The Sterile Insect Release Method for Pest Control: a Density-Dependent Model[1]

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ABSTRACT

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A logistic model of population growth is presented which describes the effects of introducing sterile individuals into a wild population regulated by density-dependent factors. It is shown that for certain levels of sterile releases two steady states exist, of which the upper state is stable and the lower state is unstable. Once a population is driven to below the lower threshold, continued releases will cause (local) extinction. The 2 steady states exist for a wide variety of density-dependent growth functions. The release of sterile males alone is less effective than the release of sterile males and sterile females but not importantly so; however, the release of sterile females alone is not a satisfactory strategy for eradication.

Insect population control by the release of sterile males is one of several available techniques for genetical pest control (Whitten and Foster 1975). The technique was suggested first by Knipling (1955). It was applied successfully in the field notably against the screwworm, *Cochliomyia hominivorax* (Baumhover et al. 1955) and against several fruit fly species (Iwahashi 1977).

Knipling (1955) examined some basic requirements for successful pest control by the sterile insect release method (SIRM), in particular the numerical relationship between the numbers of sterile and fertile males. His model was based on a simple difference equation that enabled trends in population numbers to be predicted by computer simulation for given parameter values (Knipling 1967). Some of the assumptions inherent in Knipling's model were biologically unrealistic and, in fact, were relaxed in later population studies.

The first algebraic treatments of the SIRM, based largely in Knipling's model, appear to be due to Berryman (1967) and Lawson (1967). Zouros (1969) compared the effectiveness of the method for monagamous and polygamous females. The effects of environmental stochasticity and carrying capacity were considered by Kojima (1971) in a computer simulation. Later Costello and Taylor (1975) developed an analytical stochastic model that included the environmental carrying capacity as one of the parameters. Other models that incorporated certain types of density regulation were proposed recently. Miller and Weidhaas (1974) presented a mathematical formulation that allowed for density-dependent mortality during the larval but not during the adult stage. Dietz (1975) incorporated crowding into a stochastic computer model and, in a later paper (Dietz 1976) considered the effect of immigration on sterile male releases. For the melon fly, *Dacus cucurbitae*, Itô (1977) presented a logistic growth model that allowed for density-dependent changes in the rate of population increase. Prout (1978) examined the effects of sterile male releases, with and without immigration, on a pest species in which the survival of the newly hatched larva to the adult stage is density-regulated, and Barclay and Mackauer (1980) examined the effects of predation on the SIRM.

The purpose of this paper is to extend the algebraic treatment of the SIRM to several, and more general, density-dependent situations. Because of the structural differences betwen models published so far, we were interested to determine in particular whether the steady population equilibria predicted for several specific situations are a common and a fundamental consequence of density-dependent regulation or are an artifact of certain simplifying assumptions of the models. We adopted a continuous rather than a discrete population model, but similar results would have emerged from a discrete model for a restricted range of the parameters. Logistic population growth was assumed for most cases, although some of the results were derived for more general growth functions.

The models presented below, we believe, are the first fully dynamic SIRM models; they incorporate density dependence for all levels of density and, in a separate equation, incorporate the dynamics of the sterile individuals themselves. Thus our models are appropriate for cases where breeding is continuous or where significant mortality occurs within a generation. This is in contrast to models based on difference equations, which are particularly useful for cases where all population events occur only once per generation or other time period, where breeding is synchronous, and where the intervals between breeding cycles are short.

General Format of the Models

Mathematical models for the SIRM essentially fall into one of two classes, viz. deterministic and stochastic models; either class may include discrete or continuous time elements. The advantages and disadvantages of the two classes of models were discussed in detail by Costello and Taylor (1975).

Knipling (1955) proposed a simple deterministic model assuming discrete generations and geometric population growth; his model has the form of a difference equation

$$f_{t+1} = \lambda f_t \left(\frac{m_t}{m_t + n_t} \right) \tag{1}$$

where f_t and f_{t+1} represent, respectively, the number of fertile females present in the population at times t and

$t + 1$, m_t is the number of fertile males present at time t, n_t is the number of (introduced) sterile males alive at time t, and λ is the geometric rate of population increase.

The analogue of Eq. (1) for continuous population growth is

$$\frac{df}{dt} = b \cdot f \left(\frac{m}{m + n} \right) - c \cdot f \qquad (2)$$

where $r = b-c = \ln(\lambda)$; the parameter r represents the rate of population increase per generation under ideal conditions, that is, the natural birth rate, b, minus the death rate, c, per individual. A stability analysis shows that Eq. (2) has a single, unstable steady state or threshold. If the number of sterile males being released is larger than a critical number n_c then the population will go extinct provided that the releases are continued; the magnitude of n_c depends on the number of wild females present at time t. If the number of sterile males being released is smaller than n_c, then the wild population will escape control and increase roughly exponentially.

