Neotrop Entomol (2017) 46:137–143
DOI 10.1007/s13744-016-0440-8

Functional Response and Matrix Population Model of *Podisus nigrispinus* (Dallas, 1851) (Hemiptera: Pentatomidae) fed on *Chrysomya putoria* (Wiedemann, 1818) (Diptera: Calliphoridae) as Alternative Prey

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Keywords

Biological control, hemipterous predator, ecological modeling, demographic parameters, Leslie-matrix

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Edited by Marcelo N Rossi – UNIFESP

Received 23 March 2016 and accepted 23 August 2016

Abstract

Among the predators with high potential for use in biological control, the species of the genus *Podisus* (Hemiptera: Pentatomidae) have received special attention for laboratory rearing, since they feed on different agricultural and forestry pest insects. However, the type of diet offered to insects in the laboratory may affect the viability of populations, expressed essentially by demographic parameters such as survival and fecundity. This study assessed demographic and development aspects in experimental populations of *Podisus nigrispinus* (Dallas, 1851) fed on larvae of *Chrysomya putoria* (Wiedemann, 1818) (Diptera: Calliphoridae) as an alternative prey. The demographic parameters fecundity and survival were investigated in life stages of *P. nigrispinus* with ecological modeling, by applying the Leslie matrix population model, producing histograms of life stages in successive time steps. The functional response of *P. nigrispinus* was also investigated on seven densities of *C. putoria* third-instar larvae at 24 and 48 h. The survival of predators that reached adulthood was 65% and the development time from egg to adult was 23.15 days. The predator showed a type III functional response for consumption of *C. putoria* at 24 and 48 h. The Leslie-matrix simulation of the age structure provided perpetuation of the predator population over time steps and the prey proved to be feasible for use in rearing and maintenance of *P. nigrispinus* in the laboratory.

Introduction

Biological control is essential for sustainable management of crop pests, as an alternative to chemical products, which cause environmental damage and lead to the development of genetic resistance (Thacker 2002). However, pest management programs depend on the successful production of natural enemies, which requires systematic rearing to produce satisfactory biological and reproductive performance and high efficiency in the field release (Lemos 2005).

Stinkbugs of the subfamily Asopinae are predators and considered very useful in biological control (Molina-Rugama *et al* 1998, Oliveira *et al* 1999, Vivian *et al* 2002). Although the subfamily includes 63 genera, with 357 species around the world and 23 genera with 100 species present in Neotropics (Grazia *et al* 2015), little is known about the biology of these species (De Clercq *et al* 2000). The genus *Podisus* (Heteroptera: Pentatomidae: Asopinae) is the most important, being widely studied in the Neotropics (De Clercq 2000, Torres *et al* 2006). The generalist predator *Podisus nigrispinus* (Dallas, 1851) (Hemiptera: Pentatomidae) is the species most often studied in Brazil (Torres *et al* 2006) and shows great potential for use in integrated pest management (IPM) for control of larvae in agricultural and forestry areas (De Clercq *et al* 1998). The species can be found in different environments, including forest, especially on *Eucalyptus* spp. (Zanuncio *et al* 1994), and on economically important crops such as soybean (*Glycine max* L.) (Panizzi *et al* 1977), cotton (*Gossypium hirsutum* L.) (Medeiros *et al* 1998) and tomato (*Lycopersicum esculentum* Mill.) (Bergam *et al* 1984), and several prey species can support the growth of this predator that affects the population balance of a large number of insects (O'Neil & Stimac 1988, Wiedenmann & O'Neil 1990), mainly lepidopteran larvae (Woodward *et al* 1970).

The success of a biological control program depends on the availability of agents for large-scale release. Knowledge of insect nutrition is important to develop an appropriate diet to increase and maintain the population level and to reduce production costs, through the study of the most suitable techniques for breeding and improving the effectiveness of natural enemies in the field (Tauber *et al* 2000). It is vital to study the most suitable prey species for the production of this predator, enabling mass rearing for multiplication and release in IPM programs.

