The Joint Effects of the Release of Sterile Males and Immigration of Fertilized Females on a Density Regulated Population

TIMOTHY PROUT

Department of Entomology and Department of Genetics,
University of California, Davis, California 95616

The joint effects are studied of the release of sterilized males and immigration of mated females on a population whose discrete generation recursion is,

$$N' = N \left(\frac{RK}{K + (R - 1)N} \right)$$

where, $R \equiv$ reproductive potential, $K \equiv$ equilibrium. This form of growth is derived from life history considerations so that the impact of the release of sterile males on immatures and on adults can be compared. When the migration parameter and the sterile male release parameter are small, the system has three internal equilibriums (the middle one being unstable). Increase in immigration or in release results in one stable equilibrium. The practical conclusion is that migration must be very small in order for the release of sterile males to be effective on suppressing numbers of adults, while more migration can be tolerated if, as in many agricultural pests, immature stages are the object of concern.

This article constitutes an analytic study of a model of a density regulated population which is subjected to the release of sterilized males as well as the immigration of fertilized females. The results bear on the practical question of the extent to which a pest population can be suppressed by the release of sterile males when it is also subject to immigration.

There exists a sizeable literature consisting of simulation studies of isolated populations which are density regulated and subject to sterile male release (e.g., "Computer Models and Application of Sterile Male Technique," 1973), and at least one simulation study which is directed toward the problem of immigration (Dietz, 1975).

The following describes a system which incorporates density regulation, sterile male release, and immigration, but which is still simple enough to succumb to analytic study, thus having the virtue of revealing its near-global behavior.

The study was stimulated by a recent publication by Dietz (1976) who also obtained analytic results pertaining to a broader range of questions involving so-

called genetic control methods, than will be considered here, but he does include sterile male release and immigration. However, when impinging effects are removed, Dietz's basic model of population growth does not contain intrinsic density regulation. His population simply grows exponentially in finite generation intervals thus,

$$N_t = R^t N_0 \qquad (1)$$

where

$t =$ generation number,

$R =$ a constant > 1, often called the "reproduction potential",

$N_t, N_0 =$ number of individuals at generation t and $t = 0$, respectively.

He further stipulates a carrying capacity $\hat{K}$, such that (1) holds only for $N_t \leqslant \hat{K}$; otherwise, if $N_0 \geqslant \hat{K}$, $N_1 = \hat{K}$.

This is the classic model introduced into genetic control literature by Knipling (1955) and used extensively by others (Klassen and Creech, 1973; Kunz and Eschle; 1971, Henneberry, 1971; Davidson, 1974, p. 23; and many others) as a simple means of obtaining first guesses concerning the impact of the release of sterilized males.

This treatment is not intended to supersede Dietz's study, but rather to complement it, since there must be many explosive, "r"-type populations which are roughly described by the Knipling model as stated by Eq. (1), but there is ample evidence for the other class of populations which experience intrinsic density regulation (Pal, 1974; Hassell, 1975; "Insect Pest Management and Control", 1969, Chap. 5). Therefore, the objective is to extend the available analytic theory so as to accommodate both types of populations.

This will be a discrete generation model. The treatment will proceed as follows:

First, the basic growth characteristics of the model population will be developed, then the effects on this population of release of sterile males when it is isolated, and, finally, immigration of fertilized females will be added to the system.

1. THE BASIC MODEL OF POPULATION GROWTH

(a) Construction of the Model

A great many single population growth models have appeared recently in the literature. May (1975) presents and studies several discrete generation growth models collected from the entomological literature. Ayala *et al.* (1973) present 11 different models in their attempt to fit *Drosophila* data, and Schoener (1974), starting from basic biological assumptions has derived still more growth models.

Clearly no single model will accommodate all insect species. Indeed, it is not likely that a single model will accommodate one species at different times and in different places.

The object here is not to study a variety of models, but rather to study the interaction of sterile male release and immigration of fertilized females on some growth model which exhibits intrinsic density regulation, with the hope that the main conclusions, at least, will be reasonably robust.

The model chosen for this purpose is as follows:

$$N' = \left(\frac{RK}{K + (R - 1)\,N}\right) N. \tag{2}$$

N and N' are adult population sizes in successive generations. It can be easily shown that the two parameters R and K have their conventional meanings, viz., R is the reproductive potential or the factor by which the population grows when it is small, and K is the equilibrium size.

