FUNCTIONAL RESPONSE OF *Cosmoclopius nigroannulatus* (HEM.: REDUVIIDAE) TO DIFFERENT DENSITIES OF *Spartocera dentiventris* (HEM.: COREIDAE) NYMPHAE

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(With 2 figures)

ABSTRACT

This study evaluated the functional response of the predator *Cosmoclopius nigroannulatus* on first instar nymphae of *Spartocera dentiventris*, both species associated with *Nicotina tabacum*. The experiment was carried out in laboratory conditions: $27 \pm 1°C$; $80 \pm 5\%$, RH; 12 h, photophase. Ten newly emerged adults of each sex of *C. nigroannulatus* were used in each of five densities (5, 15, 25, 35, and 45 individuals) of *S. dentiventris* nymphae. The predators were observed every 24 h for five days, when the number of dead and/or consumed nymphae was recorded. The results showed a positive correlation between the number of ingested nymphae and the increase in prey density. Females ingested more nymphae than the males. The estimated handling time per prey (Th) was higher in males (3.07 h) than in females (1.93 h), with total handling time (Th x Na) increased with density. Other components of the functional response, such as attack rate (a'), searching time (Ts), and search efficiency (E) showed, in neither males nor females, a negative correlation regarding density. The results indicated a higher predatory efficiency in the females. The components of the functional response fitted significantly the randomic model of the Holling discs equation (Na = N {1 – exp[– a'(T – ThNa)]}), evidencing a functional response of type II.

Key words: functional response, predation, *Cosmoclopius nigroannulatus*, predator-prey interaction.

RESUMO

Resposta funcional de *Cosmoclopius nigroannulatus* (Hem.: Reduviidae) a diferentes densidades de ninfas de *Spartocera dentiventris* (Hem.: Coreidae)

Foi avaliada a resposta funcional do predador *Cosmoclopius nigroannulatus* Stal (Hemiptera: Reduviidae) em ninfas de 1º ínstar de *Spartocera dentiventris* (Berg) (Hemiptera: Coreidae), ambos associados à *Nicotiana tabacum*. O experimento foi realizado em condições de laboratório: $27 \pm 1°C$; $80 \pm 5\%$ UR; fotofase de 12 h. Dez adultos recém-emergidos de cada sexo de *C. nigroannulatus* foram usados em cada uma das cinco densidades (5, 15, 25, 35 e 45) de ninfas de *S. dentiventris*. Os predadores foram observados por cinco dias, a cada 24 h, quando era registrado o número de ninfas mortas e/ou consumidas. Os dados observados evidenciaram correlação positiva do número de ninfas ingeridas (Na) com o aumento da densidade (N), sendo que as fêmeas ingeriram mais ninfas que os machos. O tempo de manuseio por presa (Tm) estimado foi maior nos machos (3,07 h) que nas fêmeas (1,93 h), sendo que o tempo de manuseio total (Tm x Na) aumentou com a densidade. Os demais componentes da resposta funcional, como taxa de ataque (a'), tempo de busca (Tb) e

eficiência de busca (E), apresentaram, tanto em machos como em fêmeas, correlação negativa quanto à densidade. Os resultados indicaram maior eficiência predatória nas fêmeas. Os componentes da resposta funcional foram ajustados ao modelo randômico da equação dos discos de Holling (Na = N {1 – exp[–a'(T – TmNa)]}), evidenciando o tipo II de resposta funcional.

Palavras-chave: resposta funcional, predação, *Cosmoclopius nigoannulatus*, predator-prey interaction.

INTRODUCTION

To understand predator-prey interactions has been the purpose of numerous studies, specially those related to predator use in biological control in agro-ecosystems. The Reduviidae family is considered an economically important taxa because it includes an important group of generalist predators associated with many types of pests in different agricultural systems (Ambrose & Claver, 1997; Ambrose *et al.*, 2000).

Cosmoclopius nigroannulatus Stal (Hem., Reduviidae) is a predator associated with tobacco culture (*Nicotiana tabacum* L.). This insect presents great voracity with respect to nymphae of *Spartocera dentiventris* (Berg) (Hem., Coreidae) (C. R. Canto Silva, personal communication).

