

A STOCHASTIC MODEL OF PARASITISM OF THE MEXICAN  
BEAN BEETLE, *EPILACHNA VARIVESTIS* MULSANT  
(COLEOPTERA : COCCINELLIDAE), IN SOYBEANS BY  
*PEDIOBIUS FOVEOLATUS* (CRAWFORD)  
(HYMENOPTERA : EULOPHIDAE)<sup>1</sup>

Jeanne M. ALDRED\*, Merle SHEPARD\*\* and Paul T. HOLMES\*\*\*

\* Applied Physics Laboratory, The Johns Hopkins University  
Laurel, Maryland 20810, U. S. A.

\*\* Department of Entomology & Economic Zoology, Clemson  
University, Clemson, South Carolina 29631, U. S. A.

\*\*\* Department of Mathematical Sciences, Clemson University  
Clemson, South Carolina 29631, U. S. A.

INTRODUCTION

The Mexican bean beetle (MBB), *Epilachna varvestis* MULSANT, has long been an important pest of snap beans and lima beans (*Phaseolus* spp.), and in recent years its importance as a pest of soybeans (*Glycine max* (L.) MERRILL) has increased, especially in the Southeastern U. S. A. and along the eastern coast as far north as Maryland and Delaware. This pest is essentially free of naturally-occurring parasitoids and diseases. All larval stages and adults cause defoliation of host plants. Although several species of arthropod predators feed on the eggs and larvae of MBB (WADDILL and SHEPARD 1974; WADDILL and SHEPARD 1975), predation is often ineffective in preventing economic loss by the pest.

A computer simulation model of populations of MBB in soybeans (MEXSIM) has been developed and has predictive value in terms of identifying peak infestations (WADDILL *et al.* 1976). Certain biological information, such as MBB growth, development, overwintering, etc. in the soybean ecosystem, has been provided (BERNHARDT and SHEPARD 1978a, b) in order to refine the model.

Releases of the imported parasitoid, *Pediobius foveolatus* (CRAWFORD) near the coastal areas of Maryland, have shown promise for suppression of MBB populations (STEVENS *et al.* 1975a), but no quantitative information is available relative to optimum numbers of parasitoids needed for reduction of MBB population density to subeconomic levels. This information is important because *P. foveolatus* does not overwinter in the U. S. A. Thus laboratory colonies of both MBB and *P. foveolatus* must be maintained during winter months and numbers of the parasitoid increased for eventual field releases in the spring. Therefore, it is desirable to optimize the numbers of parasitoids

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to be released in order to help insure successful biological control yet minimize time and expense involved in laboratory rearing of the insect cultures.

The importance of quantitative information about numerical relationships between parasitoids and prey at various density levels in order to achieve practical biological control has been emphasized by KNIPLING (1971). Many of the inconclusive or unsuccessful attempts at controlling pests by parasitoid releases often stem from lack of understanding these numerical relationships. Results from theoretical models of the parasitoid *Trichogramma* released for control of the sugarcane borer, illustrated the importance of changes in the dynamics of parasitoid-prey interaction at different prey densities (KNIPLING, 1971).

This present study was conducted to develop a stochastic model of the interaction between the parasitoid *P. foveolatus* and the MBB, in the soybean ecosystem. The ultimate goal of using the model is to predict the response of populations of MBB when *P. foveolatus* are released into fields at various parasitoid: host ratios.

#### METHODS AND MATERIALS

Basic data inputs were obtained from reports of the biology of *P. foveolatus* (LALL, 1961; SHEPARD and GALE, 1977; GALE and SHEPARD, 1978; STEVENS *et al.*, 1975b) and MBB (BERNHARDT and SHEPARD 1978a, b; WADDILL *et al.*, 1976). The model originally selected was a stochastic bivariate birth and death model for predator-prey interaction proposed by CHIANG (1954). Basically the model depicts the two population densities (predator and prey) as coordinates of an ordered pair which move along lattice points in the first quadrant of the plane, including the axes, as the population densities change through time.

One of the assumptions made during construction of the model was that within a small change in time the maximum change in the two populations was either one birth or one death but not both. In spite of the fact that adult parasitoids emerge in very rapid succession from the parasitized larva, by selecting a sufficiently small change in time, we believe that this assumption will hold. The model also assumes that the growth of the two interacting populations depends on the frequency of encounters between the two species.

Two further assumptions of the model were less intuitively obvious, although there was no known evidence to dispute them. For example, in the model the frequency of encounters between the two species was taken to be a function of the population sizes of both species. This function was assumed by CHIANG (1954) to be proportional to the product of the two population sizes at time  $t$ . This assumption of proportionality to the product has been frequently made in the predator-prey models, notably in the LOTKA-VOLTERRA equations for a deterministic predator-prey model (GOEL *et al.*, 1971). Also, the assumption was made that the birth-death process satisfies the Markov property (BHARUCHA-REID, 1960) which means that given the

present population sizes, the past population sizes were not needed in order to predict future populations sizes.

