

Predatory capacity and intraguild interaction between aphidophagous predators in the control of rose bush aphids

Luiza Akemi Gonçalves Tamashiro¹ , Carlos Eduardo Souza Bezerra² ,
Ana Luiza Viana de Sousa³, Luiz Paulo Silvério Pereira¹, Laodicéia Lopes Pereira¹,
Alessandra de Carvalho Silva⁴, Brígida Souza¹ 

¹ Universidade Federal de Lavras (UFLA), Departamento de Entomologia, Lavras, MG, Brasil.

² Centro Universitário de Várzea Grande (UNIVAG), Laboratório de Entomologia, Várzea Grande, MT, Brasil.

³ Rutgers University, Department of Entomology, New Brunswick, NJ, USA.

⁴ Embrapa Agrobiologia, Laboratório de Artrópodes, Seropédica, RJ, Brasil.

ARTICLE INFO

Article history:

Received 06 December 2022

Accepted 12 April 2023

Available online 22 May 2023

Associate Editor: Renato Jose Machado

Keywords:

Chrysopidae

Coccinellidae

Biological Control

ABSTRACT

Chrysoperla externa (Hagen) and *Hippodamia convergens* (Guérin-Meneville) are voracious generalist predators, and important aphid control agents. In an environment containing a complex of species, the occurrence of intraguild interactions can interfere in the predator behavior and consumption. The aim of this work was to know the number of nymphs of *Rhodobium porosum* (Sanderson) and *Macrosiphum rosae* (Linnaeus) consumed by larvae of *C. externa* and *H. convergens*, and the interaction between these predators when confined together. First, second and third instar nymphs of *R. porosum* and *M. rosae* were provided in Petri dishes containing rose leaflets and second instar larvae of the predators. Intraguild interaction was studied in Petri dishes containing first instar nymphs of both aphid species and a second instar larva of *C. externa* plus one of *H. convergens*. A third treatment consisted of dishes containing a second instar larva of both predators maintained in the absence of prey. The evaluations took place throughout the entire instar of the predators. *C. externa* consumed a greater number of *R. porosum* nymphs and *H. convergens* a greater number of *M. rosae* nymphs. For both species of prey, the highest consumption was verified on the last day of evaluation. There was a positive interaction when the predator's larvae were confined in the presence of aphid nymphs, with no mortality observed for any of them. In the absence of prey, there was 70% mortality of *H. convergens* larvae due to intraguild predation.

Introduction

The use of more than one species of natural enemy can be recommended to control one or more pests simultaneously, being an important strategy for the optimization of biological control (Gardiner and Landis, 2007; Chow et al., 2010). However, the simultaneous presence of the natural enemies and, consequently, the increase in the complexity of the food chain, can cause changes in the behavior of one or all species released. These changes occur in the presence or absence of target pests, due to several interactions mediated by the density of trophic chain components, including intraguild interaction (Messelink et al., 2012; Khudr et al., 2020). The results of these interactions can be positive, due to a complementary action between the natural enemies, causing an increase in the suppression effect of pest arthropod populations (Chailleux et al., 2013; Devee et al., 2018; Souza et al., 2019). However, negative interaction can also occur, such as intraguild predation (IGP), where members of the same guild compete for resources, resulting

in the mortality of one of them. This interaction can compromise the regulation of the pest population, as the dominant predator will feed on the other, called intraguild prey (Polis et al., 1989), resulting in the reduction of control agents (Hagler and Blackmer, 2015; Fu et al., 2017).

The use of predators to reduce pest populations forms the basis of several biological control programs (Sabelis et al., 2008; Messelink et al., 2012). The ability of generalist predators to remain in the farming environment at low prey densities or even in the absence of prey, exploring other food resources, constitutes a main reason to include this category of natural enemy in such programs (Messelink et al., 2013). The green lacewing *Chrysoperla externa* (Hagen, 1861) (Neuroptera: Chrysopidae) presents a high potential to be used in biological control programs due to characteristics such as the variety of prey used as a food resource (Souza et al., 2008), high survival rate and voracity (Cuello et al., 2019), wide distribution and adaptation to agricultural environments (Carvalho and Souza, 2009; Salamanca et al., 2015), in addition to being easy to rear in the laboratory (Bezerra et al., 2017;

*Corresponding author.

E-mail: luiza.gtamashiro@gmail.com (L.A.G. Tamashiro).

Palomares-Pérez et al., 2020). Similarly, *Hippodamia convergens* (Guérin-Méneville, 1842) (Coleoptera: Coccinellidae) feeds on a wide variety of sap-sucking insects, mainly aphids (Boiça-Junior et al., 2004; Iftikhar et al., 2020) and has a wide geographic distribution and adaptation to different environments (Vargas et al., 2012; Delgado-Ramírez et al., 2019).

Among of the prey availability to generalist predators, aphids (Hemiptera: Aphididae) represent an important food source to lacewings and ladybirds (Khudr et al., 2020). These insects can colonize several agricultural crops (Riddick, 2017; Smith et al., 2018). In rose bushes (*Rosa* sp.), the aphid species *Rhodobium porosum* (Sanderson, 1901) and *Macrosiphum rosae* (Linnaeus, 1758) are important pests, both in protected environments and in the fields, colonizing plants at different times of the year (Blackman and Eastop, 2000; Barjadze et al., 2011). Due to the sap suction, these insects cause atrophy and curling of flower buds and contribute to the development of sooty mold, compromising the growth and reducing the commercial value of the plants.

Considering the relationship between aphids and their predators in rose bushes, as well as the added value to this culture, prior to establishing a biological control program involving the use of these mortality agents, it is important to understand their behavior when isolated and when there is interaction. In this work, we evaluated the consumption capacity of nymphs of *R. porosum* and *M. rosae* in different instars by second instar larvae of *C. externa* and *H. convergens*, as well as the intraguild interaction between these predators, when confined together, in the presence and absence of aphids.

Material and methods

The study was conducted in the Biological Control Laboratory of the Department of Entomology (DEN), at Federal University of Lavras (UFLA), Lavras, MG, Brazil.

The aphids were obtained from stock colonies reared on rose bushes (*Rosa* sp.), cultivar Avalanche, cultivated in greenhouse. The age standardization of the nymphs used was performed according to Fonseca et al. (2000). The predators were obtained from stock colonies maintained in the Laboratory of Entomology at UFLA, according to the methodology from Carvalho and Souza (2009) for the green lacewing *C. externa* and from Santos et al. (2009) for the *H. convergens* with the adaptation of eight pairs per cage.

