

FUNCTIONAL RESPONSE OF *Nabis punctipennis* Blanchard to *Acyrtosiphon pisum* Harris IN THE LABORATORY

Verónica Campos¹, y Jaime E. Araya^{2*}

¹ Purdue University, W. Lafayette, Indiana 47905, USA. camposvero@gmail.com

² Universidad de Chile, Facultad de Agronomía, Casilla 1004, Santiago, Chile.

* Corresponding author E-mail: jaimearaya@yahoo.com

RESUMEN

Se analizó la conducta de depredación de hembras adultas de *Nabis punctipennis* Blanchard (Nabidae) hacia *Acyrtosiphon pisum* Harris (Aphididae) en laboratorio para determinar su respuesta funcional y su potencial como agente de control biológico de este áfido. Ambos hemípteros son comunes en alfalfa, *Medicago sativa* L., en Chile. Las hembras de *N. punctipennis* presentaron una respuesta funcional tipo II, con un tiempo de manipulación de $2,757 \pm 0,1181$ h presa⁻¹ y una tasa de búsqueda de $0,353 \pm 0,3214$ h⁻¹.

Palabras clave: pulgón de la alfalfa, respuesta funcional, control natural, nábido de alas punteadas.

ABSTRACT

This study analyzed the predatory behavior of adult females of *Nabis punctipennis* Blanchard (Nabidae) towards *Acyrtosiphon pisum* Harris (Aphididae) in the laboratory in order to determine its functional response and potential as a biological control agent of this aphid. Both hemipterans are common in alfalfa, *Medicago sativa* L., in Chile. The females of *N. punctipennis* presented a type II functional response, with a handling time of 2.757 ± 0.1181 h prey⁻¹ and a searching rate of 0.353 ± 0.3214 h⁻¹.

Key words: Alfalfa aphid, functional response, natural control, punctured-winged nabid.

INTRODUCTION

Alfalfa (*Medicago sativa* L.) favors the development of many invertebrates in Chile (Gerding and Devotto, 2000), such as *Acyrtosiphon pisum* (Harris) (Hem. Aphididae). This insect pest can reach densities that reduce forage and seed production (Cardinale et al., 2003; Rojas, 2005). Although *Nabis punctipennis* Blanchard (Hem. Nabidae) have been recognized as a generalist predator (Rebolledo et al., 2005; Romero et al. 2007), there is little research on its potential as a predator for *Acyrtosiphon pisum*.

To determine the way in which predation varies with prey density, the predator-prey relationship should be understood (van Leeuwen et al., 2007), as both the capacity of finding a prey as the population growth of a predator depend of

the density of the first (O'Neill and Wiedenmann, 1987). The numerical response of a predator is the change in its reproductive rate in response to changes in prey density, while the functional response refers to the change in the consumption rate of an individual predator in response to changes in prey density in a time unit, and is expressed as a function of prey density. On the other hand, the functional response is important to provide information of the potential efficiency of a predator as a biological control agent (Omkar and Pervez, 2004; van Leeuwen et al., 2007; Cabral et al., 2009). There are three functional responses: Type I, typical of aquatic invertebrates, increases linearly until reaching a plateau, and the line slope represents the searching rate of the predator; Type II, in predator and parasitoid arthropods, increases at a decreasing rate due to

the effect of the handling time of the prey, and the searching time decreases; and Type III, used first for predator vertebrates and then to describe the behavior of some predators and parasitoid arthropods, it is sigmoid and has an accelerated increase in consumption as a function of prey density, until handling time limits it (Berryman, 1999).

Hollings' s disk equation (Skalski and Gilliam, 2001) is commonly used to characterize the response of generalist predators to an increase in prey density (Ma et al., 2005; Pakyari et al., 2009), assuming that predators search for prey at random, with a fixed encounter probability (Fernández and Corley, 2004). Using the disk equation, Ma et al. (2005) found that the consumption of *Plutella xylostella* (L.) (Lep. Plutellidae) larvae by adult *Nabis kinbergii* Reuter described a type II functional response, and Siddique and Chapman (1987) found that functional response type III described the changes in predation of *A. pisum* by 5th instar nymphs of *N. kinbergii*.

