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An analytical model for genetic control of *Heliothis virescens* incorporating the effects of sterile males

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Summary. A recent computer simulation model by Levins and Parker (1983) indicated that mass releases of male-sterile *Heliothis* hybrid moths could cause genetic suppression of the tobacco budworm, *Heliothis virescens*, without the risk of significant crop damage. We present an analytical model to explore the behavior of the Levins-Parker model. Our model shows that the length of time between matings for females when they mate with wild type fertile males to that when they mate with hybrid sterile males is extremely important to the efficacy of a suppression program. Release ratios needed to suppress a natural pest population were examined across a range of biological parameters.

Key words: Genetic control – *Heliothis virescens* – Hybrid sterility

Introduction

The tobacco budworm, *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) is a major pest of cotton and other crops. In addition, insecticidal control of the budworm is complicated by widespread resistance to several groups of insecticides. As a result, there is considerable interest in alternative controls. One possibility is genetic suppression. Laster (1972) discovered that crosses of *H. virescens* males with *Heliothis subflexa* (Guenee) females produce sterile sons and fertile daughters. These F_1 females also produce sterile sons and fertile daughters when backcrossed to *H. virescens* males. This pattern of sterility has been perpetuated continuously now for over 130 backcross generations (Laster, personal communication). A simulation model by Laster et al. (1976) (the LMP model), an analytical model by Makela and Huettel (1979) (the MH model), a more complex simulation model by Levins and Parker (1983) (the LP model) and a pilot project on St. Croix (Proshold and Smith 1982; Proshold 1983) have indicated that massive releases of backcross insects can probably suppress budworm populations.

The LMP model was conservative in that it assumed that there was "... no direct influence on the natural population from matings by sterile males". We now know that backcross hybrid (BC) males mate with both BC and *H. virescens* (V) females, and furthermore, appear to be competitive with V males for receptive females (Pair et al. 1977a; Proshold et al. 1983). When matings by BC males ("BC matings") follow matings by V males ("V matings"), the percentage of fertile eggs is reduced (Pair et al. 1977b). In addition, females apparently mate only once per night (Guerra et al. 1972). Therefore, we would expect that the total number of fertile eggs produced by a female (and hence, the rate of population growth) must decrease when a V mating (to either initiate or restore fertility) is delayed by BC matings, because of aging and mortality among the females. For example, Proshold et al. (1982) showed that both daily oviposition rates and lifetime egg production were reduced for *H. virescens* females when mating was delayed one or more nights. The LMP model also assumed that females mate "only one time with normal males". However, female *H. virescens* mate more than once in nature (Stadelbacher and Pfrimmer 1973). As already noted, females do not appear to discriminate between BC and V males. These two factors would tend to reduce the number of females inseminated (mated by V males) because, by chance, some females will mate repeatedly with V males, whereas others will never mate with V males. Lastly, the LMP model assumes that normal males mate only three times regardless of the ratio of females to V males. However, this "male mating capacity" (Makela and Huettel 1979) varies with the ♀/fertile ♂ ratio and has been shown to be as high as 6.3 in laboratory studies (Guerra et al. 1972). Makela and Huettel (1979) showed how the LMP simulation model could be treated analytically.

Although BC and V males appear to be equally competitive for receptive females, it is important to note that BC and V males are not equally "competitive" in the broader sense of impact on subsequent female mating behavior. Successful fertilization by a V male reduces the mating propensity of a female (Raulston et al. 1975), but mating with a BC male does not appear to do so (Pair et al. 1977a). Therefore, a female is likely to remate sooner after a BC mating than after a V mating, reducing the relative impact of BC matings.

The recently developed LP model uses the development and fecundity data of Smith et al. (1980) and assumptions about mortality to simulate daily population densities after release of the BC hybrids. The LP model assumes that (1) BC and V males are equally competitive for receptive females, (2) females mate repeatedly, (3) delays in V matings reduce fecundity, (4) BC and V moths mate synchronously, (5) a BC mating effectively sterilizes a female (even if she had mated previously with a V male) until she mates (or remates) with a V male and (6) a female mating with a BC male will remate the next night, but will not remate until the 3rd night following a V mating.

In this paper, we show how such a system can be modeled analytically, and explore the effects of varying assumptions (5) and (6). This treatment allows the derivation of expressions for some critical hybrid release ratios, such as those which cause an absolute decline in larval population density with each successive generation. We find that the ratio of the length of time between matings for females when the females mate with V males (female intermating period with wild-type males) to the female intermating period with BC males is extremely important in determining the behavior of the system.

