

## The role of habitat heterogeneity for the functional response of the spider *Nesticodes rufipes* (Araneae: Theridiidae) to houseflies

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### Abstract

We investigated whether or not different degrees of refuge for prey influence the characteristic of functional response exhibited by the spider *Nesticodes rufipes* on *Musca domestica*, comparing the inherent ability of *N. rufipes* to kill individual houseflies in such environments at two distinct time intervals. To investigate these questions, two artificial habitats were elaborated in the laboratory. For 168 h of predator-prey interaction, logistic regression analyses revealed a type II functional response, and a significant decrease in prey capture in the highest prey density was observed when habitat complexity was increased. Data from habitat 1 (less complex) presented a greater coefficient of determination than those from habitat 2 (more complex), indicating a higher variation of predation of the latter. For a 24 h period of predator-prey interaction, spiders killed significantly fewer prey in habitat 2 than in habitat 1. Although prey capture did not enable data to fit properly in the random predator equation in this case, predation data from habitat 2 presented a higher variation than data from habitat 1, corroborating results from 168 h of interaction. The high variability observed on data from habitat 2 (more complex habitat) is an interesting result because it reinforces the importance of refuge in promoting spatial heterogeneity, which can affect the extent of predator-prey interactions.

**Key words:** *Musca domestica*; poultry house; spatial heterogeneity; predation; population regulation

### INTRODUCTION

It is known that natural environments are heterogeneous at different spatial and temporal scales (Li and Reynolds, 1994). Despite the widespread understanding of heterogeneity as a key component of ecological systems, ecologists still struggle to understand the influence of spatial heterogeneity on many ecological variables (May, 1978; Li and Reynolds, 1994; Wellnitz and Poff, 2001). In some cases, spatial heterogeneity is positively correlated with habitat refuge (Brown, 2003), and it is believed that refuges provide a general mechanism for interpreting ecological patterns at both the community and population levels (Hawkins et al., 1993). At population levels, one important ecological pattern that is likely affected by refuge is the extent of predator-prey interaction (Huffaker, 1958; Legrand and Barbosa, 2003).

While there have been few laboratory studies

aiming to show the impact of refuges in predator-prey and host-parasitoid systems (e.g., Sih, 1981; Begon et al., 1995), detailed evaluations of the role of physical refuges in the field are rare. A notable exception is the study on the California red scale [*Aonidiella aurantii* Makell (Homoptera: Diaspididae)] and its parasitoids, particularly *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) (Reeve and Murdoch, 1986; Murdoch et al., 1989, 1995, 1996). These studies showed that scale populations were largely concentrated in the interior of citrus trees, while parasitism by *Aphytis* was significantly higher on the exterior twigs. Removal of the scales from the refuge had no effect on stability, although it did decrease the density of the exposed populations. These important results provide no clear view on whether or not refuges tend to stabilize interaction. However, model results are much clearer: refuges can have a strong stabilizing effect on populations (Hassell, 2000). Thus, under certain condi-

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tions, refuges prevent prey extinction, exert a stabilizing influence on an equilibrium point, and dampen population oscillations (Macan, 1976; McNair, 1986; Hassell, 2000).

An important feature of the introduction of refuges for prey is that it may change the characteristic of functional response fits (Wise, 1993). Functional response is defined as the temporal rate at which an individual predator kills prey. Thus, the functional response is a double rate: it is the average number of prey killed per individual predator per unit of time (Holling, 1959; Turchin, 2003). The study of functional response is important because a predator has the potential to regulate a prey population only if the predator responds to increases in prey density and inflicts greater mortality rates. Whether or not a population of predators causes such density-dependent mortality depends upon the nature of the functional and numerical responses, concepts introduced by Solomon (1949) and developed further by Holling (1959).