From these assumptions, a differential-difference equation was derived for the joint probability distribution of the two population sizes (see Appendix A). An analytic solution to this differential-difference equation would provide valuable information about the probability structure of the interaction. Unfortunately, in the search for such an analytic solution to the model, we found that this equation presents intractable problems, and no analytic solution was known. Thus the Monte Carlo simulation approach was decided upon as a way to examine the process and extract some results on the effectiveness of the three parasitoid: host ratios of interest: 1 : 20, 1 : 100, and 1 : 400.

A FORTRAN algorithm was designed to simulate a random walk in the first quadrant where  $Y$  is the number of parasitoids and  $X$  is a measure of the beetle population as explained below. In general the parasitoids prefer fourth instar MBB, so that the two species interact only when the beetle reaches the fourth larval stage. Thus a "beetle" in this simulation model was a fourth instar, a pupa, or an adult, and  $X$ =the number of adult MBB. Using the equations given in assumptions of the model and data obtained from the literature plus unpublished field and laboratory experiments, the algorithm computes the probabilities of each of the possible transitions. Then on the basis of a generated random number, the algorithm determines the direction of the transition, increments or decrements the appropriate population accordingly, and repeats the process for any desired length of time.

During the attempted implementation of this algorithm, a major limitation was found in the direct application of CHIANG's model. The probability of the birth of a beetle in CHIANG's model would be  $\lambda_1 \times \Delta t$  where  $\lambda_1$ =the birth rate of the beetles,  $x$ =the total number of beetles at time  $t$ , and  $\Delta t$ =the increments of time. However, in this situation, the probability of the birth of a beetle should be  $\lambda_1 \Delta t$  multiplied by the number of mature beetles, since the younger ones cannot reproduce. Also, the two probabilities involving the interaction of the two species, the probability of the birth of a parasitoid and the probability of the death of a beetle, are dependent on the number of fourth instars, an unknown quantity using this initial model. Thus it was apparent that a representative model of this situation must keep track of the number of beetles in each stage under consideration.

In order to account for the number of beetles in each of the last four stages of development, CHIANG's basic model was expanded to a random walk in five dimensions. Each dimension represents one of the five populations. Thus letting  $W$ =the number of parasitoids,  $L$ =the number of fourth-stage MBB,  $P$ =the number of MBB pupae,  $PA$ =number of preoviposition adult MBB, and  $MA$ =the number of mature adult MBB, the state of the system at any time can be represented by the point  $(W, L, P, PA, MA)$  in five-space. The equations for the transition probabilities are the straightforward extensions of CHIANG's model.

A FORTRAN algorithm was written to simulate the interaction between MBB and *P. foveolatus* over a period of ten weeks. Because sample beetle counts from a soybean field taken on July 9 were available, the ten weeks of the simulation algorithm began on July 9. In the simulation two releases of parasitoids were made. The first release was made on July 9, and the second release of an equal number was made on July 23. In the simulation algorithm the unit of time was one week. A listing of the simulation algorithm is available from the authors.

The simulation was scaled so as to represent an area of 192 square meters (approximately 225 square yards) of a soybean field. This area was selected in order to allow for the initial release of the parasitoids for the 1 : 400 ratio while keeping the population sizes small enough to avoid excessive use of computer time.

On the basis of the means of nine samples of four feet of row observed in a soybean field on July 9, it was expected that the initial beetle population in the simulated area would be approximately 1205 beetles distributed as follows: 568 fourth instars, 396 pupae, 12 preoviposition adults, and 229 mature adults. This implied that in order to look at three parasitoid : beetle ratios of approximately 1 : 20, 1 : 100, 1 : 400, the initial number of parasitoids should be 60, 12, and 3 respectively.

The algorithm itself begins by reading in the initial state of the system. Given this initial state, the transition probabilities are calculated using data provided from field samples taken near Sumter, South Carolina as discussed below.

A "birth" in one of the four beetle populations means that a beetle has entered a new stage in his life cycle. Likewise, a "death" means that a beetle has left that stage.