A growth model of this form has been described as the discrete time analog of the continuous time logistic (May, 1975; Pielou, 1969; Christiansen and Fenchel, 1977), or more simply as "hyperbolic" growth by Asmussen and Feldman (1977) since the factor in brackets is a hyperbolic function of N. Clark (1972) and Asmussen and Feldman (1977) have used this form of growth for studying genetic questions, and this function is a special case of a class of functions used by Hassel (1975) for purely ecological theory.

The hyperbolic model was chosen because it has the two virtues of having desirable mathematical properties, shown presently, and also a highly plausible biological rationale.

We proceed first by showing this rationale, which was first suggested by Poulsen (1975). The approach is to consider the organism's life history.

In order to describe the effects of sterile male release in its simplest terms, a minimum of two stages of the insect life history must, in some way, be taken into account: (1) The adult females, whose number will be N, constitute the stage subjected to manipulation by their mating with sterile males, and (2) the number of newly hatched larvae, n, constitute the stage receiving the direct impact of the sterile matings, which through "dominant lethal" bearing sperm or an equivalent mechanism, reduce the number of eggs hatching into young larvae.

Keeping track of the adult and immature stages has a practical aspect also, since in some pest species it is the adult which is the pest, such as mosquitoes and many other medical and veterinary pests, while in other species, such as most agricultural pests, it is the immature stage which is the object of concern.

Density regulation will be assumed to occur as density dependent survival between the newly hatched larvae, n, and the adult females of the next generation, N'.
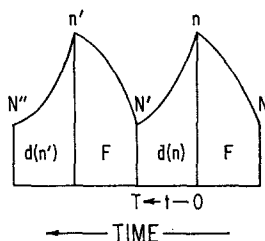
FIG. 1. Relevant life history events in some insect life cycle. The "ordinate" of this graph is numbers of individuals. n and $n' \equiv$ numbers of newly hatched larvae in successive generations. N, N', $N'' \equiv$ the numbers of adults in three successive generations. $F \equiv$ the number of newly hatched larvae per adult. $d(n) \equiv$ probability a larva will survive to become an adult. $t \equiv$ the time in the interval, larva, $t = 0$ to adult, $t = T$.

Figure 1 depicts three generations of adult numbers, N, N', and N'' which accommodate one generation of young larval numbers, n and n'. F and $d(n)$ are the factors converting the numbers of one stage to the numbers in the next. F is a constant, representing the number of young larvae produced per female. F is, therefore, the product of the number of eggs per female and the probability an egg will hatch. $d(n)$ is the probability a young larva will survive to become an adult, and, it is proposed that this be a decreasing function of n, the number of young larvae.

The recursions can therefore be constructed as follows:

$$n = FN;$$

$$N' = d(n)\, n;$$

$$\therefore N' = d(FN)\, FN, \qquad \text{adults} \tag{3a}$$

or

$$n' = Fd(n)\, n, \qquad \text{larvae.} \tag{3b}$$

Poulsen provides a rationale for arriving at the function, $d(n)$.

He supposes that during the interval of time $(0,\, T)$ as shown in Fig. 1, larvae die according to,

$$dn_t/dt = -bn_t(1 + cn_t) \tag{4}$$

where

$$b,\, c \equiv \text{constants} > 0,$$

$$n_t \equiv \text{number of larvae at time } t.$$

Integrating (4) over $(0,\, T)$ yields,

$$n_T = \frac{n_0 \exp(-bT)}{1 + (1 - \exp(-bT))\, cn_0}. \tag{5}$$

In (5), n_0 represents the number of young larvae, n; and n_T represents the number of young larvae which are transformed into adults, $N_t \cdot d(n)$ is obtained by dividing (5) by n_0 and letting $n_0 = n$ with the following result,

$$d(n) = \frac{\exp(-bT)}{1 + (1 - \exp(-bT)) \, cn}. \tag{6}$$

Thus, the survival through this stage, $d(n)$, is inversely related to the numbers entering the stage n. Let the constant, $\exp(-bT) = S$, which is simply the maximum survival when $n \to 0$, then (6) becomes

$$d(n) = \frac{S}{1 + (1 - S) \, cn}. \tag{7}$$

Substituting (7) into (3a) and (3b) yields

$$N' = \frac{SFN}{1 + (1 - S) \, cFN}, \qquad \text{adults} \tag{8a}$$

or

$$n' = \frac{SFn}{1 + (1 - S) \, cn}, \qquad \text{larvae.} \tag{8b}$$

Equations (8) are two-parameter hyperbolic growth functions of the form of (2). In (8) the parameters measure events in the organisms life history, while the parameters of (2) measure dynamical properties of the population.