Newly hatched larvae of *C. externa* and *H. convergens* were individualized in glass tubes (8.5cm height; 2.5cm diameter) and fed with eggs of *Ephestia kuehniella* (Zeller, 1879) (Lepidoptera: Pyralidae) until reaching the second-instar, when they were used in the bioassays.

Predatory capacity of *Chrysoperla externa* and *Hippodamia convergens*

The tests were carried out in Petri dishes (5cm diameter) containing rose leaflets attached to a 5 mm layer of agar-water solution (1%), with the abaxial surface facing upwards. In each plate were placed 90, 70 and 60 nymphs of first, second and third instar of *R. porosum*, respectively. The same procedure was adopted for *M. rosae*. The number of nymphs offered to predators was obtained from preliminary tests. A second-instar larva of *C. externa* and a second-instar larva of *H. convergens* were released in each plate. The plates were sealed with transparent PVC film and kept at 25±1°C, relative humidity (RH) of 70±10% and photophase of 12 hours. The surviving nymphs were counted every 24 hours after the release, throughout all the second instar of the predators.

The killed aphids, regardless of whether they were totally or partially consumed, were replaced every day, using age-standardized

nymphs from a parallel rearing. This procedure ensured feeding the predators with nymphs of the same age throughout the experiment. The following combinations were tested: second instar of *C. externa* with first, second and third-instars of *R. porosum* and *M. rosae*, and second instar of *H. convergens* with first, second and third-instars of *R. porosum* and *M. rosae*. A completely randomized design with ten replications was adopted.

Behavior and intraguild interaction between *Chrysoperla externa* and *Hippodamia convergens* in the presence and absence of aphids

Petri dishes containing rose leaflets were prepared in the same way as in the predatory capacity trial. In treatments with the presence of aphids, 150 first-instar nymphs of *R. porosum* or 150 first-instar nymphs of *M. rosae* were placed on the leaflets. The number of aphids offered to the predators was higher than the average daily consumption in order to avoid possible prey shortages and maintain the predator/prey equivalence. Prey were used in their youngest instar because the results of the test on predatory capacity showed greater consumption in this instar. As for predators, a second-instar larva of *C. externa* and a second-instar larva of *H. convergens* were released on each plate. The following treatments were tested: a) *C. externa*, *H. convergens* and *R. porosum*, b) *C. externa*, *H. convergens* and *M. rosae*, c) *C. externa* and *H. convergens* in the absence of prey. The number of prey consumed and dead larvae of *C. externa* and *H. convergens* was evaluated daily. A completely randomized design with ten replications was used. For consumption data, analysis of variance was performed, and the means were compared using the Tukey test at a significance level of 0.05, using the statistical software R (R Development Core Team, 2013). For intraguild predation, the survival rate (%) was calculated.

In order to understand the results of intraguild interaction, the behavior of predators in the first hour of release was evaluated in an additional experiment. The records were taken from the counting of time and the observation of behavioral categories (Velasco-Hernández et al., 2013), for one hour, using the Etholog 2.2 software (Ottoni, 2000). It is noteworthy that the behavioral categories "I" (intraguild predation) and "T" (try to predate) were not included in the analyses, as they were used only to record negative interactions, in the three conditions in which the predators were present simultaneously. The tests were performed in plates prepared in the same way as in the previous assays, and a second-instar larva of the predator was released with 30 first-instar nymphs of *R. porosum* or 30 first-instar nymphs of *M. rosae* or no aphids, according to the following treatments: a) *H. convergens* and *R. porosum*, b) *H. convergens* and *M. rosae*, c) *C. externa* and *R. porosum*, d) *C. externa* and *M. rosae*, e) *C. externa*, *H. convergens* and *R. porosum*, f) *C. externa*, *H. convergens* and *M. rosae* and g) *C. externa* and *H. convergens*.

Table 1

Categories used to evaluate the behavior of *Chrysoperla externa* (Chrysopidae) and *Hippodamia convergens* (Coccinellidae), in the presence and absence of *Rhodobium porosum* and *Macrosiphum rosae* (Aphididae). Temperature of 25±1°C, relative humidity of 70±10% and 12-hour photophase.

Category	Description
P (stopped)	The predator does not move
R (preying)	The predator feed on the available prey
L (cleaning/grooming)	The predator cleans its mouthparts
B (searching)	The predator search for the prey
I (IGP)	One predator feeds on the other (there's mortality)
T (attempted to IGP)	One predator attacks the other (there's no mortality)

Adapted from Velasco-Hernández et al. (2013)

For the treatments in which the two predators were released, were considered six behavioral categories (Table 1). A completely randomized design was adopted, with five replications. The time spent in each category was transformed from seconds to percentage.

Statistical analysis

For the aphid instar consumption, the data were submitted to an analysis of variance and means were compared by Tukey's test at a significance level of 0.05. The t test was used to compare the total number of aphids of each species consumed by each predator and to compare the consumption between predators. For the behavioral evaluation data were compared using the non-parametric Kruskal-Wallis and Dunn's test at a significance level of 0.05. Data analysis was performed using the R statistical program (R Development Core Team, 2013).

Results

Predatory capacity of *Chrysoperla externa* and *Hippodamia convergens*

The number of *R. porosum* and *M. rosae* nymphs consumed by the predators is related to the prey development stage, as well as the

predators' development during the second-instar, which lasted four days for *C. externa* and three days for *H. convergens*. We found that nymphs on first-instar were predated in greater numbers than those on second and third ($p < 0.001$); and regardless of prey instar, predatory activity increased with predator development, showing higher consumption on the last day ($p < 0.001$) (Tables 2 and 3).

When comparing the average total consumption of nymphs of *R. porosum* and *M. rosae*, there were significant differences according to the prey development stage and also the species of the aphid. *Chrysoperla externa* larvae fed on a greater number of first and second-instar nymphs of *R. porosum* (263.4 and 222.6, respectively) in relation to the same instars of *M. rosae*; however, when on the third-instar, there was a higher consumption of *M. rosae* nymphs (162.1) (Table 2). For *H. convergens*, the opposite occurred: nymphs of *M. rosae* on first and second-instar were predated in greater numbers (184.4 and 150.3, respectively) in relation to those of *R. porosum*, but when on the third-instar, *R. porosum* nymphs were more consumed than those of *M. rosae* (98.9) (Table 3).

When comparing the consumption of *R. porosum* nymphs, the larvae of *C. externa* fed on a greater number of individuals in the three instars, in relation to those of *H. convergens* ($p < 0.05$), resulting in a higher daily average of aphids consumed (Table 4).

