A STERILE RELEASE MODEL FOR CONTROL OF A PEST WITH TWO LIFE STAGES UNDER PREDATION

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ABSTRACT. A model is presented in which sterile pests are released into a system consisting of a pest species with two life stages and a predator species. The release of steriles affects mainly predators and, as the release rate is increased, the predator equilibrium is eventually reduced to zero. In once case, however, a bifurcation exists and the system will collapse before the predators are eliminated.

1. Introduction. The sterile insect release method (SIRM) for pest control has been used effectively against screw-worms (*Cochliomyia omnivorax*) [7], melon flies (*Dacus cucurbitae*) [12], the codling moth (*Laspeyresia pomonella*) [15], and a few other insect species. It has been tried against many other species with mixed or little success, e.g., medflies (*Ceratitis capitata*) [10]. The reasons for success in some cases and not in others are often unclear. A few general principles have been postulated by modelling and by empirical or experimental inference; these include limitations on the technique by (i) lack of sterile male competitive ability [1, 13, 17], (ii) lack of complete sterilization [8, 13] and (iii) immigration of wild fertilized individuals [9, 14].

A feature which may assist the effectiveness of the SIRM is the existence of predatory or parasitic control on the pest species. This has been investigated by modelling [3, 4, 5, 11], but appears to have never been tested experimentally. The existence of a natural enemy may lower the required sterile release rate (in the absence of immigration of pests) for eradication of the pest species [5] and it may also destabilize the system so that eradication may be achieved at considerably lower than the theoretically prescribed sterile release rates [3]. On the other hand, the existence of more than one distinct life stage in the life cycle of the pest species also complicates the outcome of a sterile release program [1]. In order to shed further light on the population dynamics of this potentially useful pest control method, a model is proposed here which incorporates two life stages (larval and adult) for the pest species and, in addition, a monophagous predator which feeds on and depresses the

pest population. This model is presented in generality, but will be examined as eight special cases.

The questions to be investigated here, motivated in part by previous results, are as follows:

(a) As the sterile release rate is increased, what are the conditions that cause the predators to go extinct before the prey?

(b) Are there conditions likely to cause an increase in the pest population equilibrium as the sterile release rate increases?

(c) How does the position of predation in the pest life cycle (larval or adult) affect the efficiency of the SIRM?

(d) How does the SIRM interact with the application of larvicides and adulticides imposed on the pest population?

2. The model. The model is based directly on a combination of the models of Barclay [1] and Barclay and Mackauer [5]; both of those models represent attempts to incorporate biological reality and have somewhat complicated behaviour. We feel that the model presented here will provide useful insight into the general behaviour of systems under sterile releases; in this spirit we confine ourselves to a consideration of gross qualitative behaviour of the system.

In the following model, the pest has two life stages, larvae (L) and adults (A), and density dependent population regulation occurs in only the pest species, possibly at each of four positions: larval recruitment or mortality and adult recruitment or mortality. Sterile pests (N) are released only as adults. Predators (P) attack either the larval or adult pests (not both) and do not exhibit crowding or other density dependent population regulation; thus they may be conveniently represented by one life stage, especially for examination of equilibria. The following four differential equations represent population changes for the pest larvae, pest adults, sterile adults and predators respectively:

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

$$\frac{dA}{dt} = L(c - eL) - A[s + u(A + N)] - jPA$$

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

$$\frac{dP}{dt} = P[g(L, A, N) - k],$$

where one of i or j is zero and the other is positive, and where $g(L, A, N) = hL$ if $j = 0$, whereas $g(L, A, N) = h(A + N)$ if $i = 0$. In addition, a, q, c and s are density independent larval recruitment and mortality, and adult recruitment and mortality, respectively. Also b, v, e and u are the density dependent respective counterparts; r is the sterile release rate, g is the predator birth rate and k the death rate. In the following analysis only one of b, v, e or u is non-zero in any given case. Thus eight special cases are examined: four positions of density dependence for each of larval (L(1)–L(4)) and adult (A(1)−A(4)) stages attacked by the predators.

Equilibrium values. Each of model L(1)–L(4) has one feasible steady state value (i.e., all variables positive) and it is easily found (Table I). In addition, each of these four models has a steady state with $\hat{L} = \hat{A} = \hat{P} = 0, \hat{N} > 0$; this steady state can easily be shown to be locally stable in each case. In addition, for certain parameter values, there is the possibility of maintaining $\hat{P} > 0$ using sterile releases alone (i.e., $\hat{A} = \hat{L} = 0$); this is of academic interest only, however, from the point of view of the pest manager.

TABLE I. Equilibrium values for
L, A and N with sterile releases.

