BIOLOGICAL CONTROL **6,** 330–339 (1996)
ARTICLE NO. 0042

A Simulation Model of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) and Mexican Bean Beetle, *Epilachna varivestis* (Mulsant) (Coleoptera: Coccinellidae), Population Dynamics in Soybean, *Glycine max* (L.)

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Received June 20, 1995; accepted October 31, 1995

We present a predator–prey model (PREDPREY) that describes the population dynamics of the generalist predator *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) and Mexican bean beetle *Epilachna varivestis* (Mulsant) (Coleoptera: Coccinellidae) in soybean, *Glycine max* (L.). PREDPREY is a state-variable model that uses a distributed-delay function to represent temperature-dependent development of both predator and prey species. The predator submodel includes descriptions of immigration, predator search, functional response, survivorship, and reproductive characteristics. The prey submodel includes descriptions of immigration, survivorship, and reproductive characteristics. The plant model describes plant growth as a function of leaf area accumulation over time. The model tracks changes in predator and prey populations over a single growing season using a 1-day time step. The model captures the essence of predator–prey dynamics to provide reasonable predictions of population patterns. Comparison of the no-predator scenario to the standard simulation (1000 predators/ha) indicates that predators bring about a 24% reduction in peak prey (larval) density and a 47% reduction in overwintering prey (adult) numbers. Sensitivity analyses indicate that reproductive and survivorship characteristics of the prey have a relatively large impact on pest density. Among predator characteristics, developmental rate and most reproductive parameters have a greater impact than do search parameters and survivorship. Plant growth rate has a greater impact than the initial size of plants. The model can be used to evaluate the relative effectiveness of natural enemies, investigate augmentative biological control strategies, and evaluate biological control strategies as part of larger IPM programs. © 1996 Academic Press, Inc.

KEY WORDS: **predator–prey dynamics; simulation modeling; *Podisus maculiventris; Epilachna varivestis.***

INTRODUCTION

For several years, we have been studying a particular predator–prey system with the goal of contributing to a broader understanding of the essential adaptations of natural enemies to crop systems. The predator, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), is a native generalist predator found throughout North America (MacPherson 1980). The prey, the Mexican bean beetle, *Epilachna varivestis* (Mulsant) (Coleoptera: Coccinellidae), is an introduced sporadic pest of soybean and other legumes throughout most of the eastern United States (Auclair, 1959). We have shown that at field-realistic prey density, *P. maculiventris* attacks relatively few prey, averaging less than one attack every 2 days (O'Neil, 1988a; Wiedenmann and O'Neil, 1992). This low rate of attack contrasts to the capability of *P. maculiventris* to attack prey under high-density laboratory conditions, where it can attack ca. 20 prey in the same 2-day period (O'Neil, 1989; Wiedenmann and O'Neil, 1991a). The maintenance of a low rate of attack, concurrent with significant changes in plant size, suggested that *P. maculiventris* alters the area it searches to find prey as a function of plant growth (O'Neil, 1988b); an hypothesis that has been validated in both soybean (Wiedenmann and O'Neil, 1992) and in potato (O'Neil, unpublished data). Further, the low rate of attack suggested that *P. maculiventris* should show trade-offs in reproductive and survival characteristics, reducing reproductive output, to survive under low prey inputs (O'Neil and Wiedenmann, 1987). This hypothesis has been validated with Mexican bean beetle (Legaspi and O'Neil, 1993) and other prey species (Wiedenmann and O'Neil, 1990; Valicente and O'Neil, 1995). We have suggested that this combina-

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tion of life history and search strategies forms the basis of adaptation of *P. maculiventris* to crop habitats, which together with its generalist feeding habits, and ability to suck moisture from plants, helps explain its subsistence in a broad diversity of crop systems (O'Neil and Wiedenmann, 1987, 1990; Wiedenmann and O'Neil, 1992; Legaspi and O'Neil, 1994a,b). We have further suggested that other generalist natural enemies common to crops should share these search and life history characteristics, which need to be measured under field-realistic conditions, as they are "transparent" when measured under high-prey density (Wiedenmann *et al.*, 1995; Legaspi and Legaspi, 1995).

This paper describes a predator–prey model that incorporates our previous results in investigating the contribution of *P. maculiventris* to prey population dynamics. Our objective in developing the model is to identify how life history characteristics and searching behavior contribute to the effectiveness of the predator in augmentative release programs. In doing so, we hope to illuminate areas needing further study and ultimately contribute to development of a broader theoretical base for augmentative biological control.

METHODS

Model structure and parameterization. The predator–prey model (PREDPREY) consists of three components, which describe soybean plant growth, *P. maculiventris* population growth, and Mexican bean beetle population growth (Figs. 1 and 2). PREDPREY is a state-variable model that uses a distributed-delay function to represent the temperature-dependent development of both predator and prey species. The model tracks changes in plant size, and predator and prey populations over a single growing season using a 1-day time step. Model parameters, inputs, and outputs are scaled to a m^2 basis; thus, predators and prey are assumed to be distributed uniformly in the field. The soybean plant model describes the accumulation of leaf area over time. The predator submodel includes descriptions of immigration, predator searching, functional response to prey density, survivorship, development, and reproduction. The prey submodel includes immigration, survivorship, development, and reproductive characteristics. The search strategy of *P. maculiventris* and consequent attack on Mexican bean beetle provide a link among the three components. The model is written in Microsoft FORTRAN (Microsoft Corp., 1985) and simulates a single season in ca. 2 s on a 486 IBM-compatible personal computer. A user interface was developed to facilitate the specification of input parameters. A graphics routine was developed to view simulation results. Model output includes estimates of adult *P. maculiventris* and Mexican bean beetle populations, leaf area index (LAI: m^2 of leaf area/m^2 of ground area), and predator search and attack rates.

