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Life stage and population density of *Plutella xylostella* affect the predation behavior of *Euborellia annulipes*

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Abstract

The diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is the main pest of brassica crops worldwide. The ringlegged earwig, *Euborellia annulipes* (Lucas) (Dermaptera: Anisolabididae), has been reported as a potential predator of lepidopteran larvae, including this pest, and may therefore be used for biological control. Knowledge about predator–prey interactions is important to establish pest management strategies. Therefore, the objective of this work was to evaluate the influence of the developmental stage (larva and pupa) and density of *P. xylostella* on the preference and functional response of *E. annulipes* adult females. We used choice and no-choice tests to evaluate the foraging behavior and preference of *E. annulipes* on DBM life stages and varied prey density to assess the type of functional response of the ringlegged earwig. Larvae were preferred over pupae, and the predator's functional response was type II for both prey stages. Our results report the potential of *E. annulipes* as a biocontrol agent of *P. xylostella*. Understanding their interactions may help in decision-making and optimization of integrated management strategies.

Introduction

The diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is the main pest of *Brassica* spp. (Brassicaceae), which have agricultural and ornamental importance worldwide (Newman et al., 2016). The DBM is responsible for great economic losses (Furlong et al., 2013; Oliveira et al., 2013), leading farmers to look for effective control strategies.

One of the barriers for the efficacy of *P. xylostella* control is its increased population growth as a function of temperature, as well as its resistance to (bio)pesticides (Zhou et al., 2011; Silva et al., 2012a; Zhang et al., 2013; Zago et al., 2014). Biological control by natural enemies of pest insects is an important component of integrated pest management (IPM) strategies for reducing insect populations and the use of synthetic products that are harmful to humans and the environment (Atlihan et al., 2010; Zappalà et al., 2013; Bacci et al., 2018).

Control agents can occur naturally in *Brassica* spp. agro-ecosystems. Earwigs were found to be predators in cruciferous crops, such as cabbage in The Philippines (Basedow, 1993) and collard greens in Brazil (Ribeiro & Gontijo, 2017). The ringlegged earwig, *Euborellia annulipes* (Lucas) (Dermaptera: Anisolabididae), is considered to be one of the most cosmopolitan species (Kocarek et al., 2015) and, although it is omnivorous, some researchers have reported this insect as a predator of lepidopteran pests, such as *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) and *P. xylostella* (Silva et al., 2009; Moral et al., 2017; Nunes et al., 2018). However, there are few studies evaluating the predation behavior of *E. annulipes* and its effect on economically important insect pests.

Earwigs are included in several studies as potential biocontrol agents capable of significantly reducing pest population densities and crop damage (Symondson et al., 2002; Romeu-Dalmau et al., 2012; Gabarra et al., 2015). The

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wide geographical distribution, natural occurrence, and predatory potential of *E. annulipes* may be important to the establishment of IPM against *P. xylostella*.

Knowledge about predator–prey interactions is fundamental to IPM and hence the success of a biocontrol program (Sultan & Khan, 2014). Presumably, the success of a predator depends on a set of behavioral attributes and characteristics of its predatory behavior, such as its searching capacity, prey preference, and predation rate. The predation behavior can be affected by many factors, such as the predator's developmental stage and prey stage and density (Farhadi et al., 2010; Queiroz et al., 2015; Santos et al., 2016).

Predation rates of entomophagous insects vary with prey density. The interaction between these two factors describes the type of functional response, which is an important tool in ecological studies of the behavior of individuals and food webs, as well as to characterize the potential of predators to reduce prey populations (O'Neil, 1989; Brouse, 2010; Toscano & Griffe, 2014). The functional response determines the number of prey that are attacked and consumed per time unit as a function of their density. Functional response curves can be represented as linear increasing functions of density (type I; attack rate is constant and independent of density), decelerating functions of density (type II; attack rate gradually declines and is inversely correlated with density), or sigmoidal functions of density (type III; attack rate initially increases as density increases, then gradually declines) (Holling, 1959, 1966; Pervez & Omkar, 2005; Sarnelle & Wilson, 2008; Shah & Khan, 2013; Kaçar et al., 2017). Handling time – the time taken by a predator to attack, kill, and consume a prey item – is a general feature of predatory behavior and has an important effect on the functional response by reducing search efficiency as prey density increases (Holling, 1959). Both attack rate and handling time of prey items by invertebrate predators are necessary to determine the functional response type (Tonnang et al., 2009).