S. dentiventris, usually referred as the tobacco gray bug, is considered a *N. tabacum* pest because of its sucking mode of feeding, causing shriveling and curling in tobacco leaves (Caldas *et al.*, 2000).

One of the fundamental aspects of a predator-prey interaction is the relationship between prey density and predator consumption, to which Solomon (1949) attributed the term "functional response". According to Holling (1959; 1961), there are four basic types of functional response: I (linear), II (curvilinear), III (sigmoidal), and IV (dome-shaped). The responses of types I and II are found in most invertebrates, wereas type III is more common in vertebrates, although some arthropods can also show this response when their preferential prey is not available (Hassel *et al.*, 1977; Jervis & Kidd, 1996). A type IV response occurs only when other prey of the same or of a different species interfere in predator handling or if the prey show some kind of defense behavior, which can intensify at higher densities (Jervis & Kidd, 1996).

According to Holling (1965) and Hassel *et al.*, (1976) the functional response has components such as exposure time, prey searching time, instant discovery rate or attack rate, search efficiency, and handling time, which includes the time spent dominating, eating, and digesting the prey. The study of the different types of functional response is important in understanding the underlining mechanisms in predator-prey interaction, in elucidating the practical role of coevolutionary relationships, and in contributing towards biological control using this kind of interaction (Houck & Strauss, 1985). In this context, many experiments about predaceous insects in agricultural systems have evaluated diverse aspects of the functional response: Veeravel & Baskaran (1997) and Vieira *et al*. (1997) with coccinelids; Heimpel & Hough-Goldstein (1994), Saini *et al*. (1997), and O' Neil (1997) with pentatomids; and Fonseca *et al*. (2000) with neuropters.

The functional response has been studied in a few species of reduvids predators. Studies done with *Rhynocoris fuscipes Fabricius*, carried out by Ambrose & Claver (1995; 1996; 1997) and Ambrose *et al*. (2000) in agricultural systems in India, represent some of the few examples.

The present study aimed, as part of this ongoing effort, to evaluate the functional response of the predator *C. nigroannulatus* on *S. dentiventris* first instar nymphae.

MATERIAL AND METHODS

The experiment was carried out in the Laboratório de Biologia e Ecologia de Insetos, Departamento de Fitossanidade, of the Universidade Federal do Rio Grande do Sul at 27 ± 1°C, 80 ± 5% RH, and a 12 h photophase.

The adults of *C. nigroannulatus* were obtained from fifth instar nymphae collected in a tobacco plot of approximately 260 m², installed in the experimental area of the Departamento de Fitossanidade in Porto Alegre (30°01'S and 51°13'W), RS. The nymphae were individualized and kept in transparent plastic recipients (13 cm diameter x 9 cm height).

They were fed daily with first and second instar nymphae of *S. dentiventris* and a honey solution at 10%, until reaching the adult phase.

The *S. dentiventris* nymphae utilized to rear the nymphae of the predator *C. nigroannulatus*, as well as the ones destined for the functional response experiment, proceeded from a mass rearing kept in the same experimental area. To obtain eggs, females of *S. dentiventris* were confined on a tobacco leaf inside cylindrical cages (19 cm diameter x 60 cm length) made of voile, which prevented parasitoid access to the eggs. The cages were daily inspected and the eggs found were transferred to Petri dishes maintained in a BOD incubator at 30°C and 12 h photophase until eclosion.

To evaluate the functional response, 10 newly emerged adults of each sex of *C. nigroannulatus* were used in each one of the densities (5, 15, 25, 35, 45) of *S. dentiventris* first instar nymphae. The predators were individually confined in transparent plastic recipients (13 cm diameter x 9 cm height). The number of ingested and remaining nymphae were registered every 24 h (T). After that, the recipients were cleaned and the same amount of nymphae was offered. The observations were carried out for five days.