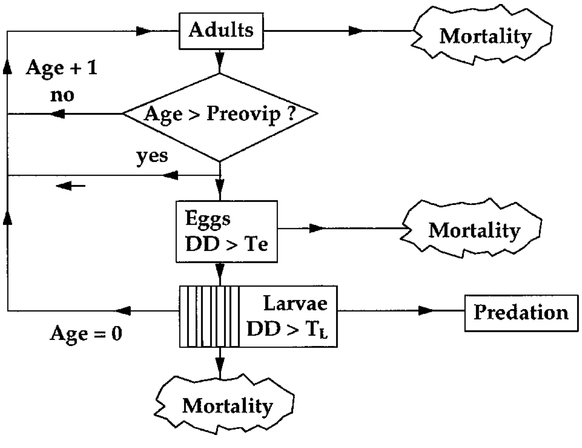

FIG. 1. Flow diagram for Mexican bean beetle submodel of PREDPREY.

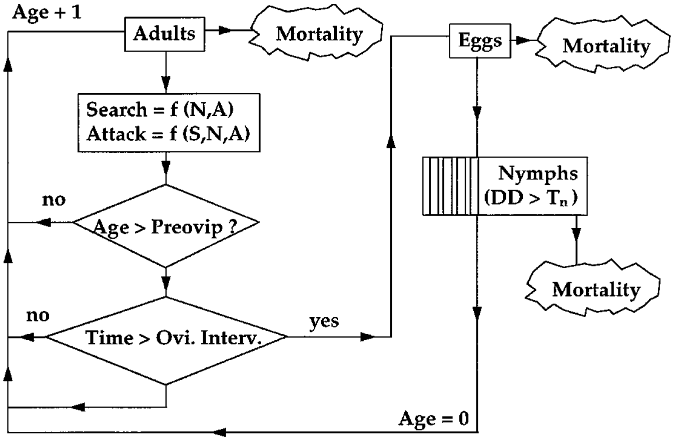

FIG. 2. Flow diagram for *Podisus maculiventris* submodel of PREDPREY.

Soybean plant growth. Only leaf area is considered (Table 1). Starting with soybean plants of an initial size, an increase in leaf area proceeds linearly for a defined time period. Following this period of growth, plant size remains constant and then begins to decline, first linearly and then exponentially. Leaf area is computed based on two surfaces of a leaf since prey are found on both leaf surfaces, and predators must traverse both surfaces to find them (see Wiedenmann and O'Neil, 1991b). Based on the typical soybean planting period in Indiana (early May to mid June), June 1 was set as the starting date for simulation. On that date, soybean is usually in the V3 (vegetative) stage (Fehr and Caviness 1977) with a leaf area index of approximately 1.1 (Day and Lorton, 1989, unpublished data). Changing the parameter values representing an initial LAI, its daily increase, and the timing of its various growth phases allows the characterization of other LAI profiles of interest (Table 1).

TABLE 1

Parameters Used for the PREDPREY Model of *P. maculiventris* and Mexican Bean Beetle Population Dynamics in Soybean

Parameter	Default value	Source
Crop		
Initial LAI	1.1	Nagarajan *et al.* (1993)
Daily increase	0.2	Nagarajan *et al.* (1993)
Day when linear increase ends (LAI is maintained)	July 25	Nagarajan *et al.* (1993)
Day when LAI starts to decline	Aug. 9	Nagarajan *et al.* (1993)
Day when linear decrease ends (exponential decline; senescence)	Sept. 12	Nagarajan *et al.* (1993)
Prey		
Reproduction		
Function	Triangular	Nagarajan *et al.* (1994)
Starting age	6 days	Nagarajan *et al.* (1994)
End age	30 days	Nagarajan *et al.* (1994)
Peak age	18 days	Nagarajan *et al.* (1994)
Peak egg lay	25 eggs/day	Nagarajan *et al.* (1994)
Development		
Egg development	75 DD	Kauffman *et al.* (1985)
Earliest development	385 DD	Nagarajan *et al.* (1994)
Latest development	584 DD	Nagarajan *et al.* (1994)
Distribution parameter, h	3.527	Nagarajan *et al.* (1994)
Mortality		
Daily adult mortality	0.0385	Kauffman *et al.* (1985)
Daily larval mortality	0.0450	Kauffman *et al.* (1985)
Total egg survival	0.8	Palmer (1978); Kauffman *et al.* (1985)
Influx		
Age of adult Mexican bean beetle	1–5 days	Assumption
Influx magnitude	$0.25/\text{m}^2$	Assumption
Predator		
Reproduction		
Minimum preoviposition age	7 days	Legaspi and O'Neil (1993)
Oviposition interval	3 days	Legaspi and O'Neil (1993)
Maximum clutch size (female eggs)	14	Legaspi and O'Neil (1993)
Development		
Earliest development	360 DD	DeClercq and Degheele (1992)
Latest development	520 DD	DeClercq and Degheele (1992)
Distribution parameter, h	4.0	Assumption
Survival		
Function	$1 - e^{-(85\text{-age})m}$	Legaspi and O'Neil (1993), Wiedenmann and O'Neil (1990)
Daily adult mortality, m	0.058	Legaspi and O'Neil (1993), Wiedenmann and O'Neil (1990)
Search		
Function	$S = C_1 e^{-C_2(N/A)} + C_3$	O'Neil (1988b), Wiedenmann and O'Neil (1992)
C_1	0.51	Wiedenmann and O'Neil (1992)
C_2	0.385	Wiedenmann and O'Neil (1992)
C_3	0.04	Wiedenmann and O'Neil (1992)
Influx		
Age	65–75 days	Assumption
Reproductive status	Based on 1 attack per day	Assumption
Influx magnitude	0.1 Adults/m^2	Assumption

