

Research Paper

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Predation by *Engytatus varians* (Distant) (Hemiptera: Miridae) on *Bactericera cockerelli* (Sulzer) (Hemiptera: Triozidae) and two *Spodoptera* species

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Abstract

Predation by *Engytatus varians* (Distant) adults on different development stages of the prey species *Bactericera cockerelli* (Sulzer) (egg, second, and third nymphal instars), *Spodoptera exigua* (Hübner) and *Spodoptera frugiperda* (J. E. Smith) (egg, first, and second larval instars) was evaluated using tomato (*Solanum lycopersicum* L.) leaflets or plants. These insects are the primary pest of several agriculturally important crops. The influence of *E. varians* age on the predation capacity was also analysed. *Engytatus varians* females consumed significantly more *B. cockerelli* eggs and nymphs than males. Additionally, female predators consumed significantly more second than third instar prey at two predator ages, while males consumed significantly more the second instar than third instar prey at all predator ages. In most of the cases, females also consumed significantly more *S. exigua* and *S. frugiperda* eggs than males; however, in terms of larvae consumption, this difference was observed only in some predator ages. Females consumed more the first than second instar *S. exigua* than males, whereas this behaviour was only observed in males when the predators were 15 and 17 days old. No significant differences were observed in the consumption of first and second instar of *S. frugiperda* for both sexes of the predators. Predator age did not cause any systematic effects on the predation rates of any prey species. Based on these results, we confirmed that *E. varians* has potential as a biological control agent for *B. cockerelli* and also for the *Spodoptera* species bioassayed.

Introduction

The tomato psyllid, *Bactericera cockerelli* (Sulzer) (Hemiptera: Triozidae), is a key pest of several solanaceous crops in the United States, Mexico, Central America, and New Zealand (Munyanza *et al.*, 2007; Liefing *et al.*, 2009; Butler and Trumble, 2012). The most important damage caused by this pest, in addition to direct plant damage, is the transmission of the bacterium *Candidatus Liberibacter solanacearum* (alternatively, *Ca. Liberibacter psyllauros*) (Hansen *et al.*, 2008), which is associated with zebra chip disease in the potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.) (Liefing *et al.*, 2009), and pepper (*Capsicum annuum* L.) (Munyanza *et al.*, 2009) crops. Without control measures, *B. cockerelli* causes yield losses up to 100%, which result in monetary losses exceeding millions of dollars per year in the potato industry in the United States and Mexico (Butler and Trumble, 2012; Munyanza, 2012).

Beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), originally from Southeastern Asia, is a cosmopolitan insect that is also particularly abundant in North and Central America, Africa, Australia and Europe (Zheng *et al.*, 2011; CAB International 2019a). This insect is one of the most important pests of various crops, such as the tomato, sweet pepper, bean, cucumber, alfalfa, cotton, and ornamentals (Zheng *et al.*, 2011). The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is the most serious maize (*Zea mays* L.) pest throughout America (Nagoshi and Meagher, 2008), including Mexico (Blanco *et al.*, 2014). Recently, this pest has become a new invasive species in West and Central Africa where outbreaks were recorded for the first time in early 2016 (Goergen *et al.*, 2016; CAB International, 2019b).

In Mexico, growers typically use several applications of broad-spectrum insecticides per month throughout the growing season to control *B. cockerelli* (Vega-Gutiérrez *et al.*, 2008) as well as *S. exigua* (Osorio *et al.*, 2008) and *S. frugiperda* (Blanco *et al.*, 2014). However, the intensive use of these chemical compounds is costly and has led to the development of resistance in these pests towards many of the active substances designed for their control

(Dávila *et al.*, 2012; Sayyed *et al.*, 2012; Wyckhuys *et al.*, 2013). Thus, chemical control has been ineffective against all three insect pests, the natural predator species of various pest organisms are decimated and pesticide residues over the maximum residue level can be found in the harvested vegetables and fruits if pesticides have been incorrectly used (Bueno *et al.*, 2013).

Miridae is a hyperdiverse family containing more than 11,020 described species, which are commonly known as *plant bugs* and are found in all major biogeographic regions of the world (Cassis and Schuh, 2012). They are phytophagous (Bryocorinae, Orthotylinae, Phylinae, and Deraeocorinae), mycetophagous (Cylapinae), carnivorous (Isometopinae and Deraeocorinae), and zoophytophagous (Bryocorinae: Dicyphini) (Cassis and Schuh, 2012). The zoophytophagous species can have great economic impact as natural enemies (e.g., *Nesidiocoris tenuis* [Reuter], *Dicyphus tamaninii* Wagner, *Dicyphus hesperus* [Knight], and *Macrolophus pygmaeus* Rambur; Urbaneja *et al.*, 2012) but they can also become major pests of some food and fiber crops (e.g., tomato, potatoes, melon, tobacco, sesame, among other) at high population levels and scarcity of the prey (Alomar *et al.*, 2006; Calvo *et al.*, 2009; Castañé *et al.*, 2011; Bhatt and Patel, 2018).