Predator search efficiency was obtained from the quantity of dead and offered prey (density) through the formula

$$E = Na/N, \text{ where}$$

E = search efficiency;
Na = number of consumed prey;
N = number of offered prey.

The handling time (Th) was estimated through the Holling discs equation by the nonlinear least square method (procedure NLIN, Marquardt method) from the SAS System software (SAS Institute, 2000). From the estimated handling time, we obtained total handling time (Th$_{total}$), search time (Ts), attack rate, and the maximum number of ingested prey per predator. Calculations were done using the following formulae:

$$Th_{total} = Th \times Na;$$
$$Ts = T - (Th_{total});$$
$$a' = Na/(N \times Ts);$$
$$Na_{max} = T/Th.$$

The number of ingested nymphae, searching and handling time, search efficiency and instantaneous discovery rate at the different densities, were submitted to Pearson linear correlation and

to ANOVA analysis. The measures were compared through the Tukey test at 5%. The observed data were transformed in $\sqrt{x+1}$ and compared with the randomic model of the Holling discs equation as suggested by Rogers (1972):

$$Na = N\{1 - \exp[-a'(T - ThNa)]\}$$

The observed values were tested with linear regression analysis, tested with nonlinear regression. These values were compared with a χ^2 test, utilizing the Bioestat 2.0 software and SAS (proc. NLIN).

RESULTS AND DISCUSSION

C. nigroannulatus males and females evidenced a positive correlation regarding the increase of *S. dentiventris* nymphae density (r = 0.6075 and p < 0.0001, and r = 0.5925 and p < 0.0001, respectively) (Table 1); females consumed more prey than males at all densities (F = 14.29; p < 0.0001). The larger amount of nymphae ingested by females of *C. nigroannulatus* could be expected since, according to Saini *et al.* (1997), those are more robust than males and require extra energy for gonads maturation and oviposition activity. The observed results in relation to female consumption fitted a polynomial quadratic model (p = 0.01). An acceleration in consumption until density 25 (Fig. 1A) was verified, after which consumption tended to decrease. However, this decrease was not statistically significant, denoting the satiation at about density 25 of newly emerged *C. nigroannulatus* females. This suggests an adjustment to type II of functional response.

As occurred in females, the number of consumed nymphae with density increase fitted a linear model (p = 0.01), with greatest consumption at about a 45 prey density (Fig. 1B). This was not significantly different from that at densities 25 and 35, suggesting, an adjustment to the type II model, the same as that for females.

The different functional response types can produce diverse effects upon the population dynamics of interacting predators and prey (Begon *et al.*, 1990). Type II functional response is found in most studies involving predator insects, including reduvids (Ambrose & Claver, 1995, 1996, 1997; Ambrose *et al.*, 2000). However, intrinsic factors in the predator, the substratum where prey is found, environmental conditions, or kinds of prey can lead to other types of response (Hassel *et al.*, 1976).

Heimpel & Hough-Goldstein (1994) verified that the type of functional response of *Perillus bioculatus* (Hemiptera: Penatomidae) to *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) larva did not fit either type II or III, probably due to the discontinuity verified in the number of ingested larvae. In relation to prey substratum, Coll & Ridgway (1995) noted different types of functional response in studying *Orius insidiosus* (Hemiptera: Anthocoridae) predatory behavior in trips in to tomato, beans, and pepper. The results evidenced type II functional response on beans and pepper leaf trips, and type I on tomato. Nordlund & Morrison (1990) also observed the type I model in *Chrisoperla rufilabris* (Neuroptera: Chrysopidae) larvae upon *Heliothis virescens* (Lepidoptera: Noctuidae) and *Aphis gossypii* (Hemiptera: Aphididae) eggs and larvae. To Hassel *et al.* (1977) type I functional response should not be accepted because any predator has a limited appetite; there has to be a prey density which exceeds consumption capacity. The almost linear consumption of *C. nigroannulatus* males can be related to other components of the functional response that will be discussed later. Although less common in insects, the type II model was verified by Kabissa *et al.* (1996) in *Chrysoperla externa* (Neuroptera: Chrysopidae) preying on *Helicoverpa armigera* (Lepidoptera: Noctuidae).