Prey dynamics. Mexican bean beetle population growth is modeled as the result of the processes of reproduction, development, mortality, and initial immigration into the field (Fig. 1, Table 1). The population begins with an initial number of adults (0.25 adults/m^2) that enter the field on June 1. The adults are assumed to be 1–5 days old, with 20% allocated into each age class. Based on field data reported by Palmer (1978), the influx population was considered to have an equal number of males and females. Incoming adults were assumed to be either newly emerged from overwintering sites or progeny of overwintered adults that emerged early and developed on alternate hosts (e.g., alfalfa, early planted bean, etc.). The timing, magnitude, and age structure of the incoming population (referred to as an "influx pattern") can be specified as part of the model inputs.

The rate of oviposition of the Mexican bean beetle is age-dependent (Hochmuth *et al.*, 1987). In the model, after a 6-day preoviposition period, the number of eggs laid increases linearly to a peak value of 25 eggs per day at 18 days. Subsequently, there is a linear decline in daily egg production until females cease reproduction at 30 days. The lifetime estimate of 300 eggs per female in the model is close to the 335 eggs per female reported by Hochmuth *et al.* (1987).

Immature development is temperature-dependent, with a lower developmental threshold of 10°C (Fan *et al.*, 1992). Eggs take about 5 days to hatch at 25°C (Kauffman *et al.*, 1985), giving a value of 75 degree-day (DD) for egg development. Following the typical hatching pattern of coccinellids, all eggs hatch simultaneously after the accumulation of 75 DD. Larvae and pupae were considered a single stage for developmental purposes. The distribution of immature development was modeled using an empirical function that approximates a bounded β function (Stinner *et al.*, 1975). The fraction of population $F(a)$ completing development by age a (days) is defined as

$$F(a) = (1 - Z)^{hZ^k}, \qquad [1]$$

where k and h are empirical parameters and $Z = (B - a')/(B - A)$, where A is time of first emergence, B is the time of last emergence, and a' is the accumulated DD by age a. For the parameter k, a value of 2.0 was used (see Stinner *et al.*, 1975). For the immature Mexican bean beetle to develop to adult, earliest and latest development times are set at 385 and 584 DD, respectively. A value of 3.527 is used for the parameter h (see Nagarajan *et al.*, 1994).

Immature and adult Mexican bean beetles are subject to mortality from factors other than predation. Egg mortality is imposed at hatching, whereas larval/pupal mortality is imposed on a daily basis. Daily adult mortality and larval mortality rates are set at 0.0385 and 0.0450, respectively (Kauffman *et al.*, 1985). Total egg survival is set as 0.8, based on reported values of 0.769 (Palmer, 1978) and 0.821 (Kauffman *et al.*, 1985). To account for plant size, "prey density" was defined as the number of Mexican bean beetle larvae/m^2 of leaf area (both surfaces).

Predator dynamics. Population growth of *P. maculiventris* is the result of the processes of immigration, reproduction, development, and mortality. The general structure of the predator submodel is similar to the prey submodel with the addition of a predator searching component (Fig. 2, Table 1). Only females are tracked by the model due to incomplete data on male and immature life history and/or searching behavior. In the model, the population begins with an influx of overwintered adults, ages 65–75 days, entering the field on June 1. The reproductive status of immigrating *P. maculiventris* females corresponds to predators that have been attacking one prey daily. The influx magnitude was set as 0.1 adults/m^2, with a distribution among 12 age classes (Fig. 3). A range of predator influx patterns (timing, age, reproductive status, and magnitude) can be specified as part of the input data.

Immature (eggs and nymphs) development is temperature-dependent, with a developmental threshold of 10°C (Warren and Wallis, 1982). Variability in development was modeled using the same distributed-delay framework used for the prey (Eq. [1]). Earliest and latest development values of 360 and 520 DD were used for A and B, respectively (Eq. [1]), based on data of DeClercq and Degheele (1992), who reported an average value of 353.5 DD to adult emergence. A value of 4.0 was assumed for the parameter h in Eq. [1].