For *M. rosae*, there was no significant difference in the consumption of first ($p = 0.193$) and second-instar ($p = 0.711$) nymphs between

Table 2

Daily average consumption (\pm standard error) of nymphs of *Rhodobium porosum* e *Macrosiphum rosae* (Aphididae) by second instar larvae of *Chrysoperla externa* (Chrysopidae). Temperature of $25 \pm 1^\circ\text{C}$, relative humidity of $70 \pm 10\%$ and 12-hour photophase.

Aphid species	Aphid instar	Average number of aphids predated during the second instar of the predator				Total average
		1 st day	2 nd day	3 rd day	4 th day	
<i>R. porosum</i>	1 st instar	54.2 \pm 0.62Ad	62.5 \pm 0.50Ac	70.7 \pm 0.47Ab	76.0 \pm 0.63Aa	263.4*
	2 nd instar	42.5 \pm 0.56Bd	52.0 \pm 0.53Bc	61.0 \pm 0.25Bb	67.1 \pm 0.40Ba	222.6*
	3 rd instar	30.1 \pm 0.56Cd	36.1 \pm 0.37Cc	42.6 \pm 0.37Cb	47.1 \pm 0.37Ca	155.9*
<i>M. rosae</i>	1 st instar	48.5 \pm 0.50Ad	58.6 \pm 0.61Ac	68.4 \pm 0.60Ab	73.5 \pm 0.54Aa	249.0*
	2 nd instar	40.8 \pm 0.62Bd	47.2 \pm 0.48Bc	53.5 \pm 0.37Bb	58.1 \pm 0.54Ba	199.6*
	3 rd instar	33.4 \pm 0.61Cd	38.3 \pm 0.59Cc	42.9 \pm 0.64Cb	47.5 \pm 0.76Ca	162.1*

Means followed by the same letters, uppercase in the columns and lowercase in the rows, do not differ from each other according to the Tukey test, $p < 0.05$. *Significant differences between the average total consumption in the first, second and third instar between each aphid species, according to the t test, $p < 0.05$.

Table 3

Daily average consumption (\pm standard error) of nymphs of *Rhodobium porosum* e *Macrosiphum rosae* (Aphididae) by second instar larvae of *Hippodamia convergens* (Coccinellidae). Temperature of $25 \pm 1^\circ\text{C}$, relative humidity of $70 \pm 10\%$ and 12-hour photophase.

Aphid species	Aphid instar	Average number of aphids predated during the second instar of the predator			Total average
		1 st dia	2 nd dia	3 rd dia	
<i>R. porosum</i>	1 st instar	49.1 \pm 0.45Ac	59.3 \pm 0.42Ab	69.0 \pm 0.39Aa	177.4*
	2 nd instar	36.8 \pm 0.59Bc	46.3 \pm 0.55Bb	53.4 \pm 0.49Ba	136.5*
	3 rd instar	27.4 \pm 0.42Cc	32.8 \pm 0.35Cb	38.7 \pm 0.47Ca	98.9*
<i>M. rosae</i>	1 st instar	51.3 \pm 0.63Ac	62.1 \pm 0.52Ab	71.0 \pm 0.51Aa	184.4*
	2 nd instar	41.4 \pm 0.54Bc	50.8 \pm 0.53Bb	58.1 \pm 0.48Ba	150.3*
	3 rd instar	24.8 \pm 0.59Cc	28.3 \pm 0.47Cb	31.5 \pm 0.68Ca	84.6*

Means followed by the same letters, uppercase in the columns and lowercase in the rows, do not differ from each other according to the Tukey test, $p < 0.05$. *Significant differences between the average total consumption in the first, second and third instar between each aphid species, according to the t test, $p < 0.05$.

Table 4

Average number (\pm standard error) of nymphs of *Rhodobium porosum* (Aphididae) consumed by second instar larvae of *Chrysoperla externa* (Chrysopidae) and *Hippodamia convergens* (Coccinellidae). Temperature of $25 \pm 1^\circ\text{C}$, relative humidity of $70 \pm 10\%$ and 12-hour photophase.

Predator	Aphid instar			
	1 st instar ¹	2 nd instar ¹	3 rd instar ¹	Daily average ¹
<i>C. externa</i> ²	65.85 \pm 0.40	55.65 \pm 0.34	38.98 \pm 0.36	53.49
<i>H. convergens</i> ²	59.13 \pm 0.36	45.50 \pm 0.35	32.97 \pm 0.40	45.87

¹Significant differences between means, the according to the t test, $p < 0.05$. ²Consumption period (second instar): four days for *Chrysoperla externa* (Chrysopidae) and three days for *Hippodamia convergens* (Coccinellidae).

Table 5
Average number (± standard error) of nymphs of *Macrosiphum rosae* (Aphididae) consumed by second instar larvae of *Chrysoperla externa* (Chrysopidae) and *Hippodamia convergens* (Coccinellidae). Temperature of 25±1°C, relative humidity of 70±10% and 12-hour photophase.

Predator	Aphid instar			
	1 st instar	2 nd instar	3 rd instar ¹	Daily average
<i>C. externa</i> ²	62.25±0.49	49.90±0.41	40.53±0.61	50.89
<i>H. convergens</i> ²	61.47±0.29	50.10±0.33	28.20±0.27	46.59

¹Significant differences between means, the according to the *t* test, *p* <0.05. ²Consumption period (second instar): four days for *Chrysoperla externa* (Chrysopidae) and three days for *Hippodamia convergens* (Coccinellidae).

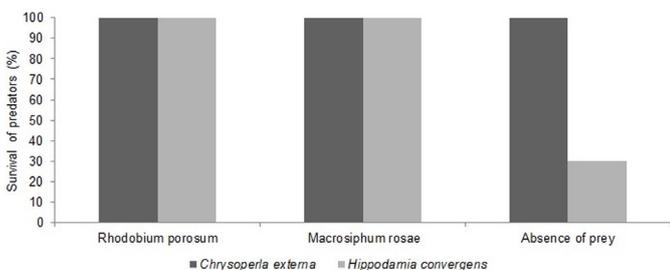


Figure 1 Survival rate of predators *Chrysoperla externa* (Chrysopidae) and *Hippodamia convergens* (Coccinellidae) in the presence and absence of *Rhodobium posorum* and *Macrosiphum rosae* (Aphididae). Temperature of 25±1°C, relative humidity of 70±10% and 12-hour photophase.

