

FUNCTIONAL RESPONSE OF SELECTED COTTON ARTHROPOD PREDATORS TO BOLLWORM EGGS IN THE LABORATORY

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Abstract

The functional response study of the ten most common arthropod predators of cotton bollworm (*Helicoverpa zea*) eggs was conducted in the laboratory. Crab spider (*Misumenops* spp.) and assassin bug (*Zelus renardii*) did not consume any bollworm eggs under laboratory conditions and the scymnus lady beetle (*Scymnus loewii*) consumed very few (avg. 0.5 eggs per beetle) bollworm eggs in a 24-hour period. Functional response was measured by offering varying densities of bollworm eggs for each predator species and the functional response was recorded for 24 hours. Soft-winged flower beetle (*Collops* spp.), minute pirate bug (*Orius* spp.), hooded beetle (*Notoxus* spp.) and damsel bug (*Nabis* spp.) showed Type-I response, while lady beetle (*Hippodamia convergens*) adult, lady beetle larva, and green lacewing larva (*Chrysoperla* spp.) showed Type-II response; big-eyed bug adult (*Geocoris* spp.) showed Type-III functional response. Among the predators with Type-I functional response, the Collops beetle had the highest slope. Lady beetle larva had the highest handling time (0.185 h) followed by lady beetle adult (0.14 h) and green lacewing larva (0.08 h). Lady beetle adult and green lacewing larva showed a significantly higher attack rate or searching rate compared to lady beetle larva.

Introduction

The cotton bollworm is a key pest of cotton, which reportably infested 79.4% of the 2002 U. S. cotton crop causing a 2.31% (613,102 bales) yield loss (Williams 2002). Although many arthropod predators of bollworm eggs and larva have been reported and studies have been conducted to evaluate the effect of different predator species in suppressing bollworm eggs and larval populations (Ewing and Thomas 1943, Lingren et al. 1968, Ridgway and Lingren 1972, Bryson and Schuster 1975, McDaniel and Sterling 1979), the information on functional response and the comparative ability of those predator species to consume the target pest is lacking. This information is very important in natural enemy conservation and biological control programs. The number of prey that an individual predator kills is a function of prey density, and is known as functional response (Holling 1966). Effectiveness of a predator is directly related to the type of their functional response. The objective of this study was to evaluate the functional response of the most common arthropod predators to bollworm eggs. Following are the three major types of functional response of arthropod predators.

Type-I Functional Response

In this type of functional response the number of prey killed increase linearly in a constant rate up to maximum and then remains constant as prey density increases (density independent).

$$N_e = \alpha + \beta N \text{ -----(1)}$$

Where, N_e = number of prey eaten, N = prey density (number of prey offered), α =Intercept and β = slope of the prediction line.

Type-II Functional Response

In this type of functional response the number of prey killed approaches asymptote hyperbolically as prey density increases (declining proportion of prey killed or the inverse density dependence). Holling's "Disc equation" (equation-2) is the most commonly used curvilinear model for Type-II functional response. This function assumes the encounter rate with prey is linearly related to the prey density. Prey density remains constant and the handling time limits the number of prey eaten within a fixed time period.

$$N_e = \frac{a N T}{1+a N T_h} \text{ -----(2)}$$

Where, N_e = number of prey eaten, a = the attack constant or instantaneous search rate, N =prey density, T = total available time, T_h =handling time (The time taken by the predator to search, capture, consume and digest one prey), and aN = encounter rate with N prey density.

Since the experiment was conducted without prey replacement, the prey density declined as the experiment continued from hour 1 to hour 24, a random predator equation (Rogers 1972, Juliano 1993) was used to represent the Type-II functional response as shown below.

$$N_e = N_0 \{1 - \exp [a (T_h N_e - T)]\} \quad \text{-----(3)}$$

Where, N_e = number of prey eaten, a = the attack constant or instantaneous search rate or area of discovery, N_0 =initial prey density, T = total time, and T_h = handling time for one prey.

Type-III Functional Response

In this type of functional response the number of prey killed approaches asymptote as a sigmoid function (increase in proportion of prey killed up to inflection point and then decrease in proportion). This is the density dependent response.