The parameters estimated in evaluating the components of functional response have been discussed in the literature by different authors with respect to non-linear models utilized for this purpose (Houck & Strauss, 1985; Juliano & Willians, 1987; Fan & Petitt, 1994). According to Streams (1994), these parameters are responsible for determining the different functional response types.
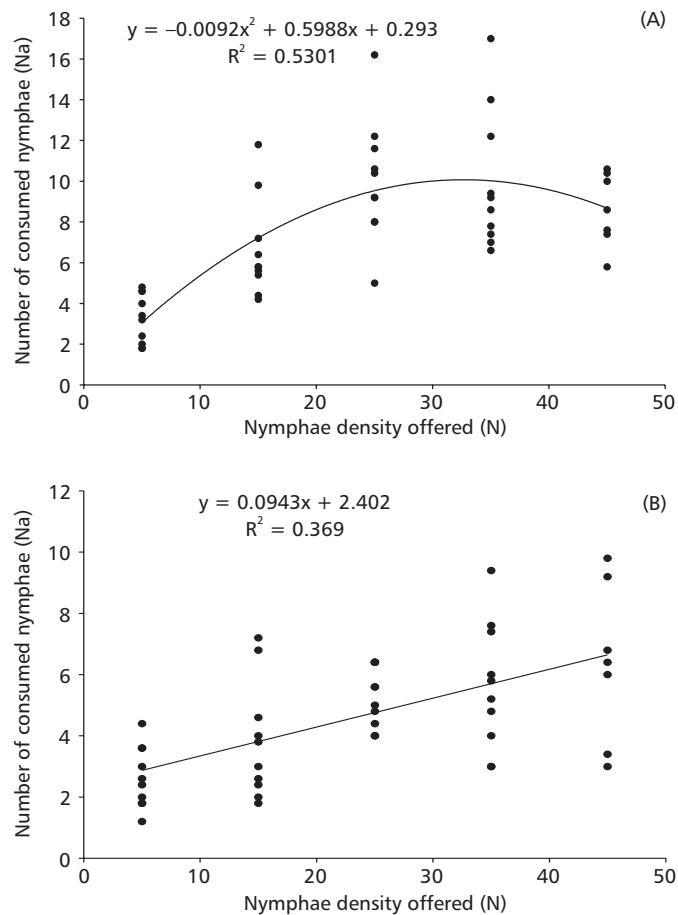

Fig. 1 — Functional response registered in *Cosmoclopius nigroannulatus* females (A) and males (B) at different densities of S*partocera dentiventris* first instar nymphae.

TABLE 1

Averages numbers, observed (raw value), observed (transformed $\sqrt{x+1}$) and estimated ($\pm$ SE) of nymphae consumed (*Na*) by *Cosmoclopius nigroannulatus* males and females in relation to different densities (*N*) of first instar nymphae of *Spartocera dentiventris*.

Consumed prey per sex	*N*				
	5	**15**	**25**	**35**	45
Females					
Observed (raw values)	$3.3 \pm 0.38a^1$	$6.6 \pm 0.76b$	$10.0 \pm 0.95c$	$9.9 \pm 1.08c$	$8.6 \pm 0.57bc$
Observed (transformed)	2.0 ± 0.09	2.8 ± 0.13	3.3 ± 0.14	3.3 ± 0.16	3.1 ± 0.09
Estimated	$(1.7 \pm 0.06)^2$	(2.5 ± 0.11)	(3.1 ± 0.13)	(3.1 ± 0.14)	(2.8 ± 0.44)
Males					
Observed (raw values)	$2.6 \pm 0.32a$	$3.8 \pm 0.60ab$	$5.3 \pm 0.30bc$	$5.6 \pm 0.66bc$	$6.4 \pm 0.82c$
Observed (transformed)	1.9 ± 0.08	2.2 ± 0.13	2.5 ± 0.06	2.5 ± 0.13	2.7 ± 0.16
Estimated	(1.7 ± 0.11)	(2.0 ± 0.11)	(2.4 ± 0.06)	(2.5 ± 0.12)	(2.6 ± 0.33)

[1] Averages followed by same letters do not differ significantly through Tukey test at 5%.