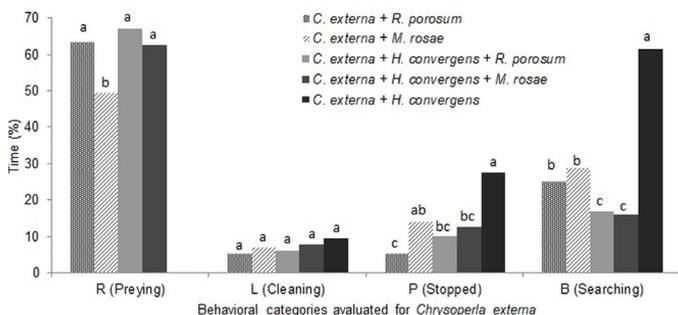


Figure 2 Time spent by *Chrysoperla externa* (Chrysopidae) in each behavioral category evaluated in the presence and absence of prey and another predator (*Hippodamia convergens*– Coccinellidae), during 60 minutes. Temperature of 25±1°C, relative humidity of 70±10% and 12-hour photophase. Average time (%) followed by the same letters do not differ from each other by the Kruskal-Wallis and Dunn's Test *p*<0.05

predators. However, *C. externa* consumed a significantly higher number of third instar nymphs of this aphid (*p* < 0.05) (Table 5). Nevertheless, this difference did not significantly reflect the average daily consumption of nymphs by both predators.

Behavior and intraguild interaction between *Chrysoperla externa* and *Hippodamia convergens* in the presence and absence of aphids

The survival rate of *C. externa* and *H. convergens* larvae was 100% when confined together, in the presence of either prey species (Figure 1). In the absence of prey, only 30% of the larvae of *H. convergens* survived, as a result of intraguild predation (Figure 1). In treatments involving both predators and the prey *R. posorum*, the total consumption during 24 hours was 119.2 nymphs, a higher value (*p* < 0.05) than the average obtained for the sum of consumption of each of them when kept separated

Table 6
Individual daily average, together and sum of individual averages of first instar nymphs of *Rhodobium porosum* e *Macrosiphum rosae* (Aphididae) consumed by second instar larvae of *Chrysoperla externa* (Chrysopidae) and *Hippodamia convergens* (Coccinellidae). Temperature of 25±1°C, relative humidity of 70±10% and 12-hour photophase.

Aphid species	Predator	24-hour consumption
<i>Rhodobium porosum</i>	<i>Chrysoperla externa</i>	54.20 c
	<i>Hippodamia convergens</i>	49.10 d
	Sum of individual averages	103.30 b
<i>Macrosiphum rosae</i>	Predators released together	119.50 a
	<i>Chrysoperla externa</i>	51.30 c
	<i>Hippodamia convergens</i>	48.50 c
	Sum of individual averages	99.80 b
	Predators released together	107.20 a

Means followed by the same letters for each prey species did not differ from each other according to the Tukey test, *p*<0.05.

(103.3 nymphs) (Table 6). In the presence of *M. rosae*, consumption was also higher (107.2) (*p* < 0.05) than the sum of consumption of each of them when evaluated individually (99.8) (Table 6).

In the presence of prey, the time spent by *C. externa* larvae to predate both aphid species was higher than the other combinations, except for the one in which the larvae were maintained individually with *M. rosae* ($X^2 = 19.70$; *p* < 0.05). The aphid species did not change the average time that *C. externa* larvae spent preying, and corresponded to 67.13% for *R. posorum* and 62.65% for *M. rosae* (Figure 2).

The time that individual *C. externa* larvae (in the absence of *H. convergens*) were preying when confined with *R. posorum* was higher (63.49%) than when confined with *M. rosae* (49.60%) ($X^2 = 19.70$; *p* < 0.05). Regarding searching time category, *C. externa* larvae were more agile in the presence of *H. convergens* than when individually. In a presence of the coccinellids larvae, *C. externa* larvae spent 16.70% of the time searching for *R. posorum* and 16.01% searching for *M. rosae*. Individually, the searching time was 25.43% e 28.89%, in the presence of *R. posorum* and *M. rosae*, respectively. In the absence of prey, the higher time of stopped category (27.65%) ($X^2 = 17.07$; *p* < 0.05) and searching (61.48%) ($X^2 = 19.57$; *p* < 0.05) was observed when *C. externa* larvae were not supplied with prey (Figure 2).

Larvae of both predators confined together spent more time preying when supplied with *M. rosae* nymphs (67.30%) than with *R. posorum* nymphs (42.30%) ($X^2 = 18.04$; *p* < 0.05). In the same conditions of confinement, the time spent to prey *M. rose* nymphs was higher than when was individually and with *R. posorum* nymphs (44.84%) ($X^2 = 18.04$; *p* < 0.05) (Figure 3).

Regarding the searching time, it was observed that, similar to *C. externa*, *H. convergens* spent more than half of the time foraging (60.57%) in the presence of the competitor and absence of prey ($X^2 = 20.87$; *p* < 0.05). Under these conditions, the coccinellid larvae remained still for a longer period (35.59%) compared to the other combinations

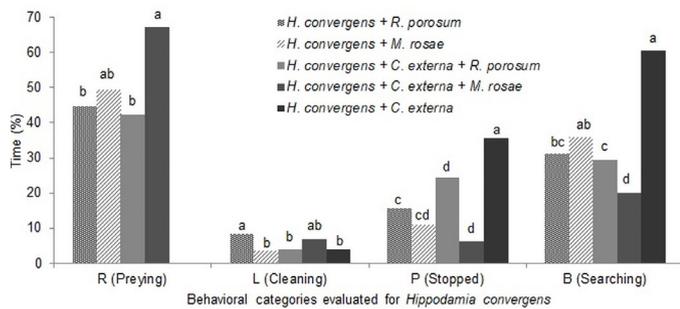


Figure 3 Time spent by *Hippodamia convergens* (Coccinellidae) in each behavioral category evaluated in the presence and absence of prey and another predator (*Chrysoperla externa* – Chrysopidae), during 60 minutes. Temperature of $25 \pm 1^\circ\text{C}$, relative humidity of $70 \pm 10\%$ and 12-hour photophase. Average time (%) followed by the same letters do not differ from each other by the Kruskal-Wallis and Dunn's Test $p < 0.05$.

($X^2 = 21.83$; $p < 0.05$). It was observed that, when the predators met each other, *H. convergens* remained inhibited with the proximity of *C. externa*, inducing them to remain still.

Discussion

The greater number of first-instar nymphs of *R. porosum* and *M. rosae* consumed by both predators is directly related to the smaller size and body mass of the aphids. The lower body content to be ingested requires less handling time and, consequently, a greater number of preys consumed. The consumption of prey with smaller body size was also higher for *C. externa* and *H. convergens* larvae fed on nymphs of *Cinara* spp. (Hemiptera: Aphididae) compared to the larger nymphs (Cardoso and Lazzari, 2003a, 2003b). These results are related to the ease of capturing smaller prey, which leads to greater consumption of nymphs in this stage, as also observed for *C. externa* larvae fed on nymphs of *Schizaphis graminum* (Rondani, 1852) (Hemiptera: Aphididae) (Fonseca et al., 2000).