The Type-III functional response can be represented by the Hassell model where the attack rate (a) is hyperbolic function of the prey density as given below.

$$a = \frac{d+bN}{1+cN}$$

By substituting the value of 'a' to the disc equation we get the Type-III model as below.

$$N_e = \frac{dNT + bN^2T}{1+cN + dNT_h + bN^2T_h} \quad \text{-----(4)}$$

Where, N_e = number of prey eaten, a = the attack constant or instantaneous search rate, N_0 =initial prey density, T = total time, T_h = handling time; b , c , and d are parameter constants.

The random predator equation (Rogers 1972, Juliano 1993) was used to represent the type-III functional response to account for the fixed prey density in our study as given below.

$$N_e = N_0 \{1 - \exp [(d+bN_0)(T_h N_e - T)/(1+cN_0)]\} \quad \text{-----(5)}$$

Where, N_e = number of prey eaten, a = the attack constant or instantaneous search rate, N_0 = initial prey density (number of prey offered), T = time, T_h = handling time; b , c , and d are parameter constants.

Materials and Methods

The study was conducted in the Cotton Entomology Laboratory at the Agricultural Experimental Station, Lubbock, Texas in July–August 2003. The functional response of the 10 most prevailing arthropod predators was evaluated (Table 1). All predators were collected from a cotton field with a sweep net or beat bucket. Uniform size, uninjured predators of mixed sex were sorted out and held without food and water for 24 hours. The 2nd and 3rd instars of both the lady beetle and green lacewing were used for the study while the remainders of the predators were in the adult stage. Bollworm eggs were used as prey, which were obtained from an insectary at USDA-ARS, SIMRU, Stoneville, MS and stored in a refrigerator at 10 °C until they were used in the experiment. The functional response was measured by randomly assigning different densities of bollworm eggs (1 to 150 eggs per density treatment) to each predator species in a petridish. Each treatment was replicated 5 to 10 times. The maximum and minimum prey densities for each predator were determined based on a preliminary feeding study. The treatment arena consisted of bollworm eggs placed singly in rows on a fresh cotton leaf in a plastic petridish (100 mm x 15 mm). The experiment was conducted at 29 °C and a photoperiod of 12:12 (L: D). Moist cotton swab and filter paper (9 cm) were used to keep the bollworm eggs and cotton leaf moist during the experiment. Predators were allowed to feed on bollworm eggs for 24 hours. The numbers of bollworm eggs eaten by each predator were recorded after 24 hours of predator exposure.

Data Analysis

Model Selection

The maximum likelihood ratio test of hypothesis was performed with logistic regression analysis of the proportion of prey eaten vs. number of prey present using SAS- 8.2 -CATMOD program for the selection of best fit model (Juliano 1993). The following cubic expression of the polynomial function was used to describe the relation between N_e/N_0 vs. N_0

$$\frac{N_e}{N_0} = \frac{\text{Exp} (P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + (\text{Exp} (P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3))} \quad \text{-----(6)}$$

Where, N_e = number of prey eaten, N_0 = initial prey density, and $P_0, P_1, P_2, P_3, \dots, P_z$ = parameters to be estimated.

This analysis tests the null hypothesis that the estimated parameters are equal to 0 ($H_0: P_0=P_1=P_2=P_3=0$). If the linear parameter (P_1) was not significantly different from 0 the Type –I (Eqn-1)) model was selected as the best-fit model. If the linear parameter $P_1 < 0$ and the quadratic parameter $P_2 > 0$ the Type-II (Eqn-3) model was selected as the best-fit model. When $P_1 > 0$ and $P_2 < 0$ the Type-III (Eqn-5) model was selected as the best fit model. The models were further verified by plotting the observed mean proportion eaten with predicted proportion eaten.

Parameter Estimation

Parameter α & β for Type –I functional response was estimated by simple linear regression analysis but for type-II and type-III functional response the parameters ‘a’ and T_h were estimated by nonlinear least square regression using nonlinear regression in JMP 4.0.2 program (SAS Institute 2000). For the predators showing Type-III functional response the full model (with all 4 parameters- b, c, d and T_h) was fitted first and if the parameters were not significantly contributing to the model or not significantly different from 0, those parameters were taken out of the model and reduced models were run step by step by deleting one parameter at a time using NLIN –SAS - Gauss Newton method (Juliano 1993).

