

## THE STERILE INSECT RELEASE METHOD ON SPECIES WITH TWO-STAGE LIFE CYCLES

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### INTRODUCTION

The sterile insect release method (SIRM) of population control has received considerable attention both experimental and theoretical since its initial formulation (KNIPLING, 1955). Much information of a general qualitative nature can be obtained by mathematical models in which various ecological elements are included with the SIRM. The consequences of these elements can then be obtained by comparing models.

The present paper seeks to extend our understanding of SIRM dynamics by examining a hypothetical species with two life stages which has density dependent processes operating at various points. The groundwork for this has been laid by MILLER and WEIDHAAS (1974) and by PROUT (1978) who constructed two stage life cycle models and to a lesser extent by BERRYMAN *et al.* (1973) whose computer model was somewhat less explicitly two-stage. All these authors treated density dependence only in larval survivorship or the transition between the two stages. To varying degrees they found a decreased efficiency of the SIRM against the adults with this mode of population regulation. MILLER and WEIDHAAS (1974) point out that many insects conform to the assumption that most of the density dependence occurs in larval survivorship. The case can also be made, however, that for comparative purposes it is worthwhile investigating the consequences of the density dependence being in various possible places in the life cycle, especially since the conclusions concerning the efficiency of the SIRM against the adults are affected by the mode of action of the density dependence.

The format of this paper is to work out the model in as great generality as appears feasible, i. e., with parameters not receiving specific values, and then to give various of the parameters specific values for comparative purposes. Mathematical proofs which are not essential to follow the thread of the development have been relegated to appendices.

### THE MODELS

The general model is based loosely on the logistic equation of population growth and assumes a life cycle consisting of two readily distinguishable parts which are ecologically distinct and do not compete with each other for resources. For insects this could be visualized as eggs and larvae lumped into one stage with pupae and

adults being lumped into the second stage. Other taxa may or may not so neatly fit this scheme. Reproduction is assumed continuous and this necessitates the inclusion of an extra equation to describe the dynamics of the released sterile individuals. Steriles are assumed to be released continuously and in equal sex ratio. Time is scaled to generations to make the parameters more interpretable.

#### *A general two stage life cycle*

Letting  $L$  be larval numbers and  $A$  be adult numbers a model of a two stage life cycle is constructed which involves density dependence in each of, larval recruitment, larval losses, adult recruitment and adult losses. The two equations of changes in numbers are:

$$\frac{dL}{dt} = A(a - bA) - L(q + vL) \quad (1)$$

$$\frac{dA}{dt} = L(c - eL) - A(s + uA) \quad (2)$$

in which the first term in each equation represents density-dependent recruitment and the second term represents density-dependent losses. The losses in the larval stage are composed of both mortality and transition to the pupal or adult stage, so  $q$  must be greater than or equal to  $c$ . At equilibrium  $(\hat{L}, \hat{A})$  the two time derivatives are zero and equations (1) and (2) represent two ellipses which both pass through the origin  $(\hat{L}=0, \hat{A}=0)$  and which have centres at  $(-q/2v, a/2b)$  and  $(c/2e, -s/2u)$  respectively. These usually intersect in two points (Figs. 1a and 1b) one of which is the origin (with the exception that tangency of the two curves reduces the second point also to  $(\hat{L}=0, \hat{A}=0)$ ). A positive steady state will exist if the slope of the

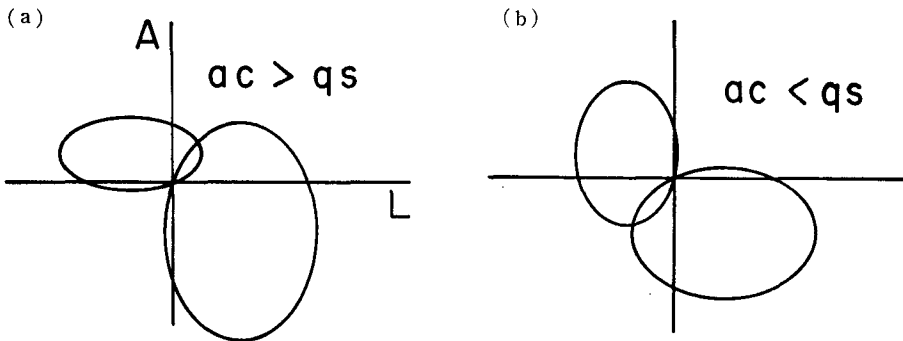


Fig. 1. Ellipses formed by the two isoclines:  $dA/dt = 0$  and  $dL/dt = 0$ . The points of intersection represent steady states. (a) The only nonzero steady state is positive. (b) The only nonzero steady state is negative.

ellipse from eq (1) at the origin is less than that from eq (2) (Fig 1a) and this will occur if  $ac > qs$  (3). If  $ac < qs$ , no positive equilibrium exists. A linearized stability analysis (see Appendix 1) indicates that a positive steady state is stable if and only if

$$(q + 2v\hat{L})(s + 2u\hat{A}) > (c - 2e\hat{L})(a - 2b\hat{A}) \quad (4)$$

However from eq (1),  $q+2v\hat{L}=\hat{A}/\hat{L}$  ( $a-b\hat{A}+v\hat{L}^2/\hat{A}$ ) and  $s+2u\hat{A}=\hat{L}/\hat{A}$  ( $c-e\hat{L}+u\hat{A}^2/\hat{L}$ ) so that the left side of (4) is always greater than the right side provided that  $\hat{L} > 0$ ,  $\hat{A} > 0$ ; ie that  $ac > qs$ .

The origin is only a stable steady state for  $qs > ac$  (Appendix 1), which condition disallows a positive steady state. Using BENDIXSON's criterion (Appendix 1) it can be shown that there are no limit cycles around any positive steady state. These facts guarantee that any single positive steady state that exists is not only locally stable but is globally stable for all positive values of  $L$  and  $A$ . One proviso must be stated here. It is possible for three positive steady states to exist if both the ellipses are greatly elongated in directions perpendicular to each other. This can occur if  $b \gg v$  and  $e \gg u$  and if  $b$  and  $e$  are not too different from each other. These conditions entail strong density dependence in the recruitment stages and weak density dependence in the losses (both larval and adult). This case is both geometrically and biologically extreme and will not be considered in the present development.