Variable	Model			
	L(1)	L(2)	L(3)	L(4)
L	k/h	k/h	k/h	k/h
A	ck/sh	ck/sh	$\frac{k(ch-ek)}{sh^2}$	$\frac{ck\hat{N}}{rh}$
N	r/s	r/s	r/s	$*$

$*$ The positive root of $u\hat{N}^2(ck/rh + 1) + s\hat{N} - r = 0$

Models A(1)–A(4) do not behave as simply; they exhibit multiple feasible steady states $(\hat{L}, \hat{A}, \hat{N}, \hat{P} > 0)$. Each of these models has two feasible steady states. In addition there are steady states with $\hat{L} = \hat{A} = \hat{P} = 0, \hat{N} > 0$, and with $\hat{P} > 0, \hat{N} > 0$. In all cases the steady state with $\hat{L} = \hat{A} = \hat{P} = 0, \hat{N} > 0$, is locally stable. The feasible steady states are not as easy to locate here as in models L(1)–L(4).

Predator extinction. In each of the eight models it is seen that there is a limiting value of k/h that just makes $\hat{P} = 0$ with no sterile releases (Table II). For predators to exist, the value of k/h must be less than this limiting value. With sterile releases the value of $\hat{P}$ may be expected to change.

TABLE II. Upper limit to the value of k/h that allows predator existence ($\hat{P} > 0$) with no sterile releases. Here $y = ac - qs$.

Position of	Non zero density dependent parameter			
predation	b	v	e	u
Larvae	sy/bc^2	y/sv	y/ae	ay/q^2u
Adults	y/bc	cy/s^2v	qy/a^2e	y/qu

As the sterile release rate is increased from zero the value of the predator equilibrium may decrease. In larval predation models the values of $\hat{L}$ and $\hat{A}$ do not vary with r so long as $\hat{P} > 0$. There is a value of $r(r')$ for each of these four models for which $\hat{P} = 0$, at which point the system reverts to the behaviour of the one species system [1]. In all cases except model A(3) the values r' are easily found (Table III). In none of the larval predation models does a bifurcation exist so long as $\hat{P} > 0$.

Setting $x = k/h$ and differentiating r' with respect to x, a maximum value of r' is found, and it can be shown in each of models L(1)–L(4) that the value of r' at this maximum coincides with the value of r^* (the bifurcation, or break point value of r) in the single species system [1]. In each of the four models, if the value of x is less than the value that maximizes r', then the system ends up on the lower limb of the isocline of the single species system when $r = r'$ (and thus $\hat{P} = 0$), whereas if x is greater than this value for maximal r', then the system ends up on the upper limb of the single species isocline. The lower limb of the single species isocline is unstable while the upper limb is stable.

TABLE III. Values of $r(r')$ that make $\hat{P}$ zero for the eight models. Here $x = k/h$, $y = ac - qs$. Also shown for models A(1)–A(4) is r^*, the break-point value of r, that yields a bifurcation. "?" indicates no information.

Stage preyed upon	Position of host density dependence			
	Larval recruitment $b \neq 0$	Larval mortality $v \neq 0$	Adult recruitment $e \neq 0$	Adult mortality $u \neq 0$
Larvae	$r'\dfrac{bc^3x[\frac{sy}{bc^2}-x]}{qs^2+bc^2x}$	$\dfrac{cx(y-svx)}{qs+svx}$	$\dfrac{x(c-ex)(y-aex)}{qs}$	$\hat{N}=\dfrac{qr'(cx+r')}{ac^2x}$
Adults	$r'\dfrac{sx(y-bcx)}{c(a-bx)}$	$\dfrac{sx(cy-vs^2x)}{ac^2-vs^2x}$	?	$\dfrac{x(s+ux)(y-qux)}{ac}$
	$r^*\dfrac{cx(a-bx)}{4q}$	$\dfrac{2ac\hat{A}^2(x-\hat{A})}{qx^2}$	?	$\dfrac{acx}{4q}$

Additionally, the strength of predation and its effects on the prey equilibrium become greater as x decreases. Thus a prey population that is strongly controlled (and thus depressed) by the predator is more likely to end up at the lower (unstable) prey steady state of the single species system as sterile releases increase, so as to drive the predators extinct, than is a prey population species less strongly controlled by predators. Thus a more efficient (smaller x) predator potentially aids the sterile release program more than a less efficient predator.

Models with predation on adult prey are less consistent. Although there is a bifurcation indicated in the equations, it is evident in models A(1) and A(2) that $\hat{P} \to 0$ as r increases before the bifurcation is reached (i.e., $r' < r^*$). Again, the value of x determines which limb of the single species isocline is reached as $\hat{P} \to 0$.

Model A(3) appears intractable analytically and no definite conclusions in this regard can be drawn. Model A(4) shows the same general behaviour as the model of Barclay and Mackauer [**5**]. Here there is a value of x that separates two general behaviours. Setting $y = ac - qs > 0$, if $(y-qs)/2qu < x < y/qu$, then $\hat{P} \to 0$ as r is increased towards the critical value r'. If $x < (y - qs)/2qu$, then a bifurcation exists and the system collapses as r achieves a value $r^* = acy/4q$, with $\hat{P} > 0$ at this value of r. This case (model A(4)) is the only one of the eight for which catastrophic behaviour clearly exists as r increases. In this model, as in most of the others, the value of x that maximizes r' separates the cases that end up on the upper from the lower limb of the single species system for those values of x that do not yield a

bifurcation. Again, strong predation assists the sterile release program by yielding a low level unstable equilibrium when $r = r'$.