The prepositional period, the number of eggs laid per egg mass, and the interoviposition interval depend on the predation rate (Legaspi and O'Neil, 1993; Wiedenmann and O'Neil, 1990). The maximum clutch size is set at 14 female eggs/egg mass (Legaspi and O'Neil, 1993). Egg survivorship is set at 94% (Mukerji and LeRoux, 1965, unpublished data). Survival through the nymphal stage was set as 55%, which compares with the 10 to 78% survival rates reported by De Clercq and Degheele (1992) and Legaspi and O'Neil (1994a).

The predation rate for *P. maculiventris* is directly related to the area searched. The area searched by *P. maculiventris* is described as a negative exponential function of prey density (O'Neil, 1988b; Wiedenmann and O'Neil, 1992):

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

where S is the leaf area searched (m^2), N/A is the prey density, with N being the number of prey and A the leaf

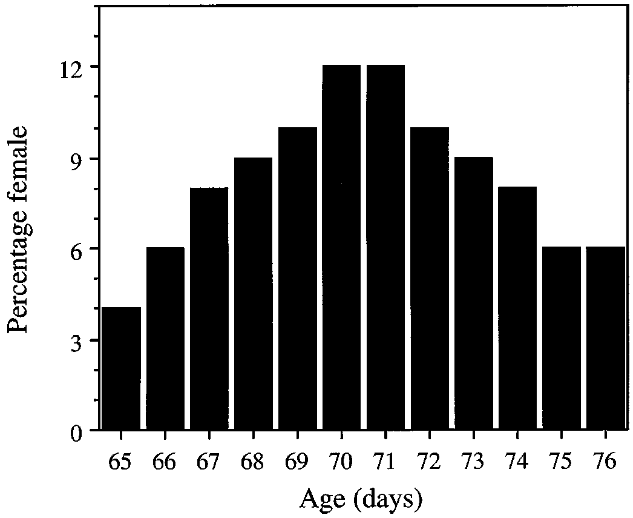

FIG. 3. Simulated age distribution of female *P. maculiventris* entering the field on June 1.

area (m^2, both surfaces). The values for the three parameters that characterize the search function, $C_1 = 0.51$, $C_2 = 0.385$, and $C_3 = 0.04$, are based on estimates given by Wiedenmann and O'Neil (1992). The per capita attack rate (N_a) is given by

$$N_a = S(N/A). \qquad [3]$$

The search (Eq. [2]) and attack (Eq. [3]) functions are based on the assumptions that *P. maculiventris* searches at random and that it attacks all encountered prey. We have shown that under field-realistic prey densities, both assumptions are reasonable (Wiedenmann and O'Neil, 1991b). The search model has also been shown to accurately describe *P. maculiventris'* search for both third and fourth instar Mexican bean beetle in soybeans (O'Neil, 1988b; Wiedenmann and O'Neil, 1992).

Adult survivorship follows a Type I schedule (Begon *et al.*, 1990), with a daily mortality value of 0.058 (Wiedenmann and O'Neil, 1990; Legaspi and O'Neil, 1993). Model output is numbers of adult (female) *P. maculiventris*. We use numbers of *P. maculiventris* rather than density (e.g., numbers/m^2 of leaf area) as the predator's search for prey incorporates the size-effect of the soybean plant (via Eq. [2]).

Model validation. Validation of ecosystem models should emphasize the need to establish the usefulness of the model, instead of focusing on the "validation problem" per se (Mankin *et al.*, 1979; Shugart and O'Neill, 1979). Our approach to validation was to gauge the "reasonableness" of the model results, and then address the utility of the model (see Harrison, 1990). Emphasis was placed on ensuring that the model captured the essence of predator–prey dynamics, particularly the timing of events, and the relative magnitudes of *P. maculiventris* and Mexican bean beetle populations. Model predictions were compared with field data and with predictions by an earlier model of Mexican bean beetle population dynamics (Nagarajan *et al.*, 1994).

Model behavior and sensitivity analysis. We used two indicators of model performance: peak density (No./m^2 of leaf area, both surfaces) of Mexican bean beetle larvae (hereafter, "peak prey density") and the number of adult Mexican bean beetles at the end of the season. Using peak prey density simplifies analysis, and since peak densities often occur during critical soybean reproductive phases (Nolting and Edwards 1989), it provides insight into the potential impact of *P. maculiventris* to Mexican bean beetle damage to soybean. The number of adult Mexican bean beetles at the end of the season is important because the species overwinters in the adult stage and thus the size of the immigrant population in the subsequent year is influenced by the number of Mexican bean beetle produced the previous field-season.