Parameter Comparison:

The ‘a’ and T_h for Type-II functional response were compared with an “indicator variable approach” using NLIN SAS – Gauss Newton method (Juliano 1993). The following equation was used to compare two Type-II functional responses.

$$N_e = N_0 \{ 1 - \exp [-(a_1 + D_a [z])([T_{h1} + D_{th} (z)] N_e - T)] \} \text{-----(7)}$$

Where, N_e = number of prey eaten, N_0 = Initial prey density, a = estimated attack rate for population 1 ($z = 0$), D_a = difference between attack rate of population 1 and population 2, z = Indicator variable that takes value 0 for population 1 and 1 for population 2, T_h = estimated handling time rate for population 1, D_{th} = difference between handling time of population 1 and population 2 and T = time. The null hypothesis ($H_0: D_a = D_{th} = 0$) was tested using a t-test, where $t = (\text{parameter}/\text{asymptotic standard error})$ with the residual degrees of freedom. Multiple tests were performed to compare parameters between different predator species.

Prey Consumption Rate Comparison

The average number of bollworm eggs eaten by different predators in lower, medium and higher level of egg density (5, 25 and 150 bollworm eggs per petridish) were compared using PROC GLM and LSD (SAS Institute 2002).

Results and Discussion

Bollworm Egg Consumption Rate

Preliminary feeding study revealed that 150 bollworm eggs per study arena was the highest density for the functional response study of Collops beetle, lady beetle adult, lady beetle larva and green lacewing larva, but it was 20 for other predators. Lady beetle adult, green lacewing larva and Collops beetle showed significantly high consumption rate (122, 119 and 85 eggs/24 h, respectively) followed by lady beetle larva (51 eggs/24 h) and big-eyed bug (45 eggs/24 h). Scymnus lady beetle, minute pirate bug, hooded beetle and damsel bug consumed 1, 2, 5 and 12 eggs/24 h, respectively. The assassin bug and crab spider did not consume any bollworm eggs in the laboratory.

Functional Response

The logistic regression analysis (Table 2) revealed that the soft-winged flower beetle, minute pirate bug, hooded beetle and damsel bug had nonsignificant linear parameter, indicating that the functional response of these predators were of Type-I (Fig. 3). Both lady beetle and green lacewing larva and lady beetle adult had significant and negative linear parameter, suggesting that these predators showed Type-II functional response (Figs. 4 and 5). The big-eyed bug showed a Type-III response as the model gave significant and positive linear and cubic parameters and the negative quadratic parameter (Fig. 6).

Parameter Estimation and Comparison

Both intercept and slope of the Type-I model were nonsignificant for minute pirate bug and damsel bug, suggesting that there is no functional response or direct relationship between prey density and the predation rate of these two predators. The slopes for the hooded beetle and Collops were significantly different from 0 and both were less than one (Table 3), suggesting that the probability of prey eaten by these predators will decrease with the increasing prey density. Among the predators with Type-II functional response, lady beetle larva (0.185 h) and lady beetle adult (0.14 h) had the significantly high handling time compare to green lacewing larva (0.08 h). The attack rates of lady beetle adult (0.26), green lacewing larva (0.059) and lady beetle larva (0.029) did not differ significantly from each other. In case of the big-eyed bug, the parameter c and d (Type-III model) were not significant; therefore, handling time was calculated by using a reduced model. The big-eyed bug had a handling time of 2.5051 ± 0.0548 h and the slope of 0.0108 ± 0.00278 .

Conclusion

Lady beetle adult, green lacewing larva and Collops beetle were the most voracious feeders of bollworm eggs. The increment in prey consumption rate was constant for soft-winged flower beetle, minute pirate bug, hooded beetle and damsel bug. The mortality of prey due to predation by lady beetle and green lacewing larva and lady beetle adult increased with the increase in prey density but at a decreasing rate (i.e., negative density dependence). However, in the case of the big-eyed bug the functional response was positively density dependence. Functional response may vary with predator sex, developmental stages of predator and prey, searching arena, and other environmental conditions like light wind and temperature. Therefore, the functional response in the field would be expected to be much different than in the laboratory setting. However, information obtained from the laboratory study such as this would provide some guidelines to relative predation rate of different predators in the field.

