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Model for Genetic Control of *Heliothis virescens*

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Summary. A model was developed which corrects and extends an earlier one proposed for the control of the tobacco budworm, *Heliothis virescens* (F.), through hybrid male sterility. Population suppression is effected through the release into natural populations of the backcross progeny of a hybrid between *H. virescens* and a related species. Thereafter, the system perpetuates itself in nature through continual backcrossing of the fertile backcross females to native *H. virescens* males. When the proportion of backcross hybrid females in the total population is large enough to draw off the insemination potential of the native males, the native females fail to replace themselves. The present model demonstrated that the ratio of released backcross hybrids to natural *H. virescens* remains constant in a closed population. Furthermore it was shown that the release ratio necessary to achieve extinction of a closed population is related to the number of females that a male can inseminate and to the population growth rate. Release ratios required to slow natural population growth and to lessen the impact damage of releases on crop plants were also examined. Effects of selection against the backcross females on the predictions of the model were explored.

Key words: *Heliothis virescens* – Genetic control – Population model – Hybrid sterility – Tobacco budworm

Introduction

The tobacco budworm, *Heliothis virescens* (F.) (Lepidoptera: Noctuidae), is a major pest of cotton, tobacco and other crops in the United States. The protection of crops from this species is particularly difficult because *H. virescens* is resistant to insecticides which are directed against it but which instead destroy its natural enemies. An effective and environmentally acceptable means of control is therefore highly desirable.

The potential for control of *H. virescens* through a genetic system was investigated by Laster (1972). He found that *H. virescens* males crossed with females of a closely related congener, *Heliothis subflexa* (Guenée), produced viable F_1 hybrids. The hybrid males from this cross were sterile but the hybrid females were fertile and produced offspring when backcrossed to *H. virescens* males. Several studies have been conducted to confirm these observations and to investigate in detail the sterility mechanism thought to be a maternally inherited cytoplasmic incompatability (Proshold and LaChance 1974; Proshold et al. 1975; Richard et al. 1975).

The pattern of male sterility and female fertility has been perpetuated for over 40 generations through continuous backcrossing of the backcross females of successive generations to *H. virescens* males (Laster et al. 1976). The mating behavior of these backcross males and females appears to be much the same as that of normal *H. virescens* (Laster et al. 1977; Pair et al. 1977a). These two factors make feasible the production of competitive backcross insects to be used in a genetic control program.

The principles of the control strategy were presented by Laster et al. (1976) and Parvin et al. (1976). In essence their model predicts that extinction of a population of *H. virescens* would result from the introduction of relatively large numbers of the backcross insects. The fertile backcross females would compete with the native females for mates, drawing off the mating potential of the native *H. virescens* males. Since few *H. virescens* females would be fertilized, not enough progeny of the pure *virescens* genotype would be produced in one generation to replace the native population.

The Laster-Parvin model, however, contains an intrinsic inconsistency which has led its authors to incorrect conclusions. This model predicts that populations eventually go to extinction regardless of the ratio of released hybrids to native moths. In the present paper we correct the model, establish mathematical relationships among its

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parameters, and explore the biological properties and their implications as they affect control strategies. Like the Laster-Parvin model, ours is completely deterministic and no assumptions about the biology of *H. virescens* have been made other than those used in the original papers.

The Model

Although the following model is logistically based on that of Laster et al. (1976) and Parvin et al. (1976), the nomenclature is specific to this paper. The present model also differs slightly from the original because of a programming error in the latter which treated the backcross and *H. virescens* females unequally in the mating algorithm, giving a spurious advantage to the backcross females. In the present model the two types of females are equally competitive. In the section discussing selection we will consider the relaxation of this assumption.

Suppose a natural population of *Heliothis virescens* (V) is closed (no in- or out-migration) and consists of N males and N females in the first generation under consideration. As the native adults emerge, backcross (BC) males and females are released in the ratio R of BC:V, giving a total of N(R + 1) males and N(R + 1) females in the mixed population. Mating is random between and within types (BC and V). Thus, the frequency of a specific mating pair is the product of the frequency of each type in the male and female mating pool. These are shown in Table 1, where $p = R/(R + 1)$, the proportion of BC in the mixed popula-