Engyptatus varians (Distant) (Hemiptera: Miridae) is also a zoophytophagous that feeds on plants and phytophagous insects living on them, such as aphids, whiteflies, pseudococcids, and lepidopterans (Bueno *et al.*, 2013; Silva *et al.*, 2016). This species is widely distributed in North (Madden and Chamberlin, 1945), Central (Maes, 1998), and South America (Schuh, 1995). In Mexico, the presence of *E. varians* was reported for the first time in 2014 under greenhouse conditions feeding on *B. cockerelli* nymphs on tomato plants (Martínez *et al.*, 2014). Later, a study by Pineda *et al.* (2016) reported that, during the whole nymphal stage, *E. varians* consumed significantly the same number of *B. cockerelli* third instars (80–85) depending on whether it was fed only with third instars of the pest or with third instars + eggs of the grain moth *Sitotroga cerealella* Olivier (Lepidoptera: Gelechiidae). Also, Martínez *et al.* (2014) found that fourth instar of this predator preyed on 46% of the *B. cockerelli* third instars offered (9) during a 24 h period. In Brazil, other studies have determined that *E. varians* is an important predator of the tomato borer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). In this regard, Bueno *et al.* (2013) observed that *E. varians* consumed 92 eggs on average, over 24 h. By direct observations, these authors reported that this predator is capable of preying on larvae of this pest by stinging through the leaf epidermis into the larvae within the mine. Silva *et al.* (2016) observed that when *E. varians* fed on eggs and first instar larvae of *T. absoluta*, the survival rate of the predator was higher than 70%. However, the potential of predation of this mirid has been poorly studied on lepidopteran pests, and it is unknown on *S. exigua* and *S. frugiperda*.

In this study, the predation by *E. varians* adults on different developmental stages of *B. cockerelli* (egg, second, and third instar nymphs) and *S. exigua* and *S. frugiperda* (egg, first, and second larval instars) was recorded. The influence of *E. varians* age on the predation capacity was also analysed.

Materials and methods

Sources of insects

Bactericera cockerelli and *E. varians* were obtained from the colonies maintained in the Entomology Laboratory of the Instituto de Investigaciones Agropecuarias y Forestales (IIAF) of the

Universidad Michoacana de San Nicolás de Hidalgo (UMSNH), El Trébol, Michoacán, Mexico. Nymphs and adults of *B. cockerelli* were reared on tomato plants (variety Saladette) (~30 cm in height with nine to ten fully expanded leaves) in three frame boxes (50 × 60 × 50 cm) entirely covered by a mesh screen. Tomato plants containing psyllid eggs were transferred to other insect-free frame boxes, and new host plants were supplied as needed. *Bactericera cockerelli* colony was maintained under laboratory conditions at ~25°C, 56% RH, and a photoperiod of 12:12 h (L:D) (Pineda *et al.*, 2016).

Nymphs and adults of *E. varians* were originally collected in March 2013 from tomato plants grown in a greenhouse of the IIAF-UMSNH. They were reared on tomato plants infested with eggs and nymphs of *B. cockerelli* plus eggs of the *S. cerealella* as a supplementary food source. Using eggs and nymphs of the psyllid as diet is inexpensive and, additionally, it does not modify the predation rate of *E. varians* on third instars of *B. cockerelli* (Pineda *et al.*, 2016). The colony of *E. varians* was maintained under the same conditions as the prey colony.

The colony of *S. frugiperda* was started using larvae collected from the maize field at El Trébol, Municipality of Tarímbaro, Michoacán, Mexico. The colony of *S. exigua* was originally supplied by the Laboratorio de la Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, San Nicolás de los Garza, Nuevo León, Mexico. The larvae of both lepidopteran species were reared on a wheat germ-based semi-synthetic diet (Poitout and Bues, 1974) in a growth chamber at 25 ± 2°C, with 70–80% RH and a photoperiod of 16:8 h (L:D). Adults were fed with a 15% honey solution. Brown paper was provided as a substrate for oviposition, which was replaced periodically, as required.

