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RESPONSE OF *NABIS ROSEIPENNIS* [*HETEROPTERA : NABIDAE*] TO LARVAE OF MEXICAN BEAN BEETLE, *EPILACHNA VARIVESTIS* [*COL. : COCCINELLIDAE*]

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Laboratory studies were done to measure predation by adult damsel bugs, *Nabis roseipennis* Reuter [*Heteroptera : Nabidae*], on 3rd instar larvae of Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant [*Coleoptera : Coccinellidae*], and to measure longevity and body weight of the nabids. In the 1st experiment, field-collected nabids were isolated for 24 h in 9 cm Petri dishes with lima bean foliage (*Phaseolus lunatus* L.) and were assigned to one of 3 prey treatments : either 4 3rd-instar MBB larvae, 4 3rd-instar larvac of boll weevil (BW), *Anthonomus grandis* Boheman [*Coleoptera : Curculionidae*], or 2 larvae of each species. No MBB larvae were attacked in either the MBB treatment or 2-species treatment. In contrast, BW larvae were attacked in both BW and 2-species treatments. Significantly more BW larvae were attacked in the BW treatment than in the 2-species treatment, and both were greater than the number of MBB larvae attacked. Nabids that did not attack prey lost weight during the 24 h, whereas those that attacked prey gained weight. In the 2nd experiment, nabids that had attacked prey were isolated with lima foliage, and nabids that had not attacked prey were kept with MBB and lima foliage until an attack or death. In no instances were MBB attacked. Longevity and the pattern of weight loss did not differ between nabids that did or did not attack prey. We discuss possible reasons for the failure of *N. roseipennis* to attack MBB larvae, as well as the implications for using nabids to influence pest populations in the field.

KEY-WORDS : *Nabis roseipennis, Nabidae, Epilachna varivestis,* Mexican bean beetle, generalist predators, predation.

Damsel bugs (*Heteroptera : Nabidae*) are generalist predators found in both natural and agricultural ecosystems. Nabids are among the most abundant foliage-inhabiting predators associated with crops such as cotton (**Bell & Whitcomb,** 1964 ; **Dinkins** *et al.*, 1970), soybeans (**Barry,** 1973 ; **Shepard** *et al.*, 1974 ; **McCarty** *et al.*, 1980), and alfalfa (**Pimentel & Wheeler,** 1973 ; **Benedict & Cothran,** 1975 ; **Wheeler,** 1977). Nabids, like other generalist predators in crops, may serve as ecological buffers by limiting or delaying the population growth of potential pests (**Rabb** *et al.*, 1984). Because of the potential importance of generalist predators to pest dynamics, it is necessary to incorporate the benefits of these indigenous natural enemies when developing pest management strategies.

In Indiana soybeans and alfalfa, 3 species of *Nabis* are encountered frequently : *N. roseipennis* Reuter, *N. americoferus* (Carayon), and *N. rufusculus* Reuter (**O'Neil,** unpubl.

data). Of these species, *N. roseipennis* is the largest and often the most numerous. This species has been evaluated in field studies for its potential as a predator against many soybean pests, where it has been shown to attack noctuid larvae (**Reed** *et al.*, 1984), eggs of *Anticarsia gemmatalis* Hubner (**Buschman** *et al.*, 1977), both eggs and larvae of *Plathypena scabra* (F.) (**Braman & Yeargan, 1989**), eggs of *Pseudoplusia includens* (Walker) (**Richman** *et al.*, 1980), and eggs and the first 3 larval instars of Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant (**Waddill & Shepard,** 1974). In laboratory studies, *N. roseipennis* has been shown to attack *Heliothis zea* (Boddie) larvae (**Donahoe & Pitre, 1977**), *H. virescens* (F.) larvae (**Nadgauda & Pitre,** 1978), both eggs and larvae of *P. scabra* (**Sloderbeck & Yeargan,** 1983), and adults and nymphs of *Empoasca fabae* Harris (**Rensner** *et al.*, 1983). In addition, *N. roseipennis* in the laboratory has been reported to attack eggs and the first 3 larval instars of *E. varivestis* (**Waddill & Shepard,** 1974). However, the acceptability of the ultimate (4^{th}) larval instar has not been tested.