In this study, we tested the following hypothesis: The predation behavior of *E. annulipes* varies as a function of *P. xylostella* life stage under choice conditions, and as a function of prey population density. Therefore, the objective was to evaluate the influence of DBM life stage and density on the preference and functional response of *E. annulipes* adult females. Moreover, we compared the efficiency of two methods of estimating the functional response parameters attack rate and handling time.

Material and methods

The experiment was conducted under laboratory conditions at 26 ± 2 °C, 70 ± 10% r.h., and L12:D12 photoperiod in the Laboratory of Entomology (LEN) of the Federal University of Paraíba (UFPB), in Areia, Paraíba, Brazil. We used *E. annulipes* adults (females) as predators and *P. xylostella* larvae and pupae as prey, both reared in the laboratory.

Predator and prey rearing

The ringlegged earwigs and the DBM were both reared at 25 ± 2 °C, 70 ± 10% r.h., and L12:D12 photoperiod. The colonies of the ringlegged earwigs were established in the Biological Control Unity of the Embrapa Algodão, Campina Grande, Paraíba, Brazil (Lemos et al., 1998) and, posteriorly, reared at LEN/UFPB, and they were supplemented with field-collected individuals every 2–3 years. Females and males of *E. annulipes* were grouped in containers with in total 32 insects each, one male per three females, and they were fed with *P. xylostella* larvae and pupae. Given that maternal care is common in dermapteran species (Butnariu et al., 2013), the eggs were collected carefully separated on moistened filter paper in Petri dishes (9 cm diameter) with their mother, until hatching.

Twenty-four hours after hatching, nymphs of the ringlegged earwigs were separated in transparent plastic containers (13 × 20 × 7 cm) containing moistened paper as a refuge, and fed with an artificial diet (Silva et al., 2009). In each container, we kept on average 40 nymphs. The containers were cleaned, and the diets were replaced every 3 days or earlier if needed until adults emerged. Sex dimorphism can be distinguished from the difference of the forceps (male presents the right branch of the forceps turning sharply inward near the tip, and in the female, the forceps are slightly and equally curved at the tips) (Klostermeyer, 1942). For this research, we chose to use only adult females as they are more aggressive predators than males (Moral et al., 2017).

Diamondback moth larvae and pupae were obtained from commercial cabbage production in Areia, Paraíba, Brazil. They were subsequently transported to the laboratory for rearing. The larvae were reared in transparent plastic containers (36 × 25 × 12 cm) sealed with mesh fabric and fed with collard green leaves (*Brassica oleracea* L. var. *acephala*). Pupae were removed from the leaves with a fine brush and placed in sealed flat-bottomed test tubes (8.5 cm high, 2.4 cm diameter) until they emerged. After emergence, males and females were placed in plastic cages (15 cm high, 6.5 cm diameter) sealed with mesh on top. As oviposition substrate, we used collard green leaves that had moistened cotton wrapped around their petioles to preserve their turgidity. The leaves with the eggs were removed and placed inside other containers (20 × 13 × 7 cm) until hatching. As adult food, we provided honey (5%) + water (95%) in hydrophilic cotton on top of the cage.

Foraging and prey preference

The predator's preference for developmental stages of *P. xylostella* was evaluated using choice and no-choice tests. One newly molted *E. annulipes* adult female was starved for 24 h and then released in the center of a Petri dish (16 cm diameter) containing 60 prey items. Four collard green leaf disks (4 cm diameter) were distributed equidistantly in each plate. In the no-choice test, we exposed 60 DBM fourth instars and 60 pupae, whereas in the choice test, we used 30 DBM fourth instars or 30 pupae. Earwigs are nocturnal predators (Klostermeyer, 1942; Naranjo-Guevara et al., 2017), so the predation behavior and the number of prey items consumed were assessed over a 12-h period (17:00–05:00 hours). We used Manly's (1974) preference index to confirm the prey stage preference by the predator, as follows:

$$\beta_1 = \log\left(\frac{\mathrm{e}_1}{\mathrm{A}_1}\right) \Big/ \left[\log\left(\frac{\mathrm{e}_1}{\mathrm{A}_1}\right) + \log\left(\frac{\mathrm{e}_2}{\mathrm{A}_2}\right)\right], \qquad (1)$$

where β_1 is the preference for prey type 1, e_1 (or e_2) is the number of prey type 1 (or 2) remaining after experimentation, and A_1 (or A_2) is the number of prey type 1 (or 2) offered. The value of the preference index can range from 0 to 1 − β_1 close to 1 indicates a preference for prey type 1, β_1 close to 0 indicates preference for prey type 2, $\beta_1 = 0.5$ indicates no preference, and thus, the predator selects prey randomly. This method considers the depletion in prey density due to predation during the experiment (Sherratt & Harvey, 1993).

To evaluate the predator foraging behavior, the time to seek, dominate, and consume the prey were timed in both of the preference tests. Ten replicates in each treatment for choice and no-choice tests were carried out, as well as for calculating Manly's preference index.

Functional response

The functional response was evaluated as function of prey density, as described in previous bioassays. We used 30, 40, 50, 60, and 70 larvae, and 5, 10, 15, 20, and 25 pupae. Recently molted adult females were starved over a 24-h period. Subsequently, they were released in Petri dishes (9 cm diameter) containing a collard green leaf disk of the same size as the dish, and the prey. Larvae presenting lesions in the integument and low mobility and pupae consumed totally or partially were considered killed. Ten replicates for each treatment were done to evaluate the functional response.

Data analysis

The experiments were analyzed following a completely randomized statistical design. Data were subjected to an ANOVA after testing for normality (Shapiro–Wilk) and variance homogeneity (Bartlett). For both preference and foraging tests, with choice and no-choice, we applied a factorial 2 × 2 scheme (choice conditions × prey life stage). The time seeking, dominating, and consuming the prey, as well as the number of larvae and pupae consumed, were compared by F-test ($\alpha = 0.05$) using Proc GLM. Differences between Manly's preference index for both prey stages were compared by t-test ($\alpha = 0.05$) using Proc TTEST. The percentage of consumption was evaluated with a non-parametric test, comparing values by χ^2, as implemented in Proc FREQ (all tests were done in SAS; SAS Institute, 2015).

The type of functional response was determined by logistic polynomial regression analysis with beta binomial model with logit link function for larvae and quasi-binomial model with cauchit link function for pupae, using the linear generalized model in R (R Development Core Team, 2014). The following polynomial function, describing the relationship between the number of prey killed and the number offered, was fitted to the data:

$$\frac{\mathrm{N_a}}{\mathrm{N_0}} = \frac{\exp\left(\mathrm{P_0} + \mathrm{P_1N_0} + \mathrm{P_2N_0^2} + \mathrm{P_3N_0^3}\right)}{1 + \exp\left(\mathrm{P_0} + \mathrm{P_1N_0} + \mathrm{P_2N_0^2} + \mathrm{P_3N_0^3}\right)}, \qquad (2)$$

where N_a represents the number of prey killed, N_0 is the number of prey offered, and P_0, P_1, $P_{2,}$ and P_3 are the constant, linear, quadratic, and cubic coefficients, respectively, related to the slope of the curve. The sign of the linear coefficient from the polynomial logistic regression analysis was used to distinguish the shape of the functional response curve, with negative and positive values indicating types II and III, respectively (Juliano, 2001).

Because prey were not replaced during the experiment, the number of larvae and pupae killed was analyzed by non-linear regression of 'random equation' (Rogers, 1972) to estimate the parameters of functional response:

$$\mathrm{N_a} = \mathrm{N_0}\{1 - \exp[\mathrm{a}(\mathrm{T_hN_a} - \mathrm{T})]\}, \qquad (3)$$

where N_a is the number of prey killed, N_0 is the initial number of prey offered, a is the attack rate, T_h is the handling time, and T is the time of exposure of the predator to prey (24 h).