Table 1. Frequency of mating types and resulting offspring

Parents		Offspring					
♀	♂	V♀	V♂	BC♀	BC♂	Sterile	Total
V	V	$q^2/2$	$q^2/2$				q^2
BC	V			$pq/2$	$pq/2$		pq
V	BC					pq	pq
BC	BC					p^2	p^2
Total		$q^2/2$	$q^2/2$	$pq/2$	$pq/2$	p	1
Total/total fertile		$q/2$	$q/2$	$p/2$	$p/2$		

Let $p = R/(R + 1)$ and $q = (1 - p) = 1/(R + 1)$, where R is the release ratio of BC to V in $g = 1$

Note: Ratio in offspring is $p/q = R$

Table 2. Population trends over generations

Row	Generation				
	1	2	3	4	. . . g
1. V adults (1 sex)	N	$N\theta\mu q$	$N\theta^2\mu^2q^2$	$N\theta^3\mu^3q^3$	$N\theta^{g-1}\mu^{g-1}q^{g-1}$
2. BC adults (1 sex)	N . R	$N\theta\mu p$	$N\theta^2\mu^2pq$	$N\theta^3\mu^3pq^2$	$N\theta^{g-1}\mu^{g-1}pq^{g-2}$
3. V + BC adults	$N(R + 1) = N/q$	$N\theta\mu$	$N\theta^2\mu^2q$	$N\theta^3\mu^3q^2$	$N\theta^{g-1}\mu^{g-1}q^{g-2}$
4. BC : V adults	R	R	R	R	R
5. V fertilized females	$N\mu q$	$N\theta\mu^2q^2$	$N\theta^2\mu^3q^3$	$N\theta^3\mu^4q^4$	$N\theta^{g-1}\mu^gq^g$
6. BC fertilized females	$N\mu p$	$N\theta\mu^2pq$	$N\theta^2\mu^3pq^2$	$N\theta^3\mu^4pq^3$	$N\theta^{g-1}\mu^gpq^{g-1}$
7. BC + V fertilized females	$N\mu$	$N\theta\mu^2q$	$N\theta^2\mu^3q^2$	$N\theta^3\mu^4q^3$	$N\theta^{g-1}\mu^gq^{g-1}$
8. V adults (pure pop.)	N	$N\theta$	$N\theta^2$	$N\theta^3$	$N\theta^{g-1}$
9. (BC + V) : (V) = M : P if $R > \mu - 1$	$R + 1 = 1/q$	μ	$\mu(\mu q)$	$\mu(\mu q)^2$	$\mu(\mu q)^{g-2}$
10. (BC + V) : (V) = M : P if $R \leqslant \mu - 1$	R + 1	R + 1	R + 1	R + 1	R + 1

N is native population size (1 sex) in $g = 1$. θ is population increase per generation, μ is the number of times a male can mate and $q = 1 - p = 1/R + 1$ where R is the release ratio of BC : V

Reference to this table in the text will take the form T2 (row, column), T2 (row _), or T2 (column _) tion, and $q = (1 - p) = 1/(R + 1)$, the proportion of V. Note that the proportion of matings that are fertile (by V males) is q and that the ratio of BC to V offspring is $p/q = R$, which is the same ratio as their parents.

Assume each male (BC or V) can inseminate a total of μ females. A female is assumed to be satisfied with a single fertile mating (by a V male) while a mating with a BC male does not change her mating behavior (Raulston et al. 1975). Therefore, the presence of BC males will be ignored during mating although they will be included in considerations of total population size relative to potential crop damage. During the first generation, $N\mu$ fertile matings occur (with V males), $N\mu q$ of which are with V females and $N\mu p$ of which are with BC females [Table 2, rows 5-7, column 1. Note that future references to Table 2 will be of the form: 'T2 (row, column)']. Fertilized BC and V females lay the same number of eggs and the same proportion of these offspring survive to adulthood in the next generation, i.e., there is no differential fertility or viability between types. Let θ be the number of offspring of one sex surviving to adulthood for each fertilized BC or V female parent. Thus, θ is the amount by which the population size increases each generation and will be treated as a constant at present.

At this point, it may be instructive to note which part of the Laster-Parvin model differs from the present model. As a result of the mating advantage erroneously attributed to the BC females in their model, the ratio of BC:V adults increased over time instead of remaining constant (T2, row 4). The effect of this increasing ratio on the total population size (BC+V) over generations is plotted in Figure 1, where the simulated data is from Table 1 in Parvin et al. (1976). Note that the BC:V ratio increases linearly until generation 14. (The irregularity of R in later generations is due to rounding error with small population sizes.) The population size, on the other hand, increases until generation six and then decreases to zero by generation 20. The reason that an increasing ratio affects the population growth curve in this way will become clear after exploring the interrelatedness of R with θ and μ.