The parameters of (2) and (8) are related as follows:

Adults:

$$R = SF; \tag{9}$$

$$K = \frac{SF - 1}{(1 - S) \, cF}; \tag{10a}$$

or letting $SF = R$,

$$K = \frac{R - 1}{(1 - S) \, cF}. \tag{10b}$$

Larvae:

$$R = SF; \tag{}$$

$$k = \frac{SF - 1}{(1 - S) \, c}; \tag{11a}$$

or, letting $SF = R$,

$$k = \frac{R - 1}{(1 - S)\,c}.$$ (11b)

where $k \equiv$ equilibrium larval numbers

(b) *Mathematical Aspects*

Both adults and larvae have the same functional form of growth.

The parameter R has the same value for both but, of course, the equilibrium parameters are different, there being many more larvae than adults at equilibrium; the relationship is simply $k = FK$.

Equation (2) assumes a simpler and also more general form if the variable N is normalized to the equilibrium K. Letting the new variable be $P = N/K$, (2) becomes

$$P' = \left(\frac{P}{1 + (R - 1)\,P}\right).$$ (12)

The explicit time dependent solution of this recurrence equation can be easily obtained, and from this its global behavior can be directly assessed. The solution is

$$P_t = \frac{P_0}{P_0 + R^{-t}(1 - P_0)}.$$ (13)

If $R > 1$, the single equilibrium ($\hat{P} = 1$) is approached monotonically. The rapidity of approach is determined simply by the magnitude of R. (R^{-1} also happens to be the eigenvalue of (13) linearized about, $\hat{P} = 1$.) The fact that the equilibrium is approached monotonically so long as $R > 1$ is a desirable property for the present purposes, because it means that large and biologically reasonable values of R can be explored without the complications of the system entering into increasing oscillations or "chaotic" behavior, a situation which May (1975) has pointed out can arise for practically all other discrete time growth functions in current use. For instance, the logistic differential equation when employed as a difference equation will produce chaotic behavior when $R \geqslant 3.692$. There are many species where R could easily be much larger than this. For example, Cuellar and Cooper (1973) studied the mosquito, *Culex pipiens*, and conclude that R could be "249 or more...."

As mentioned earlier hyperbolic growth of the form of (2) has been described by several authors as the discrete time analog of continuous time logistic growth. This is presumably because the time dependent solution (13) looks very much like the solution of the continuous time logistic differential equation when time is measured in generation intervals, and R is replaced by e^r. The recurrence equation (2) simply represents this solution over a one generation time interval.

The reason why this analogy emerges from Poulsen's formulation of survival is that Poulsen's differential equation simply represents "logistic decay" in continuous time rather than logistic growth in continuous time.

(c) Biological Aspects

The starting point in deriving (2) was Poulsen's differential equation (4). This has the virtue of simplicity, and it is presumably this appeal to parsimony that has sustained the long and continued use of the continuous time logistic differential equation. However, in this case the simple assumption appears to enjoy empirical support from a large number of experimental studies of density dependent egg to adult survival in insects. The data from many of these experiments at least roughly conform to the hyperbola (6), which results from integration of Poulsen's differential equation. For instance, Hassel (1975) has compiled data from 13 species of insects, and if one is not concerned, as he is, with literal fitting, then a hyperbola roughly describes the laboratory data he gives, and is certainly adequate to fit the field data. Additionally, Rajagopalan et al. (1973) studied density dependence of egg to adult survival of Culex fatigans in Indian village wells. They employ a negative exponential function for data interpretation, but, in fact, a hyperbola would fit better.

There is, however, a biological limitation of this model which should be identified: fertility, F, is constant and independent of adult numbers. Density dependent fertility is an important consideration in the effects of sterile male release. However, there are pest species where such an effect probably plays little role, such as the many mosquito species which breed in small receptacles, man-made or natural. Here the principle limitation, where powerful density regulation does occur, is imposed on immatures, and probably not on adults (McClelland, personal communication).

The hyperbolic growth form can therefore be said to represent a reasonable number of biological realities, at least.