We introduce density dependence into the exponential growth equation by means of the logistic equation

$$\frac{dN}{dt} = r N \left(1 - \frac{N}{K} \right) \qquad (3)$$

where N and K represent the total population size and the carrying capacity of the environment, respectively.

We incorporated into our model(s) the following explicit assumptions that would seem to apply to a rather wide range of biological situations: (a) populations exist as a continuum and reproduce continuously over time; (b) population growth follows a logistic curve, except under conditions that can be described by more general growth functions; (c) the carrying capacity of a given environment is constant; (d) sterile males are fully competitive with fertile males; (e) mating is at random, and the proportion of fertile matings is in direct proportion to the number of sterile and fertile individuals present in the population; (f) both sexes are monogamous or, if females mate more than once, sterile sperm is fully competitive with fertile sperm; (g) if polygamy occurs, each individual mates a random number of times; the number of matings follows a Poisson distribution with an identical mean for all individuals; (h) the population sex ratio is one-to-one throughout life; (i) the release of sterile individuals is continuous and at a rate constant per unit of time and per unit of habitat; and (j) the release leads to the complete and instantaneous mixing of wild and treated individuals.

Specific Models

The extent to which density dependence affects the SIRM hinges on whether either births or deaths, or both, are density-dependent. We examine the relationship by increasing, step by step, the generality of the models: from a model assuming density-independent births and density-dependent deaths to a general model assuming that all population growth parameters are density-dependent.

Density-independent Births, Density-dependent Deaths

Release of Sterile Males and Sterile Females.—We rewrite the logistic Eq. (3) to separate the population rate of increase, r, into its component elements, making the individual birth rate, b, density-independent and the death rate, c, density-dependent under ideal conditions

$$dN/dt = (b - c) N - [r (N^2/K)]. \qquad (4)$$

Because fertile females constitute exactly one half of the wild (fertile) population, by assumption h, Eq. (4) can be rewritten as

$$df/dt = f(a_1 - a_2 - 2gf) \qquad (5)$$

where a_1 is the birth rate, a_2 is the density-independent death rate, g is a crowding parameter inversely proportional to the carrying capacity, and $f = N/2$. The rate of change of the sterile male population, n, is defined by

$$dn/dt = R - a_2 n - 2g(f + n)n \qquad (6)$$

where R represents the rate of release of sterile males. With sterile males present Eq. (5) becomes

$$df/dt = f[a_1(f/f+n) - a_2 - 2g(f + n)]. \qquad (7)$$

We proceed with a stability analysis of Eq. (6) and (7). The stability characteristics for this model are shown in graphical form in Fig. 1 and have also been
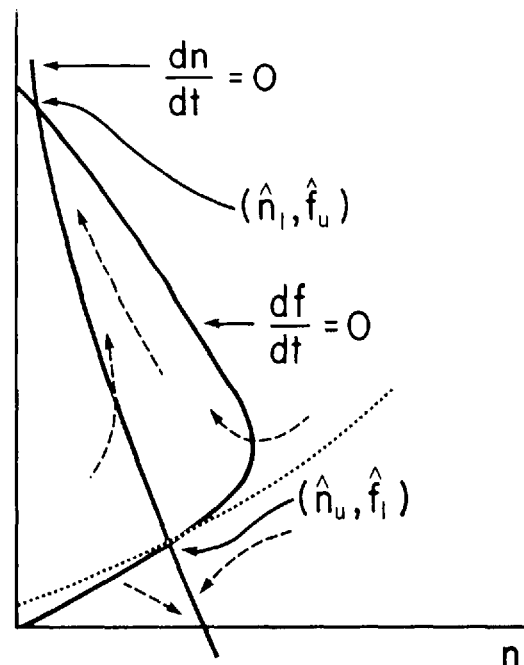

Fig. 1.—Isoclines formed by setting the two derivatives to zero from Eq. (6) and (7). Trajectories are shown as dashed lines with arrows. Systems which can be reduced to having coordinates below the dotted line, which passes through $(\hat{n}_u, \hat{f}_l)$, will go extinct.

derived algebraically[2]. The curves shown in Fig. 1 and 2 represent the zero isoclines of the time derivatives from Eq. (6) and (7) with $dn/dt = df/dt = 0$. The points of intersection of the two curves represent the steady states of the system, and the arrows represent trajectories of n and f at various points in the (n,f) plane. These trajectories illustrate the qualitative aspects of the stability of the steady states. If the two curves do not intersect, then the system is unstable, and the fertile population declines and goes extinct provided that sterile releases are continued at their previous level.