- Let  $P_1 = P$  (the birth of fourth stage MBB)  
 $P_2 = P$  (the death of a fourth stage MBB)  
 $P_3 = P$  (the death of a MBB pupa)  
 $= P$  (the birth of a preoviposition MBB adult)  
 $P_4 = P$  (the death of a preoviposition MBB adult)  
 $= P$  (the birth of a mature MBB adult)  
 $P_5 = P$  (the death of a mature MBB adult)  
 $P_6 = P$  (the birth of a parasitoid)  
 $P_7 = P$  (the death of a parasitoid)  
 $P_8 = P$  (no change in the system)

Note that the death of a fourth instar may be due to the formation of a pupa or to the instar's being parasitized. Then:

$$P_1 = \lambda_1 (MA)/s = 21.7 (MA)/s$$

where  $\lambda_1$  = the birth rate of the fourth instars

and  $s = P_1 + P_2 + P_3 + P_4 + P_5 + P_6 + P_7$

$$P_2 = \mu_1 (L)(W)/s = L^2 W / (1.00286 L - 0.50143 \text{ NOPARS})s$$

where  $\mu_1$  = the death rate of the fourth instars

and  $NOPARS = \min(6.65 W, L)$

$P3 = \mu_2 P/s = 1.42276 (P)/s$   
 where  $\mu_2$  = the death rate of the pupae

$P4 = \mu_3 (PA)/s = 0.4375 (PA)/s$   
 where  $\mu_3$  = the death rate of the preoviposition adults

$P5 = \mu_4 (MA)/s = 0.219436 (MA)/s$   
 where  $\mu_4$  = the death rate of the mature adults

$P6 = \lambda_5 (W)(L)/s = 30 (NOPARS)/s$   
 where  $\lambda_5$  = the birth rate of the wasps

$P7 = \mu_5 W/s = 0.5833 (W)/s$   
 where  $\mu_5$  = the death rate of the wasps

For detailed computation of the above equations see Appendix B.

In order to make efficient use of computer time, an event-paced simulation was used in which  $P8=0$  and  $\Delta t = -\log(R)/s$ ; where  $R$  is a random number between zero and one. For the actual simulation runs,  $\Delta t$  was set equal to its expected value,  $1/s$  at each iteration, as test runs using each showed no significant difference in the results.

Some consideration of the biological situation at hand caused an adjustment in the algorithm. As noted earlier, during each season the process of interest must undergo an initialization period. The newly released *P. foveolatus* can immediately lay eggs. However, the subsequent generation of adults will not emerge from the parasitized MBB for about 15 days under field conditions. Therefore, the probability of births resulting from newly released wasps must remain zero for 15 days. Hence, a delay mechanism was coded into the model which prohibits births from the wasps released on July 9 until July 24 and prohibits births from the wasps released on July 23 until August 7.

Once the transition probabilities were calculated, a random number  $R$  between zero and one was generated using the IBM WATFIV version of RANDU. The interval  $[0, 1]$  was partitioned so that if  $R \leq P1$  the event associated with  $P1$  was made to occur, if  $P1 < R \leq P1 + P2$  the event associated with  $P2$  occurred, if  $P1 + P2 < R \leq P1 + P2 + P3$  the event associated with  $P3$  occurred, etc. Whenever a fourth instar dies, a decision must be made as to whether the larva becomes parasitized or pupates. The decision was made by finding the probability that the larva was parasitized, generating another random number, and dividing the  $[0, 1]$  interval into two segments in a similar manner as with the transition probabilities.

In order to provide a random seed to RANDU for each new simulation, the subroutine FTIME, which returns the time of day in seconds, was called at the beginning of the algorithm. This time was manipulated to provide a seed that was between five and seven digits long and that ended in an odd number since these are IBM's specifications for a good seed for RANDU.

Each simulation run outputs the state of the system at the end of each of the ten weeks. In addition, the total number of beetles at the end of each week and the sum of all the mummies produced during each week were output.

In order to analyze the results of the simulation, the means and standard deviations of the numbers of parasitoids, fourth stage MBB, preoviposition MBB adults, and mature adults, as well as total MBB were computed week by week.

Since the underlying distributions of these population sizes are unknown, CHEBYSHEV's Inequality was used to find confidence regions for the behavior of the system. Since CHEBYSHEV's Inequality was general enough to disregard the form of the distribution, it was frequently very conservative. CHEBYSHEV's Inequality states that for any random variable  $X$  with finite variance the following is true:

$$P(|X - \mu| > \kappa\sigma) < 1/\kappa^2$$

In other words, the probability that a variable will differ from its mean more than  $\kappa$  standard deviations is less than  $1/\kappa^2$ . Weekly confidence intervals of at least 75% were tabulated for each of the three parasitoid: MBB ratios.

#### RESULTS AND DISCUSSION

Curves of the mean numbers of the four stages of the beetles, of the total beetles, and of the parasitoids for each initial ratio are given in Figures 1-6.

