

CONSERVATION AND AUGMENTATION OF MICROPLITIS CROCEIPES ^{1/}
FOR CONTROLLING HELIOTHIS SPP. ^{2/}

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ABSTRACT

Various approaches are available for conservation and augmentation of Microplitis croceipes (Cresson) to control of Heliothis zea (Boddie) and Heliothis virescens (F.). Simulations of augmentation with several models of host-parasitoid population dynamics showed that such models could reveal important parameters to measure and could help in design of augmentation programs. In a model with no dispersal between subpopulations, simulated 10-fold augmentation of M. croceipes density in spring suppressed H. virescens density throughout the season. Adding density-independent dispersal between subpopulations to this model decreased the impact of augmentation. Incorporating parasitoid aggregation in response to host density caused the behavior of the model with dispersal to return to that with no dispersal. Adding density-dependent mortality from causes other than parasitization had little effect on simulated trajectories when such mortality occurred before parasitization, but adding density-dependent mortality after parasitization reduced parasitoid impact. Although I was unable to draw on many data for several processes and parameters, the simulations suggest that augmentation of M. croceipes for control of Heliothis spp. would be technically feasible.

INTRODUCTION

To practice rational conservation or augmentation we need explicit predictions of natural enemy impact. For example, to decide when, where, and in what numbers to release parasitoids in an inoculative release program, one needs to predict what effect date/time, place, and density of release have on reduction in host density in the generation of release and in subsequent generations. To get such predictions one can use either regression models or mechanistic models. To develop a regression model, one would release wasps under various conditions and then regress parasitism on numbers released, host density, time of season,

^{1/} Hymenoptera: Braconidae

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temperature and other biotic and abiotic factors. This approach can be very expensive because of the many variables involved and because of the large areas needed for experiments with highly mobile hosts and parasitoids. Furthermore, one cannot safely extrapolate regression equations to conditions beyond those of the experimental releases.

Mechanistic models, which are based on understanding of the causal interactions between dependent and independent variables, provide an alternative to regression models. Here one has to measure the parameters of the component processes affecting damage and population dynamics, e.g. feeding, search, development, dispersal, natality, and mortality. Although these measurements are expensive, they are often less expensive than the large scale experiments needed for regression models. Furthermore, if mechanistic models are designed well, they can apply to a wide range of conditions.

In this paper, I review the forms conservation and augmentation could take with Microplitis croceipes (Cresson) (Hymenoptera: Braconidae) against Heliothis zea (Boddie) and Heliothis virescens (F.) (Lepidoptera: Noctuidae). I then describe simulations with several mechanistic models of host-parasitoid population dynamics and draw inferences about important parameters to measure and about the prospects for augmentation. H. zea and H. virescens are major insect pests in the United States (Schwartz 1984, Head 1984), and Heliothis spp. are major pests worldwide (Newsom 1972, Anonymous 1981). M. croceipes is often the most abundant parasitoid of the larvae of these moths in field surveys (Lewis and Brazzel 1968, Mueller and Phillips 1983, Stadelbacher et al. 1984, King et al. 1985), and as this paper will show, it is a promising candidate for control of these pests.

CONSERVATION

Several forms of conservation are possible for M. croceipes: (1) using cultural practices, especially weed control, with minimum impact on M. croceipes, (2) applying insecticides least toxic to M. croceipes, (3) applying insecticides only when sampled Heliothis spp. density exceeds the economic threshold, and (4) using M. croceipes density and potential impact of it and other natural enemies in deciding whether to apply an insecticide. Concerning cultural practices, Stadelbacher (1981) has recommended destruction of non-crop hosts plants in the spring to reduce Heliothis spp. numbers in crops later in the season. However, this practice could also reduce the density of M. croceipes and other natural enemies. Whether the impact on Heliothis spp. of noncrop host plant destruction is worth the loss of natural enemies depends on the relative impact on Heliothis spp. and natural enemy populations in subsequent generations and on the importance of Heliothis spp. mortality from natural enemies.

As with some other predators and parasitoids, M. croceipes is relatively tolerant of pyrethroids and carbamates and intolerant of organophosphates (Powell and Scott 1986), which suggests use of pyrethroids and carbamates rather than organophosphates to conserve this and other

natural enemies. However, using pyrethroids could mean a conflict with resistance management: some researchers are now recommending use of organophosphates in early season and reduced use of pyrethroids to prevent development of pyrethroid resistance in Heliothis spp.

Some growers and consultants already sample pest densities and use economic thresholds. Furthermore, Hartstack et al. (1976), Brown et al. (1983), and Hopper and Stark (1987) developed models for use in Heliothis spp. management that include the impact of natural enemies. However, a great problem with any explicit use of M. croceipes in decisions about Heliothis spp. management lies with the difficulty of sampling parasitoid density. Rearing host larvae until parasitoids emerge takes too long for short-term decisions; dissection is too labor intensive and requires too much expertise; and adults are difficult to sample with conventional techniques (e.g. whole plant examinations, suction collectors). Beyond using relatively non-toxic insecticides and economic thresholds, improved conservation of M. croceipes for control of Heliothis spp. at this point does not look promising.

AUGMENTATION

Three forms of augmentation are likely for M. croceipes: inundative releases, inoculative releases, and nursery crops.

Inundative releases. No parasitoid reproduction is assumed for inundative releases. Thus they are like applications of selective insecticides and are associated more with reducing damage by the host population present at release than with suppressing host density in subsequent generations. M. croceipes reduces damage to cotton by reducing the feeding rate of parasitized Heliothis spp. larvae, although parasitization does not reduce the time that host larvae spend on the host plant (Hopper and King 1984b). It is unknown whether parasitized larvae suffer higher or lower mortality than unparasitized larvae in the field, but Chrysoperla carnea (Stephens) does not prefer either type of larva in field cage experiments on cotton (Stark and Hopper 1988).