Equilibria

Eq. (6) and (7) have two positive steady states which can be obtained by setting $dn/dt = df/dt = 0$. The equilibrium value of n, called $\hat{n}$, is obtained by solving the resulting cubic equation

$$2ga_1n^3 + a_1a_2n^2 - R(a_1 + a_2)n + R^2 = h(n) = 0. \tag{8}$$

All parameters being positive, by Descartes' rule of signs Eq. (8) has exactly one negative root and either two positive real roots or two complex roots (i.e., the roots are complex if the isoclines in Fig. 1 do not intersect) for any given value of R. We will call $\hat{n}_u$ the upper (larger) positive real root, if it exists, and $\hat{n}_l$ the lower positive real root.

Equation (7) provides the steady state of f, called $\hat{f}$, in terms of $\hat{n}$

$$\hat{f} = \frac{\frac{a_1 - a_2}{2g} - 2\hat{n} \pm \sqrt{\left(\frac{a_1 - a_2}{2g} - 2\hat{n}\right)^2 - 4\hat{n}(\hat{n} + a_2/2g)}}{2}$$

$$= \frac{a_1 - a_2}{4g} - \hat{n} \pm \frac{\sqrt{\left(\frac{a_1 - a_2}{2g}\right)^2 - \frac{2a_1\hat{n}}{g}}}{2} \tag{9}$$

for which we have two possible values, one of which can be excluded by using Eq. (6). Fig. 1 shows that only $(\hat{n}_l, \hat{f}_u)$ and $(\hat{n}_u, \hat{f}_l)$ represent steady states.

Equation (9) has two positive real roots if and only if the discriminant is positive, i.e., if

$$\hat{n} < \frac{(a_1 - a_2)^2}{8ga_1} \tag{10}$$

By increasing R a point is reached at which the two zero isoclines become tangent to each other; at that point $(\hat{n}_u, \hat{f}_l) = (\hat{n}_l, \hat{f}_u)$ (Fig. 2). We label the point $(\hat{n}^*, \hat{f}^*)$ and call it the breakpoint; and we call R^* the value of R which results in it. If R is increased further beyond R^* and maintained there, then f will decline to zero since no positive equilibrium exists for $R > R^*$; ie., the zero isoclines will not intersect at all. The value of $\hat{n}^*$ can be found by differentiating Eq. (8) and setting this to zero, which yields an equation for the minimum of Eq. (8); this represents the breakpoint when the minimum falls on the n axis (Fig. 3). Solving for R and substituting this back into Eq. (8) gives
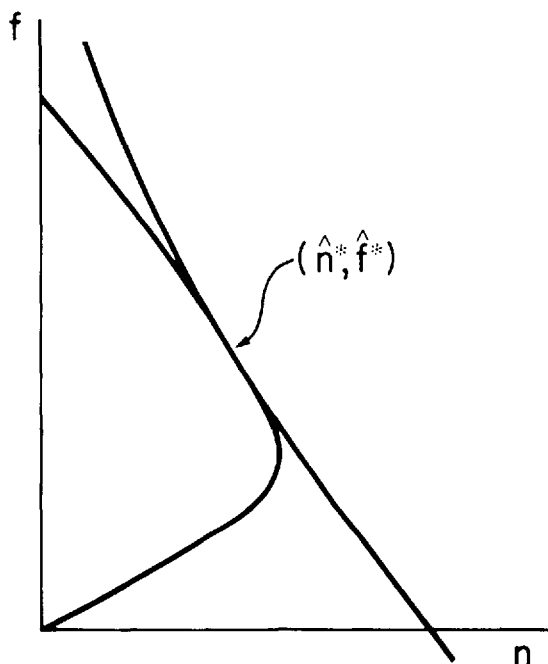
[2] Stability analysis available from the authors on request.

FIG. 2.—Isoclines which are tangent to each other. Here R $= R^*$ and the system is unstable.
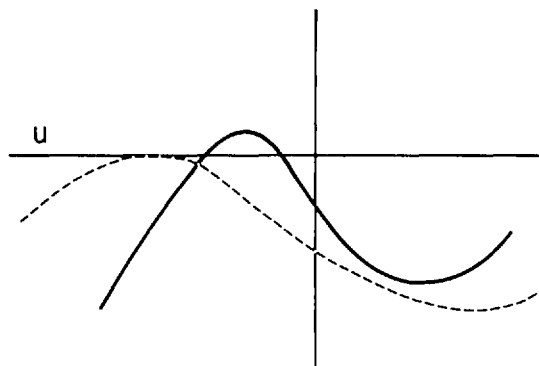