A good understanding of the predator-prey relationship allows developing biological control programs successfully (Flores et al., 2010). Studies, like the one conducted by Costamagna and Landis (2007), are important as they allow predicting the contribution of natural enemies to control pests so that producers can trust these organisms and include them in control strategies (Zalucki et al., 2009).

Due to the abundance of *N. punctipennis* in alfalfa fields in Chile (Rebolledo et al., 2005), it is important to study its behavior as a natural agent in conservative biological control programs that minimize the risks associated with the introduction of species (i.e., classical biological control) (Lavandero et al., 2006). It is important to maintain the control agents present in the crop, and enhance their abundance and activity because the increase in predator density generates a greater control of pests, as described by Chang and Snyder (2004), Ostman (2004), and Cardinale et al. (2003).

The predatory behavior of adult females of *N. punctipennis* towards *A. pisum* was studied in the laboratory to determine its functional response and potential as biological control agent of this aphid.

MATERIALS AND METHODS

Rearing *N. punctipennis* and *A. pisum*. Adults (~50) of *N. punctipennis* were collected with an entomology net at the beginning of spring (October) in alfalfa untreated with insecticides in El Noviciado (33°26' S, 70°43' W), Pudahuel commune, Metropolitan Region, Chile. These predators

were fasted 48 h in individual Petri dishes lined with slightly humid filter paper to avoid natural enemies. They were then set free to obtain eggs in 50 x 50 x 50 cm cotton mesh covered cages with 'Blanca dulce' *Vicia faba* L. plants infested with *A. pisum* obtained with the net in the same crop. *Faba* beans were used because they are easy-to-handle host plants to rear the aphids. The stems were revised after 7 d; those with eggs inserted were cut into pieces and placed in 12 x 6.05 x 17 cm transparent cages with humidified cotton, and kept at 24°C and a 14:10 h L:D regime. Nymph emergence was recorded daily; nymphs were set individually in Petri dishes, maintained at 24°C for 2 d and fed with aphids. Then, they were set free on *V. faba* plants with *A. pisum* in 50 x 50 x 50 cm cotton mesh cages of at 22-28°C in the laboratory, reaching adulthood in ~20 d.

Experimental arena (EA). The EA was a 350 mL transparent plastic cage, with a 2 cm diameter hole on the base to introduce a ~12 cm stem piece of *V. faba* var. 'Blanca agua dulce'. The hole around the stem was sealed with high density polyurethane foam, and the top of the EA was covered with cotton cloth. To keep the stem turgid, the EA was placed on a 200-mL plastic transparent container with water.

Only 10-15 d-old adult females of *N. punctipennis* from the rearing cages were used in the experiment. The selected nabids were placed individually in Petri dishes with no food, so as to guarantee similar stomach content. They were only provided with a piece of humidified cotton at 24°C and a 14:10 L:D photoperiod for 24 h. Subsequently, they were used in the experiment to determine the functional response. For this, the nabids were placed individually in the EA and exposed to five different densities of *A. pisum* of similar size: 3, 9, 18, 36, and 54 per EA. In addition, a control treatment, which consisted of an EA with 18 aphids and no predator was included to determine natural mortality. The EAs were maintained at 24°C and a 14:10 L:D regime. After 24 h, the predators were discarded and the aphids remaining in each treatment were counted.

Experiment design and statistical analysis. The experiment was conducted using a complete randomized block design with 6 treatments and 10 replications.