The attack rate (a') and handling time (T_h) parameters were analyzed by non-linear regression, as proposed by Rogers (1972), using the R package 'frair', with data estimated by bootstrap (R Development Core Team, 2014; Pritchard et al., 2017). To compare the efficiency of this method with that of least squares, using the Marquardt method (Proc NLIN; SAS Institute, 2015), we compared the 95% confidence intervals (95% CI): If they do not overlap, the difference between means is significant ($\alpha = 0.05$) (Di Stefano, 2005). We also evaluated the ratio T/T_h for each prey stage and method.

Information criteria were used to assess the fit of the model obtained in R. The determination coefficient (R^2) of non-linear models was calculated using the uncorrelated sum of squares instead of the total sum of squares. We used other indicators to compare linear models, such as adjusted determination coefficient (R^2_{adj}), and Akaike information criterion (AIC):

$$L = -\frac{n}{2}\ln\left(\frac{RSS}{n}\right), \quad (4)$$

$$AIC = -2L + 2K, \quad (5)$$

where K is the number of parameters (including error) and L indicates log maximum likelihood. L can be obtained using sample size (n) and residual sum of squares (RSS).

The R^2_{adj} measured the strength of the relationship between the model and the predation data (Santos et al., 2016). Because R^2 values do not necessarily indicate the goodness-of-fit of the models, AIC was used to compare the fit of the two functional response models (Pachú et al., 2018).

Results

Foraging and prey preference

The time to seek and dominate the prey did not depend on the choice condition ($F_{1,36} = 0.790$, $P = 0.38$) or on the interaction between prey life stage and choice condition ($F_{1,36} = 0.321$, $P = 0.57$). However, the life stage of the prey influenced the time for the predators to attack ($F_{1,36} = 3.930$, $P<0.05$). The time to consume the prey was not influenced by the choice condition ($F_{1,36} = 0.108$, $P = 0.74$) nor by the interaction between prey life stage and choice condition ($F_{1,36} = 2.609$, $P = 0.12$). However, as stated previously, the prey life stage also determined the time for consumption by the predator ($F_{1,36} = 20.264$, $P<0.0001$). *Euborellia annulipes* consumed a whole pupa in 12 min, a longer time than that taken to consume a larva (Figure 1).

Over the 12 h of evaluation, *E. annulipes* females consumed more *P. xylostella* larvae than pupae under choice ($\chi^2 = 70.71$, d.f. = 1, $P<0.001$) and no-choice tests ($\chi^2 = 229.21$, d.f. = 1, $P<0.001$) (Table 1) and, consequently, we noted that a higher percentage of larvae was killed: 23.3 vs. 80.5% (Figure 2). A Manly's index of 0.78 confirmed that *E. annulipes* females preferred DBM larvae ($t = 10.950$, $P<0.0001$).