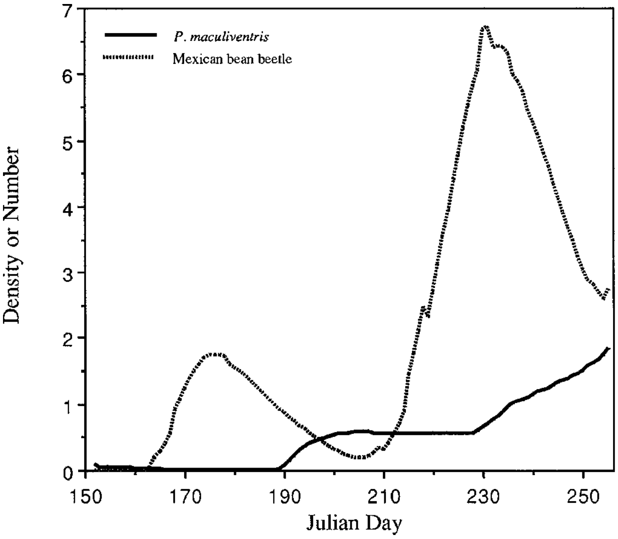

FIG. 4. Standard model output. Mexican bean beetle density is expressed as the number of larvae/m^2 of leaf area. Predator numbers/m^2 are given for adult females. Peak prey density of 6.8 prey/m^2 of leaf area occurred on Julian Day 231 (Aug. 19).

We used peak prey density in sensitivity analyses. The relative sensitivity of model performance (P) to the parameter p_i was measured using a dimensionless quantity defined by France and Thornley (1984) as

$$s(P, p_i) = (\Delta P/P)/(\Delta p_i/p_i). \qquad [4]$$

We targeted ±5% change from standard values (e.g.,

TABLE 2

Comparison of Adult Mexican Bean Beetle Populations Simulated by Indiana Soybean System Model (ISSM),[a] PREDPREY, and Field Data

Source	Influx generation		2nd generation		Time between population peaks
	Peak no.	Julian day	Peak no.	Julian day	
ISSM-high mortality[b]	3.2	152	6.3	213	61
ISSM-low mortality[c]	3.2	152	11.1	213	61
PREDPREY (with predators)	3.2	152	20.9	213	61
PREDPREY (without predator)	3.2	152	22.3	213	61
Field data (Palmer, 1978)	2.7	160	6.2	218	58

[a] Nagarajan *et al.* (1994).

[b] Using high estimates of Mexican bean beetle mortality based on Palmer (1978).

[c] Using low estimates of Mexican bean beetle mortality based on Kauffman *et al.* (1985).

[b,c] Predator populations were not included in either of the ISSM simulations. However, the "high" mortality factor of Palmer (1978) includes predation as well as weather-related factors.

$\Delta p_i/p_i = 0.05$); however, actual changes ranged from 4 to 5.3% due to rounding. Two predator characteristics, the preoviposition period and the oviposition interval, which can be changed only at increments of 1 day, were changed by 14.3 and 33.3%, respectively. In addition, selected model parameters were changed over a wider range of possible values and the percentage change in peak prey density was computed and plotted.

In addition to sensitivity analyses, model behavior was examined through a series of simulations involving changes in *P. maculiventris* searching and Mexican bean beetle reproductive schedules. Predator search was changed to reflect a constant-high (0.51 m^2), a constant-low (0.04 m^2), or a linearly increasing function of prey density. Prey reproductive schedule was changed to initiate reproduction earlier or later than the default schedule, in combination with changes in total fecundity.

RESULTS

The standard simulation showed two generations of Mexican bean beetle per season, with the first-generation density lower than the second generation (Fig. 4). Peak prey density of 6.7 Mexican bean beetle larvae/m^2 of leaf area occurred on Day 231 (August 19). The number and timing of prey population peaks predicted by PREDPREY compared favorably with those predicted by an alternate Mexican bean beetle population model (Nagarajan *et al.*, 1994) and field data (Table 2). Comparison of Mexican bean beetle larval and *P. maculiventris* adult populations predicted by PREDPREY with sampling data soybean showed a reasonable correspondence between model output and field data (Fig. 5).

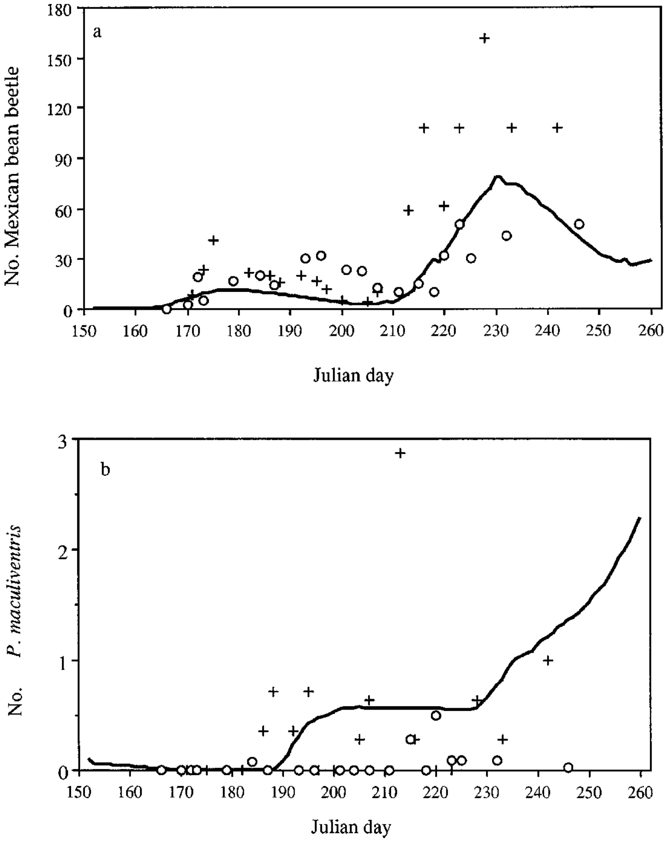

FIG. 5. Simulated and observed number/m^2 of adult Mexican bean beetle (a) and *P. maculiventris* (b). Field data are for 1976 (o) and 1977 (+) from Palmer (1978). Palmer gave no leaf area estimation; therefore, no estimate of Mexican bean beetle density (No./m^2 leaf area) is possible from his data.