FIG. 3.—The graph of the cubic equation for $\hat{n}$, the equilibrium value of the number of sterile males. When $R = R^*$ the curve is tangent to the n-axis and $\hat{n}_u = \hat{n}_l$.

$$\hat{n}^* = \frac{a_1^2 - 4a_1a_2 + a_2^2 + \sqrt{(a_1 + a_2)(a_1^3 + a_2^3)}}{18a_1g} \tag{11}$$

whence

$$R^* = \frac{2a_1^4 + 2a_2^4 - 6a_1^2a_2^2 - a_1^3a_2 - a_1a_2^3}{54a_1g(a_1 + a_2)}$$

$$+ \frac{2(a_1^2 - a_1a_2 + a_2^2)\sqrt{(a_1 + a_2)(a_1^3 + a_2^2)}}{54a_1g(a_1 + a_2)} \tag{12}$$

An equation for $\hat{f}^*$ can similarly be found by substituting $\hat{n}^*$ and R^* into Eq. (6) set to zero. It is worth noting

that if a_1 is much larger than a_2, then $\hat{n}^* \doteq \dfrac{a_1}{9g}$, or slightly less than 1/4 of $\hat{f}_u$ when $R = n = 0$

$$\text{and } R^* \doteq \frac{2a_1{}^2}{27g} = \frac{4a_1}{27} \left[\begin{array}{l} \text{times the values of} \\ \hat{f}_u \text{ when } R = n = o \end{array} \right].$$

Stability

If Eq. (6) and (7) are set equal to zero and the resulting functions plotted in the (n, f) plane, we obtain the zero isoclines, that is, the set of all points for which $\dfrac{df}{dt} = 0$ and for which $\dfrac{dn}{dt} = 0$. As noted above, the points of intersection of these two isoclines represent steady states in which both derivatives are simultaneously zero. It can be shown by differentiating each of Eq. (6) and (7) twice that $\dfrac{d^2n}{df^2} > 0$ for Eq. (6) and $\dfrac{d^2n}{df^2} < 0$ for Eq. (7) for all positive values of n and f. Thus the concavity of the two curves is opposite everywhere in the positive quarter plane; and in that region

the zero isoclines will intersect in no more than two points. One can plot qualitatively correct trajectory segments (as in Fig. 1) and determine that the upper point $(\hat{n}_l, \hat{f}_u)$ is stable while the lower point $(\hat{n}_u, \hat{f}_l)$ is unstable.

Numerical simulations confirm these conclusions and also indicate that the system is stable even under considerable perturbations provided that R is not too close to the critical value R* (Fig. 4–7). A linearized stability analysis indicates that the system is locally stable if $R < 2g(\hat{f}-\hat{n})\,(\hat{f}+\hat{n})$ which limits stability to R < R* and also to $(\hat{n}, \hat{f}) = (\hat{n}_l, \hat{f}_u)$. The actual region within which f inevitably declines to extinction is shown in Fig. 1 as the area below the broken line.