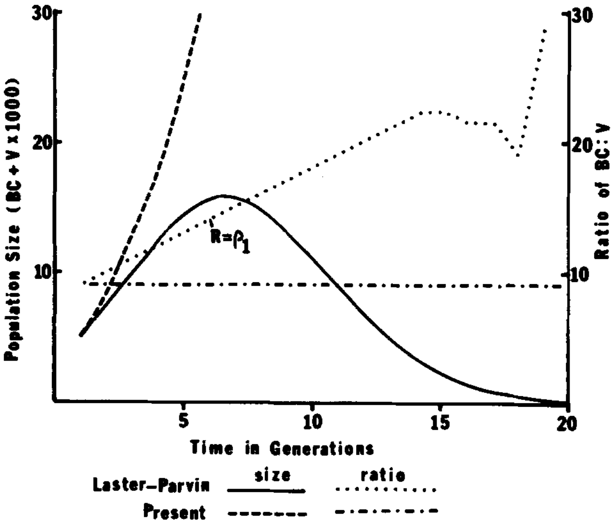

Fig. 1. Total population size (BC+V, one sex only) and BC:V ratio from Table 1 of Parvin et al. (1976) and the present model plotted over generations. Note that for the Laster-Parvin model in generation 6, $R = 14 = \mu\theta\text{-}1 = \rho_1$, after which the population decreases

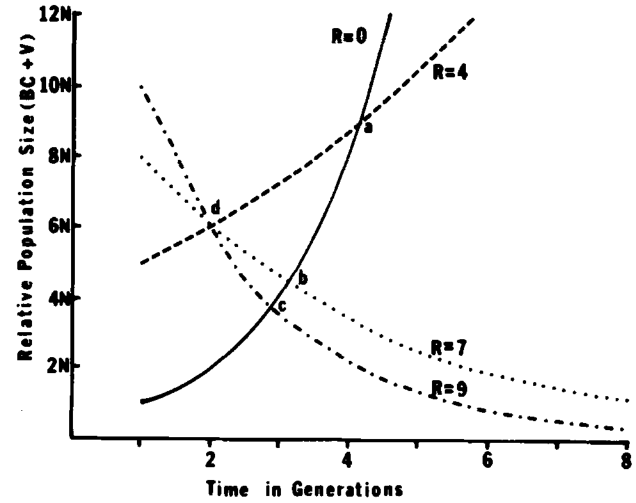

Fig. 2. Relative population size (BC+V, one sex only) over generations for three values of the release ratios to be compared with a pure V population, R = 0. For all curves $\theta = 2$, $\mu = 3$

Extinction

The present model predicts that in the second generation the total female population size is $N\theta\mu$ of which $N\theta\mu q$ are V [T2 (1, 2)]. This means that the number of V change by a factor $\theta\mu q$ from the first to the second generation (N to $N\theta\mu q$). In fact, the change between any two consecutive generations is $\theta\mu q$ [T2 (row 1)], implying that the number of V may increase or decrease depending upon whether $\theta\mu q$ is greater than or less than one. If $\theta\mu q < 1$, the mixed population will steadily decrease in size until it goes to extinction. Since $1/q = R + 1$, the rate of approach to extinction is directly proportional to the release ratio. If $\theta\mu q > 1$, the population will increase in size each generation (in spite of the sterility of the BC males), and extinction will not occur. Thus the equation $\theta\mu q = 1$ defines a critical release ratio, $\rho_1 = \mu\theta - 1$. A particular release ratio above ρ_1 will cause the successful extinction of the pest population and a ratio below ρ_1 will merely control its rate of increase. This difference is illustrated in Figure 2 where $\rho_1 = 5$. For the release in which $R = 4$ ($< \rho_1$) the population size increases, but for $R = 7$ or 9 ($> \rho_1$), the population is quickly extinguished.

In the Laster-Parvin model, release ratios initially less than ρ_1 eventually led to extinction because R increased over generations. In other words, a ratio originally less than $\mu\theta - 1$, would gradually increase until it was greater than $\mu\theta - 1$, after which the population would decrease to extinction. The example in Figure 1 shows that in generation 6, $R = 14 = \mu\theta - 1$. Concomitantly the population increased until generation 6 and after R passed ρ_1, it decreased until extinction.