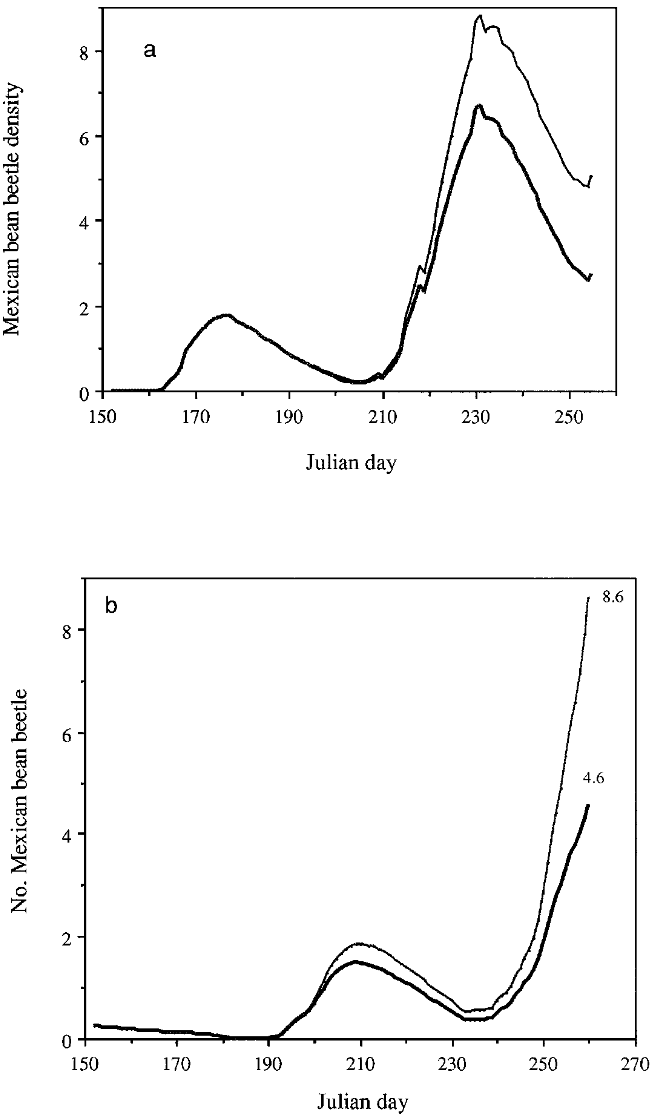

FIG. 6. Comparison of Mexican bean beetle density (No. larvae/m^2 leaf area) (a) and adult Mexican bean beetle numbers (b) with (thick line) and without (thin line) *P. maculiventris.*

As expected, simulated populations of the Mexican bean beetle in the absence of predators were larger than populations with predators present (Fig. 6a). At peak prey density on Julian Day 231, *P. maculiventris* had the effect of reducing prey density by 23.7% (6.7 for standard case vs 8.8 for the no-predator situation). The effect of predators on the number of Mexican bean beetle adults that can overwinter was much greater. By the end of the season, a 46.8% reduction in the number of Mexican bean beetle adults was observed (8.6 without predators vs 4.6 with predators; Fig. 6b).

Mexican bean beetle density was most sensitive to its reproductive characteristics and mortality factors (Table 3). Among *P. maculiventris* characteristics, development had the most effect, with relative sensitivity values of 0.51 and 0.36 for late and early development, respectively. Among plant growth parameters, changes in the rate of LAI increase had a greater impact on peak prey density than the initial value of LAI, with relative sensitivity values of 0.77 and 0.07, respectively (Table 3).

For most parameters, the direction and magnitude of model output varied in a logical fashion (Table 3). For example, a ±4% change in the maximum daily egg production by the Mexican bean beetle resulted in a +8.3%/−8.7% change in peak prey density, respectively. In contrast, ±33% change in the interoviposition interval of *P. maculiventris* resulted in a −10.8%/+6.4% change in peak prey density. Finally, counterintuitive results were found with the stadium of Mexican bean beetle eggs. Both an increase and decrease in Mexican bean beetle egg development caused a reduction in peak prey density (Table 3).

In the expanded sensitivity analysis, several parameters showed distinct nonlinearities, whereby the model's sensitivity to parametric change varied as a function of the parameter value (Fig. 7). Among *P. maculiventris* characteristics (Fig. 7a), the preoviposition time had almost no effect on peak prey density. The number of eggs/egg mass and the time of first adult emergence had a greater effect on peak prey density than the oviposition interval. Changes in Mexican bean beetle parameters (Fig. 7b) had a larger impact on peak prey density than changes in *P. maculiventris* parameters. Among prey parameters, fecundity, egg survival, and larval mortality had a greater effect on peak prey density than did development.