The two basic consequences of density dependence are: One, a much lower level of sterile releases is needed to cause population extinction with density-dependent than without density-dependent regulation. For example, considering two populations at comparable levels at the beginning of the SIRM, the minimum number required for control is n > roughly one-quarter of carrying capacity with density-dependence but n > $(\lambda - 1) \cdot f$ without density-dependent regulation. To maintain n at one-quarter of carrying capacity requires
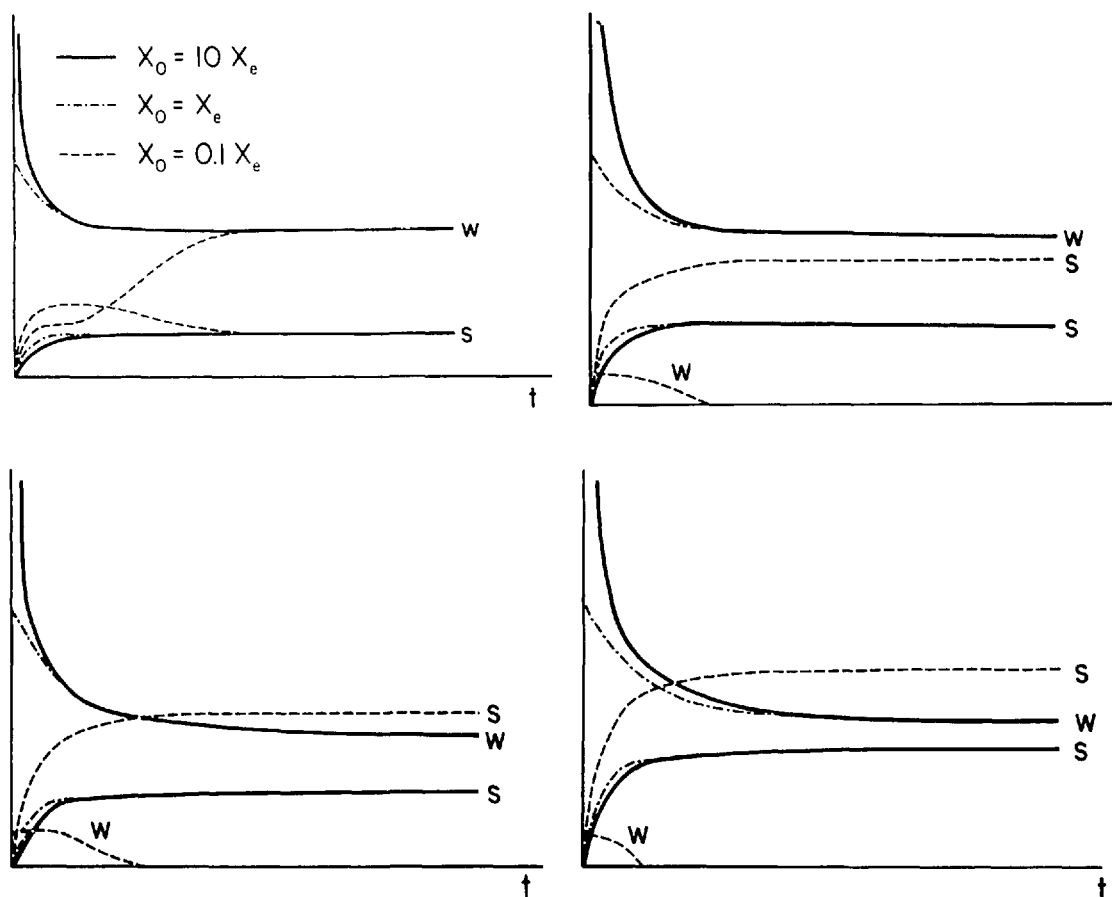

FIG. 4–7.—Computer generated solutions of Eq. (6) and (7) for selected values of the parameters. The parameter values used were as follows: $a_1 = 10$; $g = 10^{-3}$ throughout; 4(top left).—$a_2 = 1$; R = 0.75R*; 5(top right).—$a_2 = 4$; R = 0.75R*; 6(bottom left).—$a_2 = 1$; R = 0.95R*; and 7(bottom right).—$a_2 = 4$; R = 0.95R*. For each of these combinations 3 starting values were used (See Fig. 4); the wild populations were started at (a) 10% of the stable equilibrium, (b) 100% of the stable equilibrium, and (c) ten times the stable equilibrium. Sterile populations always started at zero.

a release rate of $r = \dfrac{4a_1}{27}$ times the carrying capacity, which is much less than $(\lambda - 1)f$, since $a_1 - a_2 = \ln(\lambda)$. Two, the lower of the two equilibrium points is unstable. If the population can be reduced to a level below $\hat{f}_l$, then it will continue to decline to extinction provided of course that the sterile releases continue. And further, eradication can be achieved with levels of sterile releases that would not cause extinction at population levels greater than $\hat{f}_l$. The existence of $\hat{f}_l$ has important practical implications. It is generally advisable in all cases where appreciable density-dependent factors act on a population at its usual level to reduce that population to a point below $\hat{f}_l$ prior to the SIRM, e.g., by the application of insecticides. An appropriate value of $\hat{f}_l$ can be approximated by knowing the maximum feasible release rate.

Release of Sterile Males Only.—For species in which the females transmit a medically important parasite, for example, it may be desirable to release only sterilized males. Under these conditions, Eq. (6) and (7) become

$$\frac{dn}{dt} = R - a_2 n - g(2f + n) \tag{13}$$

$$\frac{df}{dt} = f\left[\frac{a_1 f}{f+n} - a_2 - g\,(2f+n)\right] \tag{14}$$

which, when set equal to zero and solved together, yield

$$g \cdot a_1 n^3 + n^2(a_1 a_2 + Rg) - Rn(a_1 + a_2)$$
$$+ R^2 = o. \tag{15}$$

The derivative of Eq. (15) with respect to n is

$$3g \cdot a_1 n^2 + 2n(a_1 a_2 + Rg) - R(a_1 + a_2). \tag{16}$$

When Eq. (16) is solved for R and substituted back into Eq. (15) we obtain a cubic equation for $\hat{n}^*$

$$2g^3 \cdot n^3 - g^2[14a_1 + 5a_2]n^2 + 2ga_1(a_1 - 5a_2)n$$
$$+ a_2(a_1 - a_2)^2 = o. \tag{17}$$

We obtained $\hat{n}^*$ by iterative methods for a small sample of parameter values and compared these values with the corresponding values involving release of both sexes (Table 1). For the values chosen, the release of sterile

males only is not much less effective than the release of sterile individuals of both sexes. In fact, the number of males required to achieve the breakpoint with the release of males only is ca. 20% higher than the number of males needed if both sexes are being released. This suggests the rather intuitive conclusion that near the breakpoint the depression due to sterility considerably outweighs that due to density dependence.