[2] Estimated values do not differ statistically from the observed (transformed) with a χ^2 test at 5%.

The handling time (Th) per prey estimated through the nonlinear least square method, was shorter (1.93 h) in females than in males (3.07 h). The minimal number of ingested preys per predator during a 24 h period was higher in females (12.4 nymphae) than in males (7.8 nymphae). Through the standard deviation, the consumption verified in both males and females was higher than expected at densities 25 (females) and 45 (males) (Fig. 1A and B). According to Abrams (1990), these variations can occur because of behavioral and/or physiological features of predators.

Evaluating the total handling time, a tendency to increase was noticed as prey density increased ($F = 23,22$; $p < 0.0001$) both for males and females (Table 2). According to Nordlund & Morrison (1990), the handling time affects the type of functional response: the shorter it is, the faster the curve reaches the asymptote. Besides, handling time can influence other components such as attack rate and search efficiency (Beddington, 1975). In *C. nigroannulatus*, males spent more time handling the prey, producing a slower consumption acceleration, resulting in almost linear curve that contrasts with the female curve, which reaches an apparent asymptote at density 25 (Fig. 1A and B). Ambrose & Claver (1997) obtained the reverse effect with the reduvid predator *Rhynocoris fuscipes* upon *Spodoptera litura*: in that system the handling time decreased while prey density increased.

A decrease of estimated search time as prey density increased was found both for males and females ($F = 34.04$; $p < 0.0001$), with females spending more time in all tested densities (Table 2). According to Hassel *et al.* (1976), this decrease in search time occurs because at high densities prey are more easily found. The shorter search time evidenced in *C. nigroannulatus* males can be attributed to longer handling time because, according to Holling (1961), time spent handling reduces search time.

Holling (1959) mentioned that the attack rate constant can be considered independent from density. However, in *C. nigroannulatus* the attack rate estimated from the search time tended to decrease with density increase (Table 2) ($F = 26.71$; $p < 0.0001$). In accordance with Wiedenman & O'Neil (1991), this attack rate decrease can be attributed to the proportionally higher consumption at lower densities (Table 1), besides the limit imposed by the satiation evident at higher prey densities.

Likewise, the estimated search efficiency demonstrates both for males and females a decrease in response to prey density increases (F = 11.68; p < 0.0001); females were, in general, more efficient (Table 2). The search efficiency decrease with density increases occurs because the predator spends more time searching for prey at lower densities (Hassel *et al.*, 1977). Ambrose & Claver (1995) also observed, in newly emerged R. fuscipes females preying on *Riptortus clavatus* and *S. litura*, a decrease in attack rates and search efficiencies when prey density increased. Similarly, Saini *et al.* (1997) registered a decrease in these components when evaluating the functional response of *Podisus conexivus* (Hemiptera: Pentatomidae) attacking *Anticarsia gemmatalis* (Lepidoptera: Noctuidae) larvae; in that case, females showed higher search efficiency as well.

According to Hassel *et al.* (1976), the functional response model proposed by Holling (1959) did not consider prey reduction with predator consumption during a fixed exposure time. In the present study, since nymphae were replaced only after 24 h, using the randomic model seemed to be more appropriate. The nonlinear regression analysis demonstrated that the estimated components of functional response fitted the randomic model, with coefficients of $R^2 = 0,9501$ for males and $R^2 = 08539$ for females (Fig. 2). The observed values and those estimated through the equation corroborate the model, showing no statistically significant differences at any of the densities (5, 15, 25, 35, and 45 prey, respectively $\chi^2 = 0.878$, p = 0.8328, gl = 8; $\chi^2 = 0.0488$, p = 0.9298, gl = 9; $\chi^2 = 0.0053$, p = 0.9512, gl = 9; $\chi^2 = 0.0638$, p = 0.9722, gl = 6 in males, and $\chi^2 = 0.878$, p = 0.8196, gl = 9; $\chi^2 = 0.0922$, p = 0.113, gl = 9; $\chi^2 = 0.0606$, p = 0.9402, gl = 9; $\chi^2 = 0.0457$, p = 0.9543, gl = 9; $\chi^2 = 0.0325$, p = 0.9676, gl = 6 in females) (Table 1 and Fig. 2).