Prey consumption studies

The mirid predation on *B. cockerelli* and *Spodoptera* species was evaluated along its life span using 7, 9, 11, 13, 15, and 17 days old males and females except when *B. cockerelli* eggs were offered as prey. In this case, we had to stop the study when adults of the predator were 9 days old because of a temporary shortage in the number of psyllid eggs needed per days (1000–1500) to continue with the experiment for a longer period. In all experiment, 5 days old females and males (at this age they have already experience on mating and predation) were initially introduced in the cages and offered the selected prey one or two days later. Experiments with every prey were conducted under the same conditions described for the *B. cockerelli* rearing.

To obtain *E. varians* individuals of the same age for the tests, a tomato plant (~13 cm in height) with three to four fully expanded leaves, infested with a mixture of third, fourth, and fifth instar nymphs of *B. cockerelli*, was enclosed in a cylindrical plastic tube (11 cm in diameter, 15 cm in height) open at both ends. The top of the cylinder was covered with a fine mesh screen to permit air circulation and to prevent escape of the insects. Ten adult pairs (≤12 h old) were placed into the cylinder and *S. cerealella* eggs were dispersed on the tomato leaves as supplementary food. After 5 days, one of these females or males was taken randomly for the experiment and starved for 2 h before the bioassay to induce a higher feeding rate.

Prey consumption was assessed separately for females and males of *E. varians* on different types of prey: eggs or nymphs of *B. cockerelli* and eggs or larvae of *S. frugiperda* and *S. exigua*. Each experiment consisted of ten replicates per predator sex and developmental stage of the prey. In every case, ten tomato

leaflets with eggs ($n = 100\text{--}160$) or nymphs ($n = 40$) of *B. cockerelli* and eggs ($n = 50\text{--}55$) or larvae ($n = 20$) of *S. frugiperda* and *S. exigua* without predator presence, were used as controls to observe natural and manipulation mortality, unless a different method is specifically detailed below.

Predation on eggs or nymphs of *B. cockerelli*

An excised tomato leaflet bearing 100–160 eggs (≤ 24 h old) of *B. cockerelli* was placed, with its adaxial side down, into a plastic Petri dish (9 cm diameter \times 3 cm high), and then one female or one male (5 days old) was introduced to this Petri dish. The petiole of each leaflet was enveloped with a piece of moist cotton to delay dehydration. The tomato leaflets with *B. cockerelli* eggs were replaced every 24 h when females and males of *E. varians* were 6, 7, 8, and 9 days old. After each exposure, each leaflet was carefully examined using a stereoscopic microscope (40X; Zeiss Stemi DV4; Carl Zeiss, Berlin, Germany) to determine egg consumption. Consumed eggs were easily distinguished because they looked dehydrated, and no more yolk was left in them.

Predation by *E. varians* on *B. cockerelli* nymphs was evaluated separately for second- or third-instars of the psyllid. Tomato plants ~ 15 cm in height with four fully expanded leaves were used in these tests. On the adaxial surface of each leaf of the tomato plant, 10 second- or third-instar *B. cockerelli* (≤ 24 h old) ($n = 40$ for each instar/plant) were placed using a small brush. The tomato plant was enclosed into a ventilated cylindrical plastic tube as described above, and after that, one *E. varians* female or male with the same characteristics described above was introduced. Individualized 5 days old females or males of the predator were transferred to a new cylinder every 48 h when they were 7, 9, 11, 13, 15, and 17 days old. The predation by both sexes of *E. varians* at 15 and 17 days old on second instar *B. cockerelli* was not determined due to the low availability of individuals.

After each exposure, the number of consumed nymphs was recorded using a stereoscopic microscope. *Bactericera cockerelli* nymphs that had been preyed upon were distinguishable because no more haemolymph was left in the body and because of the presence of a little brown spot at their dorsum, indicating the place where the predator inserted its stylet for feeding.

Predation on eggs or larvae of *S. frugiperda* and *S. exigua*

Eggs of *S. frugiperda* or *S. exigua* (≤ 24 h old; $n = 50\text{--}55$) were placed on the adaxial side of a tomato leaflet using a small brush. After that, the tomato leaflet with its petiole wrapped in a piece of moist cotton to prevent dehydration was placed together with one female or one male predator into a plastic Petri dish. Previous tests have shown that egg mortality of both *Spodoptera* species resulting from this handling is minimal. Each female or male predator was transferred to a new Petri dish with a tomato leaflet with *S. frugiperda* or *S. exigua* eggs every 48 h for six d (when predators were 7, 9, 11, 13, 15, and 17 days old). After each exposure, leaflets were carefully examined using a stereoscopic microscope to determine egg consumption. Consumed eggs looked dehydrated and no more yolk was left in them.