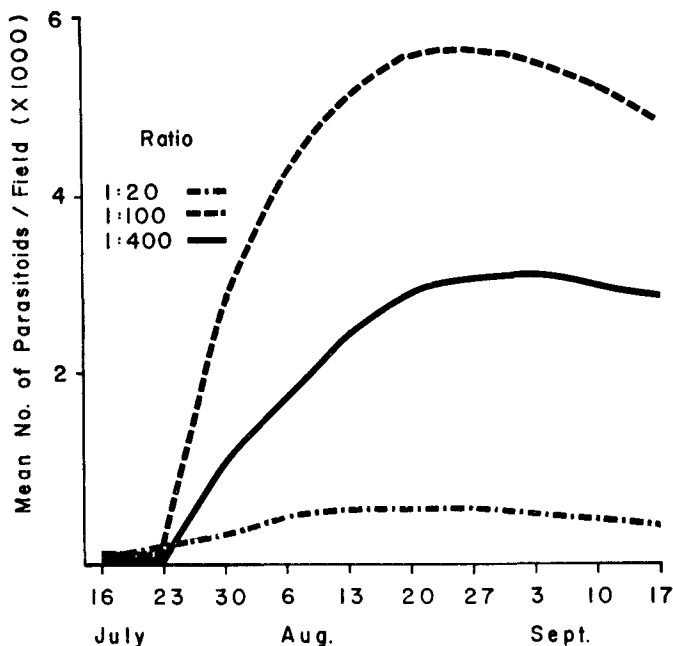


Fig. 1. Simulation of numbers of *P. joveolatus* per field (192m<sup>2</sup>) with parasitoid: host ratios of 1:20, 1:100, and 1: 400.

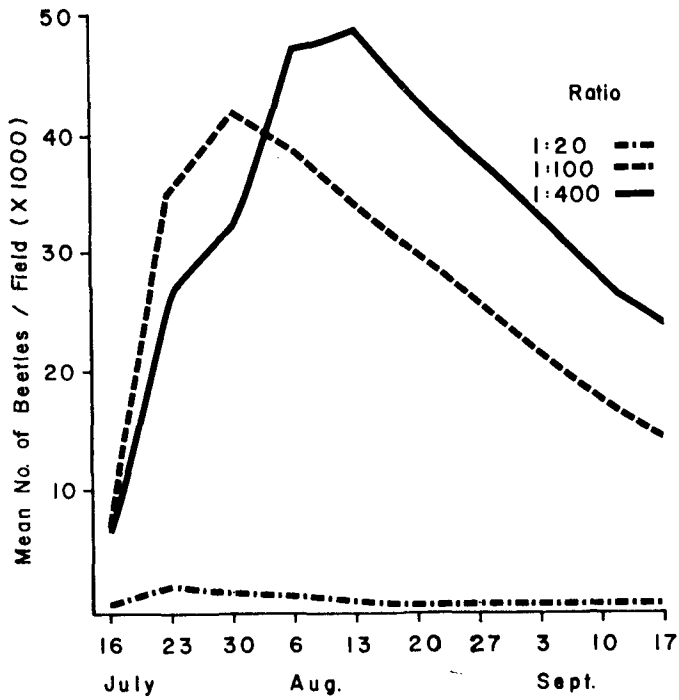


Fig. 2. Simulation of numbers of Mexican bean beetles (immatures and adults) per field (192m<sup>2</sup>) with parasitoid: host ratios of 1:20, 1:100, and 1:400.

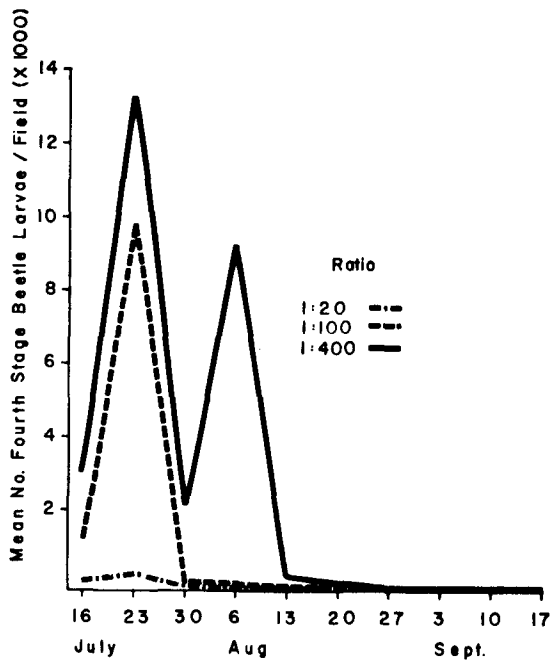


Fig. 3. Simulation of numbers of fourth stage larvae of Mexican bean beetles per field (192m<sup>2</sup>) with parasitoid: host ratios of 1:20, 1:100, and 1:400.

