Ovipositional Preference and Distribution of Eggs in Selected Field and Vegetable Crops by *Nabis roseipennis* (Hemiptera: Nabidae)¹

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Abstract Hemipteran predator abundance varies significantly among crop species. Ovipositional preference by these predators for specific crops may help explain differences in predator abundance among crops. Ovipositional preferences of *Nabis roseipennis* Reuter between a preferred standard (soybean) and four crops (corn, tomato, tobacco and squash) were determined in paired-choice tests under greenhouse conditions. Significantly more eggs or egg groups were found in soybean than in corn and tomato. Squash was the only plant preferred for oviposition over soybean. Within-plant distribution of eggs varied among plant species and appeared to be independent of prey distribution. The specific site chosen for oviposition in each plant species apparently was determined by plant physical characteristics, possibly including rind toughness and, for tomato and tobacco, glandular trichome presence and age. Patterns of ovipositional preference were similar to previous observations of field abundance and may be partially responsible for those patterns.

Key Words oviposition, habitat associations, plant-insect interactions, *Nabis roseipennis*, trichomes.

Nabids are common predators in several important field crops including soybean and cotton (Shepard et al. 1974, Donohoe and Pitre 1977, McCarty et al. 1980, Braman and Yeargan 1989). In studies to characterize the association of generalist predators with selected crops, nabids were shown to colonize and build populations readily in soybean, but not in several other nearby crops (Pfannenstiel and Yeargan 1998). Crop characteristics may affect predators in many ways that preclude their colonization: thus, the crop (1) may not support populations of preferred prey, or (2) may have morphological structures that adversely affect predators, or (3) may contain plant secondary allelochemicals that negatively affect predators that feed on prey containing these toxins.

Many hemipteran predators, including *Orius* and *Nabis* spp., oviposit by injecting eggs into the tissues of plants (Isenhour and Yeargan 1982). The ability of these predators to oviposit may be affected by plant characteristics. To determine if ovipositional preference is one of the factors mediating habitat choices by hemipteran predators, the ovipositional preference of *Nabis roseipennis* Reuter (Hemiptera: Nabidae) was evaluated on five crops: soybean, corn, tomato, tobacco, and squash.

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Nabis roseipennis is one of the most abundant predators in soybean and is much less abundant in corn, tomato and tobacco fields (Pfannenstiel and Yeargan 1998). It is not known to what degree *N. roseipennis* colonizes squash. Patterns of oviposition were compared to known patterns of predator association with these crops to determine the role of ovipositional preference in mediating abundance in these crops.

Materials and Methods

Our laboratory colony of *N. roseipennis* originated from individuals collected from the University of Kentucky's Spindletop Farm, 8 km N of Lexington, KY. Nabids were maintained individually in 9-cm Petri dishes with a moistened dental wick at $27 \pm 1^{\circ}$ C and a 15:9 (L:D) photoperiod. Throughout their development adults and nymphs of *N. roseipennis* received a constant supply of eggs of *Heliothis virescens* (F.), *Helicoverpa zea* (Boddie) and *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae). Eggs were replaced twice weekly. Prey colonies were maintained at $25 \pm 2^{\circ}$ C with a photoperiod of 15:9 (L:D):. *Heliothis virescens* and *H. zea* were reared using the methods of Ignoffo (1965); *T. ni* was reared on a modified pinto bean diet (Shorey and Hale 1965). We paired *N. roseipennis* males and females in Petri dishes within 3 d of adult eclosion and allowed them to mate. Four days later males were removed, and females received a green bean section as an ovipositional substrate. Our tests used females only after they had oviposited at least once in a green bean. After oviposition females were held without green bean sections for 48 h before a choice test. Females between 10 and 20 d old were used for all experiments.