Population Size

Regardless of whether the absolute population size increases or decreases, the deleterious effect of the BC individuals on natural populations would reduce the population growth rate. If we compare the size over generations of a mixed (BC + V) population with that of a pure V population ($R = 0$) as in Figure 2, we see that in later generations the mixed population is smaller. In the first generation, however, the total sizes of mixed populations, $R = 4$, 7 and 9, are much larger than that of a pure V population. By the second generation all mixed populations are the same size, $N\theta\mu$. Then, for $R = 7$ and 9, the mixed population becomes smaller than the pure V population by the fourth and third generations, respectively (refer to crossover points b and c). Meanwhile, for $R = 4$, the mixed population is increasing but slowly enough so that by the fifth generation its predicted size is smaller than that of pure V (crossover point a). Thus, after an initial period during which the mixed population is larger, the slowing of the growth rate produces a smaller mixed population even when the release ratio R is less than the critical value $\rho_1 = \theta\mu - 1$.

Upon the release of the BC males and females, the number of insects (the offspring of fertilized females) capable of crop damage is increased many fold. This initial increase is overcome before the third or later generations when the predicted size of the mixed population is crossed over by that of pure V. If time is of the essence, these initial effects need to be overcome as soon as possible. The earliest possible crossover point occurs between the second and third generations and is accomplished when $R > \mu^2$-1 (for example, point c in Figure 2 where $\rho_2 = 8$, $R = 9$). Of course, larger values of R will result in earlier crossover points and smaller mixed populations in subsequent generations. Thus, the second critical release ratio, $\rho_2 = \mu^2$-1, is that ratio above which the initial effects of a release are overcome by the third generation and below which the effects are not overcome until later generations.

The formulas for population sizes over generations are shown in T2 (row 3) for mixed populations and in T2 (row 8) for pure V populations. The ratio of mixed to pure V population sizes (M:P) is noted in T2 (row 9) for $R > \mu$-1 and in T2 (row 10) for $R < \mu$-1. In T2 (row 9) we find that the ratio M:P is decreased by an amount μq each generation. If μq, however, is greater than 1, implying that $R \leq \mu$-1, then as row 10 shows, the M:P ratio is restricted by the total number of females instead of μ and is constant at R + 1. Intuitively, an $R \leq \mu$-1 means that the V males are capable of mating enough times to fertilize all of the V females and all of the BC females. In this case the initial effect is never overcome; in fact damage to crops may increase as much as R-fold. Thus, the third critical release ratio is defined as $\rho_3 = \mu$-1, which separates those release ratios the initial effects of which are eventually overcome from those in which these effects are never overcome.

Time Until Extinction

If $\theta\mu q < 1$ (which implies $R > \rho_1 = \theta\mu - 1$), then the time until extinction (the state in which the number of V males is less than 1) can be calculated. By generation g, less than one V male will eclose if [T2 (1,g)] satisfies the following inequality:

$$N(\theta\mu q)^{g-1} < 1.$$

Solving for g, we have

$$(g - 1)\log\theta\mu q < -\log N$$

and

$$g > \log N/\log(\theta\mu q) + 1.$$

As an illustration, let $N = 500$, and $\theta\mu q = \frac{1}{2}$. Extinction occurs in generation 10 since $g = 10 > (8.966 + 1)$ and $N(\theta\mu q)^{g-1} = 0.977 < 1$. In the Laster-Parvin model extinction time for these parameter values was found to be five generations (Appendix A in: Laster et al. 1976).

Selection Against BC Females

So far we have assumed that the BC males are sterile but that no selective advantage or disadvantage of the BC females exists, either in competition for mates, fertility or viability of offspring. Relaxing this assumption we now explore the effects of female selection while keeping the backcross males completely sterile.

A constant selective advantage of the BC females would cause the BC:V ratio to increase over generations and accelerate the rate of extinction. Furthermore, if initially $R < \rho_1$ the mixed population would increase until advantageous selection for BC females increased R to ρ_1. After this point the population size would decrease and extinction would be only a matter of time. Selective advantage, however, would be very difficult to achieve in laboratory reared strains. Therefore, of much greater concern should be selection against the BC females and the resulting implications for a control program.

Selection against the BC female has essentially the same result regardless of the life stage at which it works. For illustration purposes, only competition for mates will be discussed in detail although the results can be generalized to any form of fitness. Two kinds of relative competitive ability will be considered: constant and increasing over generations.