The increase in the consumption of nymphs from the first to the last day of evaluations is due to the growth and development of the predator, even at the same instar, which demands greater consumption. *H. convergens* and *C. externa* also consumed more nymphs of *Myzus persicae* (Sulzer, 1776) (Hemiptera: Aphididae) as a result of their development and increase in body size (Katsarou et al., 2005; Barbosa et al., 2006). The greater demand for prey as predators develop is attributable to the increasing requirement of nutrients for their growth, as well as for other physiological processes necessary to complete their life cycle (Guedes, 2013).

The greater consumption of third-instar nymphs of *M. rosae* in relation to *R. porosum* by *C. externa* may be related to the behavior of the larva, that pierces the body of the prey and abandon them without being completely consumed. In the evaluations, the larvae were observed introducing their mouthparts in the prey, but because of their relatively large size, they release it quickly. This behavior caused higher mortality of nymphs compared to those of *R. porosum*, which are smaller and were entirely consumed. Theoretically, prey consumption involves capturing, handling, killing and ingesting its contents and/or its body parts, activities that are included in accounting for handling time (Veeravel and Baskaran, 1997; Aljetlawi et al., 2004). The fact that the prey is not completely consumed does not affect the predator's ability to search and attack; and partial consumption of the prey can result in higher mortality due to less time spent in handling (Moradi et al., 2020).

For *H. convergens*, the higher consumption of first and second-instar nymphs of *M. rosae* compared to *R. porosum* may be associated with the

nutritional quality of the prey, as well as the nutritional requirement of the predator (Eubanks and Denno, 2000; Mirhosseini et al., 2015; Farooq et al., 2018; Souza et al., 2019). Aphidophagous coccinellids depend on essential food for reproduction and embryonic and post-embryonic development. However, nutrients from other types of prey can be important for complementing their diet (Souza et al., 2019), which might vary in relation to palatability (Lundgren, 2009). Thus, the greater consumption of *M. rosae* by *H. convergens* when compared with *R. porosum* can be related to these aspects. Furthermore, the size of the prey plays important roles since *M. rosae* has a larger body volume than *R. porosum*. Another factor that may have interfered in the capture of prey is the color of the nymphs of *M. rosae*, and the shape of their body. Some species of coccinellids tend to feed on prey with coloration that distinguishes them from the host plant (Mondor and Warren, 2000). Therefore, the nymphs of *M. rosae*, may have been more easily detected by the predator. According to Lim and Ben-Yakir (2020), coccinellids use visual cues to select prey, including chromatic sensitivity and geometric perception.

The third-instar nymphs of *R. porosum* were predated in greater numbers than the nymphs of *M. rosae* probably because they are smaller. There was a certain difficulty for *H. convergens* larvae in capturing larger nymphs, compared to *C. externa* larvae. This may be due to the different types of mouthparts of these predators. A predator's efficiency and greater attack capacity are dependent on the chances of contact between it and its prey. Here, this contact is related to the maximum distance at which the predator is able to attack the prey and, therefore, the skill and speed of movement have an important impact on the predation rate (Veeravel and Baskaran, 1997; Bayoumy and Awadalla, 2018). In this regard, coccinellid larvae require greater proximity to the prey in relation to those of lacewings, generating a disadvantage in the capture activity.

The results of the intraguild interaction between predators indicated a negative response only in the absence of prey, which was characterized by the predation of *H. convergens* by *C. externa*. In the absence of extraguild prey, there is an increase in the foraging behavior of predators and, consequently, an increase in the encounter rate, contributing to the occurrence of intraguild predation (Zarei et al., 2020). Silva et al. (2022) demonstrated a reduction in intraguild predation between coccinellids and lacewings in intercrop system due to presence and increase herbivore movement, making the shared prey more vulnerable than the intraguild prey. According to Michalko; Pekár (2014), in the presence of shared prey, generalist predators choose which prey they will consume according to nutritional composition, defense behavior and size.

In the case of lacewings and coccinellids, there is a preference and competition for aphids (Khudr et al., 2020). Therefore, the results obtained in this work reiterate those obtained in other studies that demonstrated the performance of *C. externa* larvae as intraguild predators when in the absence of prey. However, in addition to the presence of extraguild prey, the density of their populations is also a factor that interferes in predation (Lucas, 2005; Nóia et al., 2008; Trotta et al., 2015; Devee et al., 2018). The results of this study show that not only the presence of the prey, but also the density of individuals, are factors that interfere in the occurrence of intraguild interaction, since the number of nymphs consumed by the two predators when confined together was higher than the daily consumption of each predator evaluated separately.

Regarding to the predators involved in the negative interaction, only *C. externa* larvae behaved as intraguild predators. Golsteyn et al. (2021) found a negative interaction between larvae of *Chrysoperla carnea* (Stephens, 1836) (Neuroptera: Chrysopidae) and larvae of *Cryptolaemus montrouzieri* (Mulsant, 1853) (Coleoptera: Coccinellidae) both in the presence and absence of prey, observing greater aggressiveness of

the lacewing in relation to the coccinellid. The fact that a predator is characterized as more aggressive compared to another is associated with body morphology and speed of movement. The lacewing larvae have prominent mandibles and are more agile compared to coccinellid larvae, which favors their success in intraguild interaction (Michaud and Grant, 2003).

Another factor that interferes in the intraguild predation is the size of the species involved, with the intraguild predator usually having greater body volume (Lucas, 2005; Devee et al., 2018). However, in the case of lacewings and coccinellids, when both are of equal size, lacewing larvae have an advantage over coccinellids in terms of competitiveness and predation behavior (Sengonca and Frings, 1985; Lucas, 2005; Zarei et al., 2020). The larvae of the predators involved in the present study were in the second instar and had similar sizes, therefore, the predation of *C. externa* on *H. convergens* is a result of its greater aggressiveness and agility.

Regarding the results obtained for predator behavior, the longer time spent by *C. externa* larvae in predating *R. porosum* nymphs, compared to *M. rosae*, is in line with that obtained for predatory capacity, since there was a higher consumption of *R. porosum* nymphs compared to *M. rosae*. For *H. convergens*, the longest time spent in predation was verified in the presence of *M. rosae*, both together with *C. externa* and individually, coinciding with the result obtained for the predatory capacity of this coccinellid.