#### *SIRM on the two stage system*

Here we assume that adult sterile individuals of both sexes in equal numbers,  $r$ , are continuously released and that they mix instantly with the wild population, and also that the sterile males are fully competitive ecologically and behaviorally with the fertiles and that mating is random; if polygamy occurs, the order of mating is either random or of no consequence. Equations (1) and (2) then become

$$\frac{dL}{dt} = A (a - b(A+N)) (A/A+N) - L (q + vL) \quad (5)$$

$$\frac{dA}{dt} = L (c - eL) - A (s + u(A+N)) \quad (6)$$

$$\frac{dN}{dt} = r - sN - uN (A+N) \quad (7)$$

in which  $A$  is the number of fertile adults,  $L$  is the number of larvae and  $N$  is the number of sterile adults in the wild population. Equations (5) to (7) usually have zero or two positive steady states for any given value of  $r$ , the release rate, depending on the parameter values (Fig. 2). The possibility exists for four positive steady states with extreme parameter values similar to those mentioned earlier, but this case will not be treated here. The origin is also a steady state (Fig. 2). The linearized stability analysis (Appendix 2) is less instructive than in the model without SIRM. The zero isoclines are much more difficult to visualize accurately in three dimensions and in addition BENDIXSON's criterion for limit cycles is not applicable in three dimensions so much less information is available for eqs (5) to (7) than for eqs (1) and (2). However, collapsing the graph onto an  $L$ - $A$  trajectory plane near the  $N$  equilibrium (Fig. 2) gives some useful information regarding stability and shows that of the two positive steady states only the upper one is stable (see Appendix 2).

It is also useful to consider special cases of the full model allowing the density

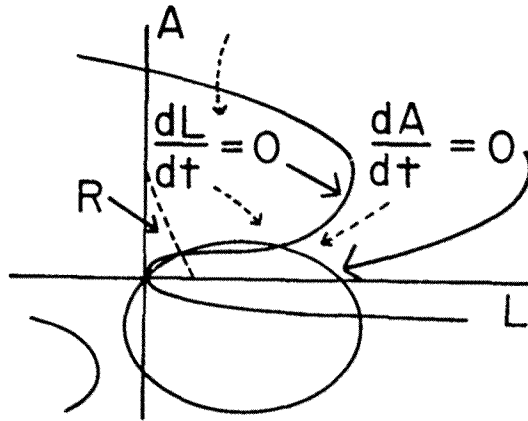


Fig. 2. Curves formed by the two zero isoclines of the derivatives when steriles are released. The dotted lines with arrows represent trajectories of the locus  $(L, A)$  as  $L$  and  $A$  progress from a starting point towards equilibrium. The region  $R$  to the left of the dashed line represents the region within which extinction occurs at a given release level due to increased efficiency of SIRM at low densities.

dependence to operate at each of only one of the four locations in turn. This allows a comparison of the effects of density dependence of each of the four kinds on the efficiency of the sterile release program.

(i) Density dependent fertility only

Here the parameters  $c$ ,  $v$ , and  $u$  all zero and equations (5) to (7) then become

$$\frac{dL}{dt} = A (aA/(A+N) - bA) - qL \quad (8)$$

$$\frac{dA}{dt} = cL - sA \quad (9)$$

$$\frac{dN}{dt} = r - sN \quad (10)$$

Equating these to zero and solving for steady states gives:

$$\hat{N} = r/s \quad (11)$$

$$\hat{A} = \frac{(acs - qs^2 - bcr) \pm \sqrt{(acs - qs^2 - bcr)^2 - 4bcs^2r}}{2bcs} \quad (12)$$

$$\hat{L} = s\hat{A}/c \quad (13)$$

in which only the upper values of  $\hat{A}$  and  $\hat{L}$  are stable (Appendix 3). For real values of  $\hat{A}$  and  $\hat{L}$  we need the discriminant of eq (12) to be non-negative. When the discriminant is zero we have the largest value of  $r$ , the rate of sterile releases, which will still allow persistence of the wild population in the face of continued releases. Solving for this largest value or  $r$ , designated  $r^*$ , gives

$$r^* = \frac{s(ac + qs - 2\sqrt{acqs})}{bc} \quad (14)$$

Substituting (14) into (12) gives the values of  $\hat{A}$  and  $\hat{L}$  (designated  $\hat{A}^*$  and  $\hat{L}^*$ ) when  $r=r^*$ . This pair of values we call the 'breakpoint', and they are:

$$\hat{A}^* = \frac{\sqrt{acqs} - qs}{bc} \quad (15)$$

$$\hat{L}^* = \frac{s(\sqrt{acqs} - qs)}{bc^2} \quad (16)$$

Also,  $\hat{L}^*/\hat{A}^* = s/c$  (17)

(ii) Density dependent survivorship through eclosion

Here  $b=v=u=0$ . Treating this case as in (i) above gives cubic equations for  $\hat{L}$  and  $\hat{A}$  which do not yield explicit solutions:

$$ae^2L^3 - e(2ac - qs)L^2 + c(ac - qs)L - qsr = f(L) \quad (18)$$

$$a^2esA^3 - qs(ac - qs)A^2 - qr(ac - 2qs)A + q^2r^2 = g(A) \quad (19)$$

The graphs of these functions differ in detail but are similar in general shape. The graph for  $L$  will always intersect the  $L$  axis in three places for  $r > 0$ . The cubic for  $A$  is shown in Figure 3. The major effect of increasing  $r$  is to raise the graph.