The type II functional response is predominant for spiders, whereas types I and III are less common (Heong et al., 1991; Mansour and Heimbach, 1993; Samu and Biro, 1993; Wise, 1993; Denno et al., 2004). However, the type of functional response exhibited by spiders is quite variable. For example, Riechert and Lockley (1984) observed the presence of type III functional response for several spiders, even though of the five papers that they cite, three provide no clear support for a type III response (Kiritani and Kakiya, 1975; Mansour et al., 1980). Nakamura (1977) found both types II and III responses by lycosids, and the most pronounced type III response occurred with leafhopper prey. The author argued that accelerated rates of predation at higher densities resulted from greater prey activity due to increased interference among leafhoppers in the rice seedlings in the experimental container. Haynes and Sisojevic (1966) also observed a type III functional response for a crab spider, due to the increased activity of the prey at higher densities. Although there are a few studies investigating the functional response of spiders, it is very difficult to establish a pattern according to foraging type because much more data is necessary to correlate foraging strategies with functional response type.

Behavioral variability characterizes many studies of spider functional responses. In an earlier

study of a lycosid feeding on vestigial-winged fruit flies, Hardman and Turnbull (1974) uncovered evidence for a weak type III response, but not among all life stages. Provencher and Coderre (1987) also uncovered considerable variation in the response of an orb weaver (Tetragnathidae) and a clubionid to different densities of two aphid species. An example of changes in the characteristics of functional response fits comes from Döbel's (personal observation) laboratory studies of feeding by two lycosids and a salticidae on planthoppers abundant in salt marshes. The addition of a refuge (*Spartina* thatch) for prey at lower densities changed the functional response of the wolf spider *Pardosa* from type II to type III. However, very little is known about the effect of refuges for prey in determining functional response curves.

*Nesticodes rufipes* Lucas (Araneae: Theridiidae) (referred to as *Theridion rufipes* in references) is widely distributed in tropical and subtropical regions, extending to temperate zones, and these spiders construct irregular webs with a disordered aspect (González, 1989). Its exact distribution is not easy to determine, since it is strongly associated with humans (Downes, 1988; González and Estévez, 1988; González, 1989). Behavioral and ecological studies considering predation by *N. rufipes* are scarce. Fox (1998) highlighted the strategic importance of these spiders to the natural control of the mosquito *Aedes aegypti* Linnaeus (Diptera: Culicidae), since the spiders incorporated a paralyzing substance in the webs that paralyzed the mosquitoes through contact, increasing their capture efficiency. Barreto et al. (1987) also mentioned the importance of *N. rufipes* as predators of *Rhodnius prolixus* Stål (Hemiptera: Reduviidae).

*Musca domestica* Linnaeus (Diptera: Muscidae) has a cosmopolitan distribution and high synanthropic indices (Smith, 1986; Ferreira and Lacerda, 1993), and is of considerable medical and veterinary importance (Harwood and James, 1979; Smith, 1986; Levine and Levine, 1991). This species lives in human dwellings, poultry houses, supermarkets and garbage, being reared on a wide variety of substrates such as food and vertebrate excrement (Axtell and Arends, 1990; Bowman et al., 2003). Although there are some chemical techniques aimed at controlling *M. domestica* in poultry houses, the inappropriate application of chemicals has intensified the search for potential natural

enemies of houseflies (Cunha and Lomônaco, 1996). Therefore, understanding the strength of interspecific interactions between *M. domestica* and its predators is of major importance.

As *M. domestica* (adult) is usually seen in *N. rufipes* webs in poultry houses (Rossi and Godoy, 2005), it is necessary to characterize the type of functional response exhibited by this predator when houseflies are offered as prey in order to determine the inherent ability of this predator to regulate densities of prey population. Yet, as the extent of predator-prey interaction may be affected by spatial heterogeneity, it is important to investigate whether or not different degrees of refuge for prey influence the characteristic of functional response fits. Thus, the specific objectives of this study were to: (i) investigate whether the addition of different degrees of refuge for prey change the characteristics of functional response exhibited by *N. rufipes* on *M. domestica*, and (ii) compare the inherent ability of *N. rufipes* to kill individual houseflies in such environments at two distinct time intervals.