The model

In the analytical model of Makela and Huettel (1979), the release ratio was defined as $R = (\text{No. of BC})/(\text{No. of V})$, the fraction of the population which is V is $1/(R+1) = q$ and the fraction which is BC is $R/(R+1) = p$. Population growth, Θ, was essentially defined as the net replacement rate (the number of female offspring surviving to adulthood for each fertilized female), which is equivalent to the multiplication rate per generation of a normal *H. virescens* ("pure") population. Initial population size for one sex was N. They further defined the male mating capacity, μ, as the number of females that a V male inseminates in his lifetime. One can define an effective mating capacity, μ_e, which accounts more realistically for the interaction between BC and V but which otherwise leaves their basic model intact. The derivation of μ_e follows.

The MH and LMP models compare a pure population to a population where BC have been released ("mixed"). In the mixed population, the N *H. virescens* males distribute their $N\mu$ matings uniformly (no multiple mating) among the N/q (i.e., $N(R+1)$) females of both types present so that the average number of fertile matings per female is $(N\mu)/(N/q) = \mu q$. Thus, when $\mu q < 1$ (a necessary condition, since the effect of $\mu q \geq 1$ on mating history was not defined), μq can be interpreted as the probability that a female mates with a V male at some point in her lifetime.

Taking into consideration female multiple mating, this formulation can be modified to consider the fraction, f, of nights that an individual female oviposits fertile eggs. For a given value of R, the probability that a female mates with a BC male and oviposits sterile eggs for, say, I_{BC} nights before remating (intermating interval for BC matings) is p (i.e., $R/(R+1)$); and the probability the female mates with a V male and oviposits fertile eggs for, say, I_V nights before remating is q (i.e., $1/(R+1)$). The average value of f when a BC mating is completely sterilizing for I_{BC} nights is simply:

$$f = \frac{I_V q}{I_V q + I_{BC} p}. \tag{1}$$

Because f is functionally equivalent to (i.e., it serves the same role as) the μq of the MH model, it is convenient to define

$$\mu_e = \frac{I_V}{I_V q + I_{BC} p} \quad \text{and} \quad I = I_V/I_{BC}$$

so that

$$f = \mu_e q = \left(\frac{I}{I q + p}\right) q = \left(\frac{I(R+1)}{I+R}\right) q. \tag{2}$$

Effective male mating capacity, μ_e, is thus a function of the release ratio, R, and the ratio, I, of the I_V and I_{BC} intermating periods.

Formula (2) can be further modified to account for incomplete sterilization by including the effects of the last previous mating. (In considering only the last previous mating, we assume that earlier matings have a relatively minor impact.) Assume that L ("leakage" of fertile sperm) indicates the fraction of fertility retained after a V then BC mating sequence. Formula (1) can now be rewritten as:

$$f = \frac{I_V q^2 + L I_{BC} q p + I_V p q}{I_V q + I_{BC} p} = \frac{(I_V + L I_{BC} p)}{I_V q + I_{BC} p} q. \tag{3}$$

where $I_V q^2$ refers to the V then V matings, $L I_{BC} q p$ refers to the V then BC matings, and $I_V p q$ represents the BC then V matings. Again defining $I = I_V/I_{BC}$:

$$\mu_e = \frac{I + Lp}{I q + p} = \frac{I(R+1) + LR}{(I+R)}. \tag{4}$$

Each female will oviposit, on average, $\mu_e q$ of her potential number of fertile eggs. This effective mating capacity, μ_e, can be substituted for μ in Table 2 of Makela and Huettel (1979) to generate our model. A portion of Table 2 of Makela and Huettel (1979) is modified and reproduced in Table 1 of this paper for reference.