For the bioassay of larvae consumption, tomato leaflets were used for both *S. exigua* and *S. frugiperda*, because tomato plants have been reported as natural host for both species (Andrews, 1988; Trumble and Alvarado-Rodríguez, 1993; Casmuz et al.,

2010; Zheng et al., 2011). One tomato leaflet was placed inside a Petri dish, 20 first or second instar *S. frugiperda* or *S. exigua* (≤ 24 h old) larvae were added with a small brush, and one *E. varians* female or male was introduced. The tomato leaflet and larvae were replaced every 48 h for six days. After each change, each Petri dish was carefully examined using a stereoscopic microscope to determine larvae consumption. Preyed-upon larvae were easily distinguished because they were flabby and empty.

Statistical analysis

Data on the number of eggs and nymphs of *B. cockerelli*, as well as those of eggs and larvae of *S. frugiperda* and *S. exigua* consumed by *E. varians* adults, were subjected to a generalized linear models procedure (GLM) to determine the influence of the mirid sex and its life stage on the number of prey consumed. Data on the number of eggs and larvae of *S. frugiperda* or *S. exigua* consumed by *E. varians* adults were also compared between both noctuid species. To separate means, a least significant difference (LSD) multiple range test ($P < 0.05$) was used. All data were submitted to normality and homoscedasticity tests of accord with Anderson-Darling and Bartlett, respectively (Zar, 2014). Differences among predation for each developmental stage of the prey (*B. cockerelli*, *S. exigua* or *S. frugiperda*) were tested through a repeated measures analysis of variance, with predator age (days) as the repeating factor, using the fixed effects model (MIXED) procedure. All data (mean \pm standard error, SE) were analysed in the SAS/STAT programme, version 9.4 (SAS Institute, Cary, NC, EE. UU.).

Results

Predation on eggs and nymphs of *B. cockerelli*

No mortality by manipulation was observed on eggs or on second or third instar *B. cockerelli* in the negative controls. *Engytatus varians* females that were 6, 7, 8, and 9 days old consumed (ranging from 74 to 83%) significantly ($P < 0.0001$) more *B. cockerelli* eggs than males (ranging from 30 to 52%) (fig. 1). However, the predation of eggs by *E. varians* females was not significantly affected by the predator age ($F_{3,27} = 0.71$; $P = 0.55$), while it decreased significantly in males ($F_{3,25} = 6.02$; $P = 0.003$) (fig. 1).

Engytatus varians females also consumed significantly more nymphs (second and third stage) than males ($F_{23,243} = 31.07$, $P < 0.0001$) in all ages bioassayed. However, *E. varians* females that were 7, 9, 11, and 13 days old consumed between 76 and 86% second instars of *B. cockerelli*, while when they were 7, 9, 11, 13, 15, and 17 days old, they consumed between 63 and 79% third instars (table 1). Female predators consumed significantly more second (81–86% nymphs) than third instar ($63 \pm 3\%$) of *B. cockerelli* than males only when they were 9 and 11 days old. In the case of *E. varians* males, they consumed significantly less third instar *B. cockerelli* (10–27 nymphs) than second instar (34–38 nymphs) for all predator ages bioassayed (table 1).

The predation of *B. cockerelli* second nymphal instars by *E. varians* females was not significantly affected by predator age (table 1). In contrast, the maximum number of consumed *B. cockerelli* third instars ($79 \pm 4\%$) was recorded when *E. varians* females were 7 days old, and then it decreased significantly between $63 \pm 3\%$ and $66 \pm 4\%$ for the remaining evaluated ages ($F_{5,42} = 3.32$; $P = 0.013$) of the predator. In the case of predation by *E. varians* males, the consumption of *B. cockerelli* third

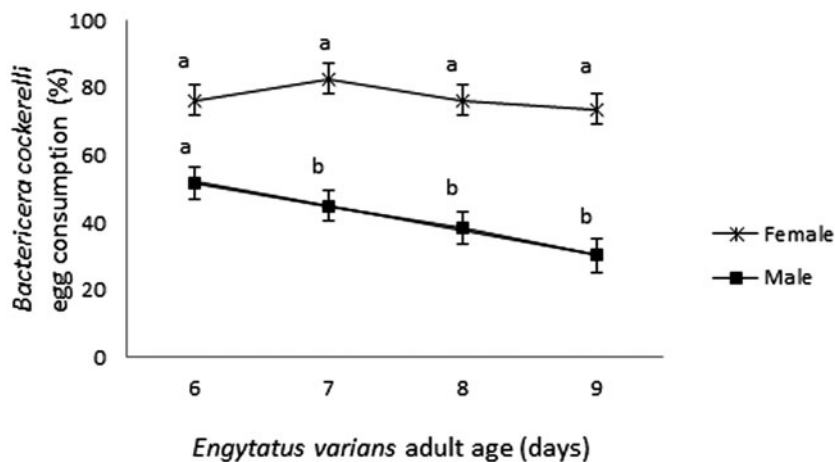


Figure 1. Predation of *Engytatus varians* females and males of different ages on *Bactericera cockerelli* eggs (means ± SE) on tomato leaves. Within the same *E. varians* age, data followed by the same letter are not significantly different ($P < 0.05$; GLM, LSD). $F_{7,52} = 19.35$, $P < 0.001$.

