PREDATION BY *PODISUS MACULIVENTRIS* (SAY) ON MEXICAN BEAN BEETLE, *EPILACHNA VARIVESTIS* MULSANT, IN INDIANA SOYBEANS[1]

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Abstract

Daily rates of predation by *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) on Mexican bean beetle larvae, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae), were measured in soybeans, *Glycine max* (L.). The number of Mexican bean beetle larvae attacked per predator per day remained consistently low throughout 2 years of study. Estimates of the area searched by *P. maculiventris* were calculated from the number of prey attacked, number of prey available for attack, and leaf area. As leaf area increased, *P. maculiventris* searched more area, demonstrating a search strategy shared with other predators of canopy-inhabiting prey in soybeans.

Résumé

Le taux journalier de prédation par *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) sur les larves du coléopteré mexicain du soja, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae) a été estimé en culture de soja, *Glycine max* (L.). Le nombre de larves du coléopteré attaqué par le predateur par jour est resté constamment bas au cours du 3 annuels d'étude. Les estimations de la superficie exploré par *P. maculiventris* ont été faites du taux d'attaque proportionnel et de la suface foliaire. Plus la surface foliaire augmente, *P. maculiventris* explore plus de superficie, demontrant une stratégie d'exploration commune aux autres prédateurs visant dans la canopie du soja.

Introduction

A large number of generalist arthropod predators inhabit soybeans, *Glycine max* (L.) (Whitcomb 1974). Most species of predators appear infrequently and do not establish resident populations. Only a small number of predator species do establish populations in soybeans (Dietz *et al*. 1980), and these predators must have adaptations that allow them to find sufficient numbers of prey to sustain population growth (O'Neil and Wiedenmann 1987). The rate that predators find prey is significantly influenced by the ability of predators to search effectively areas of habitat that contain prey (Hassell 1978). In soybeans, a complex of nine resident generalist arthropod predators maintained a near-constant level of predation and compensated for increases in the size of the soybean canopy by searching more area (O'Neil 1984). It is not known if the searching strategies of other resident generalist arthropod predators also compensate for changes in the size of the soybean canopy. If different predators share similar strategies for finding prey in the soybean canopy, then we have evidence for a common adaptation among the predators in this system.

One generalist predator consistently found in soybeans throughout the United States is *Podisus maculiventris* (Say). This predator has been studied extensively, including its reproductive, developmental, and survivorship rates (Mukerji and LeRoux 1969*a*; Evans 1982*a*; McPherson *et al*. 1982; Drummond *et al*. 1984), energy utilization (Mukerji and LeRoux 1969*b*), functional response (Morris 1963; Mukerji and LeRoux 1969*c*; Waddill and Shepard 1975), consumptive behaviors (Gallopin and Kitching 1972), pheromones (Aldrich *et al*. 1984), and distribution and population dynamics (Evans 1983; Dietz *et al*. 1980; McPherson 1982). Evans (1982*b*) assessed the search and attack behaviors of *P. maculiventris* found on goldenrod (*Solidago* spp.), including the predator's mean rate of movement, location on plant surfaces, and percentage of successful attack on various prey species (see also Marston *et al*. 1978). However, no study has reported the relationship between the number of prey attacked by *P. maculiventris* and prey density in the field, or

the effects of plant size on its search strategy. In this paper, I report the results of a 2-year study of predation by *P. maculiventris* on Mexican bean beetle, *Epilachna varivestis* Mulsant, in soybeans. My objectives were to document the changes in predation by *P. maculiventris* in relationship to field densities of Mexican bean beetle and determine if *P. maculiventris* has a search strategy similar to other generalist predators of canopy-inhabiting insects in this system.

Methods

Colonies of *P. maculiventris* and Mexican bean beetle were maintained in the laboratory following the methods of Mukerji and LeRoux (1965) and Stevens *et al*. (1975), respectively. The colony of *P. maculiventris* was started, each year, from 50–100 adults collected from March to May near Lafayette, IN. Mexican bean beetles were maintained continuously in culture since the fall of 1984. Both cultures were augmented periodically with field-collected individuals.

Research was conducted in a 2.3-ha field of soybeans (cv. Williams 82) at the Purdue Agricultural Center, Bedford, IN, in 1985, and in a 2.8-ha field (cv. Beck 301) at the O'Neall Memorial Farm, Lafayette, IN, in 1986. Daily rates of predation by adult female *P. maculiventris* on fourth-instar Mexican bean beetle were measured at approximately weekly intervals using cage-inclusion techniques.

Cages were constructed of nylon mesh screen (30 squares per 2.54 cm) supported with PVC frames. Cages were approximately 1 by 1 by 2 m, and enclosed 91 cm of soybean row. The plant canopy was isolated inside the cage by securing the cage bottom around the plant stems. For each experiment, cages were placed at randomly selected locations in the field. Before placing a cage over the foliage, plants in the selected area were vigorously shaken to dislodge resident arthropods. Cages then were secured over plants and left for 1–2 days. Prior to an experiment, plants in cages were periodically shaken to dislodge and remove remaining arthropods.