To compare the numbers of preys killed at each density, the results were analyzed with ANOVA at 5% significance, using MINITAB 13.32 (Minitab Inc., 2000) statistic software. Tukey's test was applied to separate means. To determine the functional response type (I, II, or III), a logistic regression was obtained with the Eviews 6 (QMS,

2007) statistic software, using the following cubical equation:

$$Na/Nt = \frac{\exp(P_0 + P_1Nt + P_2Nt^2 + P_3Nt^3)}{1 + \exp(P_0 + P_1Nt + P_2Nt^2 + P_3Nt^3)}$$

where Na = number of preys consumed by the predator, Nt = initial prey density, and P_0, P_1, P_2, P_3 = constant parameter, and linear, quadratic, and cubical parameters, respectively.

As the parameter is related to the slope of the curve generated between the proportion of preys consumed (Na/Nt) and the number of preys offered to the predator (Nt), and also considering that the slope allows discriminating between the types of functional response at a low prey density (Fernández and Corley, 2004), this would be type I if parameter $P_1 = 0$, type II if P_1 is negative and significant, and type III if P_1 is positive and significant (Lee and Kang, 2004).

To determine handling time and searching rate, a curvilinear regression by minimal squares was done with the Eviews 6 (QMS, 2007) statisti-

cal software, fitted to the disc equation:

$$Na = T * a * Nt / (1 + (a * h * Nt))$$

where Na = number of preys consumed by the predator, Nt = initial prey density, T = experimental period (24 h), a = searching rate, and h = handling rate.

RESULTS AND DISCUSSION

Functional response. The number of *A. pisum* preys consumed by adult females of *N. punctipennis* increased significantly when the density of aphids per EA increased from 3 to 9 and from 9 to 18 (T1, T2, and T3). However, there was no significant increase in aphid consumption when density went from 18 to 36, and from 36 to 54 aphids per EA. The mean daily consumption was 7.7 ± 0.949 aphids (Table 1). There was no natural mortality of the 18 aphids in the EA corresponding to the control treatment.

Predator satiation of adult females of *N. punc-*

Table 1. Mean consumption of *A. pisum* per female adult of *N. punctipennis* at several aphid densities per EA at 24°C for 24 h.

Treatments	Densities of <i>A. pisum</i> per EA	Mean consumption \pm SD
1	3	2.5 (0.527) c
2	9	5.0 (0.810) b
3	18	7.1 (1.370) a
4	36	7.5 (0.850) a
5	54	7.7 (0.949) a

EA: Experimental arena.

Means with different letters are significantly different, according to a Tukey test ($q < 0.05$).

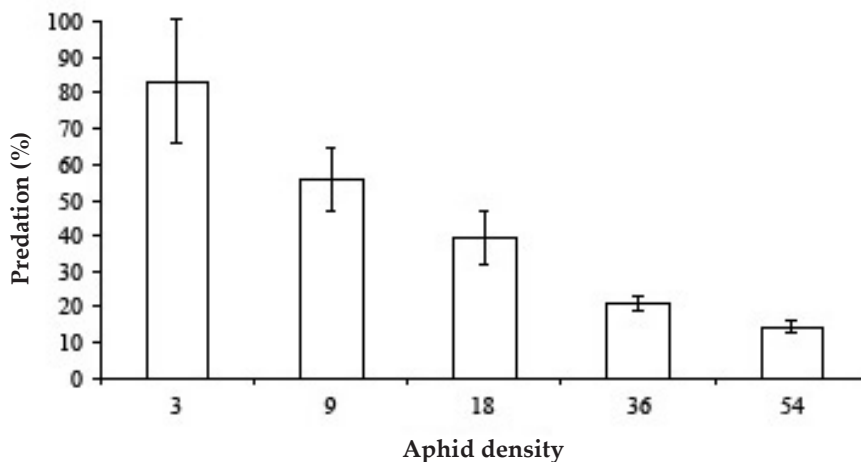


Fig. 1. Predation (%) of *A. pisum* by female adults of *N. punctipennis* in the laboratory. The columns indicate the averages of aphids consumed, with their corresponding standard deviation.