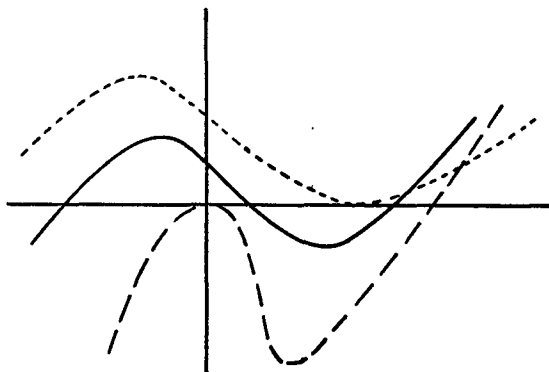


Fig. 3. Graphs of the cubic equation for  $\hat{A}$  from case (ii).

The solutions,  $\hat{A}$ , occur where the graph crosses the  $A$  axis. The three cases are: (a)  $r=0$  for the bottom (dashed) curve (b)  $0 < r < r^*$  for the solid curve (c)  $r = r^*$  for the top (dotted) curve.

When  $r=r^*$  then the graph is tangent to the horizontal axis (Fig 3) and when  $r > r^*$  the graph lies entirely above the  $A$  axis in the first quadrant and no real positive values of  $A$  exist. When  $r=r^*$  the two roots are equal and can be obtained by differentiating eq (19) and setting the derivative to zero, since eq (19) set to zero gives the three roots for  $\hat{A}$ , and its derivative gives the extrema. Solving for  $r$  in this equation gives the  $r$  which is associated with the minimum of  $g(A)$ . Then substituting this back into eq (19) gives  $\hat{A}^*$ :

$$\hat{A}^* = \frac{(a^2c^2 + 2acqs - 2q^2s^2) + (ac - 2qs) \sqrt{a^2c^2 - acqs + q^2s^2}}{9a^2es} \quad (20)$$

Similarly solving for  $\hat{L}^*$  and  $r^*$  we get:

$$\hat{L}^* = \frac{(2ac - qs) + \sqrt{(ac - qs/2)^2 + 3q^2s^2/4}}{3ae} \quad (21)$$

$$r^* = \frac{s[3a^2e\hat{A}^{*2}/q - 2(ac - qs)\hat{A}^*]}{ac - 2qs} \quad (22)$$

Of the three possible values for  $\hat{L}$ , only the middle one is stable and of the two positive values for  $\hat{A}$ , only the upper one is stable (Appendix 3).

(iii) Density dependent larval survivorship

Here  $b = e = u = 0$ , then solving the resulting equations at equilibrium gives:

$$\begin{aligned} \hat{N} &= r/s \\ \hat{A} &= \frac{[c(ac - qs) - vsr] \pm \sqrt{(c(ac - qs) - vsr)^2 - 4cqv s^2 r}}{2vs^2} \end{aligned} \quad (24)$$

$$\hat{L} = s\hat{A}/c \quad (25)$$

Then solving for the breakpoint values gives

$$r^* = \frac{c[(ac + qs) - 2\sqrt{acqs}]}{vs} \quad (26)$$

$$\hat{A}^* = \frac{c[\sqrt{acqs} - qs]}{vs^2} \quad (27)$$

$$\hat{L}^* = \frac{\sqrt{acqs} - qs}{vs} \quad (28)$$

$$\hat{L}^*/\hat{A}^* = s/c \quad (29)$$

Of the two possible values of  $\hat{L}$  and of  $\hat{A}$ , only the upper one of each is stable: i. e., there are two steady states:  $(\hat{L}_l, \hat{A}_l)$  and  $(\hat{L}_u, \hat{A}_u)$  and only  $(\hat{L}_u, \hat{A}_u)$  is stable (Appendix 3).

(iv) Density dependent adult survivorship

Here  $b = e = v = 0$  and as in (ii) above we obtain cubic equations for  $N$ ,  $L$ , and  $A$ . Proceeding as in (ii) above we obtain:

$$acsN^3 + acsN^2 - r(ac + qs)N + qr^2 = f(N) \quad (30)$$

$$acquA^3 - ac(ac - qs)A^2 + qr(2ac - qs)A - q^2r^2 = g(A) \quad (31)$$

$$\hat{L} = r\hat{A}/c\hat{N} \quad (32)$$

whence 
$$r^* = \frac{3acu\hat{N}^{*2} + 2acs\hat{N}^*}{ac + qs} \quad (33)$$

$$\hat{N}^* = \frac{a^2c^2 - 4acqs + q^2s^2 + \sqrt{(ac + qs)(a^2c^3 + q^3s^3)}}{9acqu} \quad (34)$$

$$\hat{A}^* = \frac{2a^2c^2 - 2acqs - q^2s^2 + \sqrt{(2ac - qs)^2(a^2c^2 - acqs + q^2s^2)}}{9acqu} \quad (35)$$

$$\hat{L}^* = r^*A^*/cN^* \quad (36)$$

From eq (31) it can be seen using DESCARTES's rule of signs that there are one or three positive real roots for  $\hat{A}$ . In fact there are three positive real roots if  $r < r^*$  and one if  $r > r^*$ . Only the uppermost root, however, is stable and this disappears when  $r > r^*$  (Fig. 4; Appendix 3).

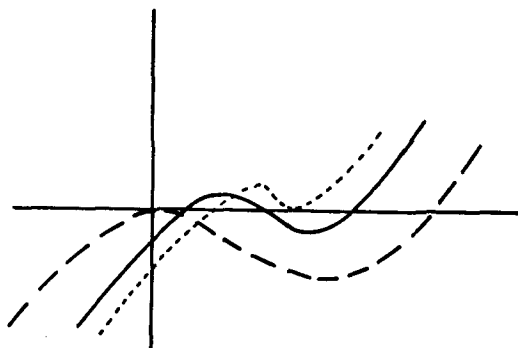


Fig. 4. The graphs of the cubic equation for  $\hat{A}$  from case (iv).  
 (a)  $r=0$  (dashed line) (b)  $0 < r < r^*$  (solid line)  
 (c)  $r=r^*$  (dotted line).