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Table 1. Predator species and prey (bollworm egg) density treatments.

Predator Species					
Common Name	Scientific Name, Family, and Order			Prey Density	
Soft-winged flower beetle	<i>Collops</i> spp.	Melyridae	Coleoptera	5, 10, 25, 50, 75, 100, 150	
Minute pirate bug	<i>Orius</i> spp.	Anthicoridae	Hemiptera	1, 2, 4, 6, 8, 10, 20, 30	
Big eyed bug	<i>Geocoris</i> spp.	Lygaeidae	Hemiptera	5, 10, 25, 50, 75, 100	
Lady beetle	Adult	<i>Hippodamia convergens</i>	Coccinellidae	Coleoptera	10, 25, 50, 75, 100, 150
	Larva	<i>Hippodamia convergens</i>	Coccinellidae	Coleoptera	5, 10, 25, 50, 75, 100, 150
Green lacewing	<i>Chrysoperla</i> spp.	Chrysopidae	Neuroptera	10, 25, 50, 75, 100, 150	
Hooded beetle	<i>Notoxus</i> spp.	Anthicidae	Coleoptera	5, 10, 20, 40	
Damsel bug	<i>Nabis</i> spp.	Nabidae	Hemiptera	5, 10, 15, 20, 30	
Scymnus lady beetle*	<i>Scymnus loewii</i>	Coccinellidae	Coleoptera	5, 10, 15, 20	
Assassin bug*	<i>Zelus renardii</i>	Reduviidae	Hemiptera	5, 10, 15, 20	
Crab spider*	<i>Misumenops</i> spp.	Thomisidae	Araneae	5, 10, 15, 20	

*= No functional response was analyzed due to zero or very low number of prey eaten.

Table 2. Selection of functional response model based on analysis of maximum likelihood estimates of Parameters (\pm SE) using a polynomial function (Juliano 1993).

Predator Species	Linear Parameter	Quadratic Parameter	Cubic Parameter	Best-fit Model
Soft-winged flower beetle	-0.0218 \pm 0.0188	-0.00027 \pm 0.000241	0.00000201 \pm 0.904 E-6	Type-I
Minute pirate bug	-0.00542 \pm 0.1518	-0.00488 \pm 0.0110	0.000096 \pm 0.000220	Type-I
Big-eyed bug	0.1842* \pm 0.0412	-0.00492* \pm .000766	0.000029* \pm 4.17E-6	Type-III
Lady beetle adult	-0.1187* \pm 0.0376	0.00176* \pm 0.000491	-0.0000075* \pm 1.866E-6	Type-II
Lady beetle larva	-0.1959* \pm 0.023	0.00232* \pm 0.000292	-0.0000083* \pm 1.085E-6	Type-II
Green lacewing	-0.2141* \pm 0.0477	0.00201* \pm 0.000541	-0.0000058* \pm 1.875E-6	Type-II
Hooded beetle	-0.7962 \pm 0.3644	0.0430 \pm 0.0204	-0.00064 \pm 0.000309	Type-I
Damsel bug	-0.3191 \pm 0.2700	0.0272 \pm 0.0170	-0.0006 \pm 0.000314	Type-I

* Significant at $p < 0.01$

Table 3. Estimated intercept and slope of different predators that displayed Type-I functional response.

Predator Species	Intercept (α)			Slope (β)		
	Parameter	SE	p>/t/	Parameter	SE	p>/t/
S.W. flower beetle	6.0168482	3.706775	0.1655	0.5101576*	0.048214	0.0001
Minute pirate bug	0.6968585	0.274217	0.044	0.031439	0.019887	0.165
Hooded beetle	0.2565217	0.727959	0.7582	0.2456522*	0.031583	0.0161
Damsel bug	1.2162162	2.225171	0.6227	0.4198198	0.122492	0.0416

* Significant at 95% significance level two-tailed test. ($P < 0.025$)

Table 4. Estimated handling time and attack rate of different predators that displayed Type-II functional response.