P. nigrispinus can be reared on several alternative prey species such as *Bombyx mori* (Linnaeus, 1758) (Lepidoptera: Bombycidae), *Musca domestica* (Linnaeus, 1758) (Diptera: Muscidae) or *Tenebrio molitor* (Linnaeus, 1758) (Coleoptera: Tenebrionidae) (Zanuncio *et al* 1990, 1992a, Zanuncio *et al* 1991). Although previous studies have compared the performance of *P. nigrispinus* (Zanuncio *et al* 2001, 2008) fed on different types of prey, no study has evaluated the use of *Chrysomya putoria* (Wiedemann, 1818) (Diptera: Calliphoridae) as a food source for this stinkbug, or the effects on demography and population dynamics with ecological modeling by means of computer simulations. The larvae of this blowfly are larger than those of *M. domestica*, with a mean length of 13.3 mm in the third instar (Oliveira *et al* 2007). In comparison with other Calliphoridae larvae, *C. putoria* is similar in size to the larvae of *Chrysomya albiceps* (Wiedemann, 1819) and is smaller than those *Chrysomya megacephala* (Fabricius, 1794), but grows faster (Prins 1982).

Knowing the temporal distribution of life stages in natural enemies or pests is of paramount importance for biological control programs because their life histories may change significantly through the time in response to biological and ecological requirements (Speight *et al* 2008). Life tables have been used to understand relevant demographic aspects in *P. nigripinus* emphasizing the influence of different prey on its growth rate (Vivian *et al* 2002). However, ecological models may also be employed to simulate the temporal distribution of life stages based on the predator performance preying its prey. A usual model to investigate the dynamics of life stage-structured populations is the Leslie matrix (1945, 1948), which has been applied to analyze the transition between different life stages in insects (Nordhein *et al* 1988, Rosa *et al* 2011).

Conventionally, functional response is known as the number of prey consumed by an individual predator as a function of prey density (Holing, 1959). The functional response study using *C. putoria* larvae is useful to better understand stinkbug predation behavior and predator-prey interactions with an alternative prey, reflecting the rate of consumption of individual consumers in response to prey density. The components of the functional response include the length of time during which the predator and prey are exposed to each other, and the successful search rate and handling time (Tostowaryk 1972). Factors that may affect the predation process are prey density, predator density, environmental characteristics, prey defense mechanisms, and predator attack strategies (Holling 1959). The functional response is suppressed when predators are satisfied or when they are prevented from attacking more prey, depending on the behavior of the predator and the prey. Thus, the functional response, the demographic parameters, and population persistence of the species can be assessed by means of key demographic parameters for population dynamics, hoping to learn more about the different population strategies employed by the predator that could affect rearing.

This study evaluated the effect of an alternative prey on demographic parameters of *P. nigrispinus* in laboratory conditions, using the demography values as components of the Leslie matrix to simulate the temporal distribution of life stages of the predator. The study also aimed to evaluate the functional response of the predator at different prey densities, providing important information to understand the stinkbug's predatory behavior as well as its development and performance in the laboratory, in order to determine optimum conditions for its rearing.

Material and Methods

Rearing and maintenance of Podisus nigrispinus

The study was conducted in the Laboratory of Insect Ecology of the Escola Superior de Agricultura "Luiz de Queiroz", Piracicaba, São Paulo state, Brazil, at 25 ± 1°C, RH = 70 ± 10% and 12 h of photophase in BOD incubation chambers throughout the experiments. The eggs were kept on moist cotton pieces in Petri dishes, to maintain humidity until hatching.

A total of 30 individuals of *P. nigrispinus* were randomly selected after the eggs hatched. First-instar nymphs received only distilled water until the second instar, and were then separated and placed in individual plastic containers of 250 mL, containing glass tubes filled with water and sealed with cotton. The food sources were *C. putoria* third-instar larvae, offered every 2 days until adult stage.