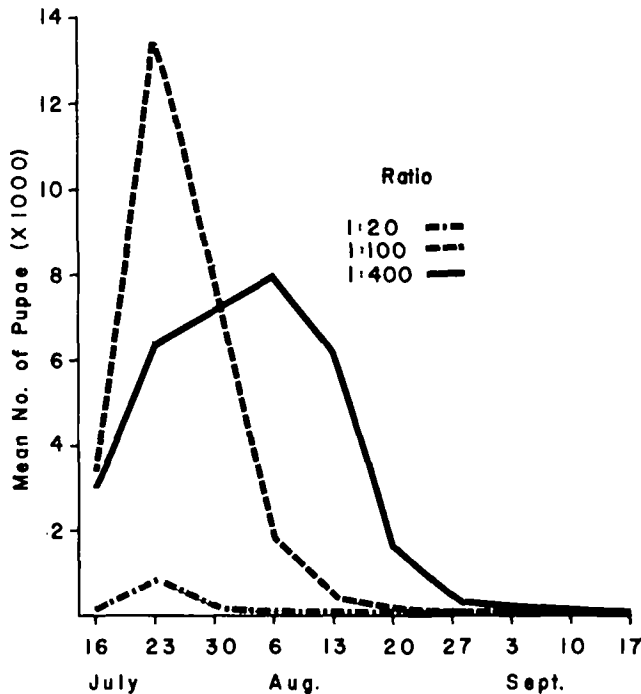


Fig. 4. Simulation of numbers of Mexican bean beetle pupae per field (192m<sup>2</sup>) with parasitoid: host ratios of 1:20, 1:100, and 1:400.

Examination of the graphs of confidence regions of at least 75% for the parasitoids versus the total beetles revealed immediately a large variance in the behavior of the thirty simulation runs for the ratio of 1:400. Consequently more simulation runs should be performed at this ratio in order to obtain better estimates of the means and the standard deviations. Additionally, the ratio of 1:400 resulted in much less suppression of the beetle population than did either of the other two ratios (Figures 1-6).

The simulations of the 1:100 ratio were rather consistent. However, this ratio allowed beetle population size to remain consistently higher than did the ratio of 1:20, in spite of the fact that after the third week the parasitoid population was larger for ratio of 1:100. This observation suggested that a key element in the success of the biological control was not the number of parasitoids present in later weeks but rather the number of wasps present in the very early weeks of the season. This was also reflected in comparison of Figures 1 and 2.

Examination of figures 3-6 reveals that the parasitoid: host ratio of 1:20 consistently results in smaller beetle populations. In these figures the ratios of 1:100 and 1:400 alternate in their effectiveness. These graphs compare only the means and thus did not reflect the erratic behavior of the populations at the ratio of 1:400.



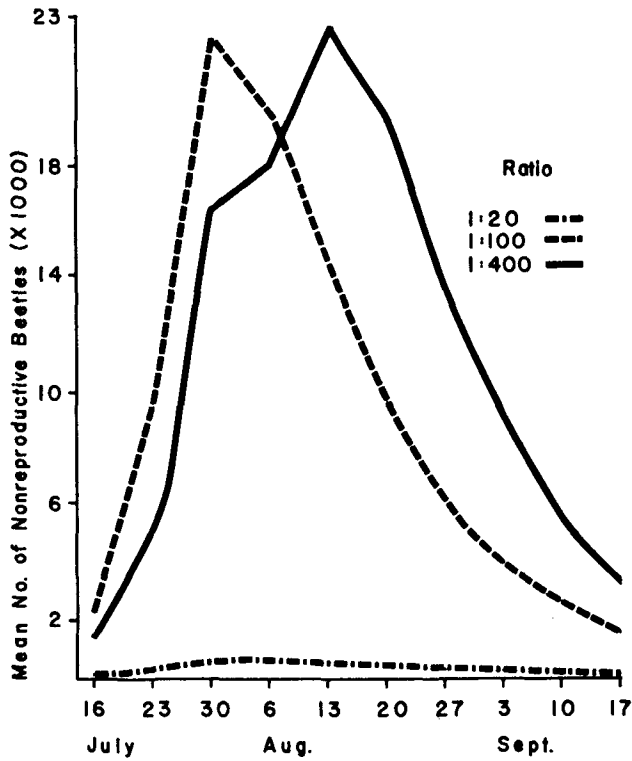


Fig. 5. Simulation of numbers of nonreproductive Mexican bean beetle adults per field (192m<sup>2</sup>) with parasitoid: host ratios of 1:20, 1:100, and 1:400.