## MATERIALS AND METHODS

**Sampling and rearing of houseflies and spiders.** An experimental poultry house located in the city of Botucatu-SP (Brazil) (22°52'20"S; 48°26'37"W) was chosen to collect the larvae of houseflies. We removed housefly larvae from small samples of chicken feces deposited below the cages, and put them into small glass tubes. All insects were then taken to the laboratory and reared in vials containing wet ground animal ration (25°C under 12 h light). After pupation, vials were kept in cages of nylon mesh on a wood frame (30 cm×30 cm×30 cm) where water and sugar were provided for adults.

Adult females of *N. rufipes* were captured in several buildings located on the campus of the University of the State of São Paulo (Botucatu, Brazil) from January–March 2003, and kept individually in cylindrical plastic containers (8.5 cm×5.0 cm) in the laboratory (25°C under 12 h light). All spiders were of similar size (15 mm body length), and were fed adult houseflies for a month (insects were randomly offered twice a week) in order to attain similar nutritional status.

**Laboratory experiments.** For the functional response experiment, spiders deprived of food for

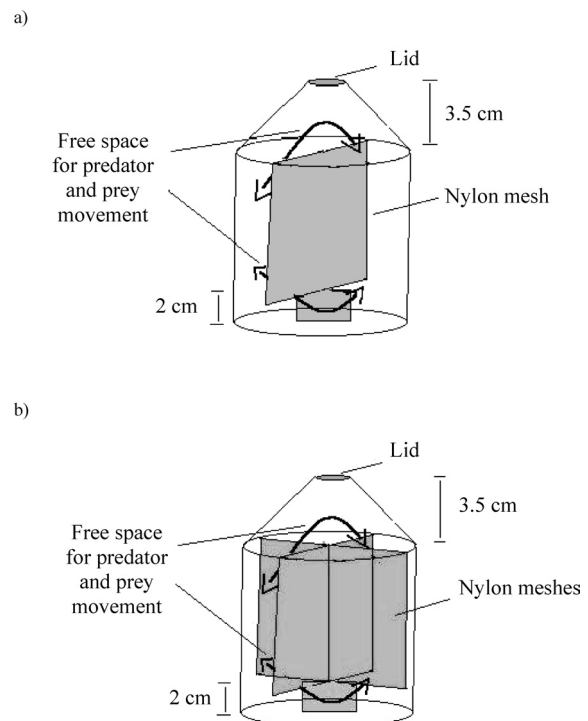


Fig. 1. The two types of experimental habitats (refuges for prey) used for the experiments. a) Habitat 1 with a nylon mesh internally fixed. b) Habitat 2 (more complex) with two nylon meshes internally fixed.

five days were individually placed in cylindrical plastic containers of 15 cm in height and 10.5 cm in diameter. These containers were previously modified in order to constitute the following two types of experimental habitats (refuges for prey): Habitat 1—a nylon mesh (9.5 cm×10.5 cm) was internally fixed in each container, separating the area (except the lid) into two equal parts (Fig. 1a). For predator and prey movement between both parts, free spaces were left between the nylon mesh and the top (3.5 cm) of the container, and between the nylon mesh and the bottom (2 cm) of the container (Fig. 1a). Habitat 2—two nylon meshes (9.5 cm×10.5 cm each) were internally fixed in each container, separating the area (except the lid) into four equal parts (Fig. 1b). As above, free spaces were left for predator and prey movement (Fig. 1b). Habitat 2 was more complex than habitat 1, thus comprising two degrees of refuge for prey. We elaborated these two experimental habitat designs because *N. rufipes* usually build their webs between walls, door crevices, and wood supports in poultry houses. Thus, the frequency of contact between prey and spider webs may be influenced by the artificial ar-

chitecture of the microhabitats where webs are fixed.