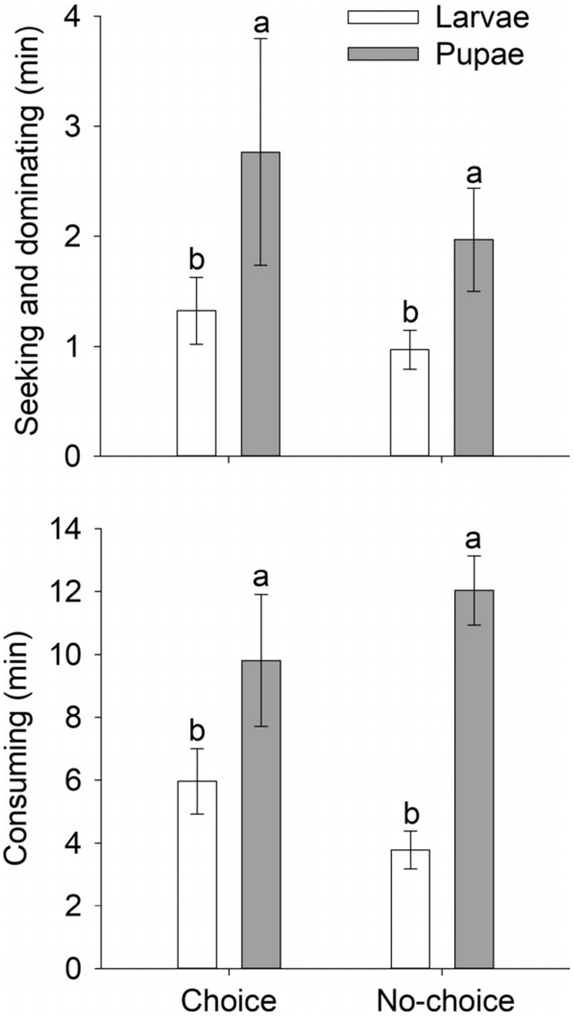

Figure 1 Mean (± SEM) foraging time (min) of *Euborellia annulipes* adult females to seek and grasp, as well as to consume *Plutella xylostella* larvae or pupae in choice and no-choice tests under laboratory conditions. Means within a panel capped with different letters are significantly different (F-tests: $P<0.001$).

Table 1 Mean (± SEM) number of *Plutella xylostella* larvae and pupae consumed over a 12-h period by *Euborellia annulipes* females in preference tests

Treatment	Larvae	Pupae	F	P
Choice	14.0 ± 1.76	4.5 ± 0.60	6.25	<0.005
No-choice	47.3 ± 1.67	17.2 ± 4.38	66.07	<0.001

Functional response

The number of *P. xylostella* larvae and pupae killed by *E. annulipes* females increased with prey density. The

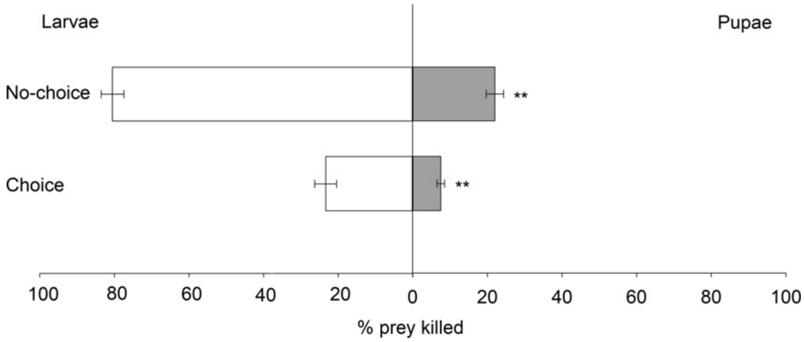

Figure 2 Mean (± SEM) percentage of *Plutella xylostella* larvae and pupae consumed by *Euborellia annulipes* adult females over a 12-h exposure period in choice and no-choice preference tests. Asterisks indicate significantly different consumption between larvae and pupae (χ^2 tests: P<0.001).

Table 2 Results of polynomial logistic regression analyses indicate the estimates and standard errors of linear coefficients for the proportion of *Plutella xylostella* larvae and pupae killed by *Euborellia annulipes* adult females

Prey	Coefficient	Estimate ± SEM	t	*P*
Larvae	Intercept (P_0)	2.01 ± 0.13	15.50	<0.0001
	Linear (P_1)	−1.95 ± 0.83	−2.33	0.024
	Quadratic (P_2)	−1.81 ± 0.86	−2.08	0.043
	Cubic (P_3)	−0.68 ± 0.87	−1.78	0.044
Pupae	Intercept (P_0)	0.32 ± 0.07	4.61	<0.0001
	Linear (P_1)	−3.76 ± 0.60	−6.26	<0.0001
	Quadratic (P_2)	−0.44 ± 0.51	−1.84	0.040
	Cubic (P_3)	0.21 ± 0.40	1.54	0.040

significantly negative value of the linear coefficient from the logistic regression strongly suggests a type II functional response for both prey stages (Rogers, 1972) (Table 2). We could distinguish that predation by *E. annulipes* increased with increasing larval and pupal density following a quadratic function (Figure 3).