In the first case, suppose that in the first generation BC females are released in the ratio R_1, but are poorer competitors for V males than are V females. Generally, in the g^{th} generation for every V female that mates with a V male, only CR_g BC females mate (where C, the relative competitive ability, is less than 1) instead of R_g as expected if the BC females were equally competitive. During the g^{th} mating, R_g is defined as the 'physical' ratio of BC:V but $R'_g = CR_g$ is the 'effective' ratio. If there are no fertility or viability differences between strains, then in the $(g + 1)^{th}$ generation the physical ratio is $R_{g+1} = R'_g$. Thus, we have the recursion equation

$$R_{g+1} = R'_g = CR_g = C \cdot CR_{g-1} = C^g R_1 .$$

The cumulative effects of constant selection are shown for several generations in the first two columns of Table 3. Since $C < 1$, the limit of C^g is zero as g goes to infinity. Figure 3 shows the decline in R_g for three values of C.

In the second case, suppose that as the BC females breed with the native V males, their relative competitive ability increases as their genome becomes more like that of the native population. This is not unlikely since each succeeding generation of BC moths looses half of its remaining *V. subflexa* genes because the male parents are

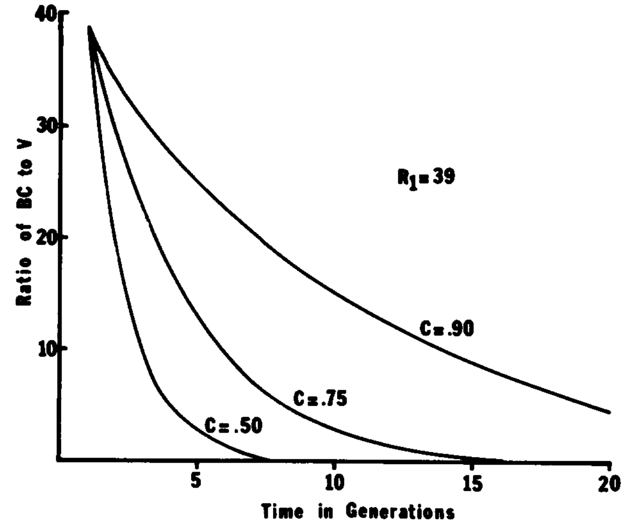

Fig. 3. Ratio of BC:V over generations declines as a function of constant competitive disability for three values of C (constant)

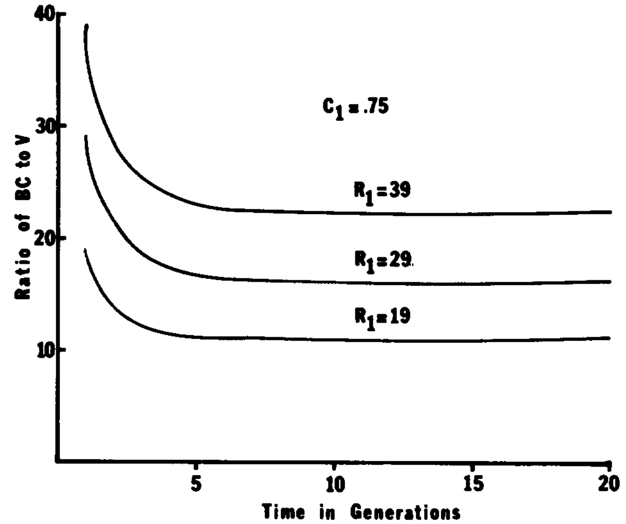

Fig. 4. Ratio of BC:V over generations when initial relative competitive ability of BC females is $C_1 = .75$. Each generation $(1 - C_g)$ is halved

Table 3. Effects of selection against BC on the ratio BC : V females

Generation	Physical ratio	Constant C effective ratio	Increasing C effective ratio
1	R_1	$R'_1 = CR_1$	$R'_1 = C_1 R_1$
2	$R_2 = R'_1$	$R'_2 = CR_2 = C^2 R_1$	$R'_2 = C_2 R_2 = C_2 C_1 R_1$
3	$R_3 = R'_2$	$R'_3 = CR_3 = C^3 R_1$	$R'_3 = C_3 R_3 = C_3 C_2 C_1 R_1$
4	$R_4 = R'_3$	$R'_4 = CR_4 = C^4 R_1$	$R'_4 = C_4 R_4 = C_4 C_3 C_2 C_1 R_1$
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.			
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g	$R_g = R'_{g-1}$	$R'_g = CR_g = C^g R_1$	$R'_g = C_g R_g = R_1 \sum_{i=1}^{g} C_i$