Response to control. Three forms of pest control are considered here: sterile releases, larvicides and adulticides. Sterile releases are quantified in the model by the parameter r, while larvicides and adulticides result in deaths of larvae and adults, respectively, and thus can be subsumed into the parameters q and s, respectively. Imposition of insecticide mortality results in an increase in q or s.

Table IV shows the direction of change of the stable feasible equilibrium with an increase in each of the three control parameters r, q and s. These changes were determined either from the explicit equilibrium value or by taking total derivatives of each of the four equations about the equilibrium and then solving for $d\hat{L}, d\hat{A}, d\hat{N}$ and $d\hat{P}$ using Cramer's rule, as was done by Barclay and van den Driessche [6]

The results are reassuringly predictable. So long as predators still have a positive equilibrium, larvae are either not affected (larval predation cases) or decrease with the imposition of steriles, larvicides or adulticides. In these cases the predators appear to be the major component affected. Adult pests are likewise either unaffected or decrease with any of the three control methods. The only exception to this regular behavior is in the case of the effects of larvicides on adult pest numbers for model A(3), with density dependence in pupal survivorship (i.e., adult recruitment). In this case, the sign is negative if $c > 2e\hat{L}$; otherwise the sign is positive.

3. Discussion. The release of sterile insects appears unlikely to cause an increase in either the larval or adult stages of the pest. In addition to the effect of depressing fertile egg production, the release of steriles increases the competition among adults, thus effectively depressing both stages simultaneously. Indeed, the model results indicate that such an increase should never occur (Table IV). This is in contrast to the model without predation [1] in which it was seen to be possible, under certain parameter conditions, for the adult stage to increase if density dependence was in adult recruitment. Apparently predators act as a buffer to prevent this from occurring.

TABLE IV. Direction of change of the equilibrium when control is imposed on the pest population, where r = sterile release rate, q = larval mortality, s = adult mortality and + = increase, − = (decrease), 0 = (no change), ∗ = (can increase or decrease), ?= (no information).

Parameter controlled	Equilibrium variable	Model							
		Larval predation				Adult predation			
		L(1)	L(2)	L(3)	L(4)	A(1)	A(2)	A(3)	A(4)
	L	0	0	0	0	−	−	−	−
	A	0	0	0	−	−	−	−	−
r	N	+	+	+	+	+	+	+	+
	P	−	−	−	−	?	?	?	?
	L	0	0	0	0	−	−	−	−
	A	0	0	0	0	−	−	∗	−
q	N	0	0	0	0	+	+	∗	+
	P	−	−	−	−	−	−	∗	−
	L	0	0	0	0	0	0	0	0
	A	−	−	−	−	0	0	0	0
s	N	−	−	−	−	0	0	0	0
	P	∗	−	−	−	−	−	−	−

Predation, however, is not sufficiently buffering to prevent an increase in adults when a larvicide is used (Table IV, model A(3)). This is the same case that displayed this type of behavior without predation [6]. This behavior may possibly be a consequence of the model used, but a similar phenomenon has been observed in mosquitoes [16], and thus this model prediction should be taken seriously.

When predation is on pest larvae, the models uniformly predict that the predator equilibrium will be driven to zero before the pest equilibrium is affected by sterile releases, the only exception being for adults in model L(4) where some depression occurs. In each of these four models there is a single stable feasible steady state until $\hat{P} = 0$, whereupon the dynamics become those of the single species system and a bifurcation exists. This behavior is reflected in the behavior of sterile releases for pest populations under attack by parasitoids [4].

With predation of adult pests, the models are less tractable and the dynamics somewhat less predictable. However, in at least two cases (models A(1) and A(2)), the predator equilibrium is again driven to zero before bifurcation is reached. Only in model A(4) is there a clear possibility of the bifurcation occurring before the predators

are eliminated. This is in contrast to the case of parasitization of adults [4] where no bifurcation exists so long as density dependence is in the hosts. Although predation and parasitism are often taken to be equivalent for modelling purposes, there are obvious ecological differences between the two processes. In the present context, one difference which may cause the difference in dynamic behavior noted above is that insects parasitized as adults can often contribute much of their potential reproductive output even after being parasitized, whereas this is not true of adults under predation. Another difference between the models presented here and those of Barclay [4] is that, in the latter models, density dependence is in the host larvae but never in the host adults.

It appears that predation assists the sterile release program more when predation is on the host adults than on host larvae, since, in the latter case, reduction of host equilibrium usually does not occur until the predators are eliminated. Again, this may be a consequence of the models, but it is worth noting. For either position of predation, efficient predators give more assistance than inefficient ones since the pest equilibrium is lower when the predators are eliminated. This allows a smaller sterile release rate to be effective and also makes it more likely for the pest population to be in the unstable region for the single species.

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