Since *N. roseipennis* is potentially an important predator of soybean pests, and MBB occasionally reaches pest status in Indiana soybeans, we designed studies to use the 2 species as a model system to understand how generalist predators search for prey in soybeans (e.g. **O'Neil,** 1988). However, in a preliminary laboratory study, we found that *N. roseipennis* failed to attack 3^{rd}-instar MBB larvae (**Wiedenmann & O'Neil,** unpublished data), in contrast to the findings of previous workers (**Waddill & Shepard,** 1974). Because of this discrepancy, we designed 2 laboratory studies to examine the predator-prey relationship between the 2 species. The objectives of the 1^{st} study were to document whether *N. roseipennis* would attack 3^{rd}-instar MBB larvae and to identify predator behavior associated with attacks. The objectives of the 2^{nd} study were to determine how feeding on prey affected predator longevity and body weight. Here we report the results of our laboratory studies, offer an hypothesis to explain the observed level of predation on MBB larvae, and relate the findings to the role played by generalist predators in agricultural crops.

METHODS

PREDATION EXPERIMENT

Adult *Nabis roseipennis* were collected from an alfalfa field near West Lafayette, IN, during September and October 1987. Within 1 hour of collection, nabids were brought into the laboratory, sexed, weighed, and isolated in 9 cm diameter Petri plates containing a lima bean leaf (*Phaseolus lunatus* L.). Experiments were conducted in the laboratory under a 14 :10 L :D photoperiod at ambient room temperature (about 23 °C). We used a total of 60 nabids : 47 ♂♂ (mean weight 8.28 mg, S.E. = 0.17) and 13 ♀♀ (mean weight 11.36 mg, S.E. = 0.33) for the experiments. Nabids were assigned randomly to one of three 24 h feeding treatments : either four 3^{rd}-instar MBB larvae (MBB), four 3^{rd}-instar larvae of boll weevil (BW), *Anthonomus grandis* Boheman (*Coleoptera : Curculionidae*), or 2 of each species. Boll weevil larvae were used as prey since prior laboratory culture of *N. roseipennis* had shown that boll weevils were attacked readily (pers. obs.). Each treatment was replicated 20 times. Because we used newly collected predators for each 24 h experiment, replication of each treatment occurred over a 2 month period. Predators were watched for the 1^{st} hour they were isolated with prey, in order to document any characteristic attack behaviors, e.g., approach, probing, and attack posture. If no attack occurred, observations concerning predator and/or prey avoidance were made. Prey that were attacked were not replaced during the 24 h experiment. Attacked prey were identified as dead individuals showing obvious signs of injury, such as gross bodily deformations, discolorations, or punctures. We did not differentiate between prey that were totally consumed and prey that were dead but only partially consumed. We recorded the number of attacks within the 1st hour and number of attacks within 24 h.

Those nabids that did not attack prey in the first 24 h were re-assigned randomly either 4 MBB or 4 BW as prey, and were kept with that prey species until either an attack occurred or the nabid died. We re-assigned the predators to ensure that the failure of the nabids to attack was not due to injury of the predator or a lack of hunger. Prey were examined daily, and were replaced if they had molted. MBB larvae (mean weight 8.43 mg) came from a laboratory culture in which they were reared on foliage of lima bean, following the methods of **Stevens** *et al.* (1975). BW larvae (mean weight 33.17 mg) were obtained from the USDA/ARS Gast Rearing Laboratory, Starkville, MS, and were reared on an artificial diet (**Lindig,** 1979).

Analysis of variance (ANOVA) was used to analyze effects of feeding treatment on the mean number of prey attacked, and Duncan's new multiple range test (DNMRT) was used to separate treatment means. We used 2-tailed t-tests to determine differences in attack rates between sexes. All statistical tests were judged at the $\alpha = 0.05$ significance level.

LONGEVITY AND BODY WEIGHT EXPERIMENT

Forty-nine nabids (38 ♂♂, 11 ♀♀) from the 3 treatments were weighed after 24 h to determine if the number of prey attacked affected body weight. We measured longevity of 10 nabids that had not attacked prey in the first 24 h and were isolated further with a lima bean leaf and MBB. Five of these nabids were weighed daily to measure body weight over time. We also measured both longevity and body weight of 27 nabids that attacked prey in the first 24 h and were further isolated with only a lima bean leaf. Plots of average body weight over time were compared for nabids that had attacked prey and nabids that had not. To correct for differences in longevity and increased fluctuations in weight when sample sizes were small, we plotted weights only over the median life span of predators.