Table 1. Predation of *Engytatus varians* females and males of different ages on nymphal instars of *Bactericera cockerelli* (means ± SE) on tomato leaves

<i>E. varians</i> sex	<i>B. cockerelli</i> instar	<i>E. varians</i> age (days)						Time analysis ^a
		7	9	11	13	15	17	
Female ^b	2nd instar	78.9 ± 6.0a	81.5 ± 7.6b	86.0 ± 5.6b	75.9 ± 5.7a	ND	ND	NS
	3rd instar	79.2 ± 3.6a	62.6 ± 2.8a	63.2 ± 3.1a	65.0 ± 3.6a	66.8 ± 3.8	65.0 ± 3.5	*
Male ^c	2nd instar	37.7 ± 5.5b	37.3 ± 3.7b	33.9 ± 5.1b	38.4 ± 5.3b	ND	ND	NS
	3rd instar	26.7 ± 5.4a	20.5 ± 5.0a	10.2 ± 1.3a	13.0 ± 3.2a	11.0 ± 2.1	13.7 ± 1.7	**

ND, not determined due to the low availability of individuals in *B. cockerelli* rearing.

Within the same column and *Engytatus varians* sex, data followed by the same letter are not significantly different ($P < 0.05$; GLM, LSD).

^aRepeated measures ANOVA on the number of consumed preys by *E. varians* at different ages (* $P < 0.05$; ** $P < 0.01$; NS = Not significant, $P > 0.05$).

^b $F_{9,67} = 2.57$, $P < 0.05$.

^c $F_{9,70} = 5.55$, $P < 0.01$.

nymphal instars decreased significantly ($F_{5,44} = 3.83$; $P = 0.006$) over the course of the study but not ($F_{3,26} = 0.2$; $P = 0.89$) when they fed on second instars of the prey (table 1).

Predation on eggs and larvae of *S. exigua* and *S. frugiperda*

No mortality by manipulation was observed on eggs or on first or second instar *S. frugiperda* or *S. exigua* in the negative controls. Similar to the *B. cockerelli* experiment, *E. varians* females consumed a significant higher number of *S. frugiperda* eggs than males across all predator ages except when they were 7 days old (table 3). Additionally, *E. varians* females consumed significantly more first instar *S. exigua* than males, except the last two bioassayed ages of the predator females (15 and 17 days old). No significant differences were observed in the consumption between *E. varians* females and males when fed on second instar *S. exigua* or when both sexes consumed first and second instars *S. frugiperda*, except for *E. varians* females at 13 days old (table 2), which consumed significantly more first instar *S. exigua* than males.

Engytatus varians females consumed significantly more *S. exigua* eggs (ranging from 74 ± 5% to 82 ± 4%) than both first (ranging from 25 ± 6% to 41 ± 6%) and second instars (ranging from 4 ± 2% to 24 ± 4%) in all ages of the predator (table 3). This was also observed in males that preyed on more eggs (ranging from 30 ± 3% to 46 ± 5%) than both first (ranging from 9 ± 3% to 33 ± 6%) and second instars (ranging from 3 ± 1% to 15 ± 3%),

with the exception of when they were 15 days old, where the number of consumed eggs and first instars was the same (table 3). In addition, no significant differences were observed in predation between first and second instars in four of the six ages tested (7–13 days old). Similarly, *E. varians* females and males consumed significantly more *S. frugiperda* eggs than both first and second instars, but no significant differences were observed between both larval instars (table 3).

In most of the cases, the predation by *E. varians* was not significantly affected by the predator age (table 3); however, in the cases where it was, for example, female predation on second instar *S. exigua* ($F_{5,42} = 6.32$; $P = 0.0002$) and *S. frugiperda* ($F_{5,44} = 4.98$; $P = 0.001$) and male predation on first ($F_{5,41} = 4.92$; $P = 0.000$) and second instar *S. exigua* ($F_{5,44} = 4.98$; $P = 0.001$), the prey consumption was, in general, positively affected.