Predator Species	Attack rate (a)		Handling time (T_h)	
	Parameter	SE	Parameter	SE
Lady beetle adult	0.2643687676*	0.06839045	0.1437737248*	0.01448963
Lady beetle larva	0.0296229172*	0.00773691	0.1857624316	0.09092348
Green lacewing	0.0595875791*	0.01032374	0.0790673603*	0.03679727

* Significant at 95% confidence interval.

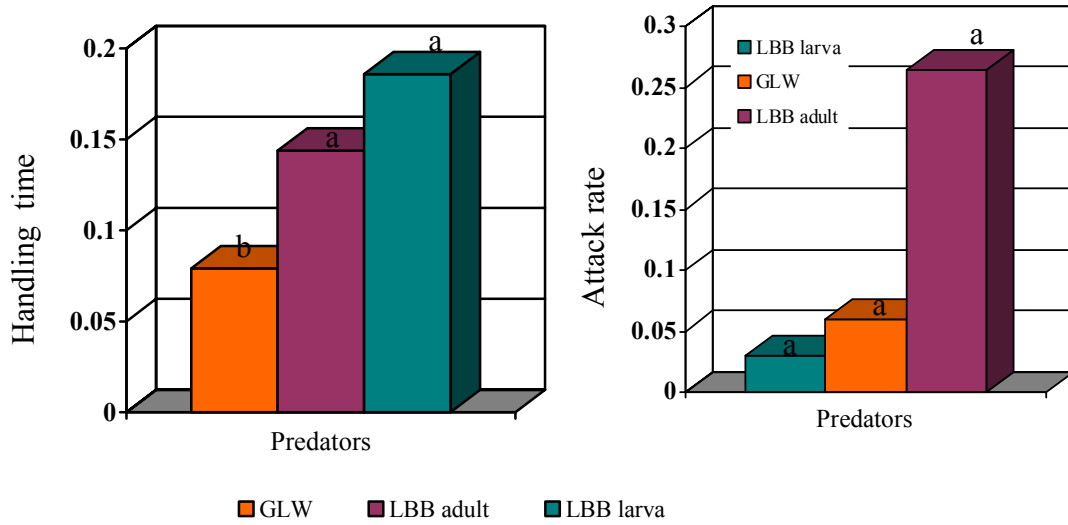


Figure 1 and 2. Comparison of handling time and attack rate of Type-II functional response.