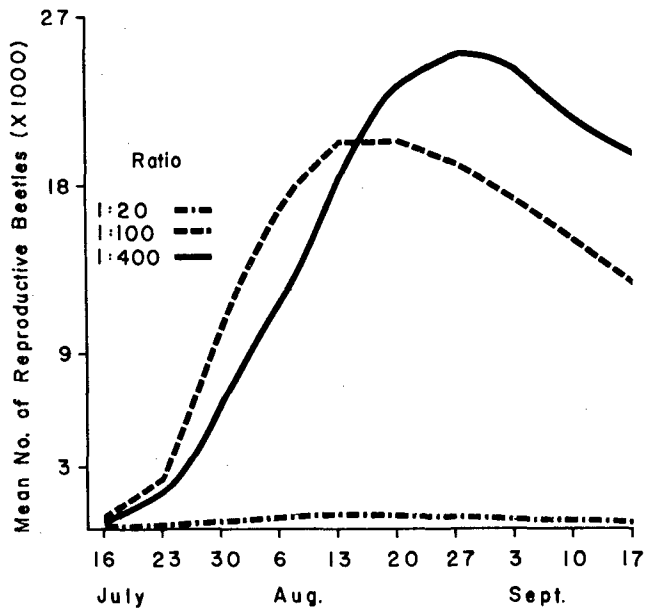


Fig. 6. Simulation of numbers of reproductive Mexican bean beetles per field (192m<sup>2</sup>) with parasitoid: host ratios of 1:20, 1:100, and 1:400.

The behavior of the simulated model was highly dependent on the values of several constants in the transition probability equations. Perturbation analysis of these constants should be performed in order to determine whether small changes in any of these constants cause great variation in the behavior of the simulated process. For example, on the basis of initial miscalculations in the implementation of the model that were later corrected, we suspected that the model was fairly sensitive to the value of the birth rate of the parasitoids. A few of the data values used in forming the constants were educated guesses or estimates based on small sample sizes. Therefore, those constants to which the model is sensitive should be investigated, and, if necessary, better data should be collected to determine their values.

The simulated model focused on the last four stages of the beetle. This was reasonable because the wasp does not significantly interact with MBB in earlier stages and the model assumes no significant changes in the beetle population due to interaction with other organisms.

Finally, throughout the building of the model it was apparent that perhaps the most important factor in the success or failure of the biological control was the size of the initial population of beetles. In other words, the numbers of MBB available during the fifteen day initialization period immediately after the release of the parasitoids. As built, the model assumes that this birth rate was the same as for MBB reproducing during the middle of the season. However, it has been shown (BERNHARDT and SHEPARD, 1978b) that the birth rate for MBB emerging from overwintering was actually lower than that of succeeding generations. Hence at present, the model probably models an extreme case. This fact implies that this model may tend to overestimate the MBB population density. However, results from these simulations reveal important numerical relationships relative to release programs with *P. foveolatus*. Actual field data from 2 years' research have provided results which agree, in general, with the model's predictions (SHEPARD and ROBINSON, 1976; SHEPARD, unpublished data).

#### SUMMARY

A stochastic model of parasitism of the Mexican bean beetle, *Epilachna varivestis* MULSANT, in soybeans by the imported parasitoid *Pediobius foveolatus* (CRAWFORD) was developed. The model was a modification of CHIANG'S (1954) predator-prey interaction model which depicts two population densities (parasitoid and host) as coordinates of an ordered pair which moves along lattice points in the first quadrant of a plane, including the axes, as the population densities change through time. At least 30 runs were made to simulate parasitoid : host ratios 1 : 20, 1 : 100, and 1 : 400 for a period of 10 weeks. Under conditions of these simulations, the parasitoid : host ratio of 1 : 400 was not satisfactory to reduce Mexican bean beetle populations in soybeans. Simulations using parasitoid : host ratio of 1 : 20 and 1 : 100 reduced beetle

populations to acceptable levels. Results from these simulations were similar to results obtained from two season's data from releases of *P. foveolatus* to control the Mexican bean beetle in soybean fields.

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APPENDIX A  
CHIANG'S predator-prey model

Part 1: The formal assumptions of the model

Let  $X(t)$ ,  $Y(t)$  be random variables representing the population sizes of the Mexican bean beetle and of the parasitoid, respectively, at time  $t$ . The following assumptions are made:

- a) The probability of a unit increase in the population size of MBB in the interval  $(t, t + \Delta t)$ , given that there are exactly  $x$  MBB at time  $t$  is  $\lambda_1 x \Delta t + o(\Delta t)$ , where  $\lambda_1$  is the birth rate of the MBB.
- b) The probability of a unit decrease in the population size of MBB in the interval  $(t, t + \Delta t)$ , given that there are exactly  $x$  MBB at time  $t$  is  $\mu_1 x y \Delta t + o(\Delta t)$ , where  $\mu_1$  is the death rate of the MBB.
- c) The probability of a unit increase in the population size of the parasitoid in the interval  $(t, t + \Delta t)$ , given that there are exactly  $y$  parasitoids at time  $t$  is  $\lambda_2 x y \Delta t + o(\Delta t)$ , where  $\lambda_2$  is the birth rate of the parasitoids.
- d) The probability of a unit decrease in the population size of the parasitoids in the interval  $(t, t + \Delta t)$ , given that there are exactly  $y$  parasitoids at time  $t$  is  $\mu_2 y \Delta t + o(\Delta t)$ , where  $\mu_2$  is the death rate of the parasitoids.
- e) The probability of a change in either population size of absolute value greater than one in the interval  $(t, t + \Delta t)$  is  $o(\Delta t)$ .
- f) The probability of no change in either population size in the interval  $(t, t + \Delta t)$ , given that there are  $x$  MBB and  $y$  parasitoids at time  $t$ , is  $1 - [\lambda_1 x + \mu_1 x y + \lambda_2 x y + \mu_2 y] \Delta t + o(\Delta t)$ .