Changing the relationship between Mexican bean beetle density and the area that *P. maculiventris* searched resulted in a significant change in peak prey densities. Under a constant-high search strategy, peak prey density declined by 17%, whereas a low-constant search strategy resulted in a 24% increase in peak prey density. When *P. maculiventris* searched as a linear

TABLE 3

Relative Sensitivity of PREDPREY to Changes in Parameter Values[a]

	Parameter value			Relative sensitivity		
Parameter	Default	Low	High	Low	High	Parameter average[b]
Crop						
Slope of LAI	0.2	0.19	0.21	0.796	−0.736	0.766
Initial LAI	1.1	1.05	1.15	0.072	−0.072	0.072
Prey						
Peak egg lay (eggs/day)	25	24	26	−2.086	2.176	2.131
Total egg survival	0.8	0.76	0.84	−2.074	2.187	2.131
Daily larval mortality	0.045	0.043	0.047	1.969	−1.801	1.885
Daily adult mortality	0.0385	0.037	0.040	1.286	−1.214	1.250
Late development, DD[c]	584	554.8	613.2	1.514	−1.490	1.502
Early development, DD	385	365.75	404.25	0.983	−1.022	1.003
Egg development, DD	75	71	79	−0.265	−0.349	0.307
Distribution parameter	3.527	3.351	3.703	0.149	−0.143	0.146
Predator						
Late development, DD	520	494	546	−0.522	0.495	0.508
Early development, DD	360	342	378	−0.373	0.352	0.362
Distribution parameter	4	3.8	4.2	−0.048	0.042	0.045
Clutch size (female eggs)	14	13.3	14.7	0.283	−0.283	0.283
Oviposition interval (day)	3	2	4	−0.323	0.192	0.257
Preoviposition period (day)	7	6	8	−0.008	0.004	0.006
Search parameter, C_1	0.51	0.485	0.535	0.252	−0.252	0.252
Search parameter, C_2	0.385	0.366	0.404	−0.094	0.085	0.089
Search parameter, C_3	0.04	0.038	0.042	0.033	−0.036	0.034
Adult mortality	0.058	0.055	0.061	0.228	−0.219	0.223

[a] Parameters are ranked according to the average value of relative sensitivity. Where applicable, parameters are grouped according to similar life history traits and ranking is done within groups.

[b] Calculated by averaging the absolute values of sensitivity under the Low and High parameter values.

[c] DD, day-degree.

increasing function of Mexican bean beetle density, peak prey density increased 20%.

Doubling the fecundity of Mexican bean beetle (600 vs 300 eggs) resulted in a two- to sixfold increase in peak prey density. In contrast, an 80% reduction in fecundity (60 vs 300 eggs) caused nearly 100% reduction in peak prey density. Changes in the Mexican bean beetle reproductive schedule alone caused a significant change in peak prey density. For instance, at a maximum production of 33 eggs/day, changes in peak prey density ranged from a 54% reduction to a 78% increase, depending on when the female oviposited (Table 4).

DISCUSSION

PREDPREY provides a reasonable approximation of the dynamics of *P. maculiventris* and Mexican bean beetle in soybean. The model suggests that *P. maculiventris* has a significant impact on within-season Mexican bean beetle dynamics and their overwintering populations, potentially influencing between-season dynamics. The life history characteristics of Mexican bean beetle, particularly those related to reproduction and survival, are key to determining its population size. The contribution of *P. maculiventris* to Mexican bean beetle dynamics is influenced more by *P. maculiventris* developmental and reproductive rates than search or survival rates. This suggests that between-generation response (Hassell, 1978) of *P. maculiventris* may be more important to Mexican bean beetle dynamics than the within-generation response.