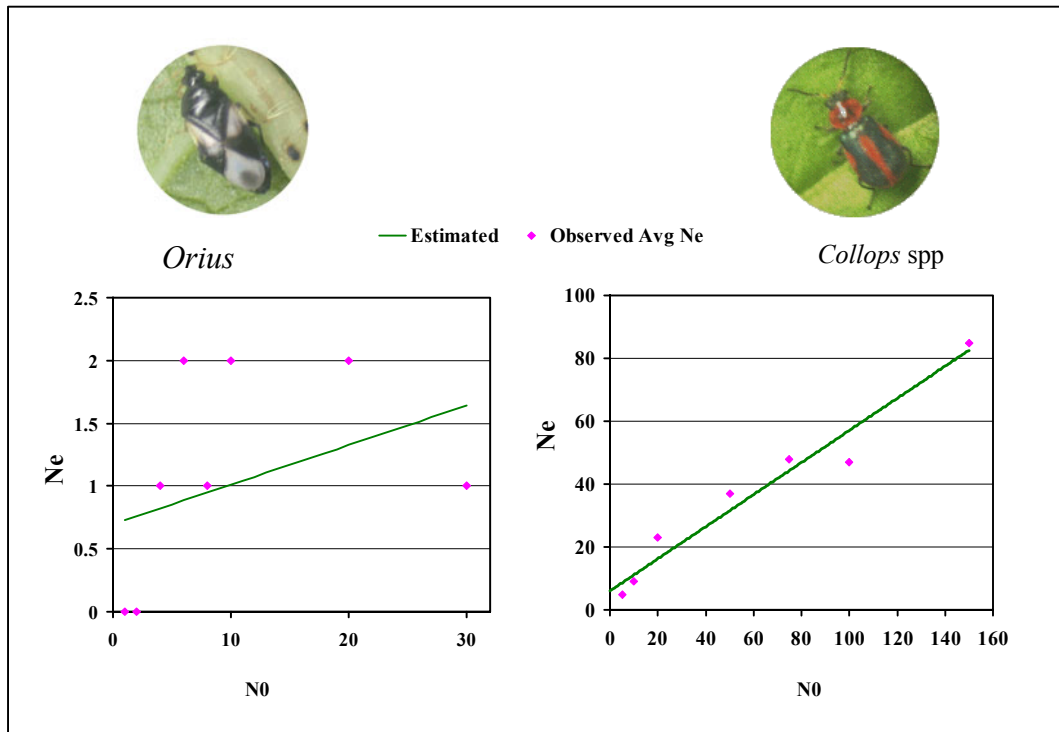


Figure 3. Type-I functional responses.

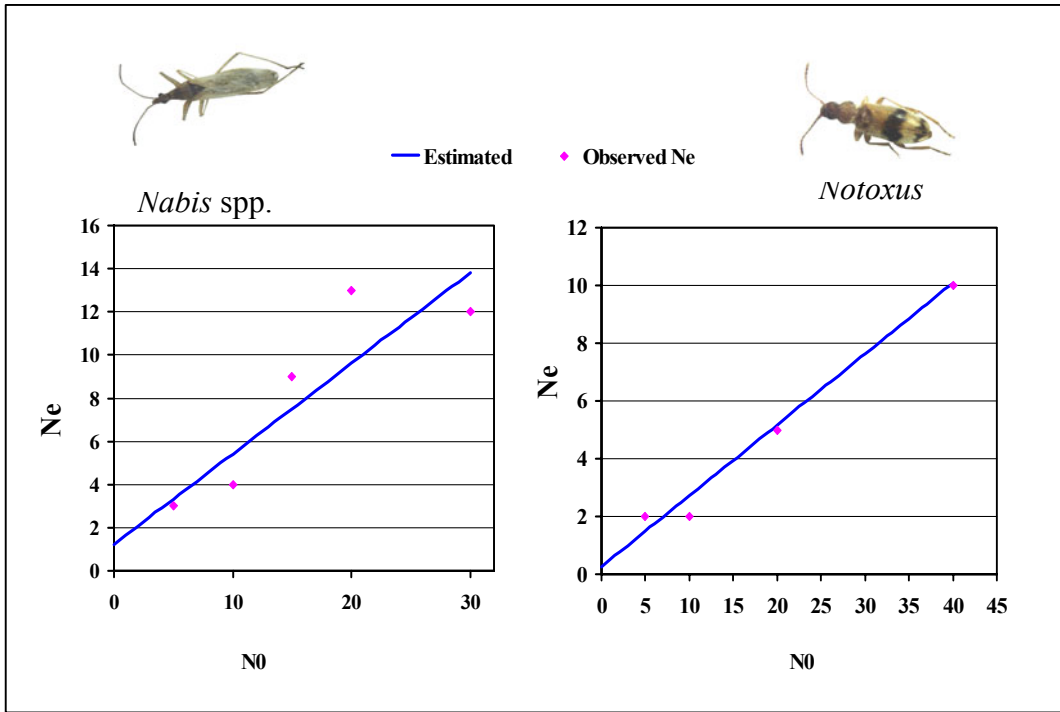


Figure 4. Type-I functional responses.