We used 2-tailed t-tests to determine differences in longevity and body weight between sexes. Longevity data for predators were placed into 2 classes : those that did not attack prey and those that attacked one or more prey. Pearson's correlation analysis was used to determine the relationship between the number of prey attacked and mean weight change. All statistical tests were judged at the $\alpha = 0.05$ significance level.

RESULTS

PREDATION EXPERIMENT

Adult nabids given BW or both prey species attacked BW readily. In contrast, none of the 20 nabids given only MBB attacked prey within 24 h. Of the nabids given BW, 50 % (10) attacked one or more prey within one hour and 90 % (18) attacked prey within 24 h. An average of 1.75 prey were attacked within 24 h (table 1). Of the nabids given both prey species, 35 % (7) attacked one or more BW within one hour and 100 % (20) attacked one or more BW within 24 h ; no MBB were attacked. An average of 1.25 prey were attacked within 24 h (table 1). Treatments significantly affected the number of prey attacked ($F = 31.40$, d.f. = 2,57, $P < 0.0001$; ANOVA). The number of prey attacked by predators in the BW treatment was significantly greater than the number attacked in the 2-species treatment, which was significantly greater than the number attacked in the MBB

TABLE 1

Mean number of prey attacked in 24 h by Nabis roseipennis *adults. Treatments consisted of four 3rd-instar Mexican bean beetle larvae, four 3rd-instar boll weevil larvae, and 2 larvae of each species.*

Treatment	Replicates	Number attacked (S.E.)
Boll weevil	20	1.75(0.26) a*
Mexican bean beetle	20	0.00(0.00) c
Both prey species	20	1.25(0.10) b**

* Means followed by different letters are significantly different at $\alpha = 0.05$ using Duncan's New Multiple Range Test.
** Only boll weevil larvae were attacked.

treatment ($P < 0.05$, DNMRT, table 1). The number of prey attacked did not differ between males and females in either the BW treatment ($t = 1.55$, d.f. = 5.9, $P > 0.05$) or the 2-species treatment ($t = 1.74$, d.f. = 16, $P > 0.05$).

The 22 nabids that did not attack prey in the first 24 h were assigned to 2nd treatments. Twelve nabids, 4 ♀♀ and 8 ♂♂, were given BW, and 10 nabids, 3 ♀♀ and 7 ♂♂, were given MBB. Of the 10 nabids assigned to MBB, 2 had previous exposure to BW. None of the nabids given MBB attacked any prey ; all 10 subsequently died, failing to attack any MBB over the remainder of their lives. Of the 12 nabids given BW, 67 % (8) attacked one or more prey within one hour, 83 % (10) attacked within 24 h, and the remaining 2 attacked prey within 48 h. An average of 1.58 prey were attacked (S.E. = 0.15).

The attack sequence began in similar ways for nabids in all 3 feeding treatments. Nabids approached prey, with mouthparts extended, and contacted the prey surface with the mouthparts. When the prey was BW, the attacks continued as the predator pierced the prey cuticle, then grasped and held the prey somewhat under the body, secured with the forelegs. When nabids were isolated with MBB, the attack sequence stopped after a few seconds of probing the surface of the prey, followed by the predator retreating from the prey. Subsequently, nabids did not initiate contact with prey and in several instances, MBB approached a nabid, whereupon the nabid would move away from the prey. In contrast, there were several cases in which nabids were isolated first with MBB, then given BW, whereupon the attack on BW occurred within 5 seconds of being placed with the prey.

LONGEVITY AND WEIGHT CHANGE EXPERIMENT

The number of prey attacked significantly affected the mean 24 h weight change. There was a significant positive correlation between the number of attacks and weight change ($r = 0.668$, $n = 49$, $P < 0.0001$). As more prey were attacked, predators gained more weight (table 2). There were no significant differences in weight change between sexes, regardless of the number of prey attacked (t-tests, $P > 0.05$).

