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A MODEL OF PREDATION BY *PODISUS MACULIVENTRIS* (SAY) ON MEXICAN BEAN BEETLE, *EPILACHNA VARIVESTIS* MULSANT, IN SOYBEANS

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Abstract

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A model of predation by *Podisus maculiventris* (Say) on Mexican bean beetle, *Epilachna varivestis* Mulsant, larvae in soybeans is presented. The attack equation described the number of prey attacked as a function of the number of prey, soybean leaf area, and the search behavior of the predator. The area searched by *P. maculiventris* was related to the amount of leaf area and the number of prey. Predictions of the number of Mexican bean beetles attacked per predator were compared with an independent field data set. The relevance of the predation model to studies of predation in other agricultural systems is discussed.

Résumé

On a élaboré un modèle de la prédation de *Podisus maculiventris* sur les larves de la coccinelle mexicaine des haricots, *Epilachna varivestis* Mulsant dans le soya. L'équation d'attaque présentée prédit le nombre de proies attaquées en fonction du nombre de proies, de la surface foliaire du soya, et des caractéristiques de la recherche du prédateur. L'aire de recherche de *P. maculiventris* est reliée à la surface foliaire et au nombre de proies. Les prévisions obtenues du nombre de coccinelles attaquées ont été comparées avec des données de terrain indépendantes. On discute de la pertinence du modèle de prédation pour d'autres systèmes agricoles.

Introduction

Soybeans, *Glycine max* (L.), have a diverse fauna of generalist arthropod predators. It has been estimated that over 1000 predator species can be found in soybeans (Whitcomb 1974), although far fewer species consistently establish populations there (Turnipseed and Kogan 1983; Dietz *et al.* 1980). The presence of similar predator complexes in widely dispersed soybean fields suggested that predators share common adaptations for maintaining populations in this system (O'Neil and Wiedenmann 1987). Because the searching behavior of predators is key to their ability to sustain populations in an environment (Hassell 1978), we can hypothesize that one adaptation that could be shared among predators commonly found in soybeans is their search strategy for finding prey.

In a previous study of predation in Florida soybeans, generalist arthropod predators were shown to maintain a low daily rate of predation over time (O'Neil and Stimac 1988*a*). The search strategy of these predators was suggested by the consistency of the predation rate while the size of the soybean canopy changed. Because predators attacked approximately the same number of prey as the plants got larger, they must have searched more to compensate for changes in the size of the canopy (O'Neil and Stimac 1988*b*). To test whether other generalist predators commonly found in soybeans also compensate for changes in the size of the plant, the daily rate of predation by *Podisus maculiventris* on Mexican bean beetle, *Epilachna varivestis*, was measured in Indiana soybeans (O'Neil 1988). This predator/prey system is similar to the one used in Florida in that a generalist arthropod predator was searching the soybean canopy to find prey. Results showed that *P. maculiventris* maintained a low daily rate of predation over time which indicated that as the size of the plant increased, *P. maculiventris* searched more area.

In this paper, the relationship between predator search and prey density is documented. This relationship is used to develop a mathematical model that describes the number of prey attacked as a function of prey density. Independent validation of the attack model is provided and the model's relevance to studies of predation in other agricultural systems is discussed.

Methods

Detailed descriptions of methods and results of the predation experiment are presented by O'Neil (1988). Only those findings needed for the development of the model are presented here.

Field Study. All predators and prey used in the study were laboratory-reared according to the methods of Mukerji and LeRoux (1965) and Stevens *et al.* (1975). Daily rates of predation by adult female *P. maculiventris* on fourth-instar Mexican bean beetle larvae were measured by placing predators and prey in 1 by 1 by 2 m field cages for a 24-h period. Cages enclosed approximately 0.91 m of soybean row. Attacked prey were identified by characteristic deformations and discolorations. Leaf area in cages (m^2, both leaf sides) was estimated as the product of the number of plants per cage and the average leaf area per plant. Average leaf area per plant was calculated from a 10-plant sample, randomly taken in the field 1 day prior to an experiment. To ensure sufficient ranges in prey density and leaf area, predation was measured over approximately weekly intervals in July and August, 1985–1987. Cages were moved to a new site for each experiment and new predators and prey used for each trial. Data from 1985 and 1986 were used to formulate the model. Data from 1987 were used in validation.