Part 2. A differential-difference equation for the joint probability distribution

Let  $P_{X,Y}(t) = P(X=x, Y=y \text{ at time } t)$ .

Then the assumptions of the model imply that

$$\begin{aligned} P_{X,Y}(t) = & P_{X,Y}(t) \{ [1 - (\lambda_1 x + \mu_1 x y + \lambda_2 x y + \mu_2 y)] \Delta t + o(\Delta t) \} + P_{X+1,Y}(t) [\mu_1 (x+1) y \Delta t \\ & + o(\Delta t)] + P_{X-1,Y}(t) [\lambda_1 (x-1) \Delta t + o(\Delta t)] + P_{X,Y-1}(t) [\lambda_2 x (y-1) \Delta t + o(\Delta t)] \\ & + P_{X,Y+1}(t) [\mu_2 (y+1) \Delta t + o(\Delta t)] + o(\Delta t). \end{aligned}$$

Thus

$$\begin{aligned} \frac{P_{X,Y}(t) - P_{X,Y}(t) \Delta t}{\Delta t} = & -(\lambda_1 x + \mu_1 x y + \lambda_2 x y + \mu_2 y) P_{X,Y}(t) + \mu_1 (x+1) y P_{X+1,Y}(t) \\ & + \lambda_1 (x-1) P_{X-1,Y}(t) + \lambda_2 x (y-1) P_{X,Y-1}(t) + \mu_2 (y+1) P_{X,Y+1}(t) \\ & + \frac{o(\Delta t)}{\Delta t}. \end{aligned}$$

Then letting  $\Delta t \rightarrow 0$  implies that

$$\begin{aligned} \frac{d}{dt} P_{X,Y}(t) = & -(\lambda_1 x + \mu_1 x y + \lambda_2 x y + \mu_2 y) P_{X,Y}(t) + \mu_1 (x+1) y P_{X+1,Y}(t) \\ & + \lambda_1 (x-1) P_{X-1,Y}(t) + \lambda_2 x (y-1) P_{X,Y-1}(t) + \mu_2 (y+1) P_{X,Y+1}(t), \\ & x, y = 0, 1, 2, \dots \end{aligned}$$

$P_{X,Y}(t) = 0$  if  $x < 0$ ,  $y < 0$  or both.

## APPENDIX B

## Calculation of transition probabilities for the adapted model

- Let  $W$  =the number of parasitoids at time  $t$   
 $L$  =the number of fourth stage MBB at time  $t$   
 $P$  =the number of MBB pupae at time  $t$   
 $PA$  =the number of preoviposition MBB adults at time  $t$   
 $MA$  =the number of mature MBB adults at time  $t$   
 $P(\cdot)$  =the probability of the event  $\cdot$  happening.

Then the straightforward extensions of the transition probability equations of CHIANG's model are as follows:

(A "birth" in one of the four MBB populations means that a MBB has entered a new stage in its life cycle. Likewise, a "death" means that a MBB has left that stage.)

- 1)  $P1 = P(\text{birth of a fourth stage MBB}) = \lambda_1(MA)/s$ , where  $\lambda_1$  = the birth rate of the fourth stage MBB and  $s = P1 + P2 + P3 + P4 + P5 + P6 + P7$ . The model assumes that the rate at which third instars become fourth instars is the same as the rate at which the MBB eggs hatch. An "egg" will, therefore, mean an egg that will hatch.

$$\begin{aligned}\lambda_1 &= (6.2 \text{ eggs/mature female/day}) (7 \text{ days/week}) (1 \text{ mature female/2 mature MBB}) \\ &= 21.7 \text{ eggs/week/mature MBB.}\end{aligned}$$

Thus  $P1 = 21.7(MA)/s$ .

- 2)  $P2 = P(\text{death of a fourth instar}) = \mu_1(L)(W)/s$   
 where  $\mu_1$  = the death rate of the fourth instar.  
 $\mu_1 = 1/\text{average life of a fourth instar}$ .