tipennis under the conditions of the bioassay would be 18 aphids per EA. Consumption did not increase at higher densities. This indicates that *N. punctipennis* would be more efficacious controlling *A. pisum* at smaller densities since predation rate was higher at lower densities (Fig. 1). This seems to be a key point because Ostman (2004) states that aphid control should occur early in the season during pest establishment, and so predators need to be already in the field when aphids develop. Therefore, it is important to note that presence of *N. punctipennis* can be found throughout all growth stages of alfalfa (Romero et al., 2007). The saturation asymptote of *N. punctipennis* occurred more quickly compared to other generalist predators, like some coccinellids (Sarmiento et al., 2007; Cabral et al., 2009), which indicates that this nabid is not too voracious. However, its abundance in alfalfa seems to contribute to aphid control in terms of consumption of the total population of nabids, more than consumption per capita.

The low prey consumption by nabids can be associated with their small size (5-6 mm), or their small energy requirements. They are expected to complete their cycle with a small predation level, and remain in the crop regardless of fluctuations in the population of *A. pisum*.

The highest predation rate was observed at a lower density, and corresponded to 3 aphids per EA. The number of aphids captured by the nabids averaged 80%, demonstrating its efficacy in capturing prey at low densities when aphids are well-dispersed. On the contrary, aphids tend to cluster on leaf undersides at greater densities. This type of behavior is important when selecting potential natural enemies, because it provides information on the predator's capacity to find its prey (Cédola and Botto, 1996).

Adult females of *N. punctipennis* presented a typical type II functional response since the estimated value of parameter P_1 was negative and significant (Table 2). As expected, predation rate decreased when prey density increased (Fig. 1).

A type III functional response is ideal for biological control because consumption rate is higher when increasing prey density (Fernández and

Corley, 2004; van Leeuwen et al., 2007). However, most natural enemy arthropods have type II responses, as is the case of *N. punctipennis*, that exhibited a lower consumption rate at higher densities (Fig. 2).

The functional response of a predator may vary, as described by Sarmiento et al. (2007). These authors evaluated the response of *Eriopis connexa* Germar (Col. Coccinellidae) to *Macrosiphum euphorbiae* (Hem. Aphididae) and found a type III response, which changed to type II when the prey was changed to *Tetranychus evansi* Baker & Pritchard (Acari Tetranychidae). This was attributed to learning (Speight et al., 1999) that could develop the coccinellid initially when attacking *M. euphorbiae*. The predator had a type II response for *T. evansi*, associated with its lack of escaping mechanisms.

Handling time to pursue, dominate, consume, and digest the prey, includes the preparation of the predator for the next search. As handling reduces the time spent to search the prey, maximum consumption is expressed when the plateau is reached in a response type II. This is equal to the quotient between the experiment time (T), herein 24 h, and handling time (h ; 2.676 h/prey in Table 3), while searching time is negligible (Begon et al., 1996; Fernández and Corley, 2004).

The handling time estimated (Table 3), which is relatively longer than in other predators (Sarmiento et al., 2007; Cabral et al., 2009), may be explained by the behavior of *N. punctipennis*. This species catches its prey approaching it from behind to avoid detection; when it is close enough, it jumps on and immobilizes its prey with the front legs to insert the stylet and feed. This activity takes some time, as observed in this study, and also by Romero et al. (2007).

When feeding from *A. pisum*, the nabid *N. kinbergii* pierces the body of the aphid and leaves it alone, and only holds the prey when this stops resisting (Siddique, 1985). Thus, considering both feeding behaviors, it is not strange to find nabids with long handling times.

Handling time can be measured, but searching rate (a) is a function of the number of contacts between predator and prey. In fact, searching time depends on the maximum distance at which

Table 2. Parameters estimated of the logistical regression to determine the functional response type of female adults of *N. punctipennis* against *A. pisum* in the laboratory.

Parameters	Estimated values (\pm SD)	q values
P_0	0.974650 (0.1574) *	0.0000
P_1	-0.091401 (0.0249)*	0.0007
P_2	0.000768 (0.0010)	0.4524
P_3	-4.91×10^{-7} (1.14×10^{-5})	0.9659

* Statistically significant with $\alpha = 0.01$.