Table 1. Population trends over generations following releases of *Heliothis* hybrids. N is initial native population size (one sex), Θ is population multiplication rate per generation for an untreated population, μ_e is the effective male mating capacity, R is the ratio of hybrid: wild type, and $q = 1/(R+1)$. Modified from Makela and Huettel 1979

	Larval generation[a]			
	1	2	3	4
Pure (wild) population (one sex)	N	$N\Theta$	$N\Theta^2$	$N\Theta^{g-1}$
Mixed (wild + hybrid) population (one sex)	$N\mu_e$	$N\Theta\mu_e^2 q$	$N\Theta^2\mu_e^3 q^2$	$N\Theta^{g-1}\mu_e^g q^{g-1}$
Mixed: pure	μ_e	$\mu_e(\mu_e q)$	$\mu_e(\mu_e q)^2$	$\mu_e(\mu_e q)^{g-1}$

[a] Generation g in this table is the same as generation g + 1 of Makela and Huettel 1979

The above results were validated, in the sense of testing the logic used in their derivation, by comparing the behavior of our model with the results of the computer simulations of the LP model, assuming that both BC and V females lay equal numbers of eggs. With the aid of R. A. Levins, we also modified the LP model such that BC matings did not cause complete sterility. Our model produced results very similar (within 1%) to the LP model in all cases studied, in spite of the fact that we make no assumptions about oviposition patterns, development time, or daily mortality rates. These specifics are not important for our purposes since some females will mate early and contribute more progeny than those which mate later, but f simply averages all of these contributions across a generation of indefinite duration.

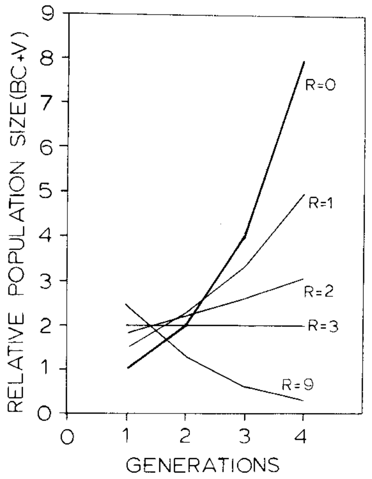

Fig. 1. Relative larval population size (BC + V) for the first generations after releases of BC for several release ratios (R) compared to a pure population (R = 0). For all curves $\Theta = 2$, I = 3, and L = 0

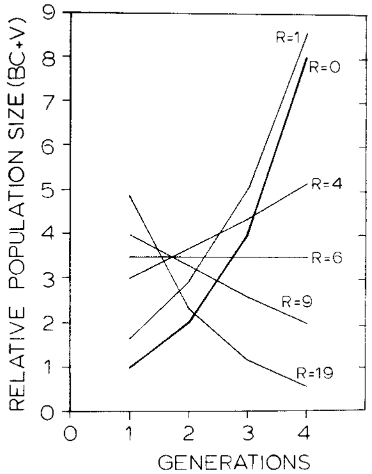

Fig. 2. Same as in Fig. 1, except I = 6

Behavior of model

Under our assumptions, any release of BC moths will result in at least a relative decline in population growth (compared to the pure V population) with successive generations. However, the mixed (where releases have been made) population is larger initially than the pure ("natural") population, and absolute suppression may not occur for several generations in cases where the release ratio is low and the ratio of the intermating intervals (I) is high. This is illustrated in Figs. 1 and 2. In Fig. 1, for example, where I = 3 and R = 1, the mixed population is suppressed, relative to what a comparable pure population would have been, by the third generation. In Fig. 2, where I = 6 and R = 1, suppression does not occur until after the fourth generation.

The ratio of the sizes of the mixed to the pure populations (M/P) is always $\mu_e(\mu_e q)^{g-1}$ (Table 1). In the first generation (g = 1), the M/P ratio is $\mu_e = (I + IR + LR)/(I + R)$ which is always ≥ 1. However, M/P will decrease after the first generation whenever $\mu_e q < 1$, and this must always occur after a release of BC has been made (R > 0). Assuming that L = 1 (there is no sterilizing effect from a V then BC mating, the most conservative case), this can be shown as:

$$\mu_e q = \frac{I + IR + R}{(I + R)}\left(\frac{1}{R+1}\right)$$
$$= \frac{I + R/(R+1)}{I + R}$$

which is always < 1.

Three aspects of our model are particularly important in the context of genetic control: (1) the larval population size in the first generation following a release; (2) larval population size in the second generation (typically the first on cotton) and (3) the release ratio, R, required to cause a decrease in larval population size with each successive generation.