Evidence for a type II response in *C. nigroannulatus*, along with estimates of its components, would contribute significantly to understanding the population dynamics of *S. dentiventris* and identifying the densities from which its prey would escape predator control. However, in functional response studies, field data are essential to complete the laboratory results, since in natural conditions other variables can interfere in predator behavior, introducing modifications in functional response components.

TABLE 2

Average values (± SE) of total handling time (Th_{total}), search time (Ts), attack rate (a'), and search efficiency (E) of *Cosmoclopius nigroannulatus* females and males at different densities (N) of *Spartocera dentiventris* first instar nymphae.

Nymphae density offered per sex	Tm_{total} (h)	Tb (h)	a'	E
Females				
5	3.8 ± 0.17a[1]	20.0 ± 0.17a	0.02 ± 1 x 10^{-3}a	0.7 ± 0.08a
15	5.1 ± 0.24b	18.9 ± 0.24b	0.01 ± 2 x 10^{-3}b	0.4 ± 0.05b
25	6.1 ± 0.26c	17.8 ± 0.26c	0.007 ± 4 x 10^{-4}bc	0.4 ± 0.04bc
35	6.1 ± 0.28c	17.9 ± 0.28c	0.005 ± 3 x 10^{-4}cd	0.3 ± 0.03c
45	5.7 ± 0.17c	18.3 ± 0.17bc	0.004 ± 4 x 10^{-4}d	0.2 ± 0.03c
Males				
5	5.8 ± 0.25a	18.2 ± 0.25a	0.02 ± 2 x 10^{-3}a	0.5 ± 0.06a
15	6.6 ± 0.40ab	17.4 ± 0.40ab	0.01 ± 1 x 10^{-3}b	0.3 ± 0.04b
25	7.7 ± 0.19bc	16.3 ± 0.19bc	0.01 ± 2 x 10^{-4}b	0.2 ± 0.01b
35	7.8 ± 0.39bc	16.2 ± 0.39bc	0.005 ± 3 x 10^{-4}b	0.2 ± 0.02b
45	8.2 ± 0.48c	15.8 ± 0.48c	0.004 ± 3 x 10^{-4}b	0.1 ± 0.02b

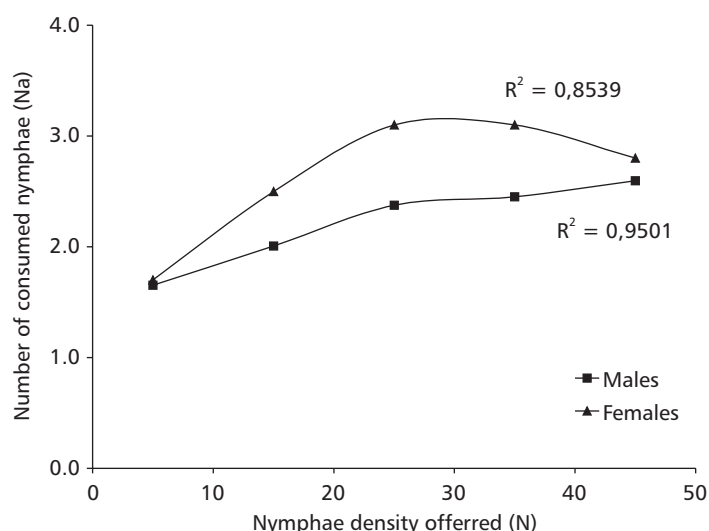[1]Averages followed by same letters do not differ significantly through Tukey test at 5%.

Fig. 2 — Estimated functional response through the randomic model in *Cosmoclopius nigroannulatus* females and males at different densities of *Spartocera dentiventris* first instar nymphae.

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