coleoptera: Coccinellidae)." *Scientific Reports* 12: 8029. <https://doi.org/10.1038/s41598-022-12078-8>.
- de Oliveira, N. C., and C. Matos. 2004. "Biological Cycle and Predation of Three Coccinellid Species (Coleoptera, Coccinellidae) on Giant Conifer Aphid." *Revista Brasileira de Entomologia* 48: 529–533.

- DeLong, J. P., and S. F. Uiterwaal. 2022. "Predator Functional Responses and the Biocontrol of Aphids and Mites." *BioControl* 67: 161–172. <https://doi.org/10.1007/s10526-021-10127-1>.
- Desneux, N., I. Kaplan, H. J. S. Yoo, S. Wang, and R. J. O'Neil. 2019. "Temporal Synchrony Mediates the Outcome of Indirect Effects Between Prey via a Shared Predator." *Entomologia Generalis* 39: 127–136. <https://doi.org/10.1127/entomologia/2019/0824>.
- Dos Santos, D. S., A. J. Barbosa, L. J. Oliveira, and J. B. Torres. 2020. "Predation of *Brevicoryne brassicae* and *Aphis craccivora* by *Eriopis connexa* Depending on Availability." *Acta Biológica Colombiana* 26: 99–104. <https://doi.org/10.15446/abc.v26n1.83303>.
- Farhoudi, F., H. Allahyari, S. M. Tabadkani, and M. Gholizadeh. 2014. "Prey Preference of *Aphidoletes aphidimyza* on *Acyrtosiphon pisum*: Effect of Prey Color and Size." *Journal of Insect Behavior* 27: 776–785. <https://doi.org/10.1007/s10905-014-9470-4>.
- Francesena, N., M. Rocca, E. Rizzo, J. D. Arneodo, and N. M. Greco. 2019. "Potential of Predatory Neotropical Ladybirds and Minute Pirate Bug on Strawberry Aphid." *Anais da Academia Brasileira de Ciências* 91: e20181001. <https://doi.org/10.1590/0001-3765201920181001>.
- He, X. Z., Q. Wang, and D. A. J. Teulon. 2011. "Host Age Preference Behavior in *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae)." *Journal of Insect Behavior* 24: 447–455. <https://doi.org/10.1007/s10905-011-9271-y>.
- Heit, G. E., G. Cohen, and G. Mareggiani. 2008. "Impact of Odor signals on *Cycloneda sanguinea* (Coleoptera: Coccinellidae) Searching Behavior." *Ciencia e Investigación Agraria* 35: 205–210. <https://doi.org/10.4067/S0718-16202008000200010>.
- Hodek, I., and E. W. Evans. 2012. "Food Relationships." In *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae)*, edited by I. Hodek, H. F. Emden, and A. Honěk, 141–274. Wiley-Blackwell Publishing.
- Holling, C. S. 1959. "Some Characteristics of Simple Types of Predation and Parasitism." *Canadian Entomologist* 91: 385–398. <https://doi.org/10.4039/Ent91385-7>.
- Islam, Y., F. M. Shah, X. Rubing, et al. 2021. "Functional Response of *Harmonia axyridis* Preying on *Acyrtosiphon pisum* Nymphs: The Effect of Temperature." *Scientific Reports* 11: 13565. <https://doi.org/10.1038/s41598-021-92954-x>.
- Jaworski, C. C., A. Bompard, L. Genies, E. Amiens-Desneux, and N. Desneux. 2013. "Preference and Prey Switching in a Generalist Predator Attacking Local and Invasive Alien Pests." *PLoS One* 8: e82231. <https://doi.org/10.1371/journal.pone.0082231>.
- Khatri, D., X. Z. He, and Q. Wang. 2017. "Effective Biological Control Depends on Life History Strategies of Both Parasitoid and Its Host: Evidence From *Aphidius colemani*—*Myzus persicae* System." *Journal of Economic Entomology* 110: 400–406. <https://doi.org/10.1093/jee/tow324>.
- Kirby, W., and W. Spence. 1826. "An Introduction to Entomology." In *Science and Visual Culture in Great Britain in the Long Nineteenth Century*, 373–379. Routledge.
- Kulkarni, S. S., and M. L. Evenden. 2024. "Functional Response of Larval and Adult *Coccinella septempunctata* to Eggs and Larvae of *Plutella xylostella* on Canola." *Entomologia Experimentalis et Applicata* 172: 334–344. <https://doi.org/10.1111/eea.13405>.
- Lira, R., D. V. do Nascimento, P. R. R. Barbosa, A. M. Simmons, and J. B. Torres. 2023. "Predation Performance and Survival of Susceptible and Pyrethroid-Resistant *Eriopis connexa* Germar (Coleoptera: Coccinellidae) to Insecticides Used in Brassica Crops." *Pest Management Science* 79: 2704–2712. <https://doi.org/10.1002/ps.7448>.
- Lira, R., D. V. Nascimento, and J. B. Torres. 2019. "Predation on Diamondback Moth Larvae and Aphid by Resistant and Susceptible Lady Beetle, *Eriopis connexa*." *Neotropical Entomology* 48: 909–918. <https://doi.org/10.1007/s13744-019-00702-8>.