The experiment was a randomized complete block ( $5 \times 2$  factorial) with five prey densities (3, 5, 10, 15, or 20 adult flies per container) and two experimental habitats. Each treatment combination was repeated 10 times with different spiders for each replicate. As five spiders died during experimentation [three in habitat 1 (densities 5, 15 and 20), and two in habitat 2 (densities 3 and 15)], predation data from 95 spiders were used for analysis. Immediately before adding prey into the spider containers, flies were immobilized by chilling in a freezer for 3 min and removed from cages into a Petri dish. When flies started to move, all of the specimens in the group were carefully dropped in the bottom of a spider container, without touching the spider web. This procedure prevented flies from being captured quickly due to their flying ability, and it insured that flies could be easily separated prior to the experiments. The flies walked around inside the spider containers for approximately the first 2 min and then started flying.

Spider and prey interacted for 168 h (7 d), after which we determined the number of prey killed (sucked and wrapped insects) by subtracting the number of remaining flies (living and intact dead individuals) from the number of prey offered. To reduce the mortality of flies during the experiment, water and sugar were provided *ad libitum* for adults (a piece of cotton embedded in a honeydew solution). The number of dead prey fixed on the web that had not been sucked or wrapped was also computed as intact dead individuals. In order to keep the densities of flies constant, intact dead individuals were replaced with new living flies in each container at 24 h intervals throughout the 168 h of experimentation. As spiders generally kill more prey than they consume, we defined functional response in terms of the number of prey killed, rather than eaten. In order to compare the immediate impact of predation among densities and between experimental habitats, we also recorded the number of prey killed over a 24 h period of predator-prey interaction. The time of 168 h for predator-prey interaction was necessary because it provided sufficient data (number of prey killed) for fitting to the functional response model.

To compare the mean number of prey killed by spiders between experimental habitats and among

densities, two ANOVA [ $5 \times 2$  factorial design (see above)] were run (Zar, 1999), one for each period of evaluation. When significant differences were found, Tukey tests for unequal N-samples (Zar, 1999) were run to compare pairs of mean values. Although non-transformed data were presented in figures, all count data (number of prey killed) were square-root transformed for statistical analysis.

We determined the relationship between prey density and the number of prey killed (functional response) by spiders in both experimental habitats by performing logistic regressions (PROC CATMOD) on the proportion of prey killed vs. density of prey offered (Trexler et al., 1988; Juliano, 2001; SAS, 2001). For predator functional response, logistic regression is particularly useful in distinguishing between type II and type III responses, which are not easily determined by nonlinear regressions that use the number of prey eaten as the dependent variable. The proportion of prey eaten declines monotonically with prey density in a type II response, but is positively density-dependent over some range of prey densities in a type III response. The sign of the linear coefficient estimated by logistic regression can be used to distinguish the shape of the functional response curve. Significant negative or positive linear coefficients from the regression indicate type II or type III, respectively (Trexler et al., 1988; De Clercq et al., 2000; Juliano, 2001).

Because logistic regression analysis indicated that our data fit the type II response for spiders in both experimental habitats, further analysis was restricted to the type II response. The "random predator equation" (Royama, 1971; Rogers, 1972) was used to describe the functional responses because it allows for prey depletion during the course of the experiment. The form of the type II equation is as follows:

$$N_e = N \left\{ 1 - \exp \left[ -a(T - T_h N_e) \right] \right\}$$

where  $N_e$  is the number of prey killed,  $N$  is the number of prey offered,  $T$  is the total time available for the predator (e.g., in this case 168 h),  $a$  is the attack rate, and  $T_h$  is the handling time. Using the SAS statistical package (SAS, 2001) we carried out nonlinear regressions (NLIN), using the least squares method to estimate the predator's attack rate ( $a$ ) and handling time ( $T_h$ ) considering predation by spiders from both experimental habitats.

Further, plots showing the observed and predicted number (data fitted to random predator equation) of prey killed at a given prey density were also determined for both experimental habitats.