Generation 1

The ratio of the mixed to pure (M/P) population size when $g = 1$ is simply μ_e as was given above. The relationship of M/P and R when $g = 1$ is shown for several values of I and L in Fig. 3. Note that when R is large, M/P is asymptotically equal to $I + L$. Data reported by Guerra et al. (1972) and Proshold and LaChance (1974) indicate that I_V is no more than three days in the laboratory. If we assume that I_{BC} is about one day (which is consistent with data from Proshold and LaChance (1974) for F_1 hybrid males), then $I = I_V/I_{BC} = 3$, as assumed in the LP model. A value for L of about 0.2 can be roughly estimated from the data of Pair et al. (1977b). Given these estimates for I and L, a "best guess" is that larval populations in the first generation would be increased no more than about 3.2 times following massive releases of BC hybrids. However, there is considerable uncertainty in this estimate, and it is reasonably possible that the increase could be twice as large. Even large increases should not cause economic damage in most cases because the releases would probably be made against the overwintering moths (because population densities are lowest), and the first larval generation feeds on wild hosts. Nonetheless, caution should be exercised when the first spring generation feeds on cultivated crops (e.g., tobacco in some areas). Population increases limited to wild hosts may actually improve control in subsequent generations on crops because the increased host/prey abundance may benefit *Heliothis* predators, parasites, and pathogens.

Generation 2

Makela and Huettel (1979) showed that the mixed population will be smaller than the pure population in the second larval generation if $R > (\mu^2 - 1)$. Substituting μ_e for μ, we can solve for R in terms of I by using the quadratic formula. When $L = 0$,

$$R > I(I-2) \text{ for } I \geq 2 . \tag{5}$$

If $I = 3$ and $L = 0$, as assumed in the LP model, R must be > 3 if the size of the second generation (generally the first attacking crops) of the mixed population is to be less than that of the pure population (Fig. 1). It can be shown that for $L > 0$, a good approximation for (5) is

$$R > I(I-2) + 2IL + L^2 . \tag{6}$$

The minimum R required for different values of L and I is illustrated in Fig. 4.

In the second generation after release, $g = 2$, and $M/P = \mu_e^2 q$ (Table 1). This is a convex, quadratic function of R for which the maximum M/P occurs at approximately $R = I - 2 + L$. This means that at low ratios and at high ratios M/P is small, but for different reasons. The maximal M/P for $I = 1$ to 7 is shown in Fig. 5. For example, using the LP assumptions of $I = 3$ and $L = 0$, the maximum M/P is 1.125 at $R = 1$ (a 12.5% increase). More conservative assumptions of $I = 6$ and $L = 0.5$ give a maximum M/P of ca. 2.0 at $R = 4.5$ (a 100% increase). Although a 12.5% increase might not even be measurable, a 100% increase might be objectionable. When $R < I - 2 + L$, M/P will be lower in generation 2 than if $R = I - 2 + L$, but it will take longer for the mixed population to become smaller than the pure population, particularly when I is large, as illustrated in Fig. 2 (compare $R = 4$ to $R = 1$). This indicates that higher ratios should always be better than lower ratios, unless a crop is particularly sensitive to pest pressure in the early season and I is large.

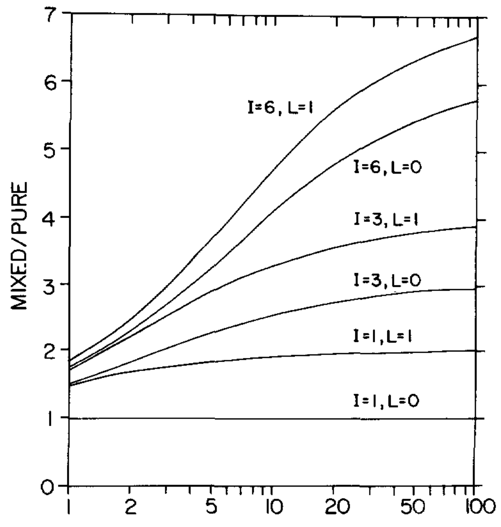

Fig. 3. The ratio (BC + V)/V (mixed/pure) of larval population sizes during the 1st generation after BC release as a function of the release ratio, R, for selected values of I and L

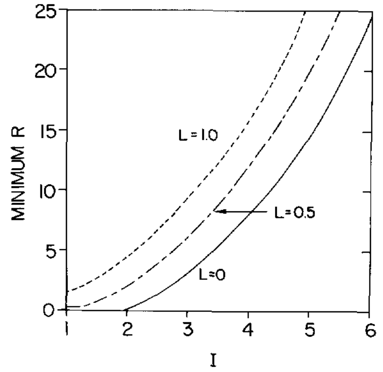

Fig. 4. The minimum release ratio, R, as a function of I and L such that the mixed population (BC + V) is no larger in the 2nd larval generation than is the pure (V) population