When sexes were combined, there was no significant difference in longevity between nabids attacking one or more prey and nabids attacking no prey ($t = 1.32$, d.f. = 35, $P > 0.05$). Nabids that attacked prey lived an average of 20.1 days (S.E. = 1.87, $n = 27$), and those that did not attack prey lived an average of 15.6 days (S.E. = 2.44, $n = 10$). Female nabids that did not attack prey lived significantly longer than males that did not attack prey ($t = 3.62$, d.f. = 5.1, $P < 0.02$, table 3). In contrast, there was no difference in

TABLE 2

Average weight change (mg) of Nabis roseipennis *as a function of the number of prey attacked in the 24 h experiment.*

Number attacked*	n	Weight change (S.E.)
0	11	− 2.2 (0.4)
1	23	+ 0.6 (0.3)
2	10	+ 1.0 (0.4)
3-4	5	+ 2.7 (0.8)

* Only boll weevil larvae were attacked.

TABLE 3

Mean longevity (days) for male and female Nabis roseipennis *that attacked prey (boll weevil larvae), and those that did not attack prey.*

Sex	No attacks (n)	One or more attacks (n)
Male	12.0 a* (7)	19.2 b (22)
Female	24.0 b (3)	24.2 b (5)

* Means followed by different letters within a column and within a row are significantly different at $\alpha = 0.05$, using t-tests.

longevity between males and females that attacked one or more prey ($t = 1.32$, d.f. = 8.4, $P > 0.05$, table 3). Within a sex, males attacking one or more prey lived significantly longer than males not attacking prey ($t = 2.36$, d.f. = 18.6, $P < 0.05$, table 3). However, there was no difference in longevity between females attacking one or more prey and females not attacking prey ($t = 0.04$, d.f. = 3, $P > 0.05$, table 3).

At median life span of predators that attacked prey (21 days), there was no difference in body weight between sexes ($t = 1.65$, d.f. = 4.2, $P > 0.05$). Small sample sizes prevented comparison of weight between sexes at median life span (22 days) for predators not attacking prey, but the trend was toward no major difference in weight between sexes. Therefore, we combined sexes for analyzing patterns of weight change. The pattern of body weight over time was similar whether prey were attacked or not (fig. 1 & 2). Over the median life span of predators that did not attack prey there was an initial sharp drop in weight, followed by a slower decline to a level of about 7.0-7.5 mg. Over the median life span of predators that attacked prey, there was an increase in weight after the attack on the 1st day, followed by the same pattern of decline as shown by nabids that did not attack prey.

DISCUSSION

In no case were 3rd-instar MBB attacked, even for predators that eventually starved to death. This was in contrast to nabids that readily attacked BW. When sexes were combined for comparison, nabids attacking prey gained weight, but did not live longer than nabids not attacking prey. The reason for the lack of difference in longevity can be seen in the

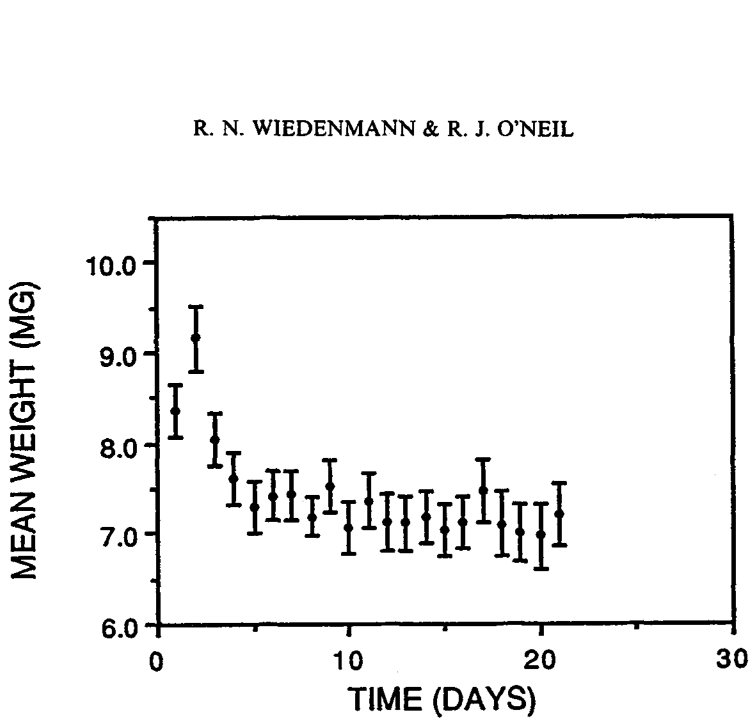

Fig. 1. Mean body weight (+/− S.E.) of *Nabis roseipennis* that attacked boll weevil larvae on day 1, then were isolated with only lima bean leaf. Weights are plotted until date of median longevity (21 days). Number of predators alive are as follows : 27 on days 1-4, 26 on day 5, 25 on days 6-9, 24 on days 10-12, 21 on days 13-14, 20 on day 15, 19 on days 16-17, 18 on day 18, 17 on day 19, 14 on day 20, and 12 on day 21.