Intrageration models can be used to predict the impact of inundative releases. Applying data from field cage experiments on host instar preferences, Hopper and King (1984a) described a simple model of the relation between the density of female parasitoids, host instar, and the proportion of hosts parasitized. They used a modified version of the search model proposed by Nicholson and Bailey (1935):

$$N_j/H_j = 1 - \exp \left(-P \sum_{i=1}^j a_i T_i \right) \quad (1),$$

where N_j is the density of parasitized hosts, H_j is the density of unparasitized hosts, P is the density of female parasitoids, a_i is the search rate (area/time) per female parasitoid for host larvae in instar i , and T_i is development time for host instar i . An important assumption of this

model is that the proportion of hosts parasitized per female parasitoid is independent of host density, and Hopper and King (1986) demonstrated this independence in field cage experiments (Fig. 1). This model predicts well the proportion of hosts parasitized vs. host instar, given an estimate of female parasitoid density (Fig. 2, Hopper and King 1984a).

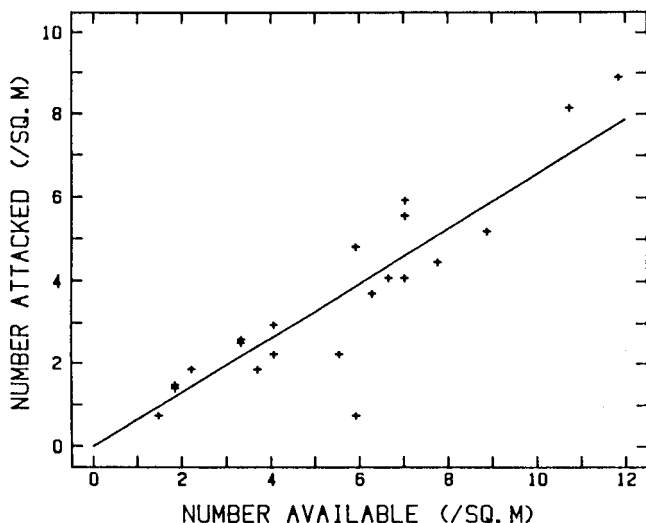


FIG. 1. Density of *H. zea* and *H. virescens* larvae parasitized by *M. croceipes* versus density of larvae available. Each point represents at least one caged population. Line is least-squares regression (from Hopper and King 1986).

With this model, one can predict the impact of various densities of *M. croceipes* on the proportion of *Heliothis* spp. larvae parasitized at each instar (Fig. 3, Hopper and King 1984a). This prediction can be combined with data on the effect of parasitization on feeding to predict the damage to a crop:

$$D = \sum_{i=1}^6 D_{pi}N_i + \sum_{i=1}^6 D_{ui}(H_i - N_i) \quad (2),$$

where D is total damage rate (number or biomass of fruit damaged per unit time), D_{pi} is the damage by parasitized hosts in instar i , N_i is the density of parasitized hosts, D_{ui} is the damage by unparasitized host in instar i , and H_i is the density of hosts in instar i . Hopper and Stark (1987) used these components in a decision model for *Heliothis* spp. management in cotton.

A problem with this formulation of *M. croceipes* impact on *Heliothis* spp. is that the parasitoid and host are assumed to be randomly distributed in the field. In field

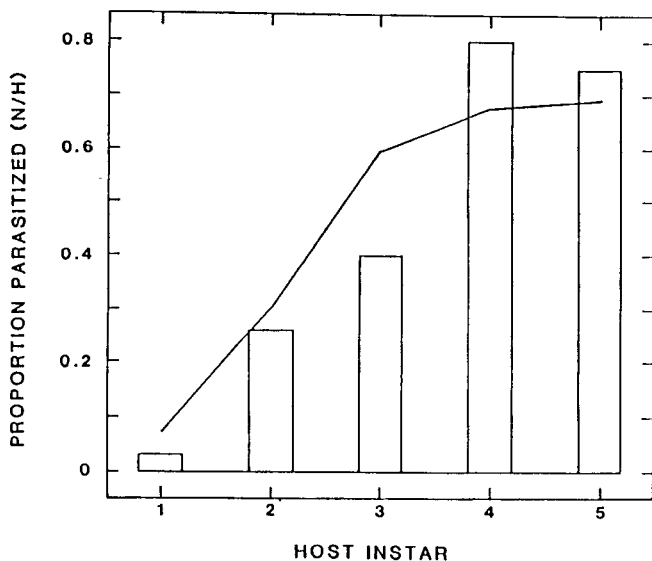


FIG. 2. *M. croceipes* parasitization versus *Heliothis* spp. instar (line) predicted using equation 1 compared with field data (bars) reported by Mueller and Phillips (1983) (from Hopper and King 1984a).

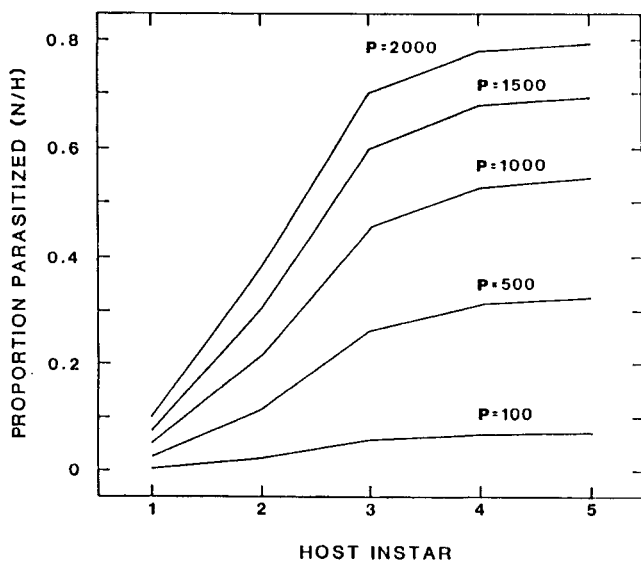


FIG. 3. Predicted parasitization by *M. croceipes* versus *Heliothis* spp. instar for various densities of female wasps (number/ha) (from Hopper and King 1984a).