Plants used for the choice tests were soybean, Glycine max (L.) Merrill (cv. "Flyer"), sweet corn, Zea mays L. (cv. "Golden Queen"), tomato, Lycopersicum esculentum Miller (cv. "Mountain Pride"), tobacco, Nicotiana tabacum L. (cv. "KY 14"), and squash, Cucurbita pepo L. (cv. "Sundance Hybrid"). Plants were grown in a greenhouse under sodium lights and a 15:9 (L:D) photoperiod. Pairwise ovipositional choice tests using soybeans as a standard were conducted under greenhouse conditions. Daily mean temperatures during the experiment ranged from 18°C to 27°C. For testing, two plants of approximately the same height, soybeans and either corn, tomato, tobacco or squash, were placed within a $0.61 \times 0.61 \times 0.82$ m (L × W × H) screened enclosure. Plants used for these studies were generally in vegetative growth stages, however, a small subset of the soybean plants used for testing against the taller corn plants had begun flowering. Before placing plants in the enclosure, we attached two 2 to 4 cm² sections of paper towel with 25 H. virescens eggs (as a food source) per sheet to each plant by stapling the paper towel sections to the upper surface of a leaf at about 1/3 and 2/3 of the plant height. Plants were placed such that their bases were 25 to 30 cm apart in the center of the enclosure and arranged so that their foliage did not touch. For the test, two reproductively active N. roseipennis females were placed on the floor in the center of the enclosure between 1600 and 1900 h. To provide a water source, two 60-ml cups of water with wicks were placed in the cage (equidistant from the two plants next to the location where the nabids were placed within the cage). The plants were watered immediately before the nabids were placed in the cage and again 24 h later. Plant foliage was lightly misted with water just after nabids were placed in the cage and again at the time of watering 24 h later. We terminated each trial after 48 h and examined each plant for N. roseipennis eggs. Trials in which no oviposition occurred were not used in the analyses. Nabis roseipennis lays eggs in groups of from 1 to about 20, so the number of egg groups and the

number of eggs per group were determined. Additionally, the plant part in which the eggs were deposited and the height of each egg group on the plant were recorded. Crop effects on total oviposition (both the number of egg groups and total eggs) within the cages were compared using analysis of variance (GLM procedure, SAS Institute 1985). Paired *t*-tests were used to compare each crop with soybean with respect to number of egg groups, total eggs and eggs per group laid on each crop. The height of the eggs on the plant was computed as a proportion of the total plant height and compared between soybean and each of the other crops using the Kruskal-Wallis test (Daniel 1990, NPAR1WAY procedure, SAS Institute 1985).

Results and Discussion

When four different plant species each were paired with soybean, total oviposition on the pair of plants was similar, regardless of which plant was paired with soybean. The mean number of egg groups and mean total number of eggs laid on both plants in a given pair ranged from 2.2 to 3.2 groups and from 14.3 to 22.0 eggs for the four combinations of plants tested. We found no differences due to plant combinations for either the total number of egg groups or the total number of eggs (F = 1.10; df = 3, 33; P = 0.365 and F = 1.27; df = 3, 33; P = 0.299, respectively). However, there were significant effects of plant species on ovipositional preference, and oviposition sites differed between plant hosts. Squash was the only crop preferred over soybean as an oviposition substrate, with an average of 12 eggs per squash plant versus 3.3 per soybean plant (t = 2.6; df = 14; P = 0.019) (Table 1). All other crops tested had fewer eggs per plant than soybean, but this difference was significant only for corn (t = 3.6; df = 13; P = 0.004). Tomato and tobacco received fewer eggs than soybean, but these differences were not significant (t = 1.4; df = 18; P = 0.178 and t = 1.1; df = 16; P = 0.286, respectively). However, there was a significant difference in the number of groups per crop in three of the four plant pairings (Table 1). Fewer groups of eggs per plant were deposited in corn and tomato than in soybean (t = 3.9, df = 11, P = 0.003

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Crop Pair	n	Groups of eggs per plant	Eggs per group	Total eggs per plant
Corn	10	$0.5 \pm 0.2^{*}$	6.8 ± 2.5	3.4 ± 1.6*
Soybean		2.7 ± 0.5	6.3 ± 0.7	16.9 ± 3.4
Tomato	10	$0.8 \pm 0.2^{*}$	9.6 ± 2.4	8.1 ± 3.0
Soybean		2.3 ± 0.3	6.3 ± 1.2	13.8 ± 2.7
Tobacco	9	0.8 ± 0.2	8.6 ± 1.0	6.2 ± 1.6
Soybean		1.4 ± 0.4	7.1 ± 1.1	9.3 ± 2.3
Squash	8	2.1 ± 0.5*	6.2 ± 1.3	12.0 ± 2.8*
Soybean		0.8 ± 0.3	4.1 ± 1.0	3.3 ± 1.7

Table 1. Ovipositional preference by *N. roseipennis* for plants of five crops. Data are means \pm SEM.