Irrespective of the age tested, *E. varians* females consumed significantly more eggs ($F_{11,105} = 6.43$; $P = 0.001$) and first instar *S. exigua* ($F_{11,91} = 4.1$; $P = 0.001$) than *S. frugiperda* (table 3). In contrast, no differences in predation on second instar *S. exigua* and *S. frugiperda* were observed ($P > 0.11$ in all cases). Moreover, *E. varians* males consumed in general similar amounts of eggs as well as first and second instar of both noctuid species ($P > 0.09$ in all cases).

Discussion

It has been reported that *E. varians* can prey upon different developmental stages of several vegetable pests (Bueno *et al.*, 2013;

Table 2. Influence of *Engytatus varians* sex on the predation rate on *Spodoptera exigua* and *Spodoptera frugiperda* (eggs, first and second instars) on tomato leaves at different predator ages

<i>E. varians</i>		Age (days)					
Females vs. males	Prey developmental stage	7	9	11	13	15	17
<i>S. exigua</i> ^a	Eggs	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	1st instar	0.0428	0.0024	0.0094	<0.0001	0.3165	0.321
	2nd instar	0.8637	0.391	0.7968	0.1516	0.0834	0.4196
<i>S. frugiperda</i> ^b	Eggs	0.5351	0.0026	0.0004	<0.0001	<0.0001	<0.0001
	1st instar	0.6404	0.0587	0.1742	0.0438	0.4543	0.1802
	2nd instar	0.2483	0.0855	0.2282	0.1216	0.1546	0.2422

^a $F_{35,308} = 32.63, P < 0.0001$.^b $F_{35,314} = 14.58, P < 0.0001$ ($P < 0.05$; GLM, LSD).**Table 3.** Predation of *Engytatus varians* females and males of different ages on developmental stages of *Spodoptera exigua* and *Spodoptera frugiperda* (means \pm SE) on tomato leaves

<i>Engytatus varians</i> sex	Species prey and developmental stage	<i>E. varians</i> age (days)						Time analysis ^a
		7	9	11	13	15	17	
<i>S. exigua</i>								
Female ^b	Egg	80.4 \pm 3.6c	81.6 \pm 4.4c	75.2 \pm 4.5c	77.8 \pm 4.4c	81.0 \pm 4.9c	74.2 \pm 5.2c	NS
	1st instar	25.0 \pm 6.5b	27.8 \pm 5.1b	35.5 \pm 7.0b	39.4 \pm 6.4b	41.0 \pm 6.4b	39.4 \pm 5.0b	NS
	2nd instar	4.5 \pm 1.7a	12.5 \pm 1.5a	15.5 \pm 2.4a	24.4 \pm 4.3a	21.5 \pm 3.9a	18.3 \pm 4.0a	***
Male ^c	Egg	46.0 \pm 5.2b	36.6 \pm 5.6b	30.0 \pm 2.6b	35.6 \pm 4.3b	34.6 \pm 4.0b	44.2 \pm 4.1c	NS
	1st instar	10.2 \pm 2.2a	9.5 \pm 2.6a	19.4 \pm 3.5a	15.0 \pm 3.3a	35.0 \pm 5.2b	33.5 \pm 6.5b	***
	2nd instar	3.5 \pm 1.3a	7.5 \pm 2.8a	14.0 \pm 1.4a	15.0 \pm 2.7a	11.1 \pm 2.0a	13.5 \pm 1.3a	**
<i>S. frugiperda</i>								
Female ^d	Egg	45.6 \pm 4.9b	44.2 \pm 7.7b	51.8 \pm 6.7b	52.4 \pm 8.3b	55.2 \pm 7.6b	53.4 \pm 6.0b	NS
	1st instar	9.37 \pm 3.0a	26.5 \pm 3.2a	16.9 \pm 1.6a	20.5 \pm 4.2a	19.3 \pm 3.5a	20.0 \pm 4.2a	NS
	2nd instar	8.8 \pm 3.1a	16.0 \pm 2.8a	10.5 \pm 1.6a	17.5 \pm 2.5a	15.0 \pm 2.9a	13.6 \pm 3.0a	*
Male ^e	Egg	42.0 \pm 3.6b	26.6 \pm 4.3b	31.0 \pm 7.3b	27.0 \pm 4.4b	24.0 \pm 3.4b	24.4 \pm 4.6b	NS
	1st instar	6.5 \pm 3.1a	15.5 \pm 3.4a	8.5 \pm 1.8a	8.5 \pm 2.8a	14.5 \pm 3.2a	12.0 \pm 1.7a	NS
	2nd instar	2.0 \pm 0.8a	6.0 \pm 2.7a	3.5 \pm 1.1a	8.5 \pm 1.83a	6.5 \pm 2.0a	7.00 \pm 0.8a	NS

Within the same column and *Engytatus varians* sex, data followed by the same letter are not significantly different ($P < 0.05$; GLM, LSD).^aRepeated measures ANOVA on the number of consumed preys by *E. varians* at different ages (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = Not significant, $P > 0.05$).^b $F_{17,151} = 35.33, P < 0.01$.^c $F_{17,157} = 13.82, P < 0.01$.^d $F_{17,152} = 12.67, P < 0.01$.^e $F_{17,162} = 11.42, P < 0.01$.