Rearing and maintenance of the blowflies

Populations of *C. putoria* were kept in entomological cages 30 × 30 × 30 cm and maintained at 25 ± 1°C, 60 ± 10% RH and photophase of 12 h, and were fed on sugar and water ad libitum. Eggs were obtained by offering about 30 g of raw ground beef to the female blowflies as an oviposition substrate, and raw liver was provided to support the maturation of ovarian follicles (Linhares 1988). Larvae were reared on an artificial diet for blowflies, adapting the methodology used by Leal *et al* (1982), which uses 2.2 g agar, 30 g yeast extract, 30 g powdered whole milk, 1.5 g casein and 1 g nipagin, added to 60 g raw chicken heart with 270 mL water per 300 g of artificial diet.

Experiments and analysis

To evaluate the influence of prey on the demographic parameters and reproductive performance, an experiment was conducted using couples of *P. nigrispinus*. After emergence, males and females were separated to obtain the egg masses, in order to determine the number of eggs per female. Pairs were formed 3 days after the females emerged, because of their post-emergence fragility, to ensure that they would survive and reach sexual maturity (Zanuncio *et al* 1992b). Third-instar larvae were offered to the predator and the larvae available were double the amount initially offered every 2 days. The fecundity and egg viability were estimated, to evaluate the reproductive performance. New eggs were recorded daily, in order to obtain the standard egg production during the lifetime of *P. nigrispinus*, for use in the matrix of life stages. Survival between life stages of the stinkbug was estimated and used as an estimate for the probability of reaching successive stages in the Leslie matrix (Leslie 1945, 1948).

The algebraic manipulation software MATLAB 8.0 (MathWorks, 2004) was used to define a classification model of life stages for 90 generations, entering the life stages of *P. nigrispinus*. The Leslie matrix (Leslie 1945, 1948) was used to describe the population dynamics and life history from the data for survival between the life stages and the fertility estimated in the laboratory. Six stages were defined (1, 2, 3, 4, 5, 6), and the sixth stage of the adult predator F and fecundity. The shape of the matrix is shown below:

$$M = \begin{bmatrix} 0 & 0 & 0 & 0 & F & F \\ S & 0 & 0 & 0 & 0 & 0 \\ 0 & S & 0 & 0 & 0 & 0 \\ 0 & 0 & S & 0 & 0 & 0 \\ 0 & 0 & 0 & S & 0 & 0 \\ 0 & 0 & 0 & 0 & S & 0 \end{bmatrix}$$

In the matrix, *F* represents the values for fecundity of the population. Each column represents one life stage of the pest. The values for fecundity of instar stages 1 to 4 were considered to be equal to zero for these immatures. Two values of fecundity were used in the matrix to represent two levels of fecundity during the adult stage of females, initial and final, according to the estimates previously mentioned. The values of *S* determine the probability that the insect will survive during an earlier life stage and will reach the next stage. The values used in the simulation were based on laboratory experiments. The simulation was performed for populations at successive times by inserting the matrix recurrence in discrete time as: $N_{t+1} = M^* N_t$, where N_t and N_{t+1} describe the populations at successive times. Thus, the population N_{t+1} depends on the population N_t as affected by fecundity and survival in the matrix. The initial values used are the same used in the experiments.

The functional response experiment used a completely randomized design composed of seven densities: 1, 2, 3, 4, 6, 7 or 9 larvae of *C. putoria* per female individual of the predator fasted for 24 h. Individual females were placed in plastic containers of 250 mL. The mean daily consumption of prey at each density was estimated, and then subjected to analysis of variance. Consumption after 24 and 48 h was evaluated taken into account prey densities, and when significant, a nonlinear regression analysis was performed. It was performed three replicates per treatment. The parameters of the nonlinear function were estimated through polynomial logistic regression (Allison 2005), for the maximum-likelihood method (Juliano 2001). The data were fitted to this function that describes the number of prey consumed as a function of density. The polynomial function is written as:

$$\frac{L_c}{L_i} = \frac{exp\left(B_0 + B_1 L_i + B_2 L_i^2 + B_3 L_i^3\right)}{1 + exp\left(B_0 + B_1 L_i + B_2 L_i^2 + B_3 L_i^3\right)},$$

where B_0, B_1, B_2 and B_3 are the parameters estimated through the nonlinear function. L_c determines the consumption of *C. putoria* larvae and L_i the initial density of prey.