TABLE I

Parameter Values for Two Populations

		Population I	Population II
Dynamical parameters	K	10^3	10^3
	R	10	50
Life history parameters	F	100	400
	S	0.10	0.125
	c	10^{-4}	1.4×10^{-4}
$d\ (n = k) = F^{-1}$		0.01	0.0025

(d) *Numerical Examples*

In what follows it will be occasionally useful to study some results numerically. For this purpose two "test" populations will be employed and these will be designated Population I and Population II. Table I shows parameter values of these two populations. Both populations have the same adult size, $K = 10^3$ but they differ in reproductive potentials, R. In Population I, $R = 10$ while in Population II, $R = 50$. The higher R of Population II confers, as will be seen, much greater resistance to the effects of sterile male release than exhibited by Population I with the lower R.

The table also shows how the two fixed R and K parameters can be translated into three plausible life history parameters with the result that in Population I each female produces 100 larvae and, at equilibrium, their probability of survival to adults becomes $d(n = k) = 0.01$, while in Population II each female produces more larvae, namely, 400, but, at equilibrium, their probability of survival is lower, namely, $d(n = k) = 0.005$ (at equilibrium, $d(n = k) = F^{-1}$).

The larval numbers at equilibrium, $k = FK$, are $k = 10^5$ and $k = 4 \times 10^5$ for Population I and II, respectively.

2. Release of Sterile Males into an Isolated Population

(a) *Introduction*

Two kinds of release procedures will be considered: (1) the number of released sterile males is constant, and (2) the ratio of released sterile males is constant, which implies that the number released declines as the population does. Borrowing from Wallace (1967, p. 427) the first kind of procedure will be termed "hard" release, and the second "soft" release.

The classic sterile male method assumes hard release. However, the consequences of soft release also will be pursued because, although most theoretical models of the process assume hard release, some have been published which apparently assume soft release (Staley *et al.*, 1971; Murdie, 1973; and Dietz, 1976) and, as will be demonstrated shortly, the hard versus soft release assumptions can lead to rather different conclusions, a fact which deserves explicit discussion.

There are general definitions and assumptions which apply to both procedures. First, we define the following:

$$A \equiv \text{number of released sterile males;}$$
$$a \equiv \text{ratio of released to native males;}$$
$$x \equiv \text{probability a female mates with a released male;}$$
$$y = 1 - x \equiv \text{probability a female mates with a fertile native male;}$$
$$N \equiv \text{number of emerging females who are all virgin.}$$

The major assumptions are random mating of females with released *vs* native males, the sex ratio is 1:1, and all matings with sterile males result in eggs which do not hatch.

The basic recursions and resulting equilibriums will be developed for adults, and larval numbers will be calculated whenever they might be of interest. Specifically, the recursions will be between the newly emerged virgin females of one generation, N, and the next, N', so that the actual population size including males, would be twice these numbers.

The following relationships result from the above:

$$a = A/N;$$

$$x = a/(1 + a) \quad \text{or} \quad A/(N + A);$$

$$y = 1/(1 + a) \quad \text{or} \quad N/(N + A).$$

(b) *Hard Release*

Assuming the mode of sterility is dominant lethality then no matter how many times the females mate, the eggs fathered by sterile males, with probability x, will not hatch while y will hatch. Using the formulation in terms of life cycle parameters (8) we therefore must multiply F by y. Thus,

$$N' = \left(\frac{SyFN}{1 + (1 - S)\, cyFN}\right) N. \tag{14}$$

Since both in the numerator and the denominator yN collapse, the recursion can be written in terms of the R and K of the undisturbed population, so that by using (9) and (10), expression (14) becomes,

$$N' = \left(\frac{RK}{K + (R - 1)\, Ny}\right) Ny. \tag{15}$$

Since $y = N/(N + A)$, (15) becomes

$$N' = \frac{RKN^2}{KN + KA + (R - 1)\, N^2}. \tag{16}$$

Denoting equilibrium by $\hat{N}$, the substitution of $\hat{N}$ for N' and N in (16) results in a cubic equation in $\hat{N}$. One root is $\hat{N} = 0$ and the other two roots are as follows:

$$\hat{N} = \frac{1}{2}\left(K \pm \left(K^2 - \frac{4AK}{R - 1}\right)^{1/2}\right) \tag{17a}$$

or in normalized form,

$$\hat{P} = \frac{1}{2}\left(1 \pm \left(1 - \frac{4a_K}{R-1}\right)^{1/2}\right). \tag{17b}$$

a_K is the normalized parameter A, defined, $a_K = A/K$.