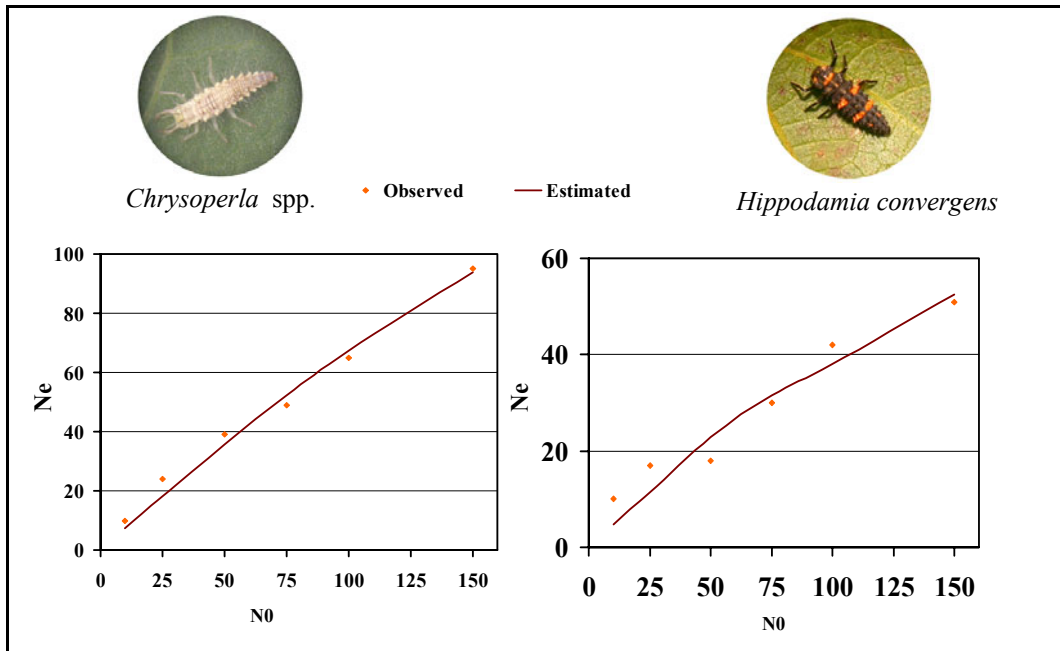


Figure 5. Type-II functional response.

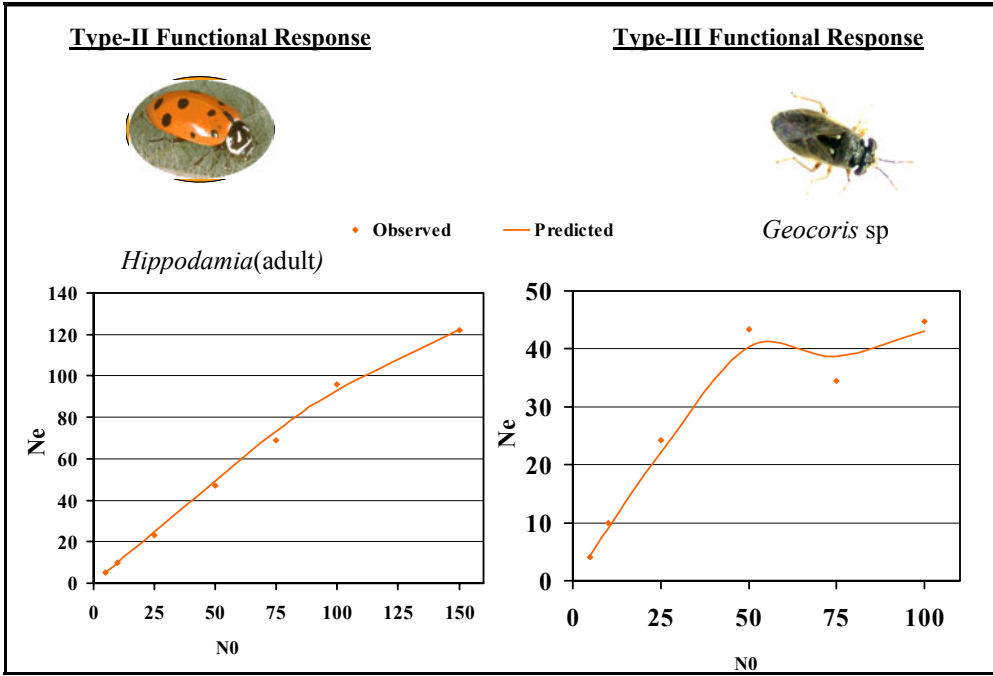


Figure 6. Type-II and Type-III functional response.