The greater time invested in predation by larvae of *C. externa* and *H. convergens*, when confined together, indicates a behavioral change, especially of those of *C. externa*, when they notice the presence of *H. convergens*. This perception may have been responsible for the increase in the number of aphids consumed, in relation to the condition in which they were kept alone, resulting in a longer predation time. Janssen et al. (1998) report that when two competitors forage in the same area, in addition to competition for the same resource, changes in search behavior may occur, reflecting changes in the attack rate. Thus, the shorter foraging time of *C. externa* larvae in the presence of the competitor may be associated with greater speed and agility in the search for prey, resulting in a greater number of prey consumed and a greater time spent in predation, as discussed earlier. On the other hand, in the absence of the competitor, *C. externa* larvae were able to search for prey more slowly, generating a longer search time. Thus, the change in the behavior of *C. externa* against another predator resulted in a positive effect defined by the reduction in the number of nymphs of both aphid species studied.

In the absence of prey, a situation in which a negative interaction was verified, only the larvae of *C. externa* attacked the larvae of *H. convergens*. It has been observed that lacewing larvae can reach coccinellid larvae at a greater distance due to their prominent mouthparts, which facilitates capture. According to Zarei et al. (2020), the confinement of *C. carnea* larvae with *Hippodamia variegata* (Goeze, 1777) larvae results in higher mortality of *H. variegata* due to the ease of capture by *C. carnea* larvae, whose mouthparts are introduced into the abdominal tergites of the coccinellid, paralyzing and making it impossible to defend itself.

Conclusion

The greater consumption capacity of *C. externa* and *H. convergens* larvae was observed when offered first-instar nymphs of *R. porosum* and *M. rosae*. During the development of the predator inside the instar an increase in the consumption capacity was observed. The intraguild interaction in the presence of prey was positive between *C. externa* and *H. convergens*, with intraguild predation only in the absence of prey. Although both *R. porosum* and *M. rosae* have consumed a greater number of different species, both preys are targets of these predators.

These results point out to the success of the isolated or simultaneous use of these predators to control aphids in rose bushes. The results obtained in this work are important to assist in biological control programs using generalist predators.

Acknowledgments

The authors thank Dr. Marcus Vinícius Sampaio, Universidade Federal de Uberlândia, Brazil, for the identification of the aphid species and to FAPEMIG and CNPq for financial support.

Conflicts of interest

The authors declare no conflicts of interest

Author contribution statement

LAGT, ALVS, BS conceived and designed the experiments. BS supervised the research. LAGT, LPSP, LLP performed the experiments. CESB analyzed the data. LAGT, BS, CESB, ACS wrote the paper. CESB, ALVS translated the paper.

References

- Aljetlawi, A. A., Sparrevik, E., Leonardsson, K., 2004. Prey-predator size-dependent functional response: derivation and rescaling to the real world. *J. Anim. Ecol.* 73 (2), 239-252. <http://dx.doi.org/10.1111/j.0021-8790.2004.00800.x>.
- Barbosa, L. R., Carvalho, C. F., Souza, B., Auad, A. M., 2006. Influência da densidade de *Myzus persicae* (Sulzer) sobre alguns aspectos biológicos e capacidade predatória de *Chrysoperla externa* (Hagen). *Acta Sci. Agron.* 28 (2), 227-231. <http://dx.doi.org/10.4025/actasciagron.v28i2.1076>.
- Barjadze, S., Karaca, İ., Yaşar, B., Japoshvili, G., 2011. The yellow rose aphid *Rhodobium porosum*: a new pest of damask rose in Turkey. *Phytoparasitica* 39 (1), 159-162. <http://dx.doi.org/10.1007/s12600-010-0133-5>.
- Bayoumy, M. H., Awadalla, H. S., 2018. Foraging responses of *Coccinella septempunctata*, *Hippodamia variegata* and *Chrysoperla carnea* to changing in density of two aphid species. *Biocontrol Sci. Technol.* 28 (3), 226-241. <http://dx.doi.org/10.1080/09583157.2018.1437597>.
- Bezerra, C. E. S., Amaral, B. B., Souza, B., 2017. Rearing *Chrysoperla externa* larvae on artificial diets. *Neotrop. Entomol.* 46 (1), 93-99. <http://dx.doi.org/10.1007/s13744-016-0427-5>.
- Blackman, R. L., Eastop, V. F., 2000. *Aphids on the World's Crops: an Identification and Information Guide*, 2nd ed. Wiley, London.
- Boiça Junior, A. L., Santos, T. M., Kuranishi, A. K., 2004. Desenvolvimento larval e capacidade predatória de *Cycloneda sanguinea* (Linnaeus, 1763) e *Hippodamia convergens* (Guérin-Méneville, 1842) alimentadas com *Aphis gossypii* Glover, 1877 sobre cultivares de algodoeiro. *Acta Sci. Agron.* 26, 239-244. <http://dx.doi.org/10.4025/actasciagron.v26i2.1892>.
- Cardoso, J. T., Lazzari, S. M. N., 2003a. Development and consumption capacity of *Chrysoperla externa* (Hagen, 1861) (Neuroptera: Chrysopidae) fed with *Cinara* spp. (Hemiptera: Aphididae) under three temperatures. *Rev. Bras. Zool.* 20 (4), 573-576. <http://dx.doi.org/10.1590/S0101-81752003000400002>.
- Cardoso, J. T., Lazzari, S. M. N., 2003b. Consumption of *Cinara* spp. (Hemiptera, Aphididae) by *Cycloneda sanguinea* (Linnaeus, 1763) and *Hippodamia convergens* Guérin-Méneville, 1842 (Coleoptera,