This average life must be weighted since the death of a fourth instar may mean its parasitization or its becoming a pupa. Now the weighted average life ( $WAL$ ) of a fourth instar is  $[NOPARS (\text{average life of a parasitized instar}) + (L - NOPARS)$

$$(\text{average life of an instar never parasitized})/L,$$

where  $NOPARS$  is the number parasitized per week and  $L$  is the total number of instars. Thus

$$\begin{aligned}WAL &= [3.51 \text{ } NOPARS + 7.02(L - NOPARS)]/L \\ &= (7.02L - 3.51 \text{ } NOPARS)/L.\end{aligned}$$

(Since a fourth instar lives an average of 7.02 days, it is assumed that if it is parasitized, it will live an average of  $7.02/2 = 3.51$  days.)

And  $\mu_1 = 1/WAL = L/(7.02L - 3.51 \text{ } NOPARS)$ .

Now scaling  $\mu_1$  on the basis of a week

$$\mu_1 = L/(1.00286L - 0.50143 \text{ } NOPARS).$$

Now consider  $NOPARS$ . The maximum number that can be parasitized per week is 6.65  $W$  since on the average a parasitoid can parasitize 11.4 larvae in its 12-day life [(11.4/12 days) (7 days/week) = 6.65/week]. However if there are not 6.65  $W$  larvae present, only  $L$  can be parasitized. Hence,

$$NOPARS = \min\{6.65 \text{ } W, L\}.$$

Thus  $P2 = L^2W/(1.00286L - 0.50143 \text{ } NOPARS)s$ .

- 3)  $P3 = P(\text{death of a pupa})$   
 $= P(\text{birth of a preoviposition adult}) = \mu_2(P)/s$   
 where  $\mu_2$  = the death rate of the pupae.

$\mu_2=1/\text{average life of a pupa}$

$= (1/4.92 \text{ days}) (7 \text{ days/week}) = 1.42276/\text{week.}$

Thus  $P3=1.42276(P)/s.$

- 4)  $P4=P(\text{death of a preoviposition adult})$

$=P(\text{birth of a mature adult}) = \mu_3(PA)/s,$

where  $\mu_3$ =the death rate of preoviposition adults.

$\mu_3=1/\text{average life of a preoviposition adult}$

$= (1/16 \text{ days}) (7 \text{ days/week}) = 0.4375/\text{week.}$

Thus  $P4=0.4375(PA)/s.$

- 5)  $P5=P(\text{death of mature adult}) = \mu_4(MA)/s,$

where  $\mu_4$ =the death rate of mature adults.

$\mu_4=1/\text{average life of a mature adult}$

$= (1/31.9 \text{ days}) (7 \text{ days/week}) = 0.219436/\text{week,}$

Thus  $P5=0.219436(MA)/s.$

- 6)  $P6=P(\text{birth of a parasitoid}) = \lambda_5(W)(L)/s,$

where  $\lambda_5$ =the birth rate of the wasps.

$\lambda_5=30 \text{ PROPOR}$ , where *PROPOR* is the porportion of encounters that result in parasitization, since parasitization results in an average of 30 births.

Now  $\text{PROPOR}=\text{NOPARS}/(L)(W).$

Thus  $P6=30 \text{ NOPARS}(W)(L)/(W)(L)s=30 \text{ NOPARS}/s.$

- 7)  $P7=P(\text{death of a parasitoid}) = \mu_5(W)/s,$

where  $\mu_5$ =the death rate of the parasitoid.

$\mu_5=1/\text{average life of a parasitoid}$

$= (1/12 \text{ days}) (7 \text{ days/week}) = 0.5833. / \text{week.}$

Thus  $P7=0.5833(W)/s.$

### 大豆畑におけるメキシコテントウムシダマシ *Epilachna varivestis* の *Pediobius foveolatus* による寄生の確率論的モデル

J. M. ALDRED · M. SHERARD · P. T. HOLMES

大豆畑におけるメキシコテントウムシダマシ *Epilachna varivestis* MULSANT の輸入捕食寄生者 *Pediobius foveolatus* (CRAWFORD) による寄生の確率論的モデルをつくった。このモデルは CHAING (1954) による捕食者-被食者相互作用モデルを改変したもので、寄生者と寄主の2つの個体群の密度を、その時間変化につれて、両軸を含む第1象限内の格子点上を動く順序対の座標として表わすものである。寄生者：寄主比を1：20, 1：100, 1：400として、10週間分のシミュレーションを少なくとも30回繰返した。これらのシミュレーションでは、寄生者：寄主比1：400は、大豆畑のメキシコテントウムシダマシ個体群を減少させるには不十分であった。寄生者：寄主比が1：20および1：100の場合には、テントウムシダマシ個体群を十分に低い水準にまで下げることができた。これらのシミュレーションの結果は、大豆畑のメキシコテントウムシダマシを制御する目的で、2年にわたって行われた *P. foveolatus* の放飼実験の結果と類似していた。