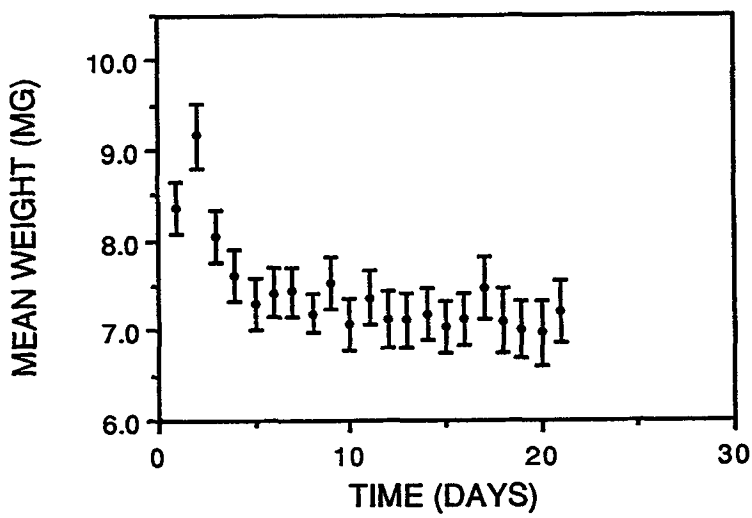

Fig. 2. Mean body weight (+/− S.E.) of *Nabis roseipennis* that attacked no prey on day 1, then were isolated with Mexican Bean Beetle larvae and lima bean leaf. No prey were attacked during the experiment. Weights are plotted until date of median longevity (22 days). Number of predators alive are : 5 on days 1-12, and 4 on days 13-22.

patterns of weight change through time (fig. 1 & 2). The weight loss approximated an exponential decline, with the majority of weight loss occurring in the 1st few days. This initial loss was followed by a long and gradual decline that led to little further weight loss. Thus, it seems that the initial weight had little effect on the duration of weight loss. Therefore, the biomass gained from attack may have shifted the onset of weight decrease by only one day, which would not have resulted in significantly greater longevity than that of the nabids not attacking prey. The same pattern of longevity and weight change during long periods of food deprivation has been shown for another heteropteran generalist predator, *Podisus maculiventris* (Say) (**O'Neil & Wiedenmann**, in prep.).

It is not clear why *N. roseipennis* adults failed to attack 3rd-instar MBB larvae. Several obvious explanations such as predator hunger or prey body size can be eliminated, as 95 % of the 40 nabids exposed to the larger BW larvae attacked BW larvae within 24 h. Also, nabids given MBB first, then BW, readily attacked BW. Reflex bleeding by MBB (see **Happ & Eisner,** 1961) could have been a deterrent to attack. However, other heteropteran predators successfully attack MBB larvae (**Waddill & Shepard,** 1974, 1975 ; **O'Neil & Wiedenmann,** 1987 ; **O'Neil,** 1988), and once the predator's mouthparts are inserted into the MBB, reflex bleeding would seem to offer little protection. Coccinellids are known to sequester toxins from host plants (**Happ & Eisner,** 1961 ; **Pasteels** *et al.,* 1973), and it is possible that the lima bean foliage provided the MBB with a chemical the nabids found « distasteful ». Larger larvae would accumulate more of the chemical, which would explain why smaller MBB larvae and eggs are attacked by *N. roseipennis* (**Waddill & Shepard,** 1974). However, other generalist predators (e.g. *Podisus maculiventris*) can attack 4th-instar MBB reared on lima foliage (**O'Neil & Wiedenmann,** 1987 ; **O'Neil,** 1988). Larger MBB larvae also have larger spines, and these may serve as a physical deterrent to attack. The size of the spines *per se* may not be sufficient deterrent, as nabids were observed probing the MBB cuticle between spines, and other heteropteran predators can attack larger MBB larvae (**Waddill & Shepard,** 1974, 1975 ; **O'Neil & Wiedenmann,** 1987 ; **O'Neil,** 1988).