Both roots are positive and, dealing with the unnormalized form (16a), if the following condition is satisfied,

$$4A < K(R-1), \tag{18}$$

then both roots are real. Thus, there are two nonzero equilibriums. Furthermore, it can be shown that the larger one, say $\hat{N}_1$, is stable and the smaller one, $\hat{N}_2$, is unstable. The $\hat{N} = 0$ equilibrium is stable, a result which will assume some significance when migration is introduced in the next section.

The lower unstable equilibrium is easily explained. It merely identifies a smaller population size below which the same release numbers, A, would result in population collapse. This is a formal statement of the often stated idea that if a given population were temporarily reduced in size, say, at the beginning of the season or as the result of pesticide treatment, then this situation would require less sterile males to bring about eradication (La Chance et al., 1967; Knipling, 1968; "Insect Pest Management and Control", 1969, Chap. 15).

Using Population I, for example, if it is possible to release only $A = 2000$ sterile males per generation ($a_\kappa = 2$), then releasing into the equilibrium population ($K = 1000$) will depress the population to a stable equilibrium of $\hat{N}_1 = 667$ ($\hat{P}_1 = 0.667$), but if the population were temporarily reduced below $\hat{N}_2 = 333$ ($\hat{P}_2 = 0.333$), then $A = 2000$ sterile males per generation would bring about eradication.

If condition (18) is not satisfied, resulting in

$$4A > K(R-1),$$

then no matter how large the population (at K or larger) it will always collapse. Thus, we have the critical release numbers, denoted by A^* or a_κ^* as follows:

$$A^* = \frac{K(R-1)}{4} \tag{19a}$$

or

$$a_\kappa{}^* = \frac{(R-1)}{4}. \tag{19b}$$

The latter more general statement defines the critical hard release numbers in terms of the release ratio at equilibrium, K.

Applying this result to Populations I and II we have,

Population	A^*	a_κ^*
I	2.250 sterile males/generation	2.25
II	12,250 sterile males/generation	12.25

As anticipated, Population II is more resistant to sterile male release than Population I.

(c) *Soft Release Procedure*

In soft release, the release ratio, a, is held constant. The number of fertile eggs is

$$Ny \quad \text{or} \quad \frac{N}{1 + a}.$$

Substituting this for N in Eq. (2) yields the recursion

$$N' = \frac{RKN}{K(1 + a) + (R - 1) N}. \tag{20}$$

This has one equilibrium,

$$\hat{N} = K \left(\frac{R - 1 - a}{R - 1} \right) \tag{21a}$$

or

$$\hat{P} = \frac{R - 1 - a}{R - 1}. \tag{21b}$$

Equation (20) is the hyperbolic growth function again, so that its time dependent behavior is normalized form is given by,

$$P_t = \frac{\hat{P}}{P_0 + \lambda^t(\hat{P} - P_0)} \quad \text{if} \quad \lambda \neq 1$$

where

$$\lambda = \frac{1 + a}{R}.$$

Thus, we have the simple condition that if

$$\lambda < 1$$

or, in other words,

$$a < R - 1,$$

the population moves monotonically to equilibrium (21). However, if

$$\lambda > 1$$

or, in other words,

$$a > R - 1,$$

then $\hat{N} < 0$, but the population, in fact, collapses to zero monotonically. Thus, the critical release ratio a^* is

$$a^* = R - 1. \tag{22}$$

This result can be compared to the hard release result by considering the normalized critical release numbers at a_κ^* (19b). This gives the hard release ratio at equilibrium, K. Comparing (22) and (19b) shows that the critical soft release ratio is four times the initial release ratio under hard release procedure. This difference stems from the soft release assumption of a constant ratio, so that as the population declines the absolute numbers released decline, resulting in the requirement of a much larger initial release (at K) in order to accomplish eventual eradication.

The critical soft release ratios as well as the initial release numbers for Populations I and II are as follows:

Population	a^*	Initial numbers (at K)
I	9	9,000
II	49	49,000

Attention has so far focused on the behavior of the adult census number, N, while it was pointed out earlier that for many agricultural pests it is the number of immatures that is of real concern.

Of course, if eradication of adults is accomplished, then larvae disappear too. However, if eradication cannot be achieved then an equilibrium will result, in which case the relation between larvae and adults becomes of interest.