- Lykouressis, D., D. Perdikis, A. Fantinou, and N. Garantonakis. 2009. "Effect of Female Size on Host Selection by a Koinobiont Insect Parasitoid (Hymenoptera: Braconidae: Aphidiinae)." *European Journal of Entomology* 106: 385–389.
- Manly, B. F. J. 1974. "A Model for Certain Types of Selection Experiments." *Biometrics* 30: 281–294. <https://doi.org/10.2307/2529649>.
- Martinou, A. F., and D. J. Wright. 2007. "Host Instar and Host Plant Effects on *Aphidius colemani*." *Journal of Applied Entomology* 131: 621–624. <https://doi.org/10.1111/j.1439-0418.2007.01220.x>.
- Messelink, G. J., R. van Maanen, S. E. F. van Steenpaal, and A. Janssen. 2008. "Biological Control of Thrips and Whiteflies by a Shared Predator: Two Pests Are Better Than One." *Biological Control* 44: 372–379. <https://doi.org/10.1016/j.biocontrol.2007.10.017>.
- Michaud, J. P. 2012. "Coccinellids in Biological Control." In *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae)*, edited by I. Hodek, H. F. van Emden, and A. Honěk. Blackwell Publishing Ltd. <https://doi.org/10.1002/9781118223208.ch11>.
- Moradi, M., M. Hassanpour, S. A. A. Fathi, and A. Golizadeh. 2020. "Foraging Behaviour of *Scymnus syriacus* (Coleoptera: Coccinellidae) Provided With *Aphis spiraeola* and *Aphis gossypii* (Hemiptera: Aphididae) as Prey: Functional Response and Prey Preference." *European Journal of Entomology* 117: 83–92. <https://doi.org/10.14411/eje.2020.009>.
- Murdoch, W. W. 1969. "Switching in General Predators: Experiments on Predator Specificity and Stability of Prey Populations." *Ecological Monographs* 39: 335–354. <https://doi.org/10.2307/1942352>.
- Nascimento, D. V., R. Lira, E. K. S. Ferreira, and J. B. Torres. 2021. "Performance of the Aphidophagous Coccinellid *Eriopis connexa* Fed on Single-Species and Mixed-Species Prey." *Biocontrol Science and Technology* 31: 951–963. <https://doi.org/10.1080/09583157.2021.1901264>.
- Nascimento, D. V., R. Lira, and J. B. Torres. 2023. "Heterosis and Reselection for Pyrethroid Resistance Trait Maintenance in the Lady Beetle *Eriopis connexa* (Germar)." *Annals of Applied Biology* 183: 148–158. <https://doi.org/10.1111/aab.12839>.
- Perdikis, D. C., A. A. Fantinou, and D. P. Lykouressis. 2004. "Instar Preference and Parasitization of *Aphis gossypii* and *Myzus persicae* (Hemiptera: Aphididae) by the Parasitoid *Aphidius colemani* (Hymenoptera: Aphidiidae)." *European Journal of Entomology* 101: 333–336.
- Pervez, A., Omkar, and M. M. Harsur. 2020. "Coccinellids on Crops: Nature's Gift for Farmers." In *Innovative Pest Management Approaches for the 21st Century*, edited by A. Chakravarthy. Springer. https://doi.org/10.1007/978-981-15-0794-6_21.
- Pervez, A., and M. Yadav. 2018. "Foraging Behaviour of Predaceous Ladybird Beetles: A Review." *European Journal of Environmental Sciences* 8: 102–108. <https://doi.org/10.14712/23361964.2018.14>.
- Pritchard, D. W., R. A. Paterson, H. C. Bovy, and D. Barrios-O'Neill. 2017. "frair: An R Package for Fitting and Comparing Consumer Functional Responses." *Methods in Ecology and Evolution* 8, no. 11: 1528–1534. <https://doi.org/10.1111/2041-210x.12784>.
- R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rashedi, A., A. Rajabpour, N. Z. Sohani, and A. Rasekh. 2020. "Prey Stage Preference and Functional Response of *Orius albidipennis* (Heteroptera, Anthocoridae) to *Aphis fabae* (Homoptera, Aphididae)." *International Journal of Tropical Insect Science* 40: 13–19. <https://doi.org/10.1007/s42690-019-00045-2>.
- Rocca, M., E. Rizzo, N. Greco, and N. Sánchez. 2017. "Intra- and Interspecific Interactions Between Aphidophagous Ladybirds: The

- Role of Prey in Predator Coexistence." *Entomologia Experimentalis et Applicata* 162: 284–292. <https://doi.org/10.1111/eea.12527>.
- Rodrigues, A. S., P. R. Barbosa, D. V. Nascimento, and J. B. Torres. 2024. "Crossbreeding and Backcrossing in the Pyrethroid-Resistant Ladybird Beetle *Eriopis connexa* (Germar) Determines Resistance in Offspring." *Insects* 15: 853. <https://doi.org/10.3390/insects15110853>.