Silva et al., 2016), being, therefore an interesting candidate to be included in IPM programmes. In the present study, we determined that eggs of *B. cockerelli*, *S. exigua* and *S. frugiperda* and some nymphal or larval instars of these species can be added to the list of prey stages that can be consumed by this predator. The information available about predation on eggs of paurometabolous insects by zoophytophagous mirids is scarce. *Deraeocoris ruber* (L.) and *Campylomma verbasci* (Meyer-Dur) can prey on eggs of the psyllid *Acizzia jamatonica* (Kuwayama) in silk acacia trees (*Albizia julibrissin* Durazzini) in parks and private gardens of Southern Bulgaria, but not information on the predation rate is provided (Harizanova et al., 2012). *Nesidiocoris tenuis* females are very voracious and can prey 140 eggs of *Bemisia tabaci*

(Gennadius) (Homoptera: Aleyrodidae) of the 450 offered in 24 h (Baños et al., 2016), whereas adults and nymphs of *D. tamarinii* and *Macrolophus caliginosus* Wagner prey a much lower number (Barnadas et al., 1998). To our knowledge, *D. hesperus* is the only mirid that has been reported feeding on *B. cockerelli* eggs, but at a low rate (5 eggs of the 10 offered in 24 h in a non-choice experiment) (Ramirez-Ahuja et al., 2017). This information contrasts greatly with our results because *E. varians* females consumed between 95 and 109 *B. cockerelli* eggs of the 100–160 offered in 24 h, and therefore this species has a much higher potential as predator and could be an attractive biological control agent for decreasing the number of spring nymphs of this important pest.

In a previous study, *E. varians* females consumed more third (3.4), fourth (1.8), and fifth (0.7) instar *B. cockerelli* than males (≤ 0.42 for all three instar nymphal) in 24 h when five nymphs of each instar were offered on a tomato leaflet (Mena-Mocino, 2016). In agreement with this, in our trials, females of this mirid consumed more second (1.9- to 2.5-fold) and third (2.9 to 6.3-fold) instars *B. cockerelli* than males across all predator ages. The rule seems to be general in mirid species because females need getting more nutrients and energy to ensure the egg production and the development and fitness of their progeny, as stated by López *et al.* (2012) for *N. tenuis*. As such, *Tupiocoris cucurbitaceus* (Spinola) females consumed more third and fourth *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) nymphs (López *et al.*, 2012) and females of *M. pygmaeus* and *Macrolophus costalis* Fieber preyed more first to third *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) nymphs (Margaritopoulos *et al.*, 2003). Besides, in our study *E. varians* females of 9 and 10 d old consumed significantly more second than third *B. cockerelli* nymphs, while males always consumed younger instars (second better than third). The lower energy demand for handling younger instars, less mobile, and sclerotized than the older, could have accounted for such a result (Ramirez-Ahuja *et al.*, 2017). Similarly, to our findings, *N. tenuis* adults (the sex was not mentioned) feed more on a mixture of first and second instars *T. vaporariorum* than on third and four instars (Valderrama *et al.*, 2007).

Predation by mirids on Lepidoptera species has been previously documented, but most studies have focused on determining the potential of these predators for controlling *T. absoluta* (Urbaneja *et al.*, 2009; Desneux *et al.*, 2010; Bueno *et al.*, 2013; van Lenteren *et al.*, 2016, 2017), *Helicoverpa armigera* Hübner (Izquierdo *et al.*, 1994), and *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae) (Wei *et al.*, 1997; Rim *et al.*, 2015). However, our study is the first contribution aiming at ascertaining if *E. varians* could be an interesting biological control agent of *S. exigua* or *S. frugiperda*. Similar to the results when using *B. cockerelli* as prey, *E. varians* females consumed in general, more *S. exigua* and *S. frugiperda* eggs than males across all predator ages. This pattern has been also reported for the mirids *Hyanchloria denticornis* Tsai Yu-Hsiao and *N. tenuis* females that consumed more eggs of *Anomis texana* Riley (Lepidoptera: Noctuidae) (Beingolea, 1959) and *S. exigua* (Aragón-Sánchez, 2017) than males, respectively.