- Coccinellidae). Rev. Bras. Entomol. 47 (4), 559-562. <http://dx.doi.org/10.1590/S0085-56262003000400004>.
- Carvalho, C. F., Souza, B., 2009. Métodos de criação e produção de crisopídeos. In: Bueno, V.H.P (Ed.), Controle biológico de Pragas: produção massal e controle de qualidade. Editora UFLA, Lavras, pp. 77-115.
- Chailleux, A., Bearez, P., Pizzol, J., Amiens-Desneux, E., Ramirez-Romero, R., Desneux, N., 2013. Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest *Tuta absoluta*. J. Pest Sci. 86 (3), 533-541. <http://dx.doi.org/10.1007/s10340-013-0498-6>.
- Chow, A., Chau, A., Heinz, K. M., 2010. Compatibility of *Amblyseius (Typhlodromips) swirskii* (Athias-Henriot) (Acari: Phytoseiidae) and *Orius insidiosus* (Hemiptera: Anthocoridae) for biological control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on roses. Biol. Control 53 (2), 188-196. <http://dx.doi.org/10.1016/j.biocontrol.2009.12.008>.
- Cuello, E. M., Andorno, A. V., Hernández, C. M., López, S. N., 2019. Prey consumption and development of the indigenous lacewing *Chrysoperla externa* feeding on two exotic *Eucalyptus* pests. Biocontrol Sci. Technol. 29 (12), 1159-1171. <http://dx.doi.org/10.1080/09583157.2019.16660958>.
- Delgado-Ramírez, C. S., Salas-Araiza, M. D., Martínez-Jaime, O. A., Guzmán-Mendoza, R., Flores-Mejía, S., 2019. Predation capability of *Hippodamia convergens* (Coleoptera: Coccinellidae) and *Chrysoperla carnea* (Neuroptera: Chrysopidae) feeding of *Melanaphis sacchari* (Hemiptera: Aphididae). Fla. Entomol. 102 (1), 24-28. <http://dx.doi.org/10.1653/024.102.0104>.
- Devee, A., Arvaniti, K., Perdikis, D., 2018. Intraguild predation among three aphidophagous predators. Bull. Insectol. 71, 11-19.
- Eubanks, M. D., Denno, R. F., 2000. Health food versus fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. Ecol. Entomol. 25 (2), 140-146. <http://dx.doi.org/10.1046/j.1365-2311.2000.00243.x>.
- Farooq, M., Shakeel, M., Iftikhar, A., Shahid, M. R., Zhu, X., 2018. Age-stage, two-sex life tables of the lady beetle (Coleoptera: Coccinellidae) feeding on different aphid species. J. Econ. Entomol. 111 (2), 575-585. <http://dx.doi.org/10.1093/jee/toy012>.
- Fonseca, A. R., Carvalho, C. F., Souza, B., 2000. Resposta Funcional de *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) Alimentada com *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae). An. Soc. Entomol. Bras. 29 (2), 309-317. <http://dx.doi.org/10.1590/S0301-80592000000200013>.
- Fu, W., Yu, X., Ahmed, N., Zhang, S., Liu, T., 2017. Intraguild predation on the aphid parasitoid *Aphelinus asychis* by the ladybird *Harmonia axyridis*. BioControl 62 (1), 61-70. <http://dx.doi.org/10.1007/s10526-016-9774-8>.
- Gardiner, M. M., Landis, D. A., 2007. Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. Biol. Control 40 (3), 386-395. <http://dx.doi.org/10.1016/j.biocontrol.2006.11.005>.
- Golsteyn, L., Mertens, H., Audenaert, J., Verhoeven, R., Gobin, B., De Clercq, P., 2021. Intraguild interactions between the mealybug predators *Cryptolaemus montrouzieri* and *Chrysoperla carnea*. Insects 12 (7), 655. <http://dx.doi.org/10.3390/insects12070655>.
- Guedes, C. F. C., 2013. Preferência alimentar e estratégias de alimentação em Coccinellidae (Coleoptera). Oecol. Aust. 17 (2), 59-80. <http://dx.doi.org/10.4257/oeco.2013.1702.07>.
- Hagler, J. R., Blackmer, F., 2015. Evidence of intraguild predation on a key member of the cotton predator complex. Food Webs 4, 8-13. <http://dx.doi.org/10.1016/j.fooweb.2015.06.001>.
- Iftikhar, A., Hafeez, F., Hafeez, M., Farooq, M., Asif Aziz, M., Sohaib, M., Naeem, A., Lu, Y., 2020. Sublethal effects of a juvenile hormone analog, Pyriproxyfen on demographic parameters of non-target predator, *Hippodamia convergens* Guérin-Méneville (Coleoptera: coccinellidae). Ecotoxicology 29 (7), 1017-1028. <http://dx.doi.org/10.1007/s10646-020-02159-7>.
- Janssen, A., Pallini, A., Venzon, M., Sabelis, M. W., 1998. Behaviour and indirect interactions in food webs of plant inhabiting arthropods. Exp. Appl. Acarol. 22 (9), 497-521. <http://dx.doi.org/10.1023/A:1006089924336>.
- Katsarou, I., Margaritopoulos, J. T., Tsitsipis, J. A., Perdikis, D. C., Zarpas, K. D., 2005. Effect of temperature on development, growth and feeding of *Coccinella septempunctata* and *Hippodamia convergens* reared on the tobacco aphid, *Myzus persicae nicotianae*. BioControl 50 (4), 565-588. <http://dx.doi.org/10.1007/s10526-004-2838-1>.
- Khudr, M. S., Fliegner, L., Buzhdygan, O. Y., Wurst, S., 2020. Super-predation and intraguild interactions in a multi-predator-one-prey system alter the abundance and behaviour of green peach aphid (Hemiptera: aphididae). Can. Entomol. 152, 200-223. <http://dx.doi.org/10.4039/tce.2020.7>.
- Lim, U. T., Ben-Yakir, D., 2020. Visual sensory systems of predatory and parasitic arthropods. Biocontrol Sci. Technol. 30 (7), 1-12. <http://dx.doi.org/10.1080/09583157.2020.1752362>.
- Lucas, E., 2005. Intraguild predation among aphidophagous predators. Eur. J. Entomol. 102 (3), 351-364. <http://dx.doi.org/10.14411/eje.2005.052>.
- Lundgren, J. G., 2009. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. Biol. Control 51 (2), 294-305. <http://dx.doi.org/10.1016/j.biocontrol.2009.05.016>.
- Messelink, G. J., Sabelis, M. W., Janssen, A., 2012. Generalist predators, food web complexities and biological pest control in greenhouse crops. In: Larramendy, M. L., Soloneski, S. (Eds.), Integrated Pest Management and Pest Control: Current and Future Tactics. InTech, Rijeka, pp. 191-214.
- Messelink, G. J., Bloemhard, C. M. J., Sabelis, M. W., Janssen, A., 2013. Biological control of aphids in the presence of thrips and their enemies. Biol. Control 58, 45-55. <http://dx.doi.org/10.1007/s10526-012-9462-2>.
- Michalko, R., Pekár, S., 2014. Is different degree of individual specialization in three closely related spider species caused by different selection pressures? Basic Appl. Ecol. 15, 496-506. <http://dx.doi.org/10.1016/j.baae.2014.08.003>.
- Michaud, J. P., Grant, A. K., 2003. Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera: Coccinellidae) serve a defensive function? Bull. Entomol. Res. 93 (6), 499-505. <http://dx.doi.org/10.1079/BER2003269>.
- Mirhosseini, M. A., Hosseini, M., Jalali, M., 2015. Effects of diet on development and reproductive fitness of two predatory coccinellids (Coleoptera: coccinellidae). Eur. J. Entomol. 112 (3), 446-452. <http://dx.doi.org/10.14411/eje.2015.051>.
- Mondor, E. B., Warren, J. L., 2000. Unconditioned and conditioned responses to colour in the predatory coccinellid *Harmonia axyridis* (Coleoptera: coccinellidae). Eur. J. Entomol. 97 (4), 463-467. <http://dx.doi.org/10.14411/eje.2000.071>.
- Moradi, M., Hassanpour, M., Fathi, S. A. A., Golizadeh, A., 2020. Foraging behaviour of *Scymnus syriacus* (Coleoptera: Coccinellidae) provided with *Aphis spiraecola* and *Aphis gossypii* (Hemiptera: Aphididae) as prey: functional response and prey preference. Eur. J. Entomol. 117, 183-192. <http://dx.doi.org/10.14411/eje.2020.009>.
- Nóia, M. B., Borges, I., Soares, A. O., 2008. Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of intra and