#### *Comparison of the four special cases*

The equilibrium values with no sterile releases and the values of  $r$ ,  $\hat{L}$ , and  $\hat{A}$  at the breakpoint were determined from the formulae given in the previous section for selected values of the parameters  $a$ ,  $c$ ,  $q$ , and  $s$ . The parameters  $b$ ,  $e$ ,  $v$ , and  $u$  were taken as  $b=ax10^{-3}$ ,  $e=cx10^{-3}$ ,  $v=qx10^{-3}$ , and  $u=sx10^{-3}$  when each of them in turn was nonzero. These values gave comparable strengths of density dependence in the four locations and the effects of each of the four parameters separately can be assessed and compared (Table 1). Multiplying each parameter (including  $r$ ) by the same constant does not change the breakpoint values  $\hat{N}^*$ ,  $\hat{L}^*$ , and  $\hat{A}^*$  so  $c$  was assigned the value unity throughout these comparisons (Table 1). Since  $c$  is a survivorship, it will always be less than or equal to unity. In addition, since the effects of the parameters on the breakpoint values are invariant with a constant proportional change of all the parameters, the effect of changing any one of them is a result of the change relative to the others rather than the actual change in itself. Thus the parameter  $c$  was held constant in Table 1 since changes in  $c$  can be assessed via changes in the others.

The following generalizations were obtained from Table 1:

(a) Density dependence in only the larval or adult recruitment stages (cases i and ii above) generally yield smaller equilibrium values for both larvae and adults than with the density dependence only in either of the mortality stages (cases iii or iv above). This is true both with and without the release of steriles and is most pronounced when  $ac$  is much greater than  $qs$ . What might be seen as the carrying

Table 1. Equilibrium and breakpoint values for selected values of the parameters.

Parameter values <sup>a</sup>				Case <sup>b</sup>	Natural equilibria		Breakpoint values				
$a$	$c$	$q$	$s$		$\hat{L}_0$	$\hat{A}_0$	$\hat{L}_0/\hat{A}_0$	$r^*/\hat{L}_0$	$\hat{L}^*/\hat{L}_0$	$\hat{A}^*/\hat{A}_0$	$\hat{L}^*/\hat{A}^*$
1	1	1	0.1	i	90	900	0.1	0.52	0.24	0.24	0.10
				ii	900	900	1.0	1.40	0.35	2.40	0.15
				iii	9000	90000	0.1	0.52	0.24	0.24	0.10
				iv	9000	9000	1.0	0.14	0.31	0.45	0.69
10	1	1	1	i	900	900	1.0	0.52	0.24	0.24	1.00
				ii	900	90	10.0	1.40	0.35	2.40	1.46
				iii	9000	9000	1.0	0.52	0.24	0.24	1.00
				iv	90000	9000	10.0	0.14	0.31	0.45	6.85
10	1	1	4	i	2400	600	4.0	0.23	0.39	0.39	4.00
				ii	600	60	10.0	0.27	0.41	0.77	5.28
				iii	1500	375	4.0	0.23	0.39	0.39	4.00
				iv	15000	1500	10.0	0.11	0.34	0.45	7.56
10	1	4	1	i	600	600	1.0	0.23	0.39	0.39	1.00
				ii	600	240	2.5	0.27	0.41	0.77	1.32
				iii	1500	1500	1.0	0.23	0.39	0.39	1.00
				iv	3750	1500	2.5	0.11	0.34	0.45	1.89
10	1	40	0.1	i	60	600	0.1	0.23	0.39	0.39	0.10
				ii	600	2400	0.25	0.27	0.41	0.77	0.13
				iii	1500	15000	0.1	0.23	0.39	0.39	0.10
				iv	375	1500	0.25	0.11	0.34	0.45	0.19
100	1	1	1	i	990	990	1.0	0.82	0.11	0.11	1.00
				ii	990	10	100.0	14.7	0.34	22.2	1.51
				iii	99000	99000	1.0	0.82	0.11	0.11	1.00
				iv	9900000	99000	100.0	0.15	0.30	0.44	66.9
100	1	5	5	i	3750	750	5.0	0.33	0.33	0.33	5.00
				ii	750	38	20.0	0.51	0.38	1.03	6.98
				iii	3000	600	5.0	0.33	0.33	0.33	5.00
				iv	60000	3000	20.0	0.13	0.32	0.45	14.3
100	1	40	1	i	600	600	1.0	0.23	0.39	0.39	1.00
				ii	600	240	2.5	0.27	0.41	0.77	1.32
				iii	1500	1500	1.0	0.23	0.39	0.39	1.00
				iv	3750	1500	2.5	0.11	0.34	0.45	1.89
100	1	1	40	i	24000	600	40.0	0.23	0.39	0.39	40.0
				ii	600	6	100.0	0.27	0.41	0.83	48.6
				iii	1500	38	40.0	0.23	0.39	0.39	40.0
				iv	150000	1500	100.0	0.11	0.34	0.45	75.6

<sup>a</sup> In each case the density dependent parameters were one one-thousandth of the corresponding density independent parameter.

<sup>b</sup> These positions were the same as the corresponding numbers of the special cases in the text.



capacity is thus dependent on the mode of action of the density dependence; specifically, equilibrium numbers will be low if mortality is largely density independent while recruitment is strongly density dependent, especially if density independent mortality is also low.

(b) The position that usually allows the largest absolute equilibrium numbers of larvae is when the density dependence is in the adult mortality (case iv) but this is not always true; if the density independent mortality of the larvae,  $q$ , is high relative to  $a$ , the fertility rate, then density dependence in the larval mortality (case iii) yields the highest equilibrium numbers.

Similarly, the position of density dependence that allows the largest adult equilibrium numbers is usually in the larval losses (case iii), except that high density independent mortality in the adults,  $s$ , allows density dependence in the adult mortality (case iv) to give the highest equilibrium adult numbers.