Table 3. Searching rate and handling time (\pm SD) estimated with the disk and attack equations of *A. pisum* by female adults of *N. punctipennis* in the laboratory.

Estimated with the disk equation	
Searching rate (hours ⁻¹)	Handling time (hours/prey)
0.055 (0.0067)	2.676 (0.1097)
Estimated with the attack equation	
0.353 (0.3214)	2.757 (0.1181)

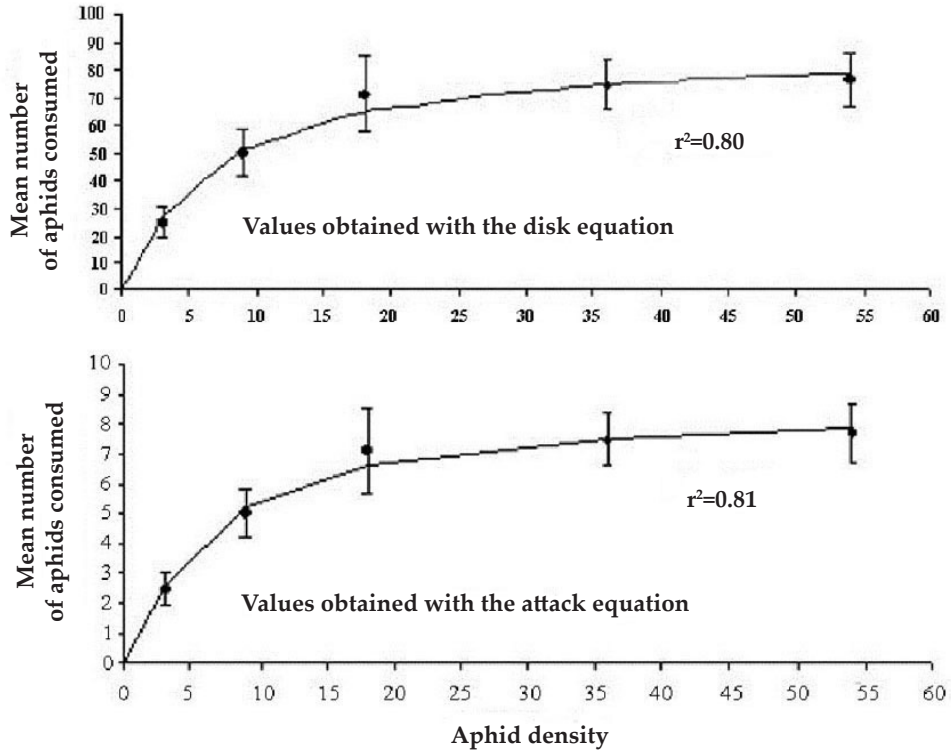


Fig. 2. Functional response of female adults of *N. punctipennis* against *A. pisum* in the laboratory, at 24°C for 24 h. The curves indicate the values expected (\pm SD) with the disk (above) and attack (below) equations.

a predator can begin attacking a prey, the quickness of movement exhibited by the predator and prey, and the amount of successful attacks (Begon et al., 1996).

The searching rate was estimated with the disk equation and reached a value of 0.055 h⁻¹ (Table 3). This seems real even though it has been described that large handling times lead to low searching rates (Smith and Smith, 2001) and, consequently, the estimated value may seem too small for the total consumption. If this value is right, 1.32 attacks would occur in 24 h, which is nonsense if *N. punctipennis* presented a maximum predation of 7.7 \pm 0.949 aphids in the same peri-

od (Table 3). This result can be explained by the fact that the disc equation assumes that the predator searches at random for preys, which are also distributed at random, with a constant handling time, and a fixed encounter probability between predator and prey, without considering the effect of decreasing the number of prey. Therefore, it is more adequate in bioassays where preys consumed are replaced, and the density is kept constant, or in large-size EA where the effect of consumption is negligible (Fernández and Corley, 2004). The limitations stated have prompted models like the attack equation (Berryman, 1999).