- Rodrigues, A. S., R. N. C. Guedes, H. Á. A. D. Siqueira, and J. B. Torres. 2020. "Stability of the Resistance to Lambda-Cyhalothrin in the Ladybird Beetle *Eriopis connexa*." *Entomologia Experimentalis et Applicata* 168: 644–652. <https://doi.org/10.1111/eea.12911>.
- Roger, C., D. Coderre, and G. Boivin. 2000. "Differential Prey Utilization by the Generalist Predator *Coleomegilla maculata lengi* According to Prey Size and Species." *Entomologia Experimentalis et Applicata* 94, no. 1: 3–13. <https://doi.org/10.1046/j.1570-7458.2000.00598.x>.
- Rogers, D. 1972. "Random Search and Insect Population Models." *Journal of Animal Ecology* 41, no. 2: 369. <https://doi.org/10.2307/3474>.
- Sarmiento, R. A., A. Pallini, M. Venzon, O. F. F. D. Souza, A. J. Molina-Rugama, and C. L. D. Oliveira. 2007. "Functional Response of the Predator *Eriopis connexa* (Coleoptera: Coccinellidae) to Different Prey Types." *Brazilian Archives of Biology and Technology* 50: 121–126. <https://doi.org/10.1590/S1516-89132007000100014>.
- Sengonca, C., S. Schirmer, and P. Blaeser. 2008. "Life Table of the Aphid Parasitoid *Aphelinus asychis* (Walker) (Hymenoptera, Aphelinidae) Parasitizing Different Age Groups of *Aphis gossypii* Glover (Homoptera, Aphididae)." *Journal of Plant Diseases and Protection* 115: 122–128.
- Silva, R. B., I. Cruz, J. C. Zanuncio, M. D. L. C. Figueiredo, T. V. Zanuncio, and J. E. Serrão. 2013. "*Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) Eggs as Alternative Food for Rearing of Lady Beetles *Eriopis connexa* (Germar) (Coleoptera: Coccinellidae)." *Biological Control* 64: 101–105. <https://doi.org/10.1016/j.biocontrol.2012.09.013>.
- Silva, R. B., J. C. Zanuncio, J. E. Serrão, E. R. Lima, M. L. C. Figueiredo, and I. Cruz. 2009. "Suitability of Different Artificial Diets for Development and Survival of Stages of the Predaceous Ladybird Beetle *Eriopis connexa*." *Phytoparasitica* 37: 115–123. <https://doi.org/10.1007/s12600-008-0015-2>.
- Ślipiński, A., and W. Tomaszewska. 2010. "Coccinellidae Latreille, 1802." In *Handbook of Zoology. Coleoptera*, edited by R. A. B. Leschen, R. G. Beutel, and J. F. Lawrence, 454–472. Walter de Gruyter GmbH & Co. KG.
- Soni, S., and S. Kumar. 2021. "Efficacy of the Parasitoid, *Diaeretiella rapae* (McIntosh) (Hymenoptera: Braconidae) Against *Myzus persicae* (Sulzer) (Homoptera: Aphididae) Infesting Rapeseed-Mustard." *Journal of Asia-Pacific Entomology* 24: 912–917. <https://doi.org/10.1016/j.aspen.2021.07.019>.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory*, Vol. 6. Princeton University Press.
- Symondson, W. O. C., K. D. Sunderland, and M. H. Greenstone. 2002. "Can Generalist Predators Be Effective Biocontrol Agents?" *Annual Review of Entomology* 47: 561–594. <https://doi.org/10.1146/annurev.ento.47.091201.145240>.
- Van Maanen, R., G. J. Messelink, R. Van Holstein-Saj, H. Hoogerbrugge, and J. C. van Lenteren. 2012. "Prey Temporarily Escape From Predation in the Presence of a Second Prey Species." *Ecological Entomology* 37: 529–535. <https://doi.org/10.1111/j.1365-2311.2012.01395.x>.
- Xue, C., J. Mao, B. Xu, et al. 2025. "Biological Control Potential of the Reduviid Predator *Rhynocoris fuscipes* (Fabricius) in Managing Noctuid Pests: Insights Into Predation and Prey Preference." *Insects* 16: 224. <https://doi.org/10.3390/insects16020224>.
- Yang, H., Y. Liu, Y. Song, Y. Zhang, and H. Liu. 2022. "Prey Stage Preference and Functional Response of the Seven-Spot Lady Beetle *Coccinella septempunctata* to the Rose Aphid, *Macrosiphum rosivorum*." *Biocontrol Science and Technology* 32: 121–131. <https://doi.org/10.1080/09583157.2021.1971622>.
- Zarghami, S., F. Kocheili, M. S. Mossadegh, H. Allahyari, and A. Rasekh. 2014. "Prey Preference and Consumption Capacity of *Nephus arcuatus* (Coleoptera: Coccinellidae): The Influence of Prey Stage, Prey Size and Feeding Experience." *Biocontrol Science and Technology* 24: 1062–1072. <https://doi.org/10.1080/09583157.2014.919376>.