The lowest adult equilibrium usually occurs when density dependence is in the survivorship over eclosion (case ii). This is often associated with lowest larval equilibrium except when  $s$  (mortality) is large relative to  $a$  (natality).

(c) The larval to adult ratio with no sterile releases,  $\hat{L}_0/\hat{A}_0$ , is usually less than unity when the density dependence is in either larval recruitment or larval losses, except when  $s$  (d.i. adult mortality) is high. On the other hand,  $\hat{L}_0/\hat{A}_0$  is high when density dependence is in either of the adult stages (cases ii or iv) except when  $s$  is low. In both of these cases  $s$  appears to be quite important in determining the size of the ratio  $\hat{L}_0/\hat{A}_0$  while  $q$ , larval d.i. mortality, is relatively unimportant. For most stable parameter values, then, it appears that larvae will outnumber adults when most of the density dependent regulation is in the adult stage, while adults may outnumber larvae when the regulation is in the larval stage.

(d) If the density dependence is in the adult recruitment (case ii), then the adult equilibrium at the breakpoint,  $\hat{A}^*$ , can be much greater than the original equilibrium before sterile releases,  $\hat{A}_0$ , providing  $ac \gg qs$ . This is due to the much greater survivorship through eclosion when larval numbers are reduced by sterile releases than when near  $\hat{L}_0$ . From eqs (1) and (2) with  $b$ ,  $v$ , and  $u$  set to zero the equilibrium values of  $L$  and  $A$  are

$$\hat{L}_0 = \frac{ac - qs}{ae} \quad (37)$$

$$\hat{A}_0 = \frac{q(ac - qs)}{a^2e} \quad (38)$$

$$\text{At equilibrium eq (2) becomes } s\hat{A} = \hat{L}(c - e\hat{L}) \quad (39)$$

and this is unchanged by the introduction of steriles. Eq. (39) is the equation of a parabola opening downwards which passes through the origin, ( $\hat{L}=0$ ,  $\hat{A}=0$ ), and with the vertex in the positive quarter plane. The curve passes through the  $L$  axis at  $(0, 0)$  and at  $(0, c/e)$ . If  $ac \gg qs$ , then  $\hat{L}_0$  is close to  $c/e$  and  $(\hat{L}_0, \hat{A}_0)$  is on the

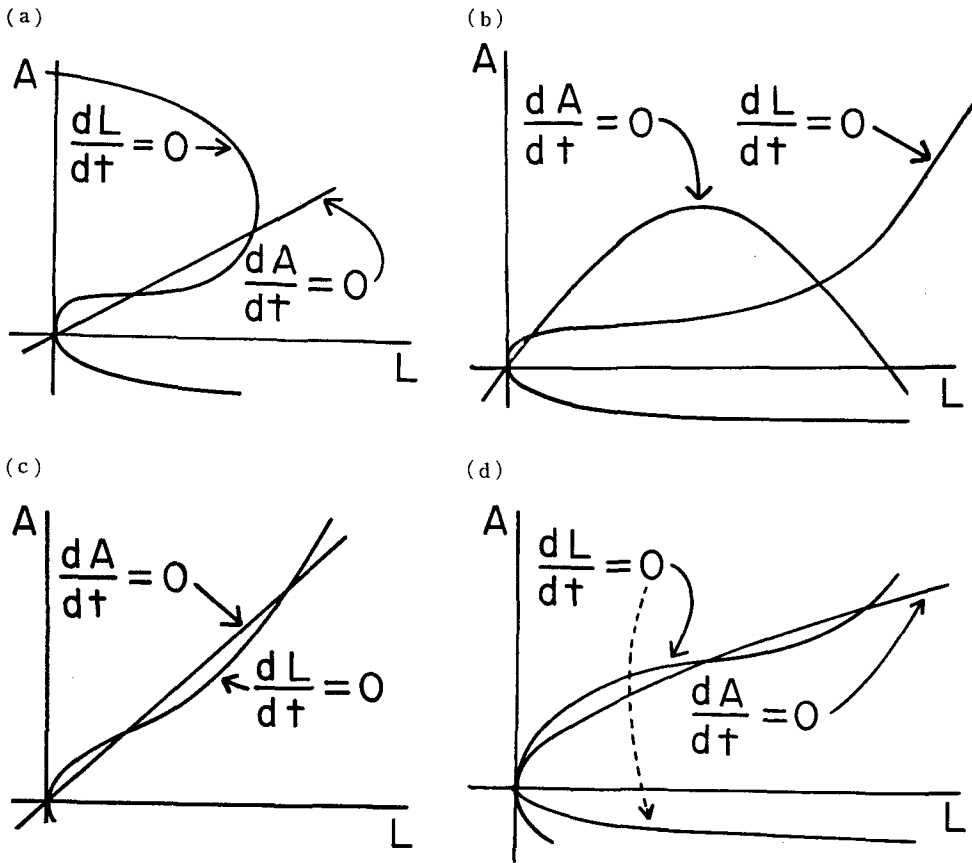


Fig. 5. Zero isoclines of the derivatives from cases (i) to (iv). In each case  $dL/dt > 0$  to the left of the curve  $dL/dt = 0$  and  $dA/dt > 0$  to the right of the curve  $dA/dt = 0$ , so that the upper right intersection and the origin are stable while the smaller positive intersection is unstable. (a) case (i);  $b \neq 0$  (b) case (ii);  $e \neq 0$  (c) case (iii);  $v \neq 0$  (d) case (iv);  $u \neq 0$

descending arm of the parabola near the  $L$  axis. With the introduction of steriles,  $\hat{L}$  decreases and the point  $(\hat{L}, \hat{A})$  slides up the parabola to the left towards the vertex. If  $ac$  is much greater than  $qs$ , then  $\hat{A}^*$  can be considerably greater than  $\hat{A}_0$  (Table 1, Fig. 5b).