In addition, we also observed that predation by *E. varians* females and males were higher in eggs than in both first and second instars across all predator ages. Similarly, females and nymphs of *N. tenuis* fed more eggs (13.4 ± 0.6 and 8.4 ± 2 per day, respectively) than first instar *S. exigua* (7.25 ± 0.4 and 1.75 ± 0.3 per day, respectively) (Aragón-Sánchez, 2017). These results confirm that egg predation seems to be common in mirids and that Lepidopteran eggs offer high quality and nutritional value for *E. varians* development. In this sense, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) and *S. cerealella* eggs have been used to mass rear several mirid species (Encalada and Viñas, 1990; Urbaneja *et al.*, 2005; Pérez-Aguilar *et al.*, 2018).

In our study *E. varians* females consumed more first than second instars *S. exigua* and this is in agreement with the behaviour of another mirid, *N. tenuis*, on the same prey (Aragón-Sánchez, 2017) and on *S. litura* (Rim *et al.*, 2015). Interestingly, Rim *et al.* (2015) reported that the preference of *N. tenuis* for young larvae was related to the total amount of volatiles detected in the host plant and to the host plant damage. Therefore, more

studies are needed to determine if the intensity of *E. varians* attraction could change with the different lepidopteran instars present in the host plant. On the contrary, *E. varians* males, in most of ages analysed, consumed similar amounts of first and second larval instars *S. exigua*. As for the second lepidopteran studied as prey, *S. frugiperda*, both sexes of *E. varians* consumed of first and second larval instars.

In general, predation rates can be greatly influenced by several characteristics of the prey (e.g., density, activity, and distribution) or predator (e.g., stadium, age, and nutritional status) (Frechette *et al.*, 2004; Lundgren, 2011; Ramirez-Ahuja *et al.*, 2017). In previous studies, our group reported that the predation rates of *E. varians* nymphs were positively affected by the predator age (Pineda *et al.*, 2016). However, in the present study, this effect was not systematically observed for adults on any prey species. For example, only predation of third instar *B. cockerelli* declined over the course of the experiment, while predation of Lepidopteran larvae increased in four of the 12 cases analysed (table 3). To confirm these results, further laboratory tests along the entire *E. varians* adult lifespan are required, which was estimated as ~17 and 22 days for males and females, respectively, when the insects preyed on *B. cockerelli* third instars + *S. cerealella* eggs on tomato leaflets (Pineda *et al.*, 2016) and as ~26 and 32 days, respectively, when the insects preyed on eggs + first instar larvae of *T. absoluta* on the same plant host (Silva *et al.*, 2016).

Interestingly, only *E. varians* females consumed both more eggs and first instar larvae *S. exigua* than the same stages of *S. frugiperda*, which could indicate, again, that females are sensitive to the prey's particular characteristics (e.g., chorion architecture, nutritional quality of the egg, cuticle characteristics, among others). This behaviour has been suggested for *D. tamaninii* and *M. caliginosus* when both fed on *T. vaporariorum* and *H. armigera* eggs (Izquierdo *et al.*, 1994). However, to confirm these results, choice experiments are needed to evaluate the mirid's preference when it is exposed to different developmental stages of different prey species. In general, the *E. varians* predation rates observed on eggs of *S. exigua* and *S. frugiperda* were lower or similar than those reported for this same predator (92 eggs per day, equivalent to 61% of predation) and other mirids such as *Campyloneuropsis infumatus* (Carvalho) and *Macrolophus basicornis* (Stål) on *T. absoluta* (51 and 101 eggs per day, equivalent to 34 and 67% of predation, respectively) (Bueno *et al.*, 2013). In addition, Mollá (2013) reported that females of *N. tenuis* of <5 days old consumed ~80% eggs ($n = 94$) of *T. absoluta* in 24 h.

Several studies have supported that the mirid predators can offer advantages as biological control agents (Urbaneja *et al.*, 2012), as they are important generalist predators that regulate arthropod populations. Also, the mirids can establish on crops early in the growing season and can remain there when prey is scarce (Castañé *et al.*, 2011), as it has been demonstrated with *N. tenuis* (Sánchez and Lacasa, 2008; Sanchez, 2009) and our predator species studied here (Pérez-Aguilar, 2016). In conclusion, we confirmed that *E. varians* is a potential candidate for biological control of *B. cockerelli*. On the other hand, further predation studies of this mirid must be performed under more realistic conditions before a final conclusion on its performance as a biological control agent against *S. exigua* and *S. frugiperda* can be reached.

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