Differences in the daily average per capita rate of predation over time (weeks) were compared with analysis of variance (ANOVA) for each weekly experiment in 1985, 1986, and the pooled 1985/1986 data. A *t*-test was used to compare average predation rates in 1985 and 1986. Linear regression was used to analyze the relationships between the average per capita rates of predation, leaf area, and prey number. All significant levels were set at 0.05. Unless otherwise stated, all predation rates refer to the number of prey attacked per predator per day.

Model. Estimates of the area searched by predators were based on the average number of prey attacked per predator, number of prey, and leaf area from the 1985–1986 field seasons. A predator search model was described as a function of the number of prey and leaf area with parameter values estimated using the Gause-Newton iterative technique of non-linear least squares (SAS Institute 1985). The number of prey attacked per predator is described as a function of the number of prey, predator search behavior, and leaf area. For validation, model-estimated predation rates were compared with field-estimated rates of predation measured in the 1987 field season. Model-estimated predation rates were obtained by inserting prey number and leaf area estimates into the attack equation. A chi-square test was used to detect a significant departure of the estimated predation rates from model-estimated predation rates. Model predictions were accepted if model-estimated rates of predation were, for a given prey number and leaf area, within the 95% confidence intervals of the field-estimated rates of predation.

Results and Discussion

The number of prey attacked, number of prey, and leaf area for each experiment in 1985 and 1986 are presented in Table 1. There were no significant differences in average predation rates in 1985 (ANOVA: df = 7, 109; $F = 1.18$; $P > 0.31$) or 1986 (ANOVA: df = 5, 24; $F = 0.11$; $P > 0.98$). Pooled data for 1985/1986 also showed no significant differences in predation rates over time (ANOVA: df = 13,133; $F = 0.63$; $P > 0.83$). There were no significant linear regressions of average rates of predation and numbers of

Table 1. Date, number of Mexican bean beetles, leaf area, and daily per capita predation rate for each experiment in 1985 and 1986 (after O'Neil 1988)

Date	No. Mexican bean beetles	Leaf area (m^2)	No. Mexican bean beetles attacked (SE)
19 June	4	1.6	0.41 (0.10)
25 June	3	2.9	0.50 (0.15)
2 July	4	4.0	0.32 (0.09)
9 July	3	5.6	0.42 (0.11)
16 July	5	4.8	0.37 (0.12)
22 July*	15	2.8	0.60 (0.40)
23 July	15	4.3	0.44 (0.13)
29 July*	12	2.6	0.40 (0.24)
8 August	2	11.3	0.22 (0.08)
12 August*	6	3.2	0.40 (0.25)
13 August	10	4.3	0.68 (0.15)
19 August*	11	2.5	0.60 (0.25)
20 August*	13	2.2	0.40 (0.40)
21 August*	9	3.3	0.60 (0.40)

*1986.

prey (df = 1, 12; $F = 4.06$; $P > 0.06$) or leaf area (df = 1, 12; $F = 4.10$; $P > 0.06$). Predators attacked an average of 0.41 and 0.50 prey per day for 1985 and 1986, respectively. A *t*-test indicated no significant difference in the average predation rate for 1985 and 1986 (df = 35.6; $P > 0.50$).

Predators maintained a nearly constant rate of predation over time whereas leaf area substantially increased (Table 1). Because predators had to have searched the soybean canopy to find prey, the maintenance of the predation rate while leaf area increased suggested that predators searched more area. This implies that *P. maculiventris* used no prey-mediated cues to locate prey in the canopy. Although we cannot discount the possibility that the predator used specific cues to locate Mexican bean beetle, the lack of prey specificity of *P. maculiventris* suggests that it does not use host-specific cues to locate prey over short distances (Hassell 1978). Because *P. maculiventris* attacks over 100 species of prey (McPherson 1980), it probably uses a combination of visual or tactile cues to locate prey over short distances (see also Morris 1963; Evans 1982).