The existence of this phenomenon appears to be much more general than simply for the present logistic based formulation since many graphs could be conceived which would qualitatively conform to the description above. In fact this same prediction was made by BERRYMAN *et al.* (1973) using an entirely different formulation as the basis of a computer simulation in which survival from the egg stage to the adult was made density dependent. This case does, however, represent an extreme (and possibly rare) case in population regulation; throughout much of the animal kingdom population regulation is generally thought to be mainly a result of mortality rather than variable recruitment (LACK, 1954). If appreciable portions of the density dependent regulation

were also in the larval stage, then  $\hat{L}_0$  would not be close to  $c/e$  and this phenomenon of adult increases with the release of steriles would not occur.

(e) The ratios  $\hat{L}^*/\hat{L}_0$  and  $\hat{A}^*/\hat{A}_0$  are usually between 0.2 and 0.4 (Table 1). They are both lowest when  $ac \gg qs$  and when density dependence is in the larval stage. There is one major exception to this range, however, and that is in case ii described just above. In this case adult equilibrium numbers can be much greater at the breakpoint than without sterile releases if  $ac \gg qs$ .

(f) When density dependence is in the larval stage (cases i and iii) the larval to adult ratios at the breakpoint,  $\hat{L}^*/\hat{A}^*$ , are always somewhat less than when density dependence is in the adult stage. Sometimes this difference is quite dramatic, as when  $ac \gg qs$ .

(g) The absolute size of  $\hat{L}^*/\hat{A}^*$  is generally greater than unity when adult d.i. mortality,  $s$ , is large and  $ac$  is not too much greater than  $qs$  (i.e., an  $r$ -selecting situation), while  $\hat{L}^*/\hat{A}^* < 1$  when  $s$  is small.

(h) The ratio  $r^*/\hat{L}_0$  is generally between 0.1 and 0.5 except in a few cases where it greatly exceeds these values. These exceptions involve case ii with  $ac \gg qs$  in which  $\hat{A}^* > \hat{A}_0$  as discussed above.

## DISCUSSION

Most species have more than one stage in their life cycle. In many insect species these stages are quite distinct morphologically and often ecologically as well, such as in many Lepidopterans. The variations on the basic theme are endless, from the Ephemeropterans with virtually no adult life to Glossinids with almost no (free living) larval stage. A single model of population dynamics based on life history features cannot hope to cover this vast array with any degree of realism. Yet it is useful to make the attempt at generality since this allows certain features of the model to be understood in a comparative context rather than trying *post hoc* to compare specific models which may be based on different premises or formulations, thus being inherently non-comparable. In the construction of such a general model we inevitably sacrifice precision and depth for breadth. The strength of a general model lies in the degree of conformity of its assumptions to reality and the generality of the formulation. Although the growth form of insects is seldom logistic and often not continuous, as the present model assumes, the model does capture certain features which are relatively independent of the functional form assumed for growth and also of the assumption of continuity. Density dependence is incorporated into four positions in the life cycle: adult and larval recruitment and adult and larval losses. The major consequences of density dependence have been demonstrated to be (a) the existence of two positive steady states, the upper of which is stable and the lower unstable, and (b) a reduction in the release rate of steriles needed to cause extinction or to facilitate control of the pest population (BERRYMAN *et al.*, 1973; MILLER and WEIDHAAS,

1974; ITÔ, 1977; PROUT, 1978). Indeed, control without extinction is infeasible without the presence of density dependence.

Another feature of the present model which is relatively independent of the growth form is the complex life cycle and the mode of action within the life cycle of the density dependence. The importance of the position of density dependence in the life cycle has been hinted at by BERRYMAN *et al.* (1973) and PROUT (1978) who pointed out the inefficiency of SIRM against adults when survivorship to adults was density dependent. The present work indicates that the exact position of density dependence is extremely important in determining (a) the size of the natural equilibrium of the wild populations, (b) the release rate need to cause either extinction or suppression, (c) the relative sizes of the larval and adult populations at the breakpoint, and (d) the degree of reduction of the population needed before the breakpoint is reached.

The inefficiency of SIRM against adults and the possible increase of the adult population with sterile releases are seen here to be largely a result of density dependence in adult recruitment rather than in larval survivorship as one is tempted to infer from the models of BERRYMAN *et al.* (1973) and PROUT (1978). Inefficiency of SIRM against adults can also occur in the present model when  $ac \geq qs$  and density dependent mortality is in the adult stage, particularly adult recruitment since in these cases the ratio of larvae to adults is less at the breakpoint than at the natural equilibrium. Inefficiency of SIRM against the larvae is apparently never a consequence of the position of density dependence since in none of the cases examined was the larval to adult ratio at the breakpoint greater than at the natural equilibrium ( $\hat{L}_0/\hat{A}_0$ ). The two ratios were equal in every case of density dependence in the larval stage while in every case of density dependence in the adult stage the SIRM was more efficient against the larvae than the adults (Table 1).

Normally in a release program it is sterile adults that are released. As KNIPLING (1972) notes, care must be taken that the insects released not be too destructive or annoying. This constraint, coupled with the greater efficiency of SIRM against larvae than adults, makes SIRM a more favourable technique for controlling species in which the larval stage is the problem than species in which the adults constitute the pests.

The implications of the present model are clearly that every effort should be made to understand the population dynamics and general ecology of a prospective candidate species for SIRM. This is not a new theme as it has been repeatedly suggested by workers in this area (e. g., WEIDHAAS, 1968; KNIPLING, 1972; PROVERBS, 1974; WHITTEN and PAL, 1974; WHITTEN and FOSTER, 1975).

In this respect the responses of the two life stages to SIRM in a pilot study together with their initial relative abundances may prove useful in assessing the regulatory processes involved in the wild population. For example, if the ratio  $\hat{L}/\hat{A}$  decreases appreciably with the application of steriles then this may indicate that the

density dependent regulation is largely in the adult stage. This information would then be useful in planning the full scale control program.

### SUMMARY

A continuous-time density dependent model was constructed of a species with a two stage life cycle. This model has a unique stable equilibrium. With the introduction of steriles at constant rate a second positive unstable steady state appears; this condition does not depend on the mode of action within the life cycle of the density dependence or its relative strength.