Results and Discussion

The survival (nymphal viability) of individuals that reached adulthood was 65 ± 0.02%, in which mortality was higher in early instars (second and third instars), probably because the prey was larger than the predator, resulting in higher mortality initially and then declining from the fourth instar. The development time from egg to adult was 23.15 ± 0.57 days (Table 1).

Mean sex ratio (female/female + male) was estimated, resulting in 0.4, from which were obtained 20.5 ± 6.36 egg masses. The number of eggs per egg mass was 27.25 ± 1.23 and the mean total number of eggs was 475 ± 73.53. The longevity of females was 13.25 ± 0.64 days and the egg viability was 69%.

Table 1 Duration and survival of the nymphal stages (mean and standard deviation) of *Podisus nigrispinus* fed on third-instar larvae of *Chrysomya putoria*. Temperature 25 ± 1°C, relative humidity 70 ± 10%, and photophase 12 h.

Life Stage	Duration (days)	Survival (%)
Egg	3*	100*
First instar	3*	100*
Second instar	4.5 ± 0.34	83 ± 0.04
Third instar	3.92 ± 0.28	73*
Fourth instar	3.91 ± 0.25	68 ± 0.07
Fifth instar	4.81 ± 0.26	65 ± 0.02

*Replicates exhibiting no variation.

Figure 1 shows the Leslie-matrix model simulation, which produced a histogram series over 90 successive time steps, using the results for survival of the nymphal stages and the fecundity data for *P. nigrispinus* obtained with *C. putoria* third-instar larvae as an alternative prey. The data showed the population distribution of all stinkbug stages at each time step. The simulation suggested high viability in the laboratory production and indicated that the predator population could be supported indefinitely.

The mean consumption of prey at 24 h, in the functional response experiment of the predator females feeding on larvae of *C. putoria*, was 0.86 (86%) for density (d) = 1; 0.63 for $d = 2$; 0.67 for $d = 3$; 0.48 for $d = 4$; 0.42 for $d = 6$, 0.31 for $d = 7$; and 0.36 for $d = 9$ larvae. At 48 h, the mean consumption was 0.9 for $d = 1$; 0.85 for $d = 2$; 0.84 for $d = 3$; 0.67 for $d = 4$; 0.7 for $d = 6$; 0.51 for $d = 7$; and 0.56 for $d = 9$ larvae.

The polynomial logistic regression analysis model indicated that the functional response pattern for the consumption of *C. putoria* by the predator was type III, since the resulting linear coefficient was positive. The type III functional response was fitted to the data with the statistical nonlinear regression protocol for obtaining adjustment to type III, with the explained variance of 78% for 24 h of exposure of the prey to the predator. The polynomial logistic regression analysis for predator consumption at 48 h also showed a type III functional response, due to the linear coefficient found with the explained variance of 87%. In type III functional response, the attack rate speeds up initially and then slows down when the predator is satiating.

The predator developed to adulthood and successfully reproduced when fed on *C. putoria* as an alternative prey, which provided adequate nutritional quality to meet the physiological requirements of the predator. The results obtained from simulations with the Leslie matrix demonstrate the importance of fecundity to ensure the perpetuation of *P. nigrispinus* in the laboratory.

Food resource is an important component of the environment, and directly influences the distribution and abundance of insects, affecting biological processes such as fertility, longevity, rate of development and behavior (Zanuncio *et al* 1991). In this sense, particularly the knowledge of predation dynamics under experimental conditions is essential for mass rearing of predators for field release as part of IPM (Parra *et al* 2002).