always pure V. Let C_g be the relative competitive ability of the BC female during the g^{th} generation. The physical and effective ratios are noted in Table 3, columns 1 and 3, for several generations. The general recursion equation is

$$R_{g+1} = R'_g = C_g R_g = (\prod_{i=1}^{g}) C_i R_1$$

If C_g approaches unity as g increases then R_g can approach a constant greater than zero. Thus, as the BC genome becomes more like that of V and selection decreases to zero (C increases to 1), the BC:V ratio will stop declining and remain constant at a value between the initial release ratio and zero. Figure 4 shows the effective ratio of BC:V for three values of R_1. In this example, $C_1 = 0.75$ and selection against BC females decreases by half each generation, $C_g = 1\text{-}(1\text{-}C_1)(\frac{1}{2})^{g-1}$. The asymptotic BC:V ratio is about $0.577 \cdot R_1$ and is approached within four or five generations. Figure 5 shows the sizes of two mixed populations with selection ($C_1 = 0.9$) where one competitive coefficient is constant while the other increases toward 1.0. For C = 0.9 (increasing) the population reaches extinction by g = 15 compared to g = 10 for C = 1.0 (no selection). For C = 0.9 (constant) low population sizes are attained in generation 5 through 11 after which the ratio BC:V is very low and the nearly pure V population is again able to increase rapidly.

One way to compensate for selection against BC would be to release them in a higher initial ratio. If in generation g (≥ 3) a total population size (BC + V) of η or less would be tolerable we have the relationship, modified from T2 (1,g),

$$N\theta^{g-1}\mu^{g-1} \prod_{i=2}^{g-1} q_i \leq \eta \,.$$

If C is constant over generations, then $q_i = 1/(C^{i-1} R_1 + 1)$; if C changes each generation then

$$q_i = 1/(1 + R_1 \cdot \prod_{j=2}^{i} C_{j-1}).$$

By the third generation (g = 3), we find that a release ratio of

$$R \geq (N\theta^2\mu^2/\eta - 1)/C_1$$

will result in a total population size smaller than any given η for either a constant or changing relative competitive ability. For $g \geq 4$, the equations are polynomials of degree two or greater. Figure 6 shows the required release ratio R which will result in a total population size of η by generation g for a constant C. For simplicity the desired total population size in the g^{th} generation is set equal to the original pure V population size of generation 1. Here $\theta\mu = 6$, and four values of constant C are plotted for comparison against C = 1.0 (no selection), for which the required release ratio asymptotically approaches $\theta\mu - 1 = 5$. For C < 1.0, however, the required R reaches a minimum around generation six and increases thereafter. This latter increase is to compensate for the rapidly decreasing BC:V ratio in later generations. It appears that if selection is acting against the BC genome, the most effective release strategy would be to aim for minimal population size in the fourth to sixth generations. To achieve a small population size by the third generation requires the release of nearly twice as many BC insects than if the same population size were desired in the fourth or later generations.

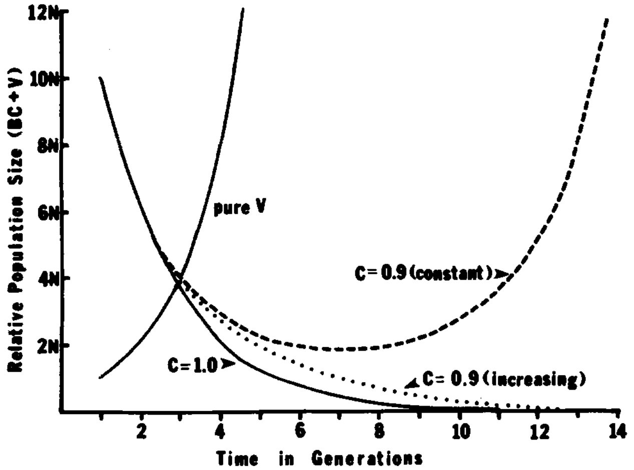

Fig. 5. Population size (one sex only) over generations for $\mu = 3$, $\theta = 2$ and R = 9. Effects of selection are shown for C = 0.9 (constant, and increasing). Pure V and no selection population curves are provided for comparison