A comparison was made of the effects of having the density dependence in each of larval and adult recruitment and larval and adult losses. It was found that if only adult recruitment is density dependent, then adult numbers can actually increase with the release of steriles provided density independent recruitment greatly exceeds density independent losses. Sterile releases were often more effective against larvae than against adults, although in some cases not importantly so.

Density dependence in recruitment gives much lower equilibrium values than when density dependence of comparable strength is in the mortality.

The release rates needed to cause extinction were generally between 0.1 and 0.5 of the larval equilibrium with no sterile releases except when the density dependence is predominantly in adult recruitment, in which case much higher release rates are required.

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## APPENDIX 1

### Linearized stability analysis

If we let  $L = \hat{L} + x$ ,  $A = \hat{A} + y$ , and if we ignore nonlinear terms, then eqs (1) and (2) become:

$$\frac{dx}{dt} = -(q + 2v\hat{L})x + (a - 2b\hat{A})y \quad (40)$$

$$\frac{dy}{dt} = (c - 2e\hat{L})x - (s + 2u\hat{A})y \quad (41)$$

Forming the matrix of coefficients,  $\mathbf{M}$ , and solving the determinant  $|\mathbf{M} - p\mathbf{I}| = 0$  gives the characteristic equation for the eigenvalues,  $p$ :

$$p^2 + \{(s + 2u\hat{A}) + (q + 2v\hat{L})\}p + (q + 2v\hat{L})(s + 2u\hat{A}) - (c - 2e\hat{L})(a - 2b\hat{A}) = 0 \quad (42)$$

which has two negative roots, or roots with negative real parts, if and only if

$$(q + 2v\hat{L})(s + 2u\hat{A}) > (c - 2e\hat{L})(a - 2b\hat{A}) \quad (43)$$

Now from eq (1) at equilibrium,  $q + v\hat{L} = \hat{A}(a - b\hat{A})/\hat{L}$  and from eq (2) at equilibrium,  $c - e\hat{L} = \hat{A}(s + u\hat{A})/\hat{L}$ . Substituting these into inequality (43) gives

$$(a - b\hat{A} + v\hat{L}^2/\hat{A})(c - e\hat{L} + u\hat{A}^2/\hat{L}) > (a - 2b\hat{A})(c - 2e\hat{L}) \quad (44)$$

which is always true if  $ac > qs$ . Equation (42) also implies that the origin ( $L=0$ ,  $A=0$ ) is unstable if  $ac > qs$  but it is stable if  $ac < qs$ . Thus there is exactly one stable equilibrium for any positive parameter values.

### BENDIXSON'S criterion for limit cycles

If we assign the label  $P(L, A)$  to eq (1) and  $Q(L, A)$  to eq (2), then BENDIXSON'S criterion says (see HAHN, 1967, for details) that if the sum

$$\frac{\partial P(L, A)}{\partial L} + \frac{\partial Q(L, A)}{\partial A}$$

does not change in sign in the region  $R$ , then there are no limit cycles in region  $R$ . Taking derivatives,

$$\frac{\partial P}{\partial L} + \frac{\partial Q}{\partial A} = -(q + 2vL) - (s + 2uA) \quad (45)$$

which is negative for all  $L, A \geq 0$  and this guarantees that no positive equilibrium has limit cycles around it.

## APPENDIX 2

## Linearized stability analysis

Letting  $L = \hat{L} + x$ ,  $A = \hat{A} + y$ ,  $N = \hat{N} + z$  in eqs (5) to (7) and ignoring nonlinear terms we get:

$$\frac{dx}{dt} = -(q + 2v\hat{L})x + [a\hat{A}/(\hat{A} + \hat{N}) + a\hat{N}\hat{A}/(\hat{A} + \hat{N})^2 - 2b\hat{A}]y - [a\hat{A}^2/(\hat{A} + \hat{N})^2]z \quad (46)$$

$$\frac{dy}{dt} = (c - 2e\hat{L})x - [s + u(2\hat{A} + \hat{N})]y - (u\hat{A})z \quad (47)$$

$$\frac{dz}{dt} = -(u\hat{N})y + [s + u(\hat{A} + 2\hat{N})]z \quad (48)$$

Then forming the matrix of coefficients,  $\mathbf{M}$ , and solving the determinant  $|\mathbf{M} - p\mathbf{I}| = 0$  gives the characteristic equation for the eigenvalues,  $p$ :

$$\begin{aligned} p^3 + [q + 2v\hat{L} + 3r/\hat{N} - u]p^2 + [(q + 2v\hat{L})(3r/\hat{N} - u) + (2r/\hat{N} - u)r/\hat{N} \\ - (c - 2e\hat{L})\{2(a\hat{A}/(\hat{A} + \hat{N}) - b\hat{A}) - a\hat{A}^2/(\hat{A} + \hat{N})^2\}]p + [(q + 2v\hat{L})(2r/\hat{N} - u)r/\hat{N} \\ - 2s\hat{N}(c - 2e\hat{L})(a\hat{A}/(\hat{A} + \hat{N}) - b\hat{A}) - (c - 2e\hat{L})\{2(a\hat{A}/(\hat{A} + \hat{N}) - b\hat{A}) - a\hat{A}^2/(\hat{A} + \hat{N})^2\}] = 0 \end{aligned} \quad (49)$$

For stability we need all the roots of eq (49) either negative or to have negative real parts, if complex. Descartes rule of signs only guarantees the sign of real roots, so we use the ROUTH-HURWITZ criterion (HAHN, 1967) for the roots of the polynomial. For a cubic equation,  $p^3 + C_1p^2 + C_2p + C_3 = 0$  the roots will all be negative or the complex roots will have negative real parts if  $C_1C_2 - C_3 > 0$ . Performing these operations on the coefficients of eq. (49) and simplifying gives:

$$T_1[T_2T_3 - S^2\hat{N}\hat{A}] - T_4[T_2T_6 - sa\hat{N}\hat{A}^2/(\hat{A} + \hat{N})^2] > 0 \quad (50)$$

in which  $T_1 = 2s + 3u(\hat{A} + \hat{N})$ ;  $T_2 = (q + 2v\hat{L}) + (s + u(2\hat{A} + \hat{N}))$ ;  $T_3 = (q + 2v\hat{L}) + (s + u(\hat{A} + 2\hat{N}))$ ;  $T_4 = (c - 2e\hat{L})$ ;  $T_6 = a\hat{A}/(\hat{A} + \hat{N}) + a\hat{N}\hat{A}/(\hat{A} + \hat{N})^2 - 2b\hat{A}$ .