Release of Sterile Females Only.—Whereas the release of sterile females may not constitute a practical approach to SIRM it is interesting to note that such releases can cause extinction purely through density-dependent depression. Modifying Eq. (7) to remove the sterile male effect, we obtain the $\hat{n}$ necessary for extinction as $\dfrac{a_1 - a_2}{2g}$, which is exactly equal to the carrying capacity of the wild population. The release rate necessary to achieve this is $R = a_1 \hat{n} = a_1 \dfrac{(a_1 - a_2)}{2g}$, which is quantitatively comparable to the value of $(\lambda - 1)f$ sterile males required in the absence of density dependence.

Density-dependent Births and Deaths

Including density dependence in the birth rate as well as in the death rate in Eq. (6) and (7) results in behaviour qualitatively similar to that of Eq. (6) and (7).

$$\frac{df}{dt} = f[\underset{\text{births}}{a_1 - a_3(f)} - \underset{\text{deaths}}{(a_2 + 2gf)}] \tag{18}$$

In the presence of steriles of both sexes Eq. (18) becomes

$$\frac{df}{dt} = f\left[\{a_1 - a_3(f + n)\}\left(\frac{f}{f+n}\right) - (a_2 + 2g(f+n)) \right] \tag{19}$$

Eq. (6) remains unchanged, so that setting the derivatives to zero and solving for the equilibria yields

$$2g(a_1 + a_2 a_4)n^3 + [a_1 a_2 + (a_2{}^2 - 2gR)a_4]n^2 \tag{20}$$
$$- R(a_1 + a_2 + 2a_2 a_4)n + (1 + a_4)R^2 = o$$

in which $a_4 = \dfrac{a_3}{2g}$.

Table 1.—Comparison of release rates required for achieving population breakpoint when both sterile males and females or sterile males only are released (a_1 = birth rate, a_2 = death rate, g = crowding parameter, $\hat{n}^*$ = number of sterile males present at equilibrium, R^* = release rate required for achieving breakpoint; see Fig. 2).

Parameter values			Sterile males & females		Sterile males		Breakpoint ratio[a]
a_1	a_2	g	$\hat{n}^*$	R^*	$\hat{n}^*$	R^*	
10	1	10^{-3}	9.2×10^2	6.3×10^3	1.2×10^3	7.6×10^3	1.21
10	1	10^{-6}	9.2×10^5	6.3×10^6	1.2×10^6	7.6×10^6	1.21
10	5	10^{-3}	3.05×10^2	2.36×10^3	3.5×10^2	2.7×10^3	1.14
10	5	10^{-6}	3.05×10^5	2.36×10^6	3.5×10^5	2.7×10^6	1.14
100	1	10^{-3}	1.1×10^4	7.4×10^5	1.4×10^4	8.8×10^5	1.19
100	1	10^{-6}	1.1×10^7	7.4×10^8	1.4×10^7	8.8×10^8	1.19
100	5	10^{-3}	1.0×10^4	6.67×10^5	1.2×10^4	8.2×10^5	1.23
100	5	10^{-6}	1.0×10^7	6.67×10^8	1.2×10^7	8.2×10^8	1.23

[a] The breakpoint ratio, $r^* \male/r^* \male + \female$, gives the factor by which the number of sterile males in males-only releases exceeds the corresponding number in males-and-female releases at the breakpoint.

We differentiate Eq. (20), set to zero, solve for R and substitute back into Eq. (20) to obtain a cubic equation for $\hat{n}^*$. The points to note here are that the two zero isoclines obtained from Eq. (6) and (19) have opposite concavity for all n and $f > o$. This is because differentiating Eq. (20) twice with respect to f and solving for $\dfrac{d^2n}{df^2}$ gives

$$\frac{d^2n}{df^2} = \frac{-4g[a_1 - a_3(f + n)]^2}{[a_2 + 4g(f + n) + a_3f]^3} \qquad (21)$$

The corresponding quantity from Eq. (6) is positive. Thus the two isoclines will intersect in no more than two points with $(\hat{n}_l, \hat{f}_u)$ being stable while $(\hat{n}_u, \hat{f}_l)$ being unstable.