The number of larvae, n, produced by N females after A sterile males are released is obtained as follows:

$$n = F \frac{N^2}{N + A}. \tag{23}$$

Larval numbers, n, can be normalized to their equilibrium numbers k in the absence of sterile male release. Let p denote this normalized variable, and define it by $p = n/k$. It was noted in Section 1(b) that without sterile male release $k = FK$. Dividing both sides of (23) by FK results in

$$p = \frac{P^2}{P + a_\kappa}$$

and at equilibrium we have

$$\hat{p} = \frac{\hat{P}^2}{\hat{P} + a_\kappa} \cdot \tag{24}$$

Solving the equilibrium expressions (17b) or (21b) for a_κ and substituting for a_κ in (24), for both soft and hard release, the result is the same, namely,

$$\hat{p} = \frac{\hat{P}}{\hat{P} + R(1 - \hat{P})} \cdot \tag{25}$$

This gives the relationship between the normalized larval and adult numbers as a function of the parameter R only, and independent of the particular release numbers, a or a_κ, involved. Expression (25) shows that even if adult numbers are not greatly reduced below 1, if R is large the larval numbers could be drastically reduced. Because this result is of some practical significance, (25) is presented graphically for Populations I and II in Fig. 2. The figure shows, for example, that if adult numbers are reduced to only 50% of their former numbers, the larval numbers are reduced to 9% of their former numbers in Population I and to 2% their former numbers in Population II. Thus, the difference between larval and adult reduction can be considerable, a fact which assumes greater significance in the next section where migration is introduced and eradication becomes impossible.
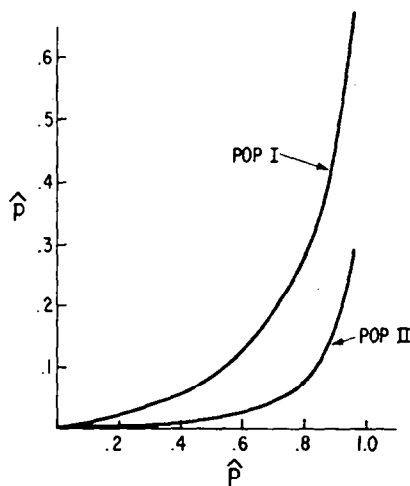

FIG. 2. Comparison of the number of newly hatched larvae, $\hat{p}$, at equilibrium to the number of adults, $\hat{P}$, at equilibrium (hard or soft model). Population I has $R = 10$ and Population II has $R = 50$. $\hat{p}$ and $\hat{P}$ are normalized to numbers at equilibrium in the absence of sterile male release.

(d) *Comparison of Hard and Soft Release Models*

Even though the hard release model better reflects the planning and actual practice of sterile male release, and so is the more important model, it might be of some value to the theoretical work in this field to compare the hard and soft release models and, in particular, to show that the soft release model can entail some pitfalls. The equilibriums produced by the two models are related. Consider the soft release equilibrium (21a). When the population achieves this equilibrium, then the absolute number of sterile males released becomes constant. It follows that this single equilibrium must be one of the two equilibriums achieved by releasing constant numbers of sterile males in the hard release model. The relationship between the two models can be most easily established by calculating the absolute numbers released when the soft release equilibrium is achieved. Under soft release the ratio $a = A/N$ is constant so that as N changes, A changes until $N = \hat{N}$. The absolute numbers released at $\hat{N}$ will be denoted by $\hat{A}$ and defined

$$\hat{A} = a\hat{N}.$$

Substituting (21a) for $\hat{N}$ in the above yields
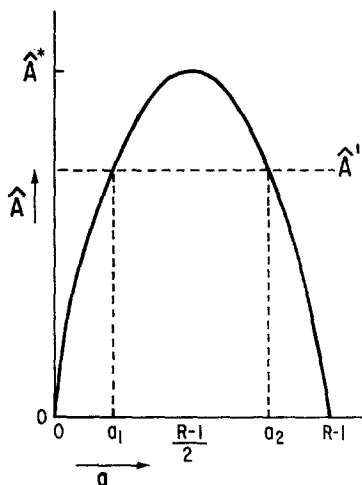
$$\hat{A} = aK - a^2 \frac{K}{R-1}. \tag{26}$$

FIG. 3. Relationship between the soft release ratio a, and the absolute numbers released, $\hat{A}$, when soft release equilibrium, $\hat{N}$, is achieved; i.e., $\hat{A} = a\hat{N}$ (see text). $\hat{A}'$ ≡ released numbers under some hard release regime. a_1, a_2 ≡ the release ratios at the two hard release equilibriums resulting from releasing $\hat{A}'$.