The size of the prey affected nymphal viability in the early stages of development, resulting in higher mortality. Prey size also influenced the durations of the second and third instars (4.5 ± 0.34 and 3.92 ± 0.28 days, respectively) because

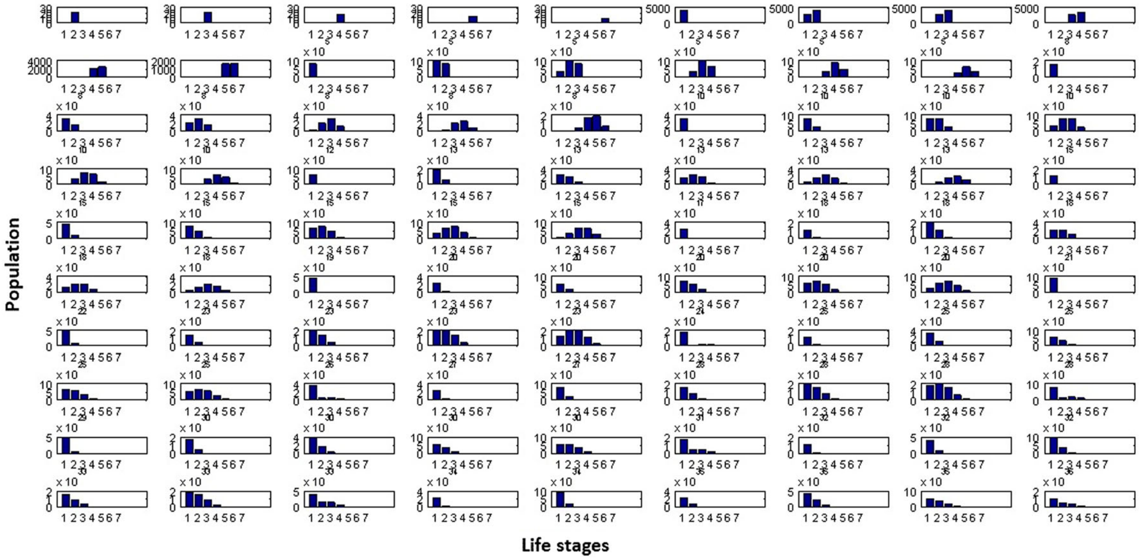

Fig 1 Leslie-matrix model simulation indicates histograms of life stages in 90 successive time steps of *Podisus nigrispinus* population reared on *Chrysomya putoria* third-instar larvae in laboratory conditions.

of the difficulty and longer time needed to capture and manipulate prey for later ingestion. An alternative procedure in the rearing of the predator in its early stages of development to improve the survival rates could be to offer smaller larvae of *C. putoria* (first-instar or second-instar larvae).

In the fourth and fifth instars, closer to adulthood, mortality decreased (mean viability of 65%) and development was faster (3.91 ± 0.25 and 4.81 ± 0.26 days, respectively). The viability of *P. nigrispinus* nymphs fed on larvae of *Alabama argillacea* (Hübner, 1818) (Lepidoptera: Noctuidae) was 98.96% (Lemos *et al* 2003), 64% with *Spodoptera frugiperda* (J.E. Smith, 1797) (Lepidoptera: Noctuidae) (Oliveira *et al* 2004), and 51.84% when fed *Musca domestica* (Lemos *et al* 2003). dos Santos *et al* (1995) reported that *P. nigrispinus* prefers to predate on small larvae of *A. argillacea* rather than on large ones, which can better defend themselves.

The reproductive functions of the predator were prioritized and probably resulted in the low longevity of the females (13.25 ± 0.64 days) because the energy used in egg production reduced the longevity. The mean numbers of egg masses and the number of eggs per mass were 20.50 ± 6.36 and 27.25 ± 1.23, respectively. With larvae of *S. frugiperda*, females produced on average 14.89 egg masses with 30.06 eggs, and with larvae of *T. molitor* they produced 17 egg masses with 19.06 eggs (Oliveira *et al* 2004). The mean fecundity of females was 475 eggs, higher than that of females fed with larvae of *M. domestica*, which produced 162.90 eggs (Molina-Rugama *et al* 1997); or females fed with larvae of *T. molitor*, which produced 325 eggs; or with larvae of *S. frugiperda*, which produced 447.62 eggs (Oliveira *et al* 2004). The viability of the eggs was high, but lower, for example, when compared to 75% for alternately *T. molitor* and *M. domestica* (Zanuncio *et al* 2001).