This model assumes that the predator search-

es for its prey at random, while searching rate and handling time are estimated similarly to those observed in bioassays where the preys are not replenished and a variation in density occurs (Lee and Kang, 2004).

The handling time estimated with the attack equation was similar to that obtained with the disc equation (Table 3). However, the searching rate was higher, which explains what was observed during the functional response bioassays when using the attack equation; a value of 0.353 h^{-1} was obtained, with a maximum consumption of 8.472 prey during the 24 h test, which is a reasonable level if maximum consumption was 7.7 ± 0.949 prey (Table 3).

A type II functional response was obtained from the results expected with the attack equation.

When comparing the curves in Fig. 2, it can be observed that the adjustment obtained was similar in both the disk and attack equations. However, the adjustment was a little higher in the attack equation, when its greater coefficient of determination was used as a parameter. This indicates that the attack equation better explains the variations in consumption of *A. pisum* by *N. punctipennis* in relation with prey density.

Type II functional responses, like those found here in for *N. punctipennis*, have been observed by other nabids in the presence of aphids. A study conducted by Siddique and Chapman (1987) also found this kind of curve when evaluating the functional response of adult females of *N. kinbergii* to *A. pisum*. The preys consumed were replenished during that study and the results indicated a searching rate and handling time of 0.312 ± 0.171 , and 2.618 ± 0.463 h, respectively, using the disc equation. When comparing the handling time and attack rate of *N. kinbergii* determined with the disk equation in their study and the values of *N. punctipennis* that we obtained with the attack equation, it can be stated that the results were quite similar because values were slightly higher in the case of *N. punctipennis* for both parameters (Table 3).

Siddique and Chapman (1987) used a much larger EA than ours for *N. punctipennis*. Greater EAs generate greater searching rates (Logan et al., 2009), and a much higher parameter should be expected in *N. kinbergii*. However, there is a slight difference between both nabids, suggesting that *N. kinbergii* is more efficient towards the same prey. This may be due to the size difference, as *N. punctipennis* is 5-6 mm long (Artigas, 1994) and *N. kinbergii* 8 mm (Wade et al., 2005). According to Hassell et al. (1976), larger species present greater searching efficiency. The distribution of aphids should also be considered, as they generally concentrate on a plant level (Rojas, 2005) and, conse-

quently, nabids do not need to search all over the EA to find their prey.

The disk and attack equations use three components that occur in all predation events, and estimate the functional response of a predator to a prey, such as attack rate, handling time and experimental time both species are exposed to. However, other unconsidered factors could affect the functional response, for example: how hungry the predator is, age (Siddique, 1985), learning (Morales et al., 2001), size of the predator and prey, prey defense strategies (Villagra et al., 2002; Sarmento et al., 2007), and its distribution (Pitt and Ritchie, 2002), as well as environment factors like temperature (Gitonga et al., 2002; Pakyari et al., 2009). To prevent these factors from affecting the functional response of the nabid, the bioassays were conducted only with 10-15 d-old adult females, which were kept with no food for 24 h to level their gut content. The preys were selected considering a relatively homogeneous size, and the tests were carried out at a stable temperature (24°C).

This laboratory study is the first evaluation of *N. punctipennis* as a biological control agent for *A. pisum*. Some authors have indicated that the functional response in the laboratory could reflect what happens in the field, particularly under high prey infestations (Lee and Kang, 2004; Omkar and Pervez, 2004). Each *A. pisum* female produces 50-100 nymphs in 7-10 d, and nymphs complete their cycle in only 12 d (Artigas, 1994) to become reproducing adults. Therefore, their density in the field increases fast, forming colonies on the tender structures (Rojas, 2005), as observed in alfalfa when collecting the predator. Then, the functional response obtained herein could predict the predation conduct of *N. punctipennis* on *A. pisum* in the field.