Though the spines alone may not have been sufficient defense, spines plus the *N. roseipennis* attack behavior may explain the failure to successfully complete an attack. *N. roseipennis* attacking BW were seen holding prey under the predator's body, while the attack was in progress (see also **Harris,** 1928). If the prey were MBB, this behavior would expose the ventral surface of the abdomen to the MBB spines, and may be dangerous to the predator. This explanation is compatible with *N. roseipennis* attacking smaller MBB larvae (**Waddill & Shepard,** 1974 ; **Palmer,** 1978), since their spines are much smaller than those of larger larvae.

We cannot explain the discrepancy between our findings and those of **Waddill & Shepard** (1974). In their study, 24 h survivorship of MBB was not controlled, and attacks by predators apparently were not directly observed. Thus, their predation rate of 0.3 (table 1 ; **Waddill & Shepard,** 1974) may reflect other sources of mortality, rather than attacks by nabids. Alternatively, since they collected their predators from soybeans, the predators may have had some prior experience with MBB and have overcome the prey's defenses. In any event, the hypothesis we offer explains our results ; however, a complete explanation may include several of the factors mentioned above. Clearly, further experiments are needed to differentiate among the possible reasons that *N. roseipennis* failed to attack 3rd-instar MBB larvae.

Our observation that *N. roseipennis* failed to attack 3rd-instar MBB carries with it some implications for the interaction between predators and prey in the field. If the failure to attack was a function of the size of the prey — whether the reason was physical, behavioral, or chemical deterrence — then we need to think of *N. roseipennis* as a predator of only eggs and early-instar MBB. Thus the effectiveness of this predator in preventing MBB from reaching pest status would be limited to the early stages of MBB infestation. Also, if we assume that a prevalent predator species attacks a particular life stage of a pest when, in fact, it does not, then different mechanisms are required to explain the pest population dynamics seen in the field.

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RÉSUMÉ

Réponse de *Nabis roseipennis* [*Heteroptera : Nabidae*] aux larves d'*Epilachna varivestris* [*Coleoptera : Coccinellidae*]

Des recherches ont été menées en laboratoire pour mesurer la prédation des adultes de *N. roseipennis* Reuter [*Heteroptera : Nabidae*] vis-à-vis des 3^{e} stades larvaires d'*E. varivestris* et pour connaître la longévité et le poids des prédateurs. Dans un premier essai, des nabis récoltés à l'extérieur ont été isolés durant 24 heures dans des boîtes de Pétri (∅ = 9 cm) avec des feuilles de haricot de Lima (*Phaseolus lunatus* L.) et soumis à l'une des trois possibilités : (1). Soit 4 troisièmes stades larvaires d'*E. varivestris* ; (2) soit 4 troisièmes stades larvaires d'*Anthonomus grandis* Boheman [*Coleoptera : Curculionidae*] ; (3) soit 2 larves de chacune des deux espèces de proie. Les larves d'*E. varivestris* n'ont pas été attaquées dans les cas 1 et 3. Par contre, les larves d'*A. grandis* ont été facilement attaquées dans les cas 2 et 3. La différence dans le nombre de larves d'*A. grandis* attaquées dans les cas 2 et 3 est significative. Le nombre de larves d'*A. grandis* attaquées est plus grand que celui d'*E. varivestis* prédatés. Les nabis qui n'ont pas attaqué de proie ont perdu du poids au cours des 24 heures, tandis que ceux qui se sont alimentés en ont gagné. Dans un deuxième essai, les nabis qui avaient attaqué une proie ont été isolés avec des feuilles de haricot de Lima et les nabis qui n'avaient pas attaqué de proie ont été gardés avec des larves d'*E. varivestis* et des feuilles de haricot de Lima, jusqu'à ce qu'ils attaquent ou meurent.

Dans aucun cas les larves d'*E. varivestis* furent attaquées. Il n'y a pas de différence dans la longévité et la perte de poids entre les nabis qui ont attaqué de 1 à 4 proies et ceux qui n'en ont attaqué aucune. Les auteurs discutent des raisons responsables de l'impuissance de *N. roseipennis* à prédater les larves d'*E. varivestis*, aussi bien que des implications de ces conclusions vis-à-vis de l'utilisation des *Nabis* pour agir sur les populations de ravageurs dans les champs.

MOTS CLÉS : *Nabis roseipennis, Nabidae, Epilachna varivestis,* prédateurs généralistes, prédation.

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