- extraguild prey densities. *Biol. Control* 46 (2), 140-146. <http://dx.doi.org/10.1016/j.biocontrol.2008.03.004>.
- Ottoni, E. B., 2000. EthoLog 2.2: a tool for the transcription and timing of behavior observation sessions. *Behav. Res. Methods Instrum. Comput.* 32 (3), 446-449. <http://dx.doi.org/10.3758/BF03200814>.
- Palomares-Pérez, M., Bravo-Núñez, M., Arredondo-Bernal, H. C., 2020. Functional response of *Chrysoperla externa* (Hagen, 1861) (Neuroptera: Chrysopidae) fed with *Melanaphis sacchari* (Zehntner, 1897) (Hemiptera: Aphididae). *Proc. Entomol. Soc. Wash.* 121 (2), 256-264. <http://dx.doi.org/10.4289/0013-8797.121.2.256>.
- Polis, G. A., Myers, C. A., Holt, R. D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20 (1), 297-330. <http://dx.doi.org/10.1146/annurev.es.20.110189.001501>.
- R Development Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, 409 pp.
- Riddick, E. W., 2017. Identification of conditions for successful aphid control by ladybirds in greenhouses. *Insects* 8 (2), 38. <http://dx.doi.org/10.3390/insects8020038>.
- Sabelis, M. W., Janssen, A., Lesna, I., Aratchige, N. S., Nomikou, M., van Rijn, P. C. J., 2008. Developments in the use of predatory mites for biological pest control. *IOBC WPRS Bull.* 32, 187-199.
- Salamanca, J., Pareja, M., Rodriguez-Saona, C., Resende, A. L. S., Souza, B., 2015. Behavioral responses of adult lacewings, *Chrysoperla externa*, to a rose-aphid-coriander complex. *Biol. Control* 80, 103-112. <http://dx.doi.org/10.1016/j.biocontrol.2014.10.003>.
- Santos, N. R. P., Santos-Cividanes, T. M., Cividanes, F. J., Anjos, A. C. R., Oliveira, L. V. L., 2009. Aspectos Biológicos de *Harmonia axyridis* alimentada com duas espécies de presas e predação intraguilda com *Eriopsis connexa*. *Pesqui. Agropecu. Bras.* 44 (6), 554-560. <http://dx.doi.org/10.1590/S0100-204X2009000600002>.
- Sengonca, C., Frings, B., 1985. Interference and competitive behaviour of the aphid predators, *Chrysoperla carnea* and *Coccinella septempunctata* in the laboratory. *Entomophaga* 30 (3), 245-251. <http://dx.doi.org/10.1007/BF02372225>.
- Silva, A. C., Cahú, R. C., Cogitskei, M. M., Kubota, K. S. G., Sujii, E. R., Togni, P. H. B., 2022. Intercropping collard plants with coriander modulates behavioral interactions among aphidophagous predators by altering microhabitat structure. *Biol. Control* 176, 1-11. <http://dx.doi.org/10.1016/j.biocontrol.2022.105084>
- Smith, G. H., Roberts, J. M., Pope, T. W., 2018. Terpene based biopesticides as potential alternatives to synthetic insecticides for control of aphid pests on protected ornamentals. *Crop Prot.* 110, 125-130. <http://dx.doi.org/10.1016/j.cropro.2018.04.011>.
- Souza, B., Costa, R. I. F., Tanque, R. L., Oliveira, P. S., Santos, F. A., 2008. Aspectos da predação entre larvas de *Chrysoperla externa* (Hagen, 1861) e *Ceraeochrysa cubana* (Hagen, 1861) (Neuroptera: Chrysopidae) em laboratório. *Cienc. Agrotec.* 32 (3), 712-716. <http://dx.doi.org/10.1590/S1413-70542008000300002>.
- Souza, B., Santos-Cividanes, T. M., Cividanes, F. J., Sousa, A. L. V., 2019. Predatory Insects. In: Souza, B., Vázquez, L., Marucci, R. (Eds.), *Natural Enemies of Insect Pests in Neotropical Agroecosystems*. Springer, Cham.
- Trotta, V., Durán Prieto, J., Fanti, P., Battaglia, D., 2015. Prey abundance and intraguild predation between *Adalia bipunctata* (Coleoptera: Coccinellidae) and *Macrolophus pygmaeus* (Hemiptera: Miridae). *Eur. J. Entomol.* 112 (4), 862-865. <http://dx.doi.org/10.14411/eje.2015.080>.
- Vargas, G., Michaud, J. P., Nechols, J. R., 2012. Larval food supply constrains female reproductive schedules in *Hippodamia convergens* (Coleoptera: coccinellidae). *Ann. Entomol. Soc. Am.* 105 (6), 832-839. <http://dx.doi.org/10.1603/AN12010>.
- Veeravel, R., Baskaran, P., 1997. Searching behaviour of two coccinellid predators, *Coccinella transversalis* Fab. and *Cheilomenes sexmaculatus* Fab., on eggplant infested with *Aphis gossypii* Glover. *Int. J. Trop. Insect Sci.* 17 (3-4), 363-368. <http://dx.doi.org/10.1017/S1742758400019196>.
- Velasco-Hernández, M. C., Ramirez-Romero, R., Cicero, L., Michel-Rios, C., Desneux, N., 2013. Intraguild predation on the whitefly parasitoid *Eretmocerus eremicus* by the generalist predator *Geocoris punctipes*: a behaviour approach. *PLoS One* 8 (11), 1-9. <http://dx.doi.org/10.1371/journal.pone.0080679>.
- Zarei, M., Madadi, H., Zamani, A. A., Nedvěd, O., 2020. Intraguild predation between *Chrysoperla carnea* (Neuroptera: Chrysopidae) and *Hippodamia variegata* (Coleoptera: Coccinellidae) at various extraguild prey densities and arena complexities. *Insects* 11 (5), 1-11. <http://dx.doi.org/10.3390/insects11050288>.