To estimate the area searched by predators, the proportional predation rate (N_a/N) was multiplied by the leaf area:

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

where S = area searched in square metres; N_a = per capita predation rate; N = number of Mexican bean beetle larvae; A = leaf area in square metres.

Equation 1 estimates the minimum effective area searched by predators as it does not include area re-searched by predators or area searched in a localized patch following an encounter with prey. To use Eq. 1 to estimate the area searched assumes that the dispersion pattern of prey does not have a significant effect on predator search. The delineation of the pattern of dispersion is predicted on the selection of a spatial unit (Taylor 1984), which is the 91-cm row of soybeans enclosed by the cage. Because *P. maculiventris* attacked a statistically constant number of prey over the range in number of prey (per 91-cm row) offered, then the "dispersion pattern" did not have a significant influence on the predation rate and therefore the estimates of area searched (see also Walde and Murdoch 1988).

Because the number of attacks remained relatively constant as prey density increased, we expect an inverse relationship between the area searched and prey density (density expressed as the number of prey per square metre of soybean foliage). To describe the

Table 2. Prey density classes, average per capita predation rate, and area searched. Prey density expressed as numbers per square metre of leaf area. Area searched estimated via Eq. 1

No. prey/m^2 of leaf area	Per capita rate of predation	Estimated area searched (m^2)
0.5	0.33	0.66
1.0	0.32	0.32
1.5	0.44	0.29
2.0	0.45	0.23
2.5	0.55	0.22
3.0	0.62	0.21
3.5	0.29	0.08
4.0	0.35	0.09
4.5	0.67	0.15
5.0	0.40	0.08
5.5	0.60	0.11
6.0	0.40	0.07

relationship between predator search and prey density mathematically, prey densities were first categorized into classes of 0.5 prey per square metre. Prey densities were categorized because, within each experiment in 1985, cages had different numbers of plants per cage resulting in different leaf area and therefore different prey densities. Average predation rates were computed for each density class (Table 2) and used to estimate the area searched (Eq. 1).