Density-Dependent Births and Deaths with More General Formulations

Considerably more general birth and death functions than those of Eq. (6), (7), or (19) can be shown to yield two positive steady states, one of which is stable and the other unstable. Here we assume a 1:1 sex ratio among the releases. Consider the population growth equation

$$\frac{df}{dt} = f[g(f) - h(f)] \qquad (22)$$

in which g(f) is a possibly density-dependent birth rate, such that g is continuous and whose first and second derivatives are both non-positive, while h(f) is a (possibly) density-dependent death rate and whose first and second derivatives are both non-negative. If either the birth rate or death rate is density-independent, then both the first and second derivatives of g or h, respectively, are zero. Density dependence makes the first derivative non-zero and generally the second derivative as well. In addition, $g(o) = b$ and $h(o) = c$ (Fig. 8). These assumptions are fairly reasonable except at extremely low density when mates are difficult to find.

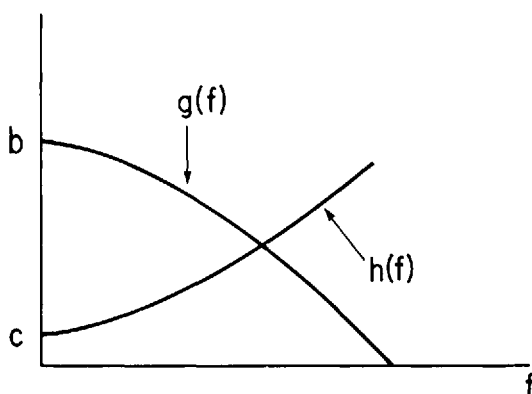For the release of sterile individuals of both sexes, we obtain

$$\frac{df}{dt} = f\left[\left(\frac{f}{f+n}\right) g(f) - h(f + n)\right] \qquad (23)$$

$$\frac{dn}{df} = R - h(f + n)\cdot n \qquad (24)$$

With the restrictions imposed on g and h it can be shown that the zero isoclines are of opposite concavity given one further provision on h.

The concavity and general shape of the zero isocline from Eq. (23) is similar to that from Eq. (7). It can be shown that $\dfrac{d^2n}{df^2} < o$ (for n, $f>1$) if one differentiates Eq. (23) twice and solves for $\dfrac{d^2n}{df^2}$. This derivation is omitted due to its length but will be supplied by the authors upon request.

Similarly, starting with Eq. (24) set to zero,

$$\frac{r}{n} = h (f + n). \qquad (25)$$

Then differentiating with respect to f and solving for $\dfrac{dn}{df}$

$$\frac{dn}{df} = \frac{-h'(f + n)}{\dfrac{R}{n^2} + h'(f + n)} \qquad (26)$$

where $h'(f + n) = \dfrac{d[h(f + n)]}{d(f + n)}$
Differentiating again and solving gives

$$\frac{d^2n}{df^2} = \frac{R}{n^4}\left[\frac{2n\{h'(f + n)\}^2 - Rh''(f + n)}{\dfrac{R}{n^2} + h'(f + n)}\right] \qquad (27)$$

which will be positive unless

$$Rh''(f + n) > 2n\{h'(f + n)\}^2. \qquad (28)$$

Inequality (28) is unlikely to be satisfied except when n is near zero. In the previous specific models considered, $h'(f + n) \geqslant o$ while $h''(f + n) \equiv o$ for all f, n. Thus this final restriction may not really be so restrictive in fact.

Since the two isoclines are of similar qualitative shape to those of Fig. 1, the same qualitative stability criteria apply to Eq. (23) and (24) as to Eq. (6) and (7).

The conditions outlined here are sufficient but not necessary for the two zero isoclines to have opposite concavity throughout their range of possible intersections. Furthermore, the two isoclines often will intersect in no more than two points even if the isoclines are not everywhere of opposite concavity. Thus, although the restrictions put on the functions g and h guarantee that there are at most two intersections, many other functions not so restricted would also have at most two equilibria, one of which will be unstable. For example, the condition that $g'(f) \leqslant o$ for all $f > o$ precludes the Allee effect, that is, growth at low densities is depressed due

Fig. 8.—The birth function g(f) and the death function h(f).

to the difficulty of finding mates. However, the Allee effect is likely to help rather than to hinder any SIRM program. A large proportion of existing growth models are special cases of Eq. (22) including its restrictions. We therefore believe that the result derived is a very robust one; that is, density dependence in a SIRM program will virtually always result in two steady states, the lower of which is unstable.