## RESULTS

The mean number of prey killed by *N. rufipes* over 24 h of predator-prey interaction was significantly different between experimental habitats ( $F=6.328$ ;  $MS=2.507$ ;  $p<0.05$ ), and spiders kept in habitat 1 ( $1.672\pm0.526$  SD) killed significantly more prey than the spiders that interacted with prey in habitat 2 ( $1.349\pm0.768$  SD) [means ( $\pm$ Standard Deviation) differed statistically by the Tukey test for unequal N-samples ( $p<0.05$ )]. Significant differences of prey consumption were also observed among densities ( $F=3.406$ ;  $MS=1.349$ ;  $p<0.05$ ), but little variation of mean values was observed as prey density increased (Fig. 2a). Even though the mean number of prey killed among densities was significant, data did not fit well into the random predator equation ( $R^2=0.21$  and  $R^2=0.09$  for habitats 1 and 2, respectively). Therefore, only data for prey killed during 168 h of predator-prey interaction were fitted to the model.

The mean number of prey killed by *N. rufipes* during 168 h of predator-prey interaction was not significantly different between experimental habitats ( $F=2.719$ ;  $MS=0.309$ ;  $p>0.05$ ) when prey densities were not considered. However, the mean number of prey killed among densities was significantly different ( $F=70.391$ ;  $MS=7.992$ ;  $p<0.001$ ) and the interaction between densities and experimental habitats had a significant influence on prey consumption by spiders ( $F=4.638$ ;  $MS=0.527$ ;  $p<0.01$ ). Prey capture by spiders increased significantly as prey density increased (Fig. 2b). However, a significant decrease in prey capture at the highest prey density was observed when habitat complexity was increased (Fig. 2b).

Logistic regression analyses indicated a type II functional response for both experimental habitats (Fig. 3), and estimates of the linear coefficients were significantly different from zero ( $p<0.05$ ) (Table 1). For predator-prey interactions that occurred in habitats 1 and 2, the model-estimated attack rates for *N. rufipes* were  $0.0506\text{ h}^{-1}$  [ $\pm0.0376$  (SE)], and  $0.2168\text{ h}^{-1}$  [ $\pm0.9458$  (SE)], while estimated handling times were  $6.9217\text{ h}$  [ $\pm1.6823$

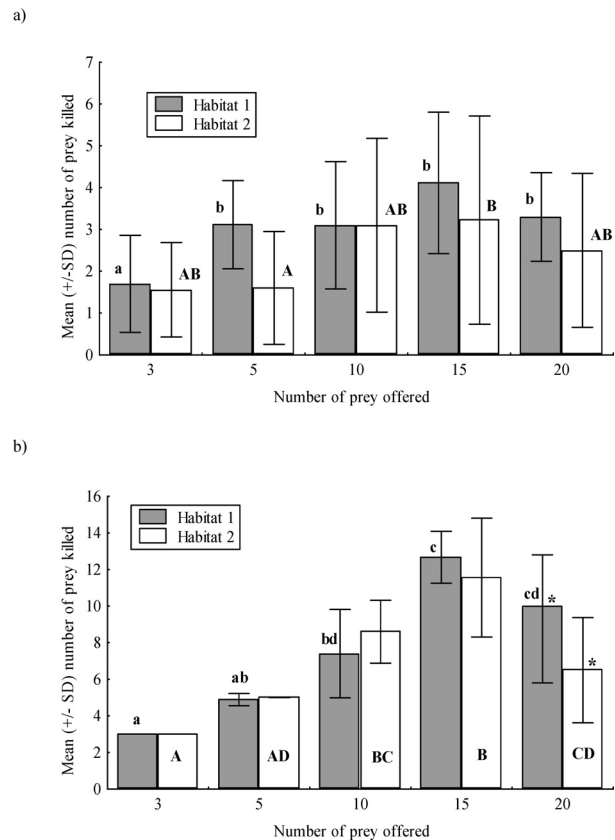


Fig. 2. Comparisons of mean ( $\pm$ Standard Deviation) number of prey killed. Means followed by different letters differed statistically from each other (Tukey tests for unequal N-samples) at  $p<0.05$ . Small and capital letters represent comparisons among densities for habitats 1 and 2, respectively. a) Comparisons computed for 24 h of predator-prey interaction. b) Comparisons computed for 168 h of predator-prey interaction. In this case, a significant decrease in prey capture at the highest prey density was observed when habitat complexity was increased. The asterisk (\*) represents a significant difference in the mean number of prey killed between habitats at a density of 20.