experiments with free-ranging wasps female, M. croceipes aggregated in areas of high host density, although the search rate per female parasitoid was independent of host density (unpublished data). The next step in developing a model for inundative, intrageneration control of Heliothis spp. by M. croceipes would be to incorporate spatial distribution of host and parasitoid. Below, I describe one approach to incorporating spatial distribution in a model for inoculative, intergeneration control of Heliothis spp. by M. croceipes.

Inoculative releases and Nursery Crops. A frequent problem with biological control of insect pests is that pest populations often increase to high densities before natural enemy densities reach sufficient levels for control. Inoculative releases, which unlike inundative releases do assume parasitoid reproduction in the field, are intended to solve this problem by starting parasitoid populations when and where needed in sufficient numbers to keep up with host populations. Such releases are associated more often with suppressing the host population in subsequent generations than with reducing damage by the host population in the field at the time of release. This tactic is closely related to the use of nursery host plants to provide reservoirs of parasitoids: nursery plants provide an insectary in the field from which parasitoids can disperse to attack host larvae.

Intergeneration models are needed to predict the impact of both inoculative releases and nursery crops. Here, I describe simulations of augmentation with several models of intergeneration dynamics of H. virescens and M. croceipes (The models also apply to H. zea.) I discuss (1) a model without dispersal between subpopulations, (2) models with various levels of density-independent dispersal between subpopulations, (3) a model with dispersal between subpopulations in which parasitoid dispersal depends on host density, and (4) a model with dispersal between subpopulations, density-dependent parasitoid dispersal, and density-dependent host mortality from other causes. The period simulated was one season, which is five Heliothis spp. generations in Mississippi.

The goals were to explore the possible results of inoculative releases and to find where further research would most improve such releases. I report simulated trajectories of host density and proportion of host larvae parasitized because these are frequently measured and most readily compared with experience.

Model with No Dispersal between Subpopulations. The equations for dynamics of host and parasitoid were:

$$H_{t+1/2} = H_t e^{-aP_t} \quad (3),$$

$$P_{t+1/2} = sH_t(1 - e^{-aP_t}) \quad (4),$$

$$H_{t+1} = rH_{t+1/2} e^{-aP_{t+1/2}} \quad (5),$$

$$P_{t+1} = sH_{t+1/2}(1 - e^{-aP_{t+1/2}}) \quad (6),$$

where H_t is the density of host larvae at the beginning of host generation t , $H_{t+1/2}$ is the density of host larvae at the midpoint of host generation t , P_t is the density of adult female parasitoids at the beginning of host generation t , $P_{t+1/2}$ is the density of adult female parasitoids at the midpoint of host generation t , a is the area searched per female parasitoid during her lifetime, s is the proportion of parasitized larvae that produce adult female parasitoids (thus it combines survival and sex ratio), and r is the host rate of increase per generation in the absence of parasitism by M. croceipes. The term $\exp(-aP_t)$ is the proportion of hosts escaping parasitism, and the term $1-\exp(-aP_t)$ is the proportion of hosts parasitized at least once (Nicholson and Bailey 1935, Royama 1971). In the results of simulations reported here, the host densities are H_t and $H_{t+1/2}$ from equations 3 and 5 and the proportions of hosts parasitized are $1-\exp(-aP_t)$ and $1-\exp(-aP_{t+1/2})$ from equations 4 and 6.

M. croceipes develops twice as fast as Heliothis spp. (Nadgauda and Pitre 1983, Jones and Lewis 1971, Hopper and King 1984a), and asynchrony of Heliothis spp. development within a generation means that M. croceipes adults emerging from a generation of host larvae can attack that generation. Therefore, I assumed two parasitoid generations per host generation. I used host generation as the time unit.

The search rate per female M. croceipes measured in field cage experiments is about $1 \text{ m}^2/\text{day}$ (Hopper and King 1986), and the mean longevity of adult female M. croceipes in the laboratory is 28 days (Hopper 1986). Assuming females live about $1/3$ to $1/2$ as long in the field as in the laboratory, I used a search area (a) of 10 m^2 ($=[1 \text{ m}^2/\text{day}][10 \text{ days}]$). M. croceipes females prefer to parasitize third instar larvae (Hopper and King 1984a), and Hogg and Nordheim (1983) found that about 60% of Heliothis spp. larvae which reached the end of the third instar survived to sixth instar in the field (i.e. essentially to pupation). I assumed that M. croceipes larvae in H. virescens larvae survive at this rate. Pupal survival for M. croceipes in laboratory experiments varies between 0.55 and 0.95 depending on the host instar parasitized (Hopper 1986). The sex ratio has been 1:1 in the colonies at Stoneville and in field collections of parasitized larvae. Putting these parameters together, I used $s=0.2$ ($=[0.6][0.75][0.5]$).