The Possibility of Limit Cycles

The trajectories in Fig. 1, while demonstrating general stability or instability, do not exclude the possibility of limit cycles. A criterion demonstrating the absence of limit cycles in a region D has been given by Bendixson and extended by Dulac (Hahn, 1967). By Dulac's criterion, if $\dot{x} = P(x,y)$, $\dot{y} = Q(x,y)$ and if $\dfrac{\partial l \cdot P(x,y)}{\partial x} +$ $\dfrac{\partial l \cdot Q(x,y)}{\partial y}$ does not change sign in region D, then there cannot be any limit cycles in region D. Here l is any differentiable function and it is multiplied onto both P and Q. In the present case

$$P(f, n) = \frac{df}{dt} = f\left[g(f)\left(\frac{f}{f+n}\right) - h(f + n) \right] \quad (29)$$

and $Q(f, n) = \dfrac{dn}{dt} = R - n \cdot h(f + n)$. $\quad (30)$

Letting $l = \dfrac{1}{f^2}$ purely for convenience, we find that

$$\frac{\partial [l \cdot P(f,n)]}{\partial f} + \frac{\partial [l \cdot Q(f,n)]}{\partial n}$$

$$= \frac{g'(f) \cdot (f+n) - g(f)}{(f + n)^2} - \frac{\dfrac{\partial [h(f+n)]}{\partial f}}{f}$$

$$- \frac{\dfrac{n \cdot \partial [h(f+n)]}{\partial n}}{f^2} \quad (31)$$

in which every term is zero or negative (for n, f ≥ o) since g'(f) ≤ o, g(f) > o, and the two partial derivatives of h are both zero or positive since h'(f+n) ≥ o. Hence Dulac's criterion is satisfied for all f, n ≥ o, a fact proving the absence of limit cycles. It can be shown that this general result applies to all models considered including releases of one sex only.

Discussion

The potential of the SIRM for pest control has not always been recognized because analytical models appeared oversimplified and, therefore, unsuitable for assessing the decline of target populations. In early models, discrete population processes were assumed and, in particular, density dependence was disregarded as an important factor of population regulation (Berryman 1967, Knipling 1955, Lawson 1967).

We have presented several models, based on continuous population processes, that examine the effects of density dependence on the requirements for a release

program. Three main points emerged from the models with regard to density dependence.

The number of sterile males that must be released to cause a decline in, and the eventual eradication of, the target population is considerably less than the number required for controlling a population of the same size that is not density regulated.

There exist two steady states for any release rate of steriles below the breakpoint level. The upper steady state is stable, and a population will return to it after a moderate perturbation. The lower steady state is unstable, and a population will decline to extinction once its numbers have been reduced to below that threshold provided, of course, that sterile releases are continued. The lower steady state exists for a wide variety of types of density-dependent birth and death rates (Itô 1977, Miller and Weidhaas 1974, Prout 1978).

The impact of the release of sterile males on the wild population is increased by the release of sterile females; this is because of an increase in density-dependent depression. Whereas control and eradication might be achieved by releasing sterile females only, the efficiency of that technique is much less than that of releasing both sexes. However, the efficiency of releasing sterile males only is not much reduced as compared with the release of both sexes.

The reason for the existence of a lower unstable steady state is that, as the population declines, both the individual reproductive rate as well as the efficiency of the SIRM increases. However, whereas the efficiency of the SIRM increases rapidly as the population becomes very small, the reproductive rate approaches its maximum near zero density only asymptotically.

The position of the unstable steady state depends on all parameters incorporated into the model; the position, therefore, cannot be readily predicted unless the pest's biology and phenology are precisely known. The approximate value of the threshold can be estimated if growth is approximately logistic. For ease of control, it is obviously desirable that the value of the lower steady state is high relative to the environmental carrying capacity. Conditions that will contribute to such a situation are a low intrinsic birth and a high intrinsic death rate, a relatively low carrying capacity, and a high rate of sterile releases.

The existence of a lower threshold has implications, also, for what the appropriate prerelease strategy should be. The model predicts that eradication can be achieved at a lower level of sterile releases than would be required if the target population had not been suppressed initially below the threshold, e.g., by insecticide treatments. That conclusion is contrary to the one reached by Costello and Taylor (1975), who used a probabilistic population model employing density-independent growth below the carrying capacity.

Although several of the results derived here have been described earlier by Miller and Weidhaas (1974), Itô (1977), and Prout (1978), their models were considerably less general than those that we have used. In particular, Miller and Weidhaas (1974) and Prout (1978) assumed that only larval survival to the adult stage was density-dependent. As we have shown in this study, density-dependent regulation of either fertility or sur-

vivorship has several robust consequences for any SIRM programme. Pest control strategy, thus, should take into account the existence of the equilibrium states which, we suggest, are a consequence of fundamental regulatory processes rather than of simplifying assumptions incorporated into the models.

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