Small EAs may generate searching efficiency values that may vary considerably from those observed in the field, which represents a limitation for the study of functional responses under laboratory conditions (Murdoch, 1983, Symondson et al., 2002). In addition, the characteristics of the plant affect predation, and its structure affects searching efficiency (Carter et al., 1984) and handling time (Symondson et al., 2002). Prey density varies greatly in crop systems due to interactions between predators related to predator density, interference, and cannibalism (Symondson et al., 2002). Romero et al. (2007) observed cannibalism by neonate nymphs I of *N. punctipennis* emerging from the egg. This behavior decreases the number of predators, but it may also cause an increase in the per capita functional response (Symondson et al., 2002), which would not necessarily reduce consumption. Deficiencies when estimating the functional response in the laboratory could be

solved with field studies. However, obtaining an adequate number of predation events requires a lot of time, and it does not seem feasible for moving predators that feed on ungrouped prey (Schenk and Bacher, 2002).

When comparing *N. punctipennis* to generalist predators commonly found in alfalfa, prey consumption is greater in the coccinellids (Grez et al., 2007; Sarmiento et al., 2007), considering predation by the three most abundant species, *E. connexa*, *Adalia bipunctata* (L.), and *Hippodamia variegata* (Goeze) (Col. Coccinellidae) (Zaviezo et al., 2004, 2006). However, their presence in alfalfa is very dynamic (Zaviezo et al., 2004; Rebolledo et al., 2009). Although the nabid per capita consumption is not high, it is the most common predator in alfalfa in the Metropolitan Region throughout crop growth, reaching maximum density in the spring, from November through December (Romero et al., 2007). This is important for aphid control since predation of aphids early in the season is a key issue to control them (Ostman et al., 2003; Ostman, 2004). Aphid population in alfalfa in the Central Valley of Chile is higher during the spring (Grez et al., 2010), as we could also confirm when collecting the material. Thus, it seems that *N. punctipennis* would be controlling the aphids in a key period. Besides, *N. punctipennis* can feed from the first nymph stage on even larger prey, as observed herein and by Romero et al. (2007). Finally, adults have a 59.9 ± 25.34 d lifespan (Rebolledo et al., 2005), and females lay an average of 200 eggs (Romero et al., 2007). On this respect, Costamagna and Landis (2007) evaluated the consumption of *Aphis glycines* Matsumura (Hem. Aphididae) by generalist predators in soybean crops and indicated that when predators are more stable in a crop, such as nabids in alfalfa, they control a pest better as a result of its abundance more than due to per capita consumption.

In general, *N. punctipennis* may contribute to control *A. pisum* mainly because it is a stable resource in alfalfa; it is present in the key periods for aphid control; and its abundance makes up for its low per capita consumption.

The simplified environment a predator is exposed to in the laboratory does not always allow predicting its efficiency as a biological control agent in the field (Lester and Harmsen, 2002). Therefore, studies in the laboratory can be complemented with studies under conditions that are more similar to those in the field, including all moving stages and sexes of *N. punctipennis*.

If *N. punctipennis* turns to be an efficient biological control agent, some strategies should be considered to protect nabids, for example, using preferably insecticides like spinosad, which affects it relatively less than other chemicals (Rome-

ro et al., 2009). In addition, alfalfa could be grown in smaller patches, as for Ostman et al. (2003), aphid density relates inversely with the margins of the crop.

CONCLUSIONS

The functional response of adult females of *N. punctipennis* to *A. pisum* in the laboratory was type II, and it was characterized by a high efficiency of consumption at low prey density.

The methodology used was adequate, as it allowed simulating the predation behavior of *A. pisum* by adult females of *N. punctipennis* in the laboratory. However, the estimation of handling time and searching rate of *A. pisum* by *N. punctipennis* adult females with the disc equation did not yield satisfactory results. Because of this, the attack equation model was also used, obtaining results that explained in a better way the observations made during this study.

Further studies on the functional response for all the prey stages of *N. punctipennis* should be conducted as they all consume *A. pisum*.

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