(SE)], and  $19.0797\text{ h}$  [ $\pm2.9295$  (SE)], respectively. Although the same type of functional response was observed for both experimental habitats, predation data from habitat 1 presented a greater coefficient of determination (Fig. 3a) than that from habitat 2 (Fig. 3b), indicating a higher variation of predation in the latter.

## DISCUSSION

*Nesticodes rufipes* exhibited a type II functional response on *M. domestica* in both experimental habitats for 168 h of interaction. Although the same

type of functional response was observed for both experimental habitats, predation data for spiders kept in habitat 1 presented a greater coefficient of determination (Fig. 3a) than that for spiders kept in habitat 2 (Fig. 3b), indicating a higher variation of

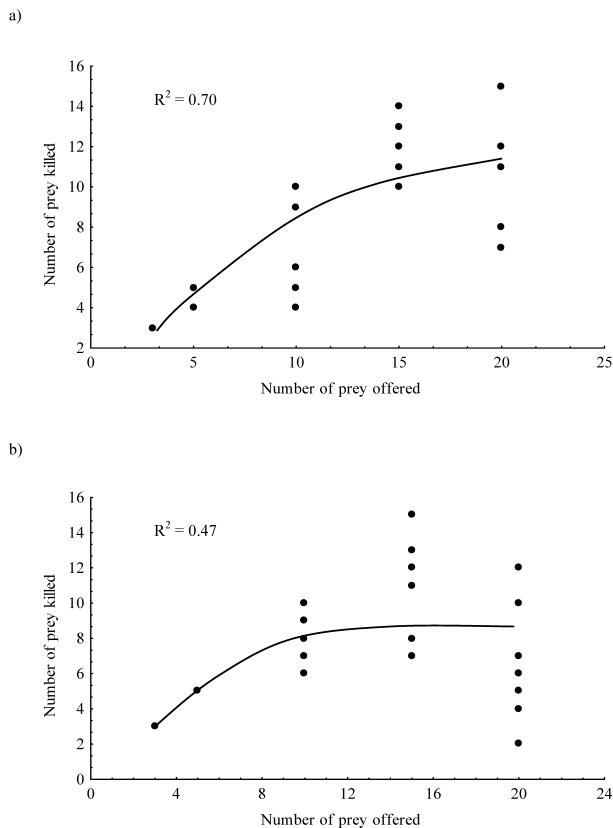


Fig 3. Functional responses of *N. rufipes* to increasing densities of adult *M. domestica* during 168 h period. Logistic regressions show that spiders exhibited type II functional responses in both habitats across the range of prey densities offered. Each data point represents the observed number of prey killed. In habitat 1 (a) data fitted better to the model than data from habitat 2 (b) (curves were fitted using the random predator equation).

predation in the latter. Yet, the higher variation of predation observed in habitat 2 seemed to be due to a significant decrease in prey capture at the highest prey density (Fig. 2b). Results of the 24 h interaction experiment suggest that the increase of habitat complexity decreases the number of prey killed by spiders. Although prey capture did not enable data to fit properly in the random predator equation in this case, predation data from habitat 2 presented a higher variation than data from habitat 1 (see low  $R^2$  values in Results), corroborating results from 168 h of interaction.

Parameters estimated by the random predator equation demonstrated that spiders kept in habitat 2 had a greater handling time and attack rate than those spiders that interacted with prey in habitat 1. However, as spiders in habitat 2 caught fewer prey than those in habitat 1 at the highest density, we suggest that handling time was more important than attack rate in determining the predation behavior observed.