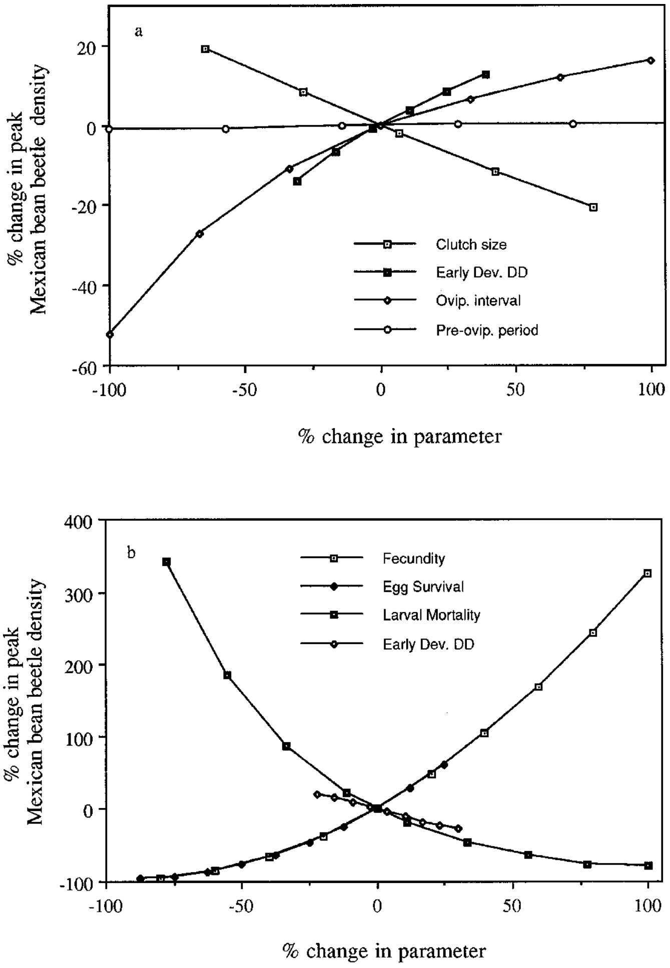

FIG. 7. Expanded sensitivity analysis of PREDPREY for changes in *P. maculiventris* (a) and Mexican bean beetle (b) characteristics. *Y*-axis is the percentage change in peak prey density. A positive percentage change indicates more prey present than the standard simulation run (peak prey density of 6.7 Mexican bean beetle larvae/m^2 of leaf area). *X*-axis is the percentage change in parameter values. See Table 1 for description of parameters.

TABLE 4

Effect of Changes in Mexican Bean Beetle Reproductive Schedule and Fecundity on Its Peak Larval Density (No./m^2 of Leaf Area)

Peak no. eggs/day	Age when reproduction Starts	Peaks	Ends	Total fecundity	Percentage change in peak prey density[a]
Changes in timing and magnitude[b]					
5	6	18	30	60	−94.77
25	6	18	30	300	0.00[c]
50	6	18	30	600	325.66
5	0	12	24	60	−91.85
25	0	12	24	300	65.67
50	0	12	24	600	584.12
5	12	24	36	60	−96.75
25	12	24	36	300	−54.23
50	12	24	36	600	122.53
Changes in timing with total fecundity at approximately standard level[d]					
33	0	18	18	297	77.70
25	0	18	24	300	33.91
20	0	18	30	300	10.19
17	0	18	36	306	−7.88
50	6	18	18	300	81.21
33	6	18	24	297	25.34
25	6	18	30	300	0.00[c]
20	6	18	36	300	−25.73
100	12	18	18	300	92.79
50	12	18	24	300	17.76
33	12	18	30	297	−18.00
25	12	18	36	300	−40.96
100	18	18	24	300	−3.96
50	18	18	30	300	−35.22
33	18	18	36	297	−53.99

[a] Peak prey density = 6.7 Mexican bean beetle larvae/m^2 of leaf area.

[b] Represents standard schedule (6-18-30) and 6 day earlier and later schedules combined with a 80% reduction and 100% increase in total fecundity.

[c] Standard values for PREDPREY.

[d] Represents changes to peak reproductive rate and schedule while the total fecundity (ca. 300 eggs per female) and timing of peak reproductive rate (18 days) are maintained at standard levels.

Nonlinearities between life history characteristics and population dynamics are common (Begon *et al.*, 1990) and serve to illustrate the importance of prey density in the measurement of predator life history characteristics. Many of the *P. maculiventris* life history and searching characteristics used in the model were measured under low density of Mexican bean beetle. This was because measurement of the functional response of *P. maculiventris* under field-realistic prey density showed that it attacked few Mexican bean beetles per day (O'Neil, 1988a; Wiedenmann and O'Neil, 1992). Had we not had the results from the field experiments, we would have measured the life history characteristics under high Mexican bean beetle density that characterize most laboratory situations. Because of the nonlinearities involved, we would not have been able to predict the contribution of selected life history characteristics to Mexican bean beetle dynamics, particularly at low Mexican bean beetle density, and thus we would have had a biased view of the relationships between *P. maculiventris* search and life history characteristics and Mexican bean beetle density.

Higher Mexican bean beetle density resulted when *P. maculiventris* searched as a linearly increasing function of Mexican bean beetle density than when it searched as a negative exponential function of Mexican bean beetle density [2]. Predators that search more leaf area at low prey densities will attack more prey than those predators that search less at low prey densities. Predators with a search strategy typified by Eq. [2] will attack more prey earlier in the season than those predators whose search strategy is to search as a linear-increasing function of prey density. Thus, the major impact of *P. maculiventris* to Mexican bean beetle population dynamics arises early in the season, when Mexican bean beetle densities are relatively low, rather than later in the season, when Mexican bean beetle densities are relatively high. This reinforces the concept that natural enemies like *P. maculiventris* may serve as "buffers" to prey population growth—their contribution to prey dynamics being more to prevent or delay pest outbreaks rather than suppress prey outbreaks once they have begun. The use of natural enemies like *P. maculiventris* in augmentative biological control should take their search strategy into consideration, with releases targeted to prevent rather than suppress pest population outbreaks.

ACKNOWLEDGMENTS

Thanks go to the many students who used versions of the model in class exercises in biological control courses taught at Purdue, Honduras and Brazil—their comments and insights improved it tremendously. Also thanks to the many people who helped evaluate various aspects of the biology of *P. maculiventris,* Mexican bean beetle, and soybean. Finally, thanks to the financial support of the USDA/CSRS, Purdue University, and Gardens Alive (Lawrenceburg, IN). This is Purdue Agriculture Research Programs Paper No. 14687.

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