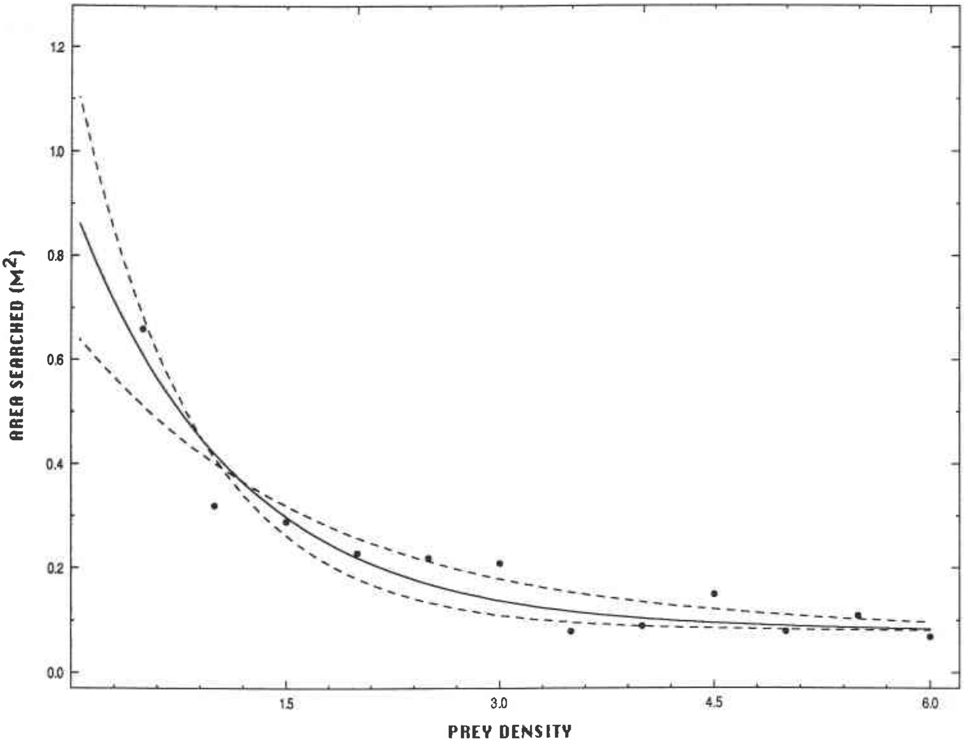

FIG. 1. Area searched (m^2) as a function of prey density (no. prey/m^2 of leaf area) in 1985 and 1986. The solid line represents the search equation (Eq. 2). Dotted lines use the 95% asymptotic values of parameter estimates.

Plotting area searched as a function of prey density shows that as prey density increased, area searched decreased (Fig. 1). To develop an equation for the search and prey density relationship we assume two additional attributes of predator search behavior. First, there is a minimum area searched at high prey densities, which is evidenced in Figure 1 by a plateau region in the search estimates at higher prey densities. This minimum area searched may reflect the need of the predator to search some area to find prey, or could be the result of area-restricted search following an attack (Hassell 1978). The second assumption is that predators cannot search indefinitely, and there is a maximum amount of area searched in the 24-h period. Furthermore, we expect the maximum area searched to occur when prey density is zero.

To incorporate these attributes of predator search with the observed form of the search – prey density relationship, a negative exponential function was used:

$$S = C_1 e^{-C_2 N/A} + C_3 \qquad [2]$$

where C_1 = maximum amount of area searched (m^2) above C_3 when prey density is zero; C_2 = rate of change in search inversely proportional to prey density; C_3 = minimum area searched (m^2) at high prey density.

Parameter estimates for C_1, C_2, and C_3 (and asymptotic 95% confidence limits) were 0.825 (0.58, 1.10), 0.887 (0.59, 1.20), and 0.08 (0.08, 0.08), respectively. Search curves using these parameter estimates, as well as their 95% asymptotic values, are shown in Figure 1.

Inserting Eq. 2 into Eq. 1 and solving for N_a gives:

$$N_a = (N/A) \cdot (C_1 e^{-C_2 N/A} + C_3) \qquad [3]$$

Equation 3 represents the functional response of *P. maculiventris* and as such can be used to describe the numbers of prey attacked as a function of Mexican bean beetle density in soybeans. Model-estimated predation rates were calculated by inserting weekly measures of leaf area and prey number for 1987 into Eq. 3. Comparison of model-estimated and field-measured rates of predation for 1987 showed that in six of seven prey densities tested, model-estimated predation rates fell within the 95% confidence interval of the field data. Only at the lowest prey density (2 July) did the model-estimated rate of predation exceed the confidence interval of the field data. The confidence intervals of some of the 1987 data were relatively large, particularly in comparison with most confidence intervals in 1985/1986. This difference in variabilty is largely due to the number of multiple attacks in 1987. In 1985 and 1986 only 6% of predators attacked more than one prey, whereas in 1987, 10% of predators attacked more than one prey. In 1985/1986, no predators attacked more than two prey, but in 1987, six predators attacked more than two prey. The reasons for these differences are not known, but the increase in the frequency of multiple attacks did increase the variability of the data set. Even so, the χ^2 estimate of the correspondence between model-estimated and field-measured rates of predation in 1987 found no significant difference ($\chi^2 = 2.36$; df = 4; $P > 0.05$). On average the model predicted 0.42 attacks per predator and the average predation rate measured in the field was 0.57.