Pairs with an asterisk (*) are significantly different by paired t-test (P < 0.05).

and t = 4.2; df = 18; P < 0.001, respectively), no significant difference was detected in the number of egg groups deposited in tobacco and soybean (t = 1.5, df = 16, P = 0.147), and more egg groups were detected in squash than in soybean (t = 2.3, df = 14, P = 0.039). Therefore, females selected the preferred crop for more oviposition bouts instead of depositing more eggs per oviposition event.

The plant strata selected for oviposition differed significantly between soybean and three of the other crops. Nabis roseipennis oviposited in the lower third of corn, tomato, and tobacco plants and in the middle and upper parts of the soybean plant except for the terminal bud and developing leaves (χ^2 = 18.5; df = 1; P < 0.001 and $\chi^2 = 21.7$; df = 1; P < 0.001 and $\chi^2 = 10.4$; df = 1; P < 0.002 for corn, tomato and tobacco versus soybeans, respectively) (Fig. 1). The distribution of N. roseipennis eggs in our greenhouse-grown soybean plants closely approximated the distribution of eggs observed in soybean plants in the field (Isenhour and Yeargan 1982). The lower third of the soybean plant generally was avoided as an oviposition substrate. In squash, the distribution of eggs was similar to that in soybeans ($\chi^2 = 0.35$; df = 1; P = 0.553). Oviposition in tomato and tobacco may be negatively affected by trichomes as oviposition only occurred either at the base of these plants (on the stalk or older petioles) or on the midribs of senescing tobacco leaves (Table 2). On older plant parts the "stickiness" of the plant surfaces may be reduced due to lower production of leaf exudates (e.g., in tobacco: Chang and Grunwald 1976) or a coating of dust and soil. Very few eggs were laid on corn, and they always were deposited at the base of the plant, sometimes on the supporting roots. The leaf midribs and leafsheaths may not be suitable oviposition sites for N. roseipennis. In squash, eggs were deposited primarily in the petioles with only occasional egg groups observed in the stalk or leaf midrib. Eggs deposited in soybeans during this study generally were in the petioles; none were observed in the petiolules, where Isenhour and Yeargan



Proportion

Fig. 1. Vertical distribution of *N. roseipennis* egg groups in five crops. Bars indicate the proportion of egg groups within each crop observed at different heights expressed as a proportion of the total plant height.

	Percent								
Location	Soybean	Corn	Tomato	Tobacco	Squash				
Stalk	8.7	100.0	44.4	57.1	11.7				
Petiole	91.4	0	55.6	0	82.4				
Leaf midrib	0	0	0	42.9	5.9				

Table	2.	Distribution	of	Ν.	roseipennis	eggs	(%	of	total	within	each	crop)
		among plant	ра	rt ir	1 five crops							

(1982) observed 79% of the *N. roseipennis* eggs in the soybean cultivar "Williams" in the field. This difference may be due to characteristics of the soybean cultivar "Flyer", which has shorter median petiolules than some other soybean cultivars.

Tomato, tobacco, and squash have glandular trichomes that produce exudates, whereas soybeans have simple trichomes. Tobacco has many glandular trichomes which produce exudates that cause the plants to be very sticky and, thus, to negatively affect some predators (Elsey 1974, Katanyukul and Thurston 1979, Belcher and Thurston 1982, Crutchfield 1990), primarily through inhibition of movement and, possibly, increased mortality of early immature stages. *Nabis roseipennis* adults have difficulty walking on green tobacco leaves of the variety "KY 14" (R. S. Pfannenstiel, pers. observ.). Glandular trichomes in tomato and their associated exudates reduce predation rates in another predatory hemipteran, *Geocoris punctipes* (Say) (Barbour et al. 1993). Squash has a combination of spines and trichomes. The glandular trichomes on squash produce exudates, but they are considered to be extrafloral nectaries which may be beneficial to some natural enemies (Olson and Nechols 1995).

Isenhour and Yeargan (1982) hypothesized that the distribution of N. roseipennis eggs on soybean plants in the field may be affected by the distribution of eggs of the green cloverworm Plathypena scabra (F.) (Lepidoptera: Noctuidae). The data presented here indicate that factors other than prey distribution, in part, determine the distribution of *N. roseipennis* eggs. Prey were distributed similarly on all of the plants used in this study, yet N. roseipennis egg distribution differed. If overall leaf area affected oviposition, then eggs on squash plants should have been more common near the top of the plants and eggs in corn, tomato, and tobacco would have been spread throughout the middle of the plants. Egg distribution within each group appears to be dependent on plant morphological characteristics associated with the plants stalk or petiole tissue and not leaf area. In tobacco and tomato, glandular trichomes and their exudates confined oviposition to the oldest parts of the plants. Conversely, in soybeans and squash older tissues near the base of the plants become tough and woody, and thus may prevent ovipositor penetration. Nabis alternatus Parshley did not oviposit in the lower portions of alfalfa stems that may have been too hard or too wide to permit oviposition (Richards and Harper 1978). The youngest tissues at the soybean plants apex may have been too soft or hirsute for N. roseipennis oviposition.