The interpretation of this condition is not easy since we don't have explicit formulas for  $\hat{N}$ ,  $\hat{L}$ , and  $\hat{A}$ . Numerical evaluations, however, indicate that the region of stability for the upper values of  $\hat{L}$  and  $\hat{A}$  is not too different from the region without SIRM; the lower values of  $\hat{L}$  and  $\hat{A}$  appear unstable.

A good notion of the stability properties of eqs. (5) to (7) can be obtained graphically (Fig. 2). For any given value of  $\hat{N}$ , the phase diagram collapsed to two dimensions can be constructed. Analysis of such a slice of the three dimensional state space, however, is at best heuristic unless the third variable is uncoupled from the two being graphed. Since eqs (5) to (7) are fairly well behaved and have no singularities, however, examination of the  $L$ - $A$  phase plane is at least instructive, if not rigorous.

For any given value of  $r$ , the value of  $\hat{N}$  will change somewhat with  $\hat{A}$  (from eq (7)) but in general the picture presented in Fig. 2 will remain qualitatively unchanged by changes in  $\hat{N}$  with  $\hat{A}$ . There are four intersections of the curves in Fig. 2 for certain values of the parameters and two for other values. Two of the intersections are in the positive quarter plane and consideration of the signs of the derivatives in eqs (5) and (6) leads to the trajectory segments shown with arrows in Fig. 2. Of these two intersections only the one furthest from the origin is an attracting point. Thus any set of coordinates falling inside region  $R$  in Fig. 2 (to the left of the dashed line) will lead to extinction (for  $r < r^*$ ) while any values of  $(L, A)$  outside this region leads to the stable equilibrium. Fig. 2, of course, is specific to a particular set of parameter values and assumes that  $r < r^*$ , the value causing extinction.

## APPENDIX 3

In special cases (i), (ii), and (iii)  $\hat{N}$  is independent of  $\hat{L}$  and  $\hat{A}$  so examination of the phase plane gives a completely valid idea of the stability of the system. In case (iv)  $\hat{N}$  is not independent of  $\hat{L}$  and  $\hat{A}$  and phase plane methods are useful but not rigorous.

Figures 5(a) to 5(d) show the  $L$ - $A$  phase planes at the level  $N=\hat{N}$ ; all assume that  $r$  is small enough to allow existence of the wild population. In each case there are two positive steady states and in each case the upper one is stable and the lower one is unstable.

Linearized stability criteria for the four special cases are as follows. The system is stable if and only if,

- (i)  $2s(q+s) > c \cdot \{a\hat{A}/(\hat{A}+\hat{N}) + a\hat{N}\hat{A}/(\hat{A}+\hat{N})^2 - 2b\hat{A}\}$
- (ii)  $2s(q+s) > (c-2e\hat{L}) \cdot \{a\hat{A}/(\hat{A}+\hat{N}) + a\hat{N}\hat{A}/(\hat{A}+\hat{N})^2\}$
- (iii)  $2s \cdot (q+2v\hat{L}+s) > ac \{a\hat{A}/(\hat{A}+\hat{N}) + \hat{N}\hat{A}/(\hat{A}+\hat{N})^2\}$
- (iv)  $\{2s+3u(\hat{A}+\hat{N})\} \cdot [(q+s+u(2\hat{A}+\hat{N}))(q+s+u(\hat{A}+2\hat{N})) - u^2\hat{N}\hat{A}]$   
 $> c[\{q+s+u(2\hat{A}+\hat{N})\} \{a\hat{A}/(\hat{A}+\hat{N}) + a\hat{N}\hat{A}/(\hat{A}+\hat{N})^2\} - sa\hat{N}\hat{A}^2/(\hat{A}+\hat{N})^2]$

These four conditions are obtained from the general condition in Appendix 2 by setting all except one of  $b$ ,  $e$ ,  $v$ , and  $u$  to zero depending on which special case is being considered.

## 2つの発育段階のある生活史をもつ場合の不妊化昆虫放飼法

H. J. BARCLAY

時間的に連続した関数を用いた密度依存モデルを、2つの発育段階（幼虫と成虫で代表）のある生活史をもった種について作成した。このモデルは一意的な安定平衡点をもつ。一定の割合で不妊化虫を放飼する場合には、正の不安定な定常状態が得られる。その条件は発育段階における密度依存的作用の形やその相対的な強さには依存しない。

幼虫・成虫の個体群への加入と、個体群からの消失が密度依存である場合のそれぞれについて、密度依存性の効果を比較した。もし成虫の加入が密度依存であれば、密度に依存しない加入が密度に依存しない消失よりも十分大きい場合、成虫数の平衡レベルは不妊化虫の放飼を行う以前の平衡レベルよりも高くなる。不妊化放飼は成虫に対してよりも、幼虫に対してしばしば効果的である。ただし違いがわずかな場合もある。

加入が密度依存であれば、同じくらいの密度依存性が死亡に見られる場合よりも平衡値ははるかに低い。

絶滅するための放飼数として、不妊化放飼をしない場合の幼虫の平衡値の10から50%の間に相当する数が必要である。ただし成虫の加入が主に密度依存的に起こる場合には上のようにならず、もっと放飼数を増やす必要がある。