Estimated values and confidence intervals of the attack rate (a') and handling time (T_h) of *E. annulipes* varied with *P. xylostella* life stage and across statistical methods used for estimation. The ringlegged earwig presented values of $a' = 0.182$ h^{-1} for larvae when estimated by least squares, and $a' = 0.150$ h^{-1} when estimated by bootstrap. For pupae, a′ was estimated by the two methods as 0.085 h^{-1} and 0.219 h^{-1}, respectively. T_h for larvae was 0.268 and 0.223 h, and for pupae 1.514 and 1.982 h by least squares and bootstrap methods, respectively (Table 3). Parameters estimated by bootstrap appeared to adjust better to the data than those estimated by least squares, as indicated by higher R^2_{adj} and lower AIC values for both stages. In addition, the confidence intervals for the parameters a′ and T_h estimated by least square were the largest, for both larvae and pupae, whereas those estimated by bootstrap were the smallest. This can easily be seen for T/T_h in both prey types (Table 3).

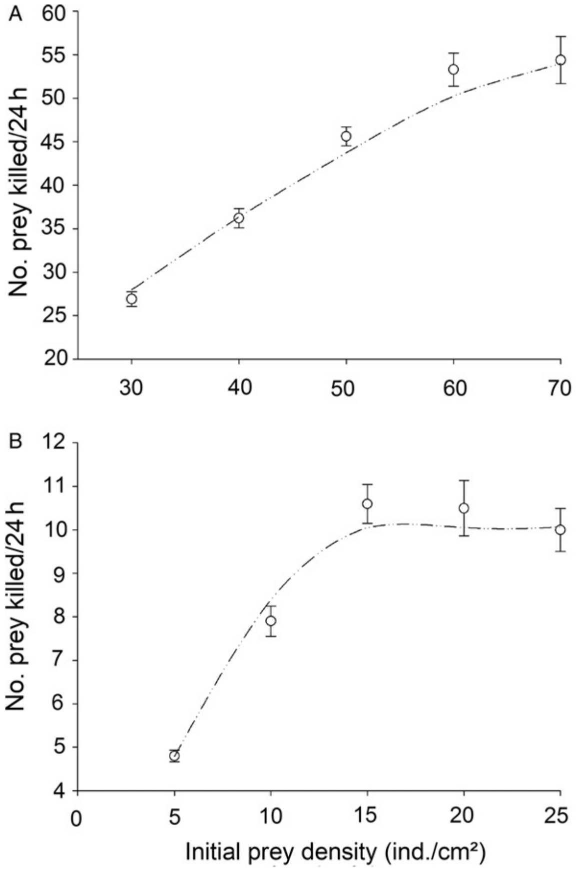

Figure 3 Mean (± SEM) number of *Plutella xylostella* (A) larvae and (B) pupae killed over a 24-h period by *Euborellia annulipes* females as function of initial density (ind. cm^{-2}).

Discussion

In this study, we found that *E. annulipes* females took less time to forage on larvae over pupae of *P. xylostella* and they preferred to feed on larvae. The preference behavior observed of the ringlegged earwig has previously been described for others, for instance, the feeding preference of the pentatomid *Podisus nigrispinus* (Dallas) for

Table 3 Attack rate (a′), handling time (T_h), T/T_h ratio (95% CI in parentheses), and evaluation criteria of functional response models of *Euborellia annulipes* females consuming *Plutella xylostella* larvae and pupae over a 24-h period, estimated using two statistical methods

	Least squares					Bootstrap				
Prey	a′ (h^{-1})	T_h (h)	T/T_h	R^2_{adj}	AIC	a′ (h^{-1})	T_h (h)	T/T_h	R^2_{adj}	AIC
Larvae	0.182 (0.092-0.457)	0.268 (0.021-0.556)	89.5 (43.17-1142.86)	0.9004	15.9937	0.150 (0.093-0.201)	0.223 (0.115-0.341)	107.6 (70.38-208.69)	0.9472	−9.1251
Pupae	0.085 (0.0246-0.415)	1.514 (1.185-4.843)	15.9 (4.96-20.25)	0.0600	82.1488	0.219 (0.104-0.314)	1.982 (1.749-2.208)	12.1 (10.87-13.72)	0.9527	14.9144
P>F	<0.05	<0.05	–	–	–	<0.05	<0.05	–	–	–

R^2_{adj}, adjusted determination coefficient; AIC, Akaike information criterion.

lepidopteran larvae over pupae in choice tests (Vacari et al., 2012; Santos et al., 2016). Besides the discovery of Sueldo et al. (2010) for *Doru lineare* (Eschscholtz) on *S. frugiperda* larvae, the type of functional response observed for *E. annulipes* on DBM prey life stage is new for earwigs.