Over the course of the study, between 1 and 16 Mexican bean beetle larvae were added per cage. One to three predators were added per cage in 1985, and a single predator was added per cage in 1986. All predators were reproductively active females that were denied access to prey but provided a green bean slice for 24 h preceding each experiment. Control cages, containing only Mexican bean beetle larvae, were used to estimate the 24-h survivorship of beetles in the absence of predators. Prey were placed first into cages with aid of a camel's-hair brush. Predators were added by dropping open plastic shell vials containing predators to the floor of the cage. Predators and prey were left in the cages for 24 h; then the enclosed plants were destructively sampled and the numbers of *P. maculiventris* and Mexican bean beetles were recorded. Attacked Mexican bean beetles were identified by characteristic discolorations and deformations. For each experiment, treatment (cages with predators) and control were replicated five times. Leaf area per cage was estimated as the product of the number of plants per cage and the average leaf area per plant (both leaf sides). Average leaf area was computed from 10 plants randomly selected from the field 1 day prior to each experiment. Leaf area was measured with a Li-Cor 3000® area meter.

Analysis of variance (ANOVA) was used to test for weekly differences in the number of Mexican bean beetles attacked per predator per day for cages with one, two, or three predators (1985). ANOVA was also used to compare differences in the average number of Mexican bean beetles attacked per predator per day across each weekly experiment both within and between years. A *t*-test was used to compare differences in the average number of Mexican bean beetles attacked per predator per day in 1985 and 1986. Linear regressions (SAS Institute 1985) were used to determine the relationships between average predation rates and the number of Mexican bean beetles and leaf area. Unless otherwise stated, all

Table 1. Date, number of replicates, number of Mexican bean beetles, average leaf area, and daily per capita predation rate for each weekly experiment in 1985 and 1986

Date	n	Number Mexican bean beetles per cage	Leaf area (m²) per cage	Per capita predation (SE)
19 Jun.	15	4	1.6	0.41 (0.10)
25 Jun.	16	3	2.9	0.50 (0.15)
2 Jul.	16	4	4.0	0.32 (0.09)
9 Jul.	15	3	5.6	0.42 (0.11)
16 Jul.	15	5	4.8	0.37 (0.12)
22 Jul.*	5	15	2.8	0.60 (0.40)
23 Jul.	14	15	4.3	0.44 (0.13)
29 Jul.*	5	12	2.6	0.40 (0.24)
8 Aug.	15	2	11.3	0.22 (0.08)
12 Aug.*	5	6	3.2	0.40 (0.25)
13 Aug.	11	10	4.3	0.68 (0.15)
19 Aug.*	5	11	2.5	0.60 (0.25)
20 Aug.*	5	13	2.2	0.40 (0.40)
21 Aug.*	5	9	3.3	0.60 (0.40)

*1986.

predation rates refer to daily per capita predation rates, the number of Mexican bean beetles attacked per predator per day.

Results and Discussion

Daily percentage survivorship of Mexican bean beetle in control cages was 98.4 and 99.2% for 1985 and 1986, respectively. In 1985, 117 rates of predation were measured over 8 weeks (Table 1). Average number of Mexican bean beetles attacked per predator per day ranged from 0.22 to 0.68. On average, predators attacked 0.41 Mexican bean beetle larvae per day. ANOVA of each weekly experiment found no significant difference in the number of Mexican bean beetles attacked per predator per day for one, two, or three predators per cage. There were no significant differences in predation rates over time (ANOVA: df = 7, 109; F = 1.18; P > 0.31).

In 1986, 30 rates of predation were measured (Table 1). Average number of Mexican bean beetles attacked ranged from 0.40 to 0.60 per predator per day. Predators attacked an average of 0.50 Mexican bean beetles per day. There were no significant differences between predation rates over time (ANOVA: df = 5, 24; F = 0.11; P > 0.98).

Over the 2 years of study, *P. maculiventris* attacked an average of 0.43 Mexican bean beetle larvae per day. ANOVA of the combined data for 1985 and 1986 showed no significant differences in number of Mexican bean beetles attacked per predator per day over time (df = 13,133; F = 0.63; P > 0.83). A *t*-test detected no significant difference between the average predation rates in 1985 versus 1986 (df = 35.6; P > 0.50). Data for both years were combined for regression analyses. Linear regression of the average predation rates and the number of Mexican bean beetles used for each weekly experiment showed a non-significant model (df = 1, 12; F = 4.06; P > 0.06) and a slope coefficient not significantly different from zero (*t* = 2.01, P > 0.06). Linear regression of the average predation rates and average leaf areas per cage leaf area showed a non-significant model (df = 1, 12; F = 4.10; P > 0.06) and a slope coefficient not significantly different from zero (*t* = 2.03; P > 0.06).