Functional response experiments conducted under laboratory conditions may have limited application for determining the characteristics of predation under field conditions (Lee and Kang, 2004). O'Neil (1997) described the discrepancy between the laboratory and field functional responses of the pentatomid, *Podisus maculiventris* Say (Heteroptera: Pentatomidae), based on a series of experiments (O'Neil, 1988a, b; Wiedenmann and O'Neil, 1991a, b, 1992). Although we attempted to simulate the architecture of *N. rufipes*'s natural web sites, our laboratory-measured functional response of *N. rufipes* may not correspond exactly to field situations. However, our functional response study has value because spiders may be faced with many levels of habitat complexity in the field, represent-

Table 1. Results of a logistic regression analysis of the proportion of adults of *M. domestica* killed by *N. rufipes* during 168 h of predator-prey interaction against initial prey numbers offered. Analyses were determined for interaction occurring in habitats 1 and 2.

Experimental habitat	Parameter	Estimate	SE	$\chi^2$	<i>p</i>
Habitat 1	Intercept	-0.1198	0.5076	0.06	0.8135
	Linear	-0.0537	0.0940	0.33	0.5678
	Quadratic	-0.0018	0.0038	0.23	0.6301
Habitat 2	Intercept	4.6308	1.3230	12.25	0.0005
	Linear	-0.1785	0.1834	0.95	0.3303
	Quadratic	-0.0044	0.0061	0.51	0.4764

ing different levels of refuge that can affect the population dynamics of spiders and their prey.

The addition of refuge is important because it is known that the extent of predator-prey interactions may be affected by refuge. For example, Finke and Denno (2002) studied the combined impact of two salt-marsh-inhabiting invertebrate predators, the mirid *Tytthus vagus* Knight (Hemiptera: Miridae) and the wolf spider *Pardosa littoralis* Banks (Araneae: Lycosidae), on suppression of their shared prey, the planthopper *Prokelisia dolus* Wilson (Hemiptera: Delphacidae), in simple (thatch-free) and complex (thatch-rich) vegetation. They observed that, in structurally simple habitats in the laboratory, the predators interacted antagonistically due to the intraguild predation of mirids by spiders, and predation pressure on the planthopper population was relaxed. However, structurally complex habitats dampened this antagonistic interaction by providing mirids a refuge from spider predation, thereby increasing the combined effectiveness of these predators in suppressing planthopper populations.

It has been argued that a predator has the potential to regulate the densities of its prey if the mortality rate it inflicts is density dependent, which can occur if the predator displays a type III functional response (Holling, 1959; Wise, 1993). However, when members of the host/prey populations are heterogeneous in the risk of being killed by natural enemies, the density dependence is not a necessary condition for stable regulation. Summarizing many field studies of spatial host-parasitoid interactions, Hassell and Pacala (1990) found that stability existed not only when parasitism was directly related to host density, but also in cases of an inverse density dependent relation and in cases where the variation of parasitization was uncorrelated with host density (Argov et al., 2003). With a more theoretical approach, Chesson and Murdoch (1986) also showed that both host density dependence and host density independence contribute to stability. Although host density dependence (both direct and inverse) and host density independence can be stabilizing, more studies focused on temporal predator-prey interactions (mainly with polyphagous predators) are needed for a better understanding of the stabilizing mechanisms. Because spiders are voracious and polyphagous predators, they are suitable organisms for investigating regulation and sta-

bility in predator-prey interactions.

Robust type III functional responses are probably not common among spiders. Many results suggest that most type III responses by spiders result from elevated prey activity at higher prey densities rather than from learning or modification in foraging behavior by spiders (Haynes and Sisojevic, 1966; Nakamura, 1977; Riechert and Lockley, 1984). Although we observed a type II functional response, which corroborates with most studies of functional response by spiders (Kajak, 1978; Heong et al., 1991; Mansour and Heimbach, 1993; Samu and Biro, 1993; Finke and Denno, 2002), the high variability observed on data from habitat 2 (Fig. 3b) is an interesting result because it reinforces the importance of refuge in promoting spatial heterogeneity, which can affect the extent of predator-prey interaction (Huffaker, 1958; Hassell, 2000; Legrand and Barbosa, 2003).

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