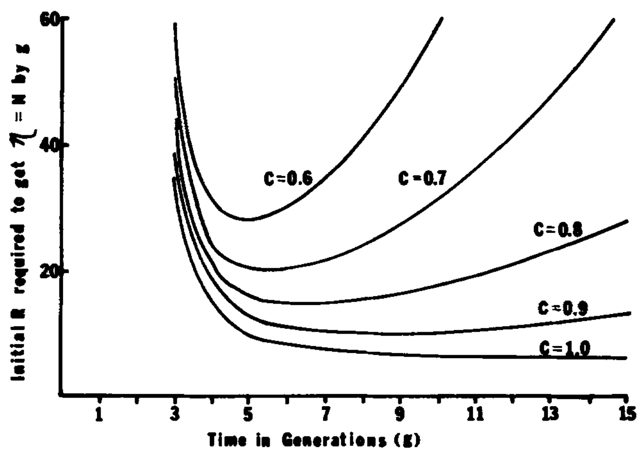

Fig. 6. Initial release ratio required if a population size of η = N is desired by the generation given for four values of competitive ability (C is constant)

Biological Implications of the Model

Up to this point, several implications of the present model have been explored from a mathematical point of view. It is equally important to understand from a biological and economical standpoint the implications of this model for the planning and implementation of a genetic control program against *H. virescens* using releases of BC strains.

The cost of a release program must be balanced against its benefit; that is, the cost of rearing and releasing a given number of BC insects should be weighed against the increased value of a crop from reduced insect damage. We have seen that high release ratios cause a more rapid decimation of V populations. Low values of R may be more economical to produce but may have undesirable effects and may even be completely contrary to the goals of the control program. In order to calculate a release ratio which has the properties consistent with the goals of a particular control program, several parameters of the populations must be known. The necessary parameters are θ, μ, and C over generations. N, the size of the native population, must also be known to calculate the number of BC insects to be released once a suitable R has been determined.

θ, Population Increase per Generation

The parameter θ, the amount of population increase per generation, has been assumed to be constant over generations and independent of population size or density. Clearly, however, the reproductive capacity of a population will depend a great deal on weather, time of the season, availability and type of host plant, winter severity and several other environmental factors (Hartstack 1976). In Texas, for instance, θ may vary between two and ten within a single season. (A.W. Hartstack, Jr., personal communication).

In the BC control model, θ partially determines whether a mixed population will increase or decrease in absolute numbers. If $R > \theta_g \mu - 1$, where θ_g is the growth rate of the g^th^ generation, then the population will decrease in that generation. The size of the population, therefore, may fluctuate with θ_g if the release ratio is near an 'averaged' $(\theta\mu - 1)$. Also, a constant or randomly fluctuating θ implies that all mortality is density-independent, a necessary condition for the mixed population to go to extinction. If, however, θ increases as the population size decreases a balance may be achieved if θ approaches $(R + 1)/\mu$. Regardless of whether the mixed BC + V population decreases or increases with time, however, its capacity to reproduce is significantly impaired when compared to that of a pure V population. Recall that the mixed to pure population ratio (M:P) is $\mu(\mu q)^{g-2}$ in the g^{th} generation. If economic damage is directly proportional to the absolute population size, the relative benefit of a release would be related to this ratio in which θ is cancelled out.

Pair et al. (1977b) showed that females mated to fertile males may have lower fertility if subsequently mated to sterile males. Since this infertility appears to be the same for both V and BC females, only θ is affected. Thus, while we have so far ignored the sterile BC males, their presence may have the effect of lowering the rate of population increase, θ.

μ, Male Mating Capacity

While θ varies considerably over generations and is difficult to estimate, μ, the capacity of V males to inseminate females should be more constant and is extremely important.

Recall that the central idea in the model is that the overwhelming number of BC females draw off the majority of V males and thereby reduce the number of V females that are fertilized. If the release ratio is small, i.e., $R \leq \rho_3 = \mu - 1$, then all females of both types could be accommodated by the fertile V males each generation. The population would increase at the same rate as a pure population. No benefit would be realized in this situation since damage to crops would be increased as much as R-fold.

The effect in the first generation of releasing a very large number of virgin female insects into an area is that the number of eggs laid is μ times the number of eggs which would have been laid had not the release been made. Clearly, the release of BC insects should not be made at a time when females are laying eggs on valuable crops. By releasing several generations prior to crop susceptibility, the initially large number of insects is reduced since the crossover point is reached before the crops can serve as host plants. If adults of the second generation lay their eggs on cotton crops, as is often the case (Laster et al. 1976), then the population size in the third generation should be smaller than if the release were not made. This means that R must be greater than $\rho_2 = \mu^2 - 1$, as it is for $R = 9$ in Fig. 2.