Podisus maculiventris maintained a low rate of predation while soybean leaf area changed approximately 5.4-fold. As Mexican bean beetles were dispersed in the plant canopy, the size of the canopy defined the searching of *P. maculiventris*. Although the soybean canopy is a three-dimensional structure comprising leaves, stems, and petioles,
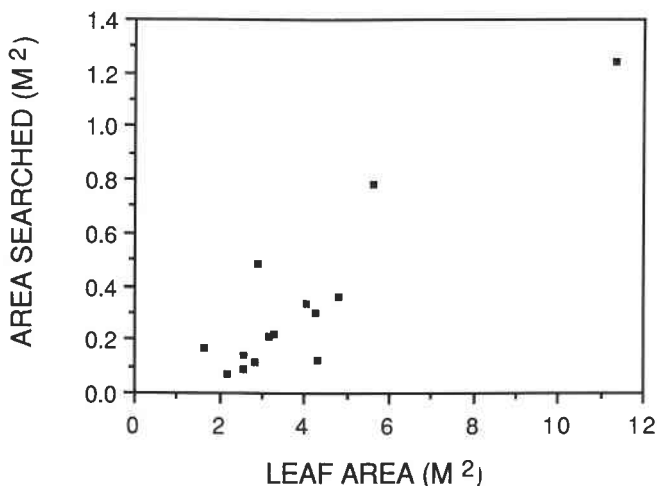
FIG. 1. Area searched (square metres) by *Podisus maculiventris* as a function of leaf area (square metres) per cage.

the leaf area is a major constituent and a consistent index of total canopy volume. As the rate of predation remained relatively constant while the leaf area increased, *P. maculiventris* had to have searched more area to compensate for leaf area changes. To estimate the area searched, I used the relationship between searching and predation:

$$N_a/N = S/A \qquad [1]$$

where N_a = per capita rate of predation; N = number of Mexican bean beetles; S = area searched (in square metres); and A = leaf area (in square metres).

Equation 1 implies that predators search a certain proportion of available area and attack a similar proportion of available prey. Rearranging Eq. 1, the area searched can be estimated from the proportional predation rate (N_a/N) and leaf area:

$$S = N_a/N \cdot A. \qquad [2]$$

Area searched estimated using Eq. 2 is the minimum effective area searched, as it does not account for area re-searched, nor area searched in a localized patch following an encounter with prey. Because we know N, N_a, and A (Table 1), the area searched can be estimated. Plotting the area searched as a function of leaf area shows the compensation for changes in leaf area (Fig. 1).

The relationship between S and A is linear. For a constant N, the proportional attack rate N_a/N is the slope of the line. However, because N varied while N_a remained relatively constant (Table 1), we cannot say N_a/N is the slope of the line in Figure 1. The points in Figure 1 are taken from a family of S and A curves, with each line describing search for a constant N and slope N_a/N.

Conclusions

By compensating for increases in leaf area by searching more area, *P. maculiventris* maintained a near-constant rate of predation on Mexican bean beetle larvae in soybeans. This compensatory search strategy also was found to be characteristic of search by other generalist arthropod predators attacking a different canopy-inhabiting prey in Florida soybeans (O'Neil 1984). The daily attack rate of predators in Florida averaged 0.38 attacks per predator per day whereas that recorded in Indiana was 0.43. The similarity in the strategy of different predators searching for prey in the soybean canopy suggests a common

adaptation for finding prey in a dynamic searching universe. A common search strategy indicates that the constraints of finding prey in soybeans select for a certain type of predator, which would explain why soybean fields with different pest complexes share a similar group of predators.

Estimating search from the proportional attack rate and total leaf area assumes prey are equally vulnerable to attack and the entire soybean canopy serves as the searching arena of predators. Undoubtedly prey refugia exist in the canopy, but the importance of refugia seem limited in the present study. The location of prey, predators, and attacks in the canopy did not seem to be affected by the size of the soybean plants (unpublished data). Predators attacked approximately the same number of prey regardless of the number of prey available or the size of the soybean canopy (Table 1). If the number of refugia were a positive function of canopy size, then we would expect fewer attacks when the canopy was large or when few prey were present. The relatively low numbers of prey used in the present study may limit the importance of prey refugia. In other studies, where prey are more dense, prey refugia may be more important.

In soybeans, the density of prey relevant to searching predators is defined by the size of the canopy. Prey density, expressed as the number per square metre of leaf area, can change either through changes in the number of prey or through leaf area growth. The probability of predator/prey encounters is therefore affected by the rate predators search the canopy, the number of prey, and the dynamics of canopy growth. In other agricultural systems, plant growth characteristics may also influence predator/prey interactions if prey are dispersed in plant parts that change over time.

Acknowledgments

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