Figure 3 shows (26) with $\hat{A}$ expressed as a function of soft release ratio, a. This is a parabola passing through $(0, 0)$ and $(R - 1, 0)$ with a maximum at $a = (R - 1)/2$ where $\hat{A} = K(R - 1)/4$ which is A^* in the hard release case. Consider the hard release model, and a hard release of $\hat{A}'$ $(\hat{A}' < A^*)$. As shown in the figure, this gives two soft release ratios a_1 and a_2 which it can be proved are related to the two hard release equilibriums, as follows:

$$a_1 = \hat{A}'/\hat{N}_1;$$

$$a_2 = \hat{A}'/\hat{N}_2 .$$

Recalling that $\hat{N}_1$ is the larger stable equilibrium and $\hat{N}_2$ the smaller unstable equilibrium, it follows that with the soft release model if

$$(R - 1)/2 < a < R - 1$$

the resulting soft equilibrium given by (21) corresponds to the lower unstable equilibrium of the hard release model. While if

$$0 < a < (R - 1)/2,$$

the soft equilibrium corresponds to the larger stable equilibrium of the hard release model. The same situation appears in the next section when migration is introduced, except that there, this same kind of simple analytic demonstration of the relationship between the models cannot be made.

The point is that the soft release model lacks robustness in important ways. Analysis of the model results in the conclusion that if a nonzero equilibrium exists there is only one, and it is always stable. This conclusion is strictly dependent on the assumption of a constant release ratio, a. The hard release model shows there can be two equilibriums; furthermore, if the soft release equilibrium is produced by $a > (R - 1)/2$ then perturbations of population size, N, would show this equilibrium to be unstable, unless the numbers released tracked the perturbations in such a way as to keep the ratio a constant.

3. RELEASE AND MIGRATION

(a) Formal Analysis

We now add migration to the system, and in this case unlike the last section, the emphasis will be on finding equilibriums since eradication will no longer be possible.

The kind of migration which is the most serious threat to the effectiveness of sterile male release is where the immigrant females have already mated and so are immune to the release of sterile males. We let the number of such immigrant females per generation be denoted by M.

Migration could be soft or hard, that is, soft migration would assume a constant ratio of immigrants to natives and hard migration would assume constant numbers, M.

Soft migration is conceivable under some natural conditions where a favorable location will produce more native individuals and also be more attractive to immigrants, and vice versa, but in the artificial situation being considered here, at least, the local abundance is being externally manipulated so that the most reasonable assumption is hard migration where M is constant.

We will therefore consider the two plausible models both involving hard migration—one with hard release and the other with soft release. (Formally there are two more models involving soft migration and more where migration is inversely related to local N.) The recursion for hard migration, hard release is as follows:

$$N' = \frac{RK(N^2 + M[N + A])}{K(N + A) + (R - 1)(N^2 + M[N + A])}. \qquad (27)$$

The recursion for hard migration and soft release is

$$N' = \frac{RK(N + M[1 + a])}{K(1 + a) + (R - 1)(N + M[1 + a])}. \qquad (28)$$

Equation (27) where both release and migration are hard yields at equilibrium a cubic equation which is

$$\hat{N}^3 + \hat{N}^2(M - K) + \hat{N}\frac{MR(A - K) - A(M - K)}{R - 1} - \frac{MARK}{R - 1} = 0 \quad (29a)$$

or

$$\hat{P}^3 + \hat{P}^2(m_\kappa - 1) + \hat{P}\frac{m_\kappa R(a_\kappa - 1) - a_\kappa(m_\kappa - 1)}{R - 1} - \frac{m_\kappa a_\kappa R}{R - 1} = 0 \quad (29b)$$

where, $m_\kappa = M/K$, or the migration parameter normalized to K.

Investigation of (29b) has not resulted in discovering everything that one would like to know about it. However, a number of important properties can be determined. The only case of interest is where the migration rate, m_κ is small, so

that $m_\kappa < 1$. In this case the quadratic term is negative. If release numbers are high, say, $a_\kappa > 1$ or even

$$a_\kappa > \frac{