It has been assumed that each time a male mates, he fertilely mates with a virgin or with a female who has previously mated only with BC males. This made μ represent both the number of times a male mates and the number of females he fertilizes. These female moths, however, are multiple maters (up to six times) although their mating drive is reduced for several days following a fertile mating. Also not every mating attempt with a V male results in her laying fertile eggs. Therefore, the number of fertilized females/male is something smaller than the number of times he mates. On the other hand, multiply mated females more often lay fertile eggs and these eggs have a higher hatch rate than singly mated females (Pair et al. 1977b). While these differences may quantitatively change predictions they do not change the way the model works because most of these 'refinements' can be accommodated by adjusting the values of the parameters already in the model or by changing them over generations.

The estimation of μ, the number of times a male mates, should be done under circumstances similar to those found in an actual release situation: males with an overwhelming number of females. Previous estimators equated μ with the mean number of spermatophores found in a sample of wild caught females (Laster et al. 1976). This is probably an underestimate of μ because (1) it does not represent a lifetime mean since the females were of varying ages and (2) satiated females probably impose behavioral limitations on the total amount of mating. These limitations would not occur with a large excess of unmated females. If a male can mate with a single female on any given night and if he can mate every night, μ may be close to his adult life span, 8 to 10 days. Environmental factors, however, such as adverse weather, phases of the moon, or non-uniform spatial distribution may reduce the male coupling rate. Also, multiply mating females and the fact that not all mating attempts result in fertilization make adjustments on μ necessary before it can be used in the model to obtain estimates of optimal release ratios and make predictions. While such determinations are not trivial undertakings (Wiedhaas et al. 1968), we feel that their importance is paramount.

C, the Relative Competitive Ability

Some preliminary investigations (Laster et al. 1977; Pair et al. 1977; Laster et al. 1978) indicate that BC females are as attractive to V males as are V females and that under laboratory conditions BC eggs and larvae survive as well as those of the V type, even though the males are sterile. However, since the potential for selection of laboratory-adapted strains does exist, it could possibly be controlled by the incorporation of genetic material from fresh natural strains of V males every few generations. It is not anticipated that selection against BC females will be a serious problem although assortative mating might be. One potential problem has recently come to light due to two discoveries. First, sequential matings of the type 'V first, BC second' resulted in greatly reduced fertility compared with single matings to V males (Pair et al. 1977b). Secondly, male BC moths were not observed mating to V females in field experiments where V males were readily mating with both BC and V females (Raulston et al. in press). Thus, BC females may experience lower fertility due to their reduced egg lay and hatch rate from secondarily mating with BC males which the V females are reluctant to do. Thus, experiments under natural conditions may determine whether BC females can compete for V and BC males, survive under natural conditions and overwinter as well as V females.

Discussion

We have assumed in our model that the native population is closed; i.e., no immigration occurs. If, however, a control program based on this model were to be implemented in a small target area within a continental population, the effects of the migration of V and BC insects would be complex but crucial to the success of the program. At the time of release, R has meaning only within the well defined target area. As migration occurs between the target area and the surrounding population the BC:V ratio would inevitably decrease. Also, after several generations, the mixed population in the target area would be smaller (less dense) than populations in surrounding areas where the BC moths would have had little effect. The diluting effect of immigration would, therefore, be enhanced by the low population density and R would be reduced still further. Thus, a large native population outside the release area would eventually swamp the BC insects in the target area resulting in a drastically reduced and ineffectual ($< \rho_3$) BC:V ratio.

An idea inherent in the Laster-Parvin model is that the diluting effect of in-migrating V insects would be overcome by the apparently increasing BC:V ratio over generations. If this were true, a circular wave of extinction could propagate outward from the target area as the BC females diffuse into new native populations. An analogy can be made to an epidemic in which the disease organism feeds on its host and grows ever more abundant. In this paper, we have amply demonstrated that R is constant (or decreasing in the presence of migration) and, therefore, such a genetic epidemic cannot occur.

Local releases will eventually be rendered ineffective by migration, so that periodic monitoring or R will be necessary to maintain control within a target area. Gassner and Proshold (1978) have described an immunoelectrophoretic assay which holds promise for distinguishing the backcross from the pure *H. virescens* type. Thus, once control has been achieved within an area, small periodic BC releases may be necessary to keep R above a certain level by counteracting the effects of immigration.

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