The results of the functional response were compared at 24 and 48 h of prey consumption, in order to determine if time affects the functional relationships. When fed on third-instar larvae of *C. putoria*, the predator showed a type III functional response at 24 and 48 h. The increase in the number of prey reflected in the predator consumption, stabilizing the attack rate with increasing prey density. At lower densities, the predator needs to move over larger areas to find new prey, slowing its rate of consumption. Some factors affecting the functional response include the size of the prey and its defense capability, which need to be taken into account to better understand the interaction (Azevedo & Ramalho 1999). Third-instar larvae of *C. putoria* are larger in relation to the predator, and their mobility provides some protection from capture and manipulation.

Therefore, the predator efficiency alone does not completely define the interaction. The defensive behavior of the prey needs to be taken into consideration, because the predatory capacity may decrease with increasing size of the prey (dos Santos *et al*. 1995). According to Gaylord & Weston (2008), the handling time of the prey varies according to the sizes of both the prey and predator: the greater the weight/size of the prey, the longer the time that the predator spends in handling it.

Oliveira *et al* (2001) obtained a type II functional response at 24 h of experiment with *P. nigrispinus* females fed on *A. argillacea*. Zanuncio *et al* (2008) used this predator females fed on larvae of *S. frugiperda* with and without defensive ability, and obtained type II and type I functional responses, due to changing defensive conditions, showing that the functional response interactions are dynamic and may change under specific conditions. These authors also observed that the lower the density, the longer the time spent searching for new prey and the lower the consumption rate. They noted, however, high consumption in small densities after 24 h, and in most cases, the predator fed on all prey offered during this period.

Type I is the linear functional response in which the attack rate increases linearly with the density of prey while type II functional response is typical of predators that specialize in few prey, which the attack rate increases at a decelerated rate to the density of prey until becoming constant (Holling 1959, Juliano 2001).

The results indicate that consumption fell at 48 h, which can probably be explained by the decreased encounter rate, the increased handling time, and predator satiation. At higher densities, the daily consumption was more homogeneous, with increased consumption during the first 24 h after fasting, but without consuming all of each individual prey.

In general, the predators are affected by the quality of prey offered (Strohmeyer *et al* 1998). They use different prey to maximize energy savings depending on the encounter rates relative to the size of the prey, with larger prey at first providing more nutritional benefit (Charnov 1976). However, there may be higher energy costs to capture large prey and greater resistance and possible aggression. The differences in the development of the predator are probably responses to the nutritional quality of the prey. A suitable prey will support more rapid development, a higher survival rate, and greater reproductive success of the predator, resulting in rapid population growth in a short time (Beddington *et al* 1976), which is essential for mass rearing for biological control programs.

The larvae of *C. putoria* are easy to rear, develop rapidly, and the results indicate that are a suitable prey for rearing and maintaining populations of *P. nigrispinus* in the laboratory over time. Leslie-matrix simulation of the age structure of the predator population, fed on *C. putoria* third-instar larvae as alternative prey, provided a satisfactory outcome, as the generations of the predator population were perpetuated for over 90 time steps, indicating a high number of individuals based on the fecundity data.

Acknowledgments Support for this research was provided by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP - 2011/10829-7). We are grateful to the Laboratório de Biologia dos Insetos and the Laboratório de Resistência de Artrópodes a Táticas de Controle of the Departamento de Entomologia e Acarologia (ESALQ-USP) and to the Centro de Tecnologia Canavieira (CTC) for providing larvae to feed the stinkbugs. We also thank the anonymous reviewers for important comments and suggestions that helped us to improve the clarity of the manuscript.

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