Ovipositional preference of two other predatory hemipterans common in soybeans has been examined. Naranjo and Stimac (1987) studied ovipositional preference of

G. punctipes between soybeans and 10 species of weeds common in soybean fields and found in choice tests that soybean usually was the preferred substrate for oviposition. In their tests there was no effect of prey abundance or the presence of a non-preferred plant on oviposition rate. Ovipositional preference was recently examined for another hemipteran predator, Orius insidiosus (Say), which is known to feed frequently on plant material. Coll (1996) determined that on some plants O. insidiosus ovipositional preference was correlated with nymphal performance (e.g., survival and growth); oviposition and nymphal performance were highest on lima beans [Phaseolus lumatus (L.)] and lowest on corn. Oviposition and performance were not correlated on tomato and pepper [Capsicum anuum (L.)] (Coll 1996). While ovipositional preference may be correlated with nymphal performance on some plants, the results from Coll's (1996) study may have been affected by an experimental design in which only foliar parts of the plants were used. Orius insidiosus oviposits preferentially on the stalk, petiole and petiolules of soybean (Isenhour and Yeargan 1982) and Coll's use of only the distal 15 cm of corn leaves may have precluded oviposition. Corn has been well documented (along with soybean) as a habitat commonly inhabited by O. insidiosus in North America (e.g., Dicke and Jarvis 1962, Coll and Bottrell 1992, Yeargan 1998). Evaluation of predator distribution on plants or the use of whole plants may provide a more accurate evaluation of predator performance on particular plants. Omnivory appears to be of relatively little importance for nabids (Ridgway and Jones 1968, Stoner 1972) and greater importance for O. insidiosus (Kiman and Yeargan 1985), thus ovipositional preferences by N. roseipennis are less likely to be related to plant suitability as a food source for nymphs.

Previous studies in Kentucky indicated that soybean is the only crop among soybean, corn, tomatoes and tobacco in which *N. roseipennis* is typically abundant (Pfannenstiel and Yeargan 1998). We chose to examine ovipositional preference as one of many possible reasons for this pattern. If no ovipositional preference for soybean had been observed between soybean and corn, for example, then the observed patterns in the field would likely be attributed to other factors. Our results, however, suggest that ovipositional preferences may contribute to the greater abundance of *N. roseipennis* in soybean. The magnitude of differences observed in our greenhouse studies, however, did not totally explain observed patterns of habitat association in the field.

An additional factor affecting colonization may be the timing of crop colonization in relationship to plant phenology. Colonization of annual crop habitats by *N. roseipennis* in Kentucky occurs in late June and July (Braman and Yeargan 1990). At this time tomato and tobacco plants are still relatively young and rapidly growing; thus, appropriate oviposition sites may be uncommon during early summer. Additionally, crops with glandular trichomes vary in the amount of exudates they produce under varying environmental conditions. Laboratory determination of plant resistance to insects may not always be a good predictor of effects in the field (Obrycki and Tauber 1984). Tomato and tobacco growing under field conditions may be less suitable for oviposition by *N. roseipennis* than those developing under greenhouse conditions. In the field, ovipositional nonpreference appears to be important for *G. punctipes* populations in certain tobacco cultivars (including "KY 14"), where adults colonize but do not reproduce well (Crutchfield 1990). For other predators, including *N. roseipennis*, colonization of suitable habitats by adults is quickly followed by reproduction. If plant suitability for oviposition plays an important role in habitat colonization by adult preda-

tors, then knowledge of the factors affecting oviposition will improve our understanding of crop choice by these predators. Additionally, plant characteristics that inhibit oviposition by *N. roseipennis* (and probably other predators) may be purposefully incorporated into resistant crop cultivars during development of those cultivars. The potential negative impact of these plant characteristics on natural enemies should be considered during evaluation of new crop cultivars.

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