The rate of increase of the H. virescens population in the absence of M. croceipes (r) is the most difficult to estimate of these parameters. It depends on natality and mortality of Heliothis spp. in the field, which are likely to be highly variable and for which there are few estimates. Heliothis spp. natality varies with species, age, diet, and temperature (Lukefahr and Martin 1964, Proshold et al. 1982, Nadgauda and Pitre 1983, Tollefson and Watson 1981). However, 100 eggs/day appears an adequate approximation for the models presented here. Snow et al. (1969) report mortality of adult moths that indicates a survival rate of 0.5/day, assuming constant mortality. Laster et al. (1987) report adult male survival rates in the field of \bar{x} 0.83-0.87/day. With these values, each female moth would lay an average of 200-769 eggs over her lifetime. If mortality during the period from oviposition to adult

eclosion were 95-99% and the sex ratio were 1:1, the rate of increase would be 5-fold per generation. These values for juvenile mortality are reasonable given egg and larval mortality observed in the field (Hogg and Nordheim 1983). Therefore, I used $r=5$ in the simulations below.

Heliothis spp. larval densities range from 0 to 40/m² on spring host plants in the delta region of Mississippi (Stadelbacher 1981 and Stadelbacher et al. 1984). However, most often densities lie between 0.1 and 10/m² so I used an initial host density of 5 larvae/m². Laster et al. (1987) found that 5.7 to 243 overwintering H. virescens emerged per ha of land area. If 160 host larvae/ha survived the winter, sex ratio for M. croceipes were 1:1, and about half the overwintering host larvae were parasitized, adult female parasitoid density would be 100/ha in spring, which is what I used for the initial parasitoid density.

In the delta region of Mississippi, host plant area increases greatly from the first Heliothis spp. generation, which is on spring noncrop plants, to the second Heliothis spp. generation, which is on summer crop plants, thus the number of insects per unit area of suitable habitat decreases dramatically (Stadelbacher et al. 1984). I assumed host plant habitat increased 20-fold between the first and second Heliothis spp. generations.

Simulations with Model without Dispersal between Subpopulations. Given these parameter estimates, initial conditions, and equations 3-6, simulation of 5 H. virescens generations yielded the solid-line trajectories for host density and proportion of hosts parasitized in Fig. 4. The trajectory of host density mimics reasonably well the dynamics of H. virescens in the field. The precipitous decline from first to second generation resulted from the increase in host plant habitat, not from parasitism. The fourth generation density of 4 larvae/m² (40,000/ha) falls in the range found in the field, although it considerably exceeds 5000/ha, a frequently used economic threshold for Heliothis spp. in cotton. The decline from fourth to fifth generation resulted from the high level of parasitism (Fig. 4b). Such declines are sometimes observed, but they probably rarely result from parasitism alone.

Augmenting parasitoid densities to 1000 females/ha ($P(0) = 0.1$) gave the dotted-line trajectories in Fig. 4. In this simulation, first generation female M. croceipes parasitized such a high proportion of first generation hosts that the H. virescens population did not exceed the economic threshold in cotton (0.5/m²) by the end of the season. The parasitoid population also failed to recover, as shown by the low levels of parasitism after the first generation. Although this result is encouraging for the prospects of augmentation, this model tends to let the parasitoids drive the host to very low levels through high levels of parasitism. This may be because the model is overly simple; in particular, it lacks dispersal and density-dependent processes, such as parasitoid aggregation and density-dependent mortality from other causes. Below I will add each of these phenomena to test the effects on simulated augmentation.

Models with Dispersal between Subpopulations. I assumed that the populations of host and parasitoid occurred

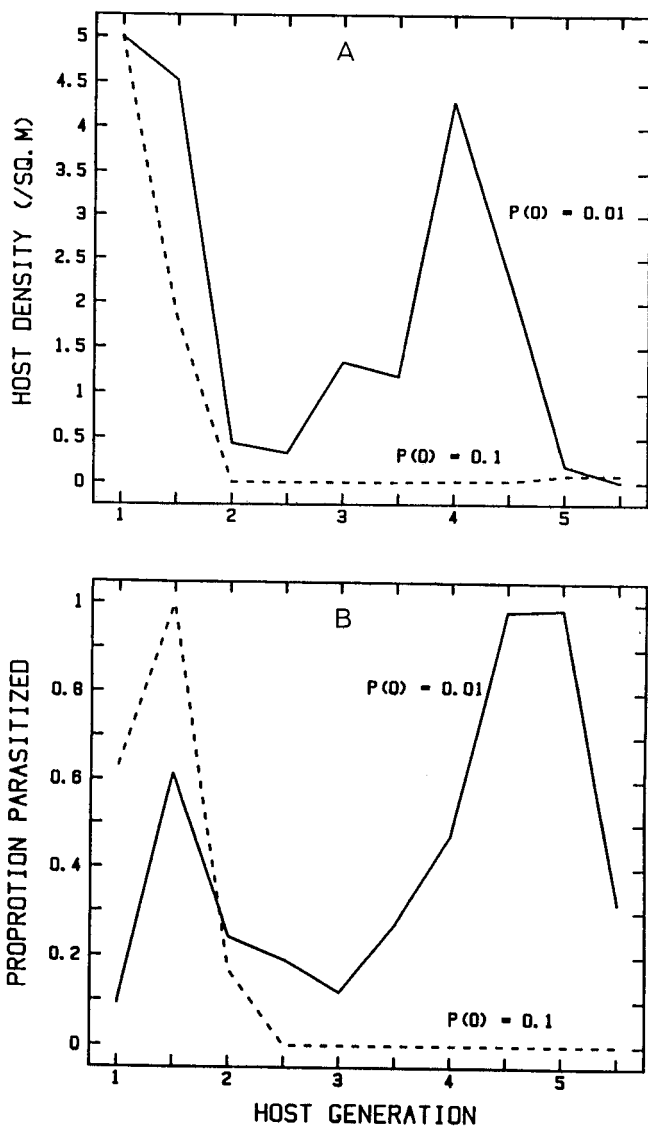


FIG. 4. Simulated host density (A) and proportion of hosts parasitized (B) versus host generation assuming no dispersal or density dependence. $P(0)=0.01$ and $P(0)=0.1$ indicate initial parasitoid densities of $0.01/m^2$ and $0.1/m^2$.

in a 40x40 km area, divided into subpopulations in cells 1 km on a side, and that interactions between host and parasitoid occurred within each subpopulation according to equations 3-6. This system size and spatial subdivision are reasonable given dispersal distances of Heliothis spp. (Snow et al. 1969, Hendricks et al. 1973, Haile et al. 1975, Sparks et al. 1975, Sparks 1979, Hartstack and Witz 1981) and M. croceipes (unpublished data).