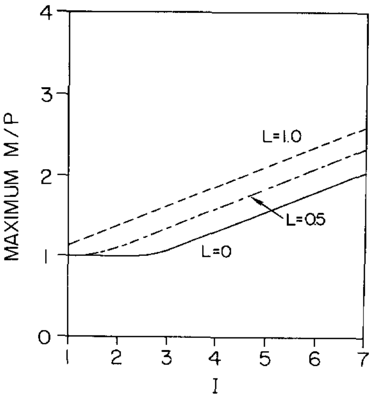

Fig. 5. The maximum population size of a mixed population (BC + V) in the 2nd generation compared to the pure (V) population (M/P) as a function of I and L

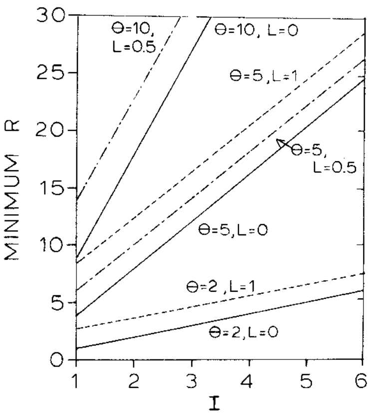

Fig. 6. The minimum release ratio, R, as a function of I, L, and Θ such that the absolute size of the mixed population declines with successive generations

Later generations

For the LMP and MH models, extinction of the mixed population will occur when $R > (\Theta\mu - 1)$. However, extinction is a theoretical possibility that will probably not be met in practice because of density dependent mortality (discussed below) and long range dispersal of the pest (Raulston et al. 1982). Another interpretation of $R > (\Theta\mu - 1)$ is that it is the ratio which will cause an absolute decrease in population size with each successive generation within a season. For our model, an absolute decrease occurs each generation when

$$R > I(\Theta - 1) \quad \text{for} \quad (\Theta \geq 1), \tag{7}$$

assuming $L = 0$. Some minimum ratios for different values of I, Θ, and L are illustrated in Fig. 6. When $L > 0$, the minimum ratio is approximately

$$R > I(\Theta - 1) + \Theta L. \tag{8}$$

In our Fig. 2, where $\Theta = 2$, $I = 6$, and $L = 0$, the critical ratio is $R > 6$. Using the LP model assumptions of $\Theta = 5$, $L = 0$, and $I = 3$, R would have to be > 12.

Conclusions

An implication of both the LMP and MH models was that populations on crops would increase, at least temporarily, following BC releases. As observed in the LP model, and as illustrated more explicitly in our model, these increases are much smaller or non-existent under a more realistic set of assumptions. Any initial increases would probably be reasonably small, less than four fold, on crops such as tobacco attacked by the first generation and less than two fold on crops such as cotton attacked by the second generation.

Our model emphasizes the importance of I (where $I = I_V/I_{BC}$) to the effects of hybrid releases. The parameter L is somewhat less important. In Figs. 3–6, change in L of 0 to 1, its entire range, is less important than a 2–3 fold increase in I. Thus, the impact of temporary "sterilization" resulting from matings with BC males following matings with V males is not nearly as important as the "fertilization delays" that occur when a female mates repeatedly with BC males instead of a V male. Such delays have their greatest impact when I is short and R is large. Because it is possible that I_V and I_{BC} are differentially density dependent, we believe that they will have to be measured simultaneously under field conditions to obtain estimates of I.

Finally, two assumptions of this model which are not explored in this paper deserve further consideration. First, although we assume a closed population with uniform R, the effects of variation in R due to immigration and spatially heterogeneous distributions of V and BC can cause a decline in R and loss of suppression (Makela and Huettel, pers. com.). Second, we assume that all mortality is density independent and, therefore, that Θ is not affected by population suppression resulting from hybrid releases. However, in view of the importance of potentially density dependent mortality by natural enemies of *Heliothis* (Ridgway and Lingren 1972; Varley et al. 1973) and because insecticide use is in some sense density dependent (insecticides are used more frequently when pest densities are high than when they are low), the possibility of compensatory increases in Θ following suppression by BC releases should be considered. Increases in Θ would not affect R, but might result in higher population densities than our model would predict.

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