Conclusions

Two alternative, but related, explanations for the pattern of predation and the predator search strategy can be advanced. The first alternative is that predators may have been satiated by the number of prey attacked. The predation rate would then be constant, and the search and prey density relationship (Fig. 1) would be an artifact. However, when *P. maculiventris* females were starved for 24 h, and then provided prey in the laboratory, they attacked up to an average of 4.4 prey per day (unpublished data). Also, other measures of predation by this predator on similar-sized prey (Morris 1963; Mukerji and LeRoux 1969; Waddill and Shepard 1975; Marston *et al.* 1978; Drummond *et al.* 1984) have shown

Table 3. Date, number of replicates, number of Mexican bean beetles, average leaf area, prey density, field-estimated predation rate, and model-estimated predation rate in 1987

Date	*n*	No. Mexican bean beetles	Leaf area (m^2)	No. prey/m^2 of leaf area	Field-estimated predation rate (conf. limit)	Model-estimated predation rate
2 July	15	2	5.3	0.4	0.00 (0.00)	0.26
7 July	15	12	3.7	3.2	1.00 (0.66)	0.41
14 July	15	16	2.6	6.1	0.33 (0.34)	0.51
16 July	12	6	4.6	1.3	0.75 (0.68)	0.44
29 July	15	3	0.8	3.9	0.33 (0.27)	0.41
3 August	15	14	6.7	2.1	1.07 (0.79)	0.44
5 August	15	10	1.8	5.5	0.53 (0.36)	0.47

that *P. maculiventris* can attack up to 10-fold as many prey as they did in the field-predation study. Thus the predators were most likely not satiated by the number of prey they attacked in the field.

Alternatively, the pattern of predation and the predator search strategy could be explained in terms of the effect of handling time on the time budget of the predator (Holling 1961; Beddington 1975; Luck 1985). The constancy of the predation rate could represent the plateau region of a Type II functional response (Holling 1959, 1961), which is determined by the relationship between handling time and the total time available to the predator (Hassell 1978). However, the low number of prey attacked argues against handling time being responsible for the pattern of predation. If we assume that handling time is constant (which is assumed for the majority of functional response models (Hassell 1978)), then we must conclude that a predator that "handles" up to 4.4 prey per day in the laboratory cannot "handle" more than 0.42 prey per day in the field. To see what magnitude of handling time would be required to explain the constancy of the predation rates measured in the field, we must convert the number of prey attacked per day to the amount of time between attacks. If, on average, the predators attacked 0.42 prey per day, then they, on average, attack one prey every 2.38 days (1/0.42). If handling time determined the maximum number of attacks, then we must conclude that the predators took more than 2 days to handle a single prey item, an estimate that does not conform with previous observations of predation by *P. maculiventris* (unpublished data; Drummond *et al.* 1984; Morris 1963; Waddill and Shepard 1975; Mukerji and LeRoux 1969; Evans 1982).

In soybeans, prey density of foliar-inhabiting prey is determined by the size of the plant and prey number. To a searching predator, the probability of a predator/prey encounter will be influenced by prey dynamics, crop growth, and the predator's search strategy. For a generalist predator that relies on visual or tactile cues to locate prey, plant growth dynamics must be incorporated into its search strategy. For a specific predator that uses prey-mediated cues the changes in plant size may not be as critical to host location.

In both Florida and Indiana soybeans, generalist arthropod predators exhibited similar search strategies. In both systems predators compensated for leaf area changes by searching more area as leaf area increased (O'Neil 1988), and in both systems predators were "conservative" searchers, showing a decrease in area searched as a function of prey density (O'Neil and Stimac 1988*b*). The possession of similar search strategies by different predators in soybeans suggests that predators share a common adaptation for finding prey in this system (O'Neil and Wiedenmann 1987). The similarity in the search strategies of predators helps to explain why the same predator species are consistently found in widely dispersed soybean fields. Interestingly, the predators common to soybeans are also found in other agricultural systems. As prey in other crops are found on plant parts that change over time, a search strategy similar to that seen in soybeans may be employed by generalist predators in those systems as well (see Ullyett 1943; Elsey 1972; Frazier and Gilbert 1976; Risch *et al.* 1982; Naranjo and Stimac 1987).

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