The voracity of earwigs as predators may explain that the time of *E. annulipes* to seek, dominate, and consume DBM larvae and pupae did not vary in the choice and no-choice tests. However, factors such as integument thickness, visual clues for active hunters, defensive behavior, handling time, and others (Silva et al., 2012b) were probably decisive for the observed differences in foraging behavior across prey stages. Huang & Enkegaard (2010) observed that *Chrysoperla carnea* (Stephens) prefers to consume *Pieris brassicae* (L.) larvae rather than eggs, which may have been influenced by chorion hardness and/or egg immobility. DBM larvae are much more agile than pupae, stimulating *E. annulipes* females to attack, as also observed for *P. nigrispinus* (Vacari et al., 2012).

Besides the integument of the prey, predator mouthparts can be an important factor mediating the choice for and the predation behavior on prey (Morrison et al., 2016). The ringlegged earwig has chewing mouthparts and, before using them, the predator uses forceps to capture DBM larvae, impede their escape, and begin consumption. The silk fiber wrapping of the pupae can hinder attack and successful predation, as well as provide higher energetic cost to the predator. Even so, *E. annulipes* detects the pupa, breaks its protection with the chewing mouthparts until reaching the least rigid part, and consumes practically the whole pupa (Nunes et al., 2018). Stink bugs, as well as other hemipterans, have piercing-sucking mouthparts and may decrease energetic cost because they do not need to break the pupal protection prior to killing the prey directly through extra-oral intake (Martínez et al., 2016).

The linear coefficient of the logistic regression model was negative, hinting at a type II functional response of *E. annulipes* preying upon *P. xylostella* larvae and pupae (Shah & Khan, 2013; Khan et al., 2015; Li et al., 2017). The deceleration or decrease in prey consumption that characterizes a functional response of type II is common among invertebrate predators (Milonas et al., 2011; Vieira et al., 2012) and was documented for other females preying upon lepidopteran larvae and pupae (Ma et al., 2005; Sueldo et al., 2010; Vacari et al., 2012). According to van Lenteren (2012), predators with this type of functional response can be used in programs of inundative biological control that aim to directly reduce target pest populations.

The functional response of predators may vary depending on prey size (Aljetlawi et al., 2004), prey evasive behavior (such as movement), or due to the predator's attack stimuli and food satisfaction (Botteon et al., 2016). Our laboratory trials did not provide the same situations that the predator would be exposed to in the field, where many factors may contribute to changes in functional response, such as the generalist predation habit (Schenk & Bacher, 2002), the complexity of the natural environment, intraguild predation and prey limitation (Michaelides et al., 2017), the time to learn the environment and to search for prey (Holling, 1959), temperature conditions (Englund et al., 2011), and structure or chemical compounds of host plants (Malaquias et al., 2014, 2015; Jalali & Ziaaddini, 2016). The size of the predator–prey contact arena under laboratory conditions may force the predator to maintain greater or lesser contact with the prey densities provided and increase the probability of obtaining type II responses (Hassanpour et al., 2010; Papanikolaou et al., 2014; van Lenteren et al., 2016). Therefore, studies conducted under field conditions are warranted to ensure the predatory efficiency of *E. annulipes*.

Our study has demonstrated that *E. annulipes* adult females are voracious predators of *P. xylostella* larvae and pupae, with a preference for larvae. Functional response experiments are often the first step in determining whether an organism is a candidate for biological control, and the rates of predation obtained for a range of prey densities provide information on the potential of predation to reduce pest density (van Lenteren et al., 2016). Our results emphasize the role of the ringlegged earwig in reduction of DBM infestations, and understanding its attack behavior is fundamental to the success of DBM control programs using this predator species.

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