Dispersal between subpopulations can be modeled in many ways. For simplicity, I assumed that moths disperse between subpopulations once per generation and oviposit after dispersing and that wasps disperse twice per host generation and parasitize after dispersing. Two extremes of dispersal are possible under these assumptions: stepping-stone dispersal where dispersers can only move to adjacent cells, and island dispersal where dispersers can move to any cell in the system with equal probability, no matter how far from their starting cell. Below, I report simulations of four models of dispersal involving various combinations of stepping-stone and island dispersal, but first I describe how these forms of dispersal were represented.

For stepping-stone, density-independent dispersal of host and parasitoids, I used these equations for movement:

$$H(x,y) = [H(x-1,y)+H(x+1,y)+H(x,y-1)+H(x,y+1)]/4 \quad (7),$$

$$P(x,y) = [P(x-1,y)+P(x+1,y)+P(x,y-1)+P(x,y+1)]/4 \quad (8),$$

where $H(x,y)$ and $P(x,y)$ are the density of host larvae and adult female parasitoids, respectively, in subpopulation x,y after dispersal. Host and parasitoids dispersing beyond the borders of the system were considered lost.

For density-independent, island dispersal of hosts and parasitoids, I used these equations for movement:

$$H(x,y) = R(x,y) \sum_{i=1}^k \sum_{j=1}^l H(i,j)/n \quad (9),$$

$$P(x,y) = R(x,y) \sum_{i=1}^k \sum_{j=1}^l P(i,j)/n \quad (10),$$

where $R(x,y)$ is a random number between 0 and 2 chosen independently for each subpopulation (with the condition that the number of dispersers is limited to the number available to disperse); k (=40) and l (=40) are the dimensions of the system; and n is the number of subpopulations in the system (=1600).

Simulations with Models with Dispersal between Subpopulations. I used the same parameters and the same mean initial densities of host and parasitoid as in the model without dispersal between subpopulations. I distributed the host and parasitoids across subpopulations at the start of each simulation using random values drawn from a uniform distribution between 0 and twice the mean density. Since island dispersal made the model stochastic, I repeatedly ran each model with island dispersal to test for differences between runs. The host density for the whole system (i.e.

averaged across subpopulations) differed little between runs (Fig. 5). Therefore, below I report the results of one representative run for each simulation.

When the initial parasitoid density was 0.01/m², the trajectories for host density (averaged across subpopulations) with island dispersal for host and parasitoid did not differ much from those without dispersal (compare Fig. 4a and 5a). However, when parasitoid density was augmented to 0.1/m², the behavior was very different from that without dispersal (compare Fig. 4a and 5b).

Fig. 6 shows simulated trajectories of host density and proportion of hosts parasitized (both averaged across subpopulations) for augmented parasitoid density ($P(0)=0.1$) with (1) no dispersal, (2) stepping-stone dispersal for host and parasitoid, (3) island dispersal for host and stepping-stone dispersal for parasitoid, and (4) island dispersal for both species. The increase in host density from trajectory 1 to 4 in the fourth and fifth host generation indicate that adding dispersal to the model decreased the impact of M. croceipes on H. virescens. Furthermore, the greater the dispersal, whether it was of host or parasitoid, the less the parasitoid impact on host dynamics. Host density exceeds economic threshold in generation five with stepping-stone dispersal for one or both species and in generation four with island dispersal for both species. The reason for this effect of dispersal was that augmentation succeeded in the model without dispersal by driving host density so low that it did not recover by the end of the season. In models with density-independent dispersal, the host had refuges with low or zero parasitoid density from which moths could recolonize areas where the parasitoids had driven them to low density.

Since both hosts and parasitoids dispersed independently in these models, the parasitoids could not differentially exploit areas where host density was high. However, as pointed out above, field experiments show that M. croceipes aggregates in areas of high host density. Therefore, I added parasitoid aggregation to a model with island dispersal to test whether such aggregation could counteract the effects of dispersal.

Model with Density-Dependent Parasitoid Dispersal. In this model, parasitoids dispersed into a subpopulation in proportion to the relative host density in that subpopulation. Thus parasitoid abundance after dispersal was given by:

$$P(x,y) = \left[\frac{\sum_i \sum_j P(i,j)}{\sum_i \sum_j H(i,j)} \right] H(x,y) \quad (11),$$

where the variables are as described above. Such a perfect response to host density is unlikely given that parasitoids would not have complete knowledge of host distribution. However, without a firmer understanding of parasitoid aggregation, this model serves as a limiting case. I used island dispersal for the host and equations 3-6 to describe interactions within a subpopulation.

Simulation with Model with Density-Dependent Parasitoid Dispersal. Again, I used the same parameters and the same mean initial densities of host and parasitoid as in the model

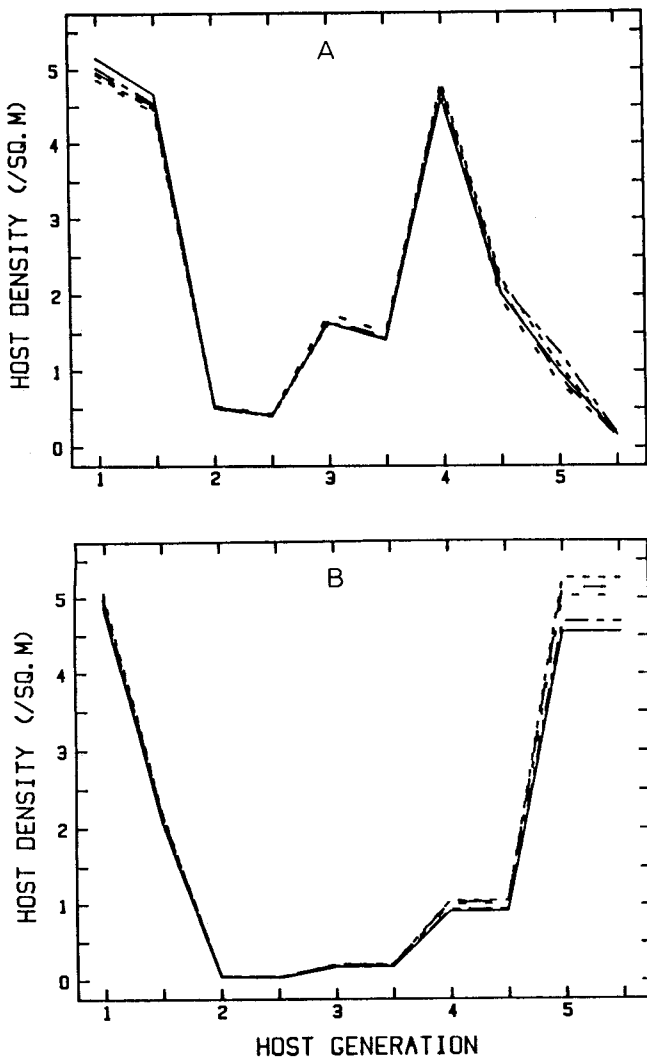


FIG. 5. Repeated simulations of host density versus host generation assuming island dispersal but no density dependence. (A) initial parasitoid density = $0.01/m^2$ and (B) initial parasitoid density = $0.1/m^2$.

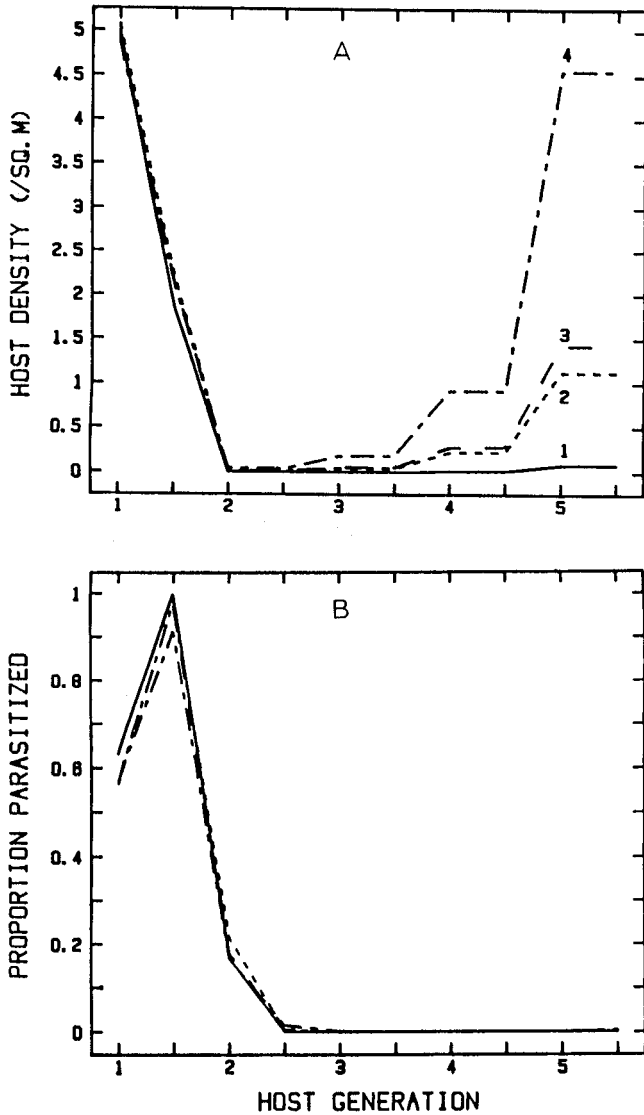


FIG. 6. Simulated host density (A) and proportion of hosts parasitized (B) versus host generation for various assumptions concerning dispersal: (1) no dispersal, (2) stepping-stone dispersal for host and parasitoid, (3) island dispersal for host and stepping-stone dispersal for parasitoid, (4) island dispersal for host and parasitoid. Initial parasitoid density = $0.1/m^2$.

without dispersal between subpopulations. Again, I distributed the host and parasitoids across subpopulations at the start of each simulation using random values drawn from a uniform distribution between 0 and twice the mean density.

Simulated trajectories of host density and proportion of hosts parasitized (both averaged across subpopulations) with this model (Fig. 7) resembled trajectories from the model with no dispersal (Fig. 4). The refuge from parasitism found with density-independent, island dispersal was no longer available, so the parasitoids again reduced host densities to low levels. There were two main differences between the simulations with models with no parasitoid dispersal and with density-dependent parasitoid dispersal. First, density-dependent dispersal prevented the host population from increasing so rapidly when parasitoid density was low, i.e. the parasitoids were more efficient at preventing an outbreak. Second, dispersal prevented high density parasitoid populations from driving the host population to such low levels that it could not recover at all before the end of the season.

Model with Density-Dependent Host Mortality from Other Causes. As Wang and Gutierrez (1980), May et al. (1981), May and Hassell (1988) have pointed out, the relative timing of density-dependent processes in an insect's life-cycle can greatly affect the impact of a natural enemy. To test whether density-dependent mortality from causes other than parasitization by *M. croceipes* affected simulated augmentation, I modified equations 3-6. For host subpopulation dynamics with density-dependent mortality before parasitization, I used the following equations:

$$H_{t+1/2} = H_t(1-H_t/c)e^{-aP_t} \quad (12),$$

$$H_{t+1} = (r/(1-1/c))H_{t+1/2}e^{-aP_{t+1/2}} \quad (13),$$

where c is the maximum number of host larvae that can be supported per unit area of host plant. The other variables and parameters were as described previously. The equations for parasitoid dynamics remained unchanged with this model.

For dynamics of host and parasitoid with mortality after parasitization, I used the following equations:

$$H_{t+1/2} = H_t(1-H_t[1+(1-e^{-aP_t})]/c)e^{-aP_t}$$

$$P_{t+1/2} = sH_t(1-H_t[1+(1-e^{-aP_t})]/c)(1-e^{-aP_t})$$

$$H_{t+1} = (r/(1-1/c))H_{t+1/2}(1-H_{t+1/2}[1+(1-e^{-aP_{t+1/2}})]/c)e^{-aP_{t+1/2}}$$

$$P_{t+1} = sH_{t+1/2}(1-H_{t+1/2}[1+(1-e^{-aP_{t+1/2}})]/c)(1-e^{-aP_{t+1/2}})$$

where the parameters and variables were as described above.

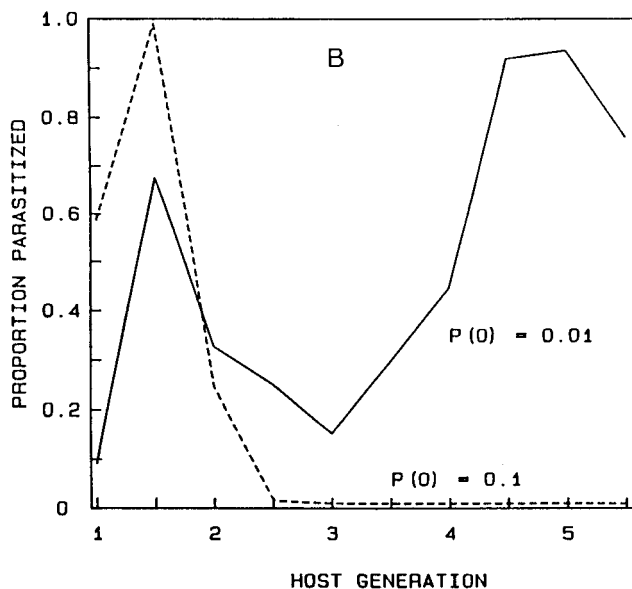
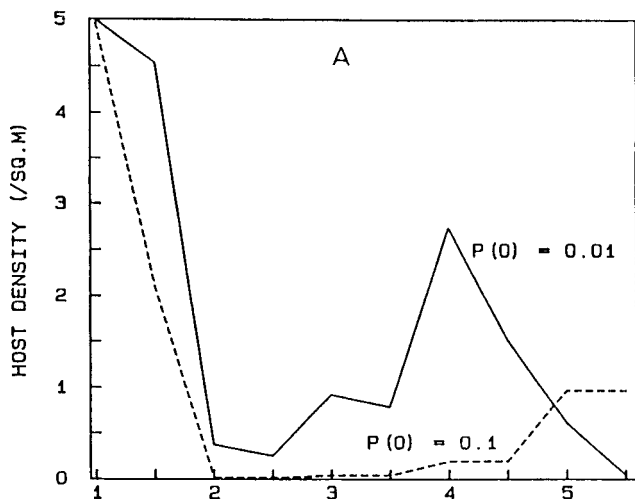


FIG. 7. Simulated host density versus host generation assuming island dispersal and parasitoid aggregation. $P(0)=0.01$ and $P(0)=0.1$ indicate initial parasitoid densities of $0.01/m^2$ and $0.1/m^2$.

The maximum host density (c) in these models could result either from competition between host larvae or from predation by natural enemies other than M. croceipes. I assumed $c = 10$ larvae/m², which was double the initial density in spring. For both models, I used equations 7 and 11 for host and parasitoid dispersal, respectively, i.e. island dispersal with parasitoid aggregation.

Simulations with Models with Density-Dependent Mortality from Other Causes. Density-dependent mortality before parasitoid attack had little affect on simulated trajectories of host density and proportion parasitized both with normal parasitoid density (Fig. 8) and augmented parasitoid density (Fig. 9). This is not surprising since such mortality only limits the growth rate of the host population. On the other hand, density-dependent mortality after parasitoid attack reduced the impact of normal parasitoid density (Fig. 8) and of augmented parasitoid density (Fig. 9). Even with augmentation, the host population exceeded the economic threshold in cotton by the fourth generation when density-dependent mortality occurred after parasitoid attack.

SUMMARY AND CONCLUSIONS

M. croceipes can be conserved by using insecticides to which it is relatively tolerant and by applying insecticides only when Heliothis spp. populations exceed economic threshold. The difficulty of measuring M. croceipes density prevents explicit use of parasitoid density data in deciding whether to spray insecticides.

Simulations with several models of the population dynamics of M. croceipes and Heliothis spp. showed that augmentative control may be technically feasible. With a model incorporating host dispersal and density-dependent parasitoid dispersal, 10-fold augmentation of M. croceipes density in spring suppressed H. virescens below the economic threshold in cotton.

Simulations also showed that the greater the level of density-independent dispersal of host and parasitoid the less the impact of augmentative releases on host density. However, dependence of parasitoid dispersal on host density increased parasitoid impact on host population dynamics. Furthermore, the timing of other density-dependent processes was crucial: density-dependent host mortality before parasitism had little effect on host dynamics, but density-dependent mortality after parasitism greatly reduced parasitoid impact on host dynamics.

Eventually, models such as those described here could predict where, when, and how many M. croceipes to release to control Heliothis spp.

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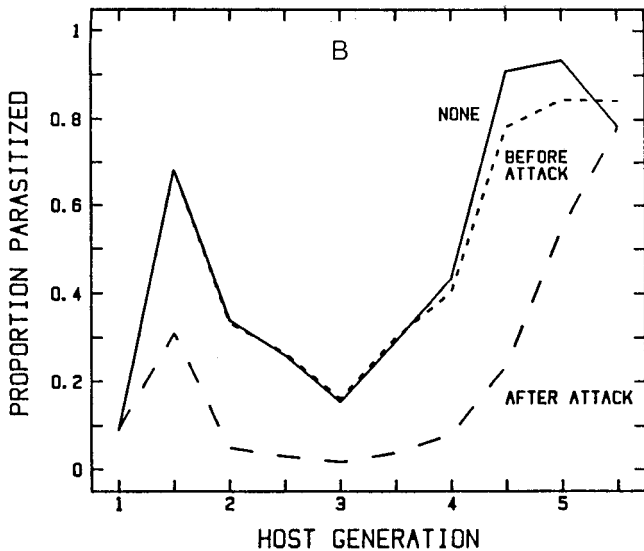
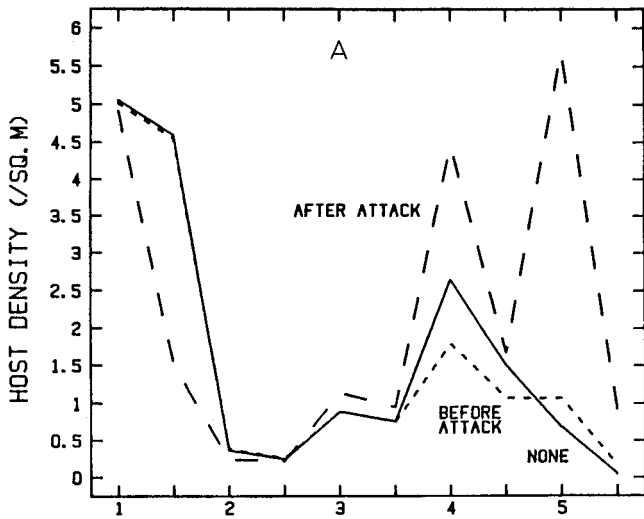


FIG. 8. Simulated host density (A) and proportion of hosts parasitized (B) versus host generation assuming island dispersal and parasitoid aggregation. NONE indicates no density-dependent mortality from other causes; BEFORE ATTACK indicates density-dependent mortality before parasitization; AFTER ATTACK indicates density-dependent mortality after parasitization. Initial parasitoid density = $0.01/m^2$.

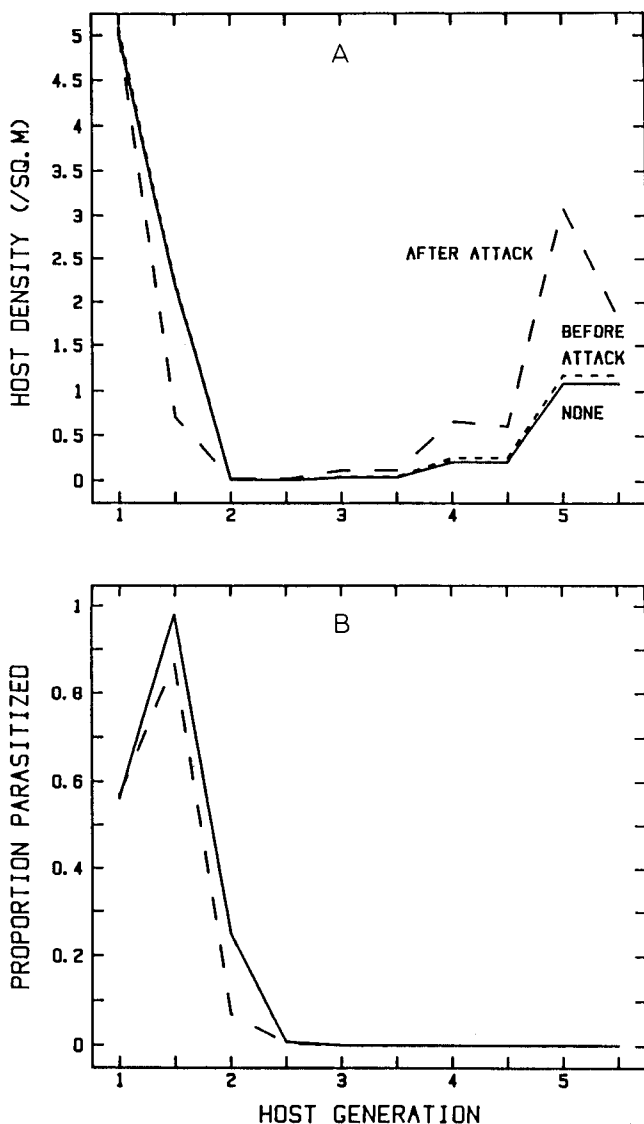


FIG. 9. Simulated host density (A) and proportion of hosts parasitized (B) versus host generation assuming island dispersal and parasitoid aggregation. NONE indicates no density-dependent mortality from other causes; BEFORE ATTACK indicates density-dependent mortality before parasitization; AFTER ATTACK indicates density-dependent mortality after parasitization. Initial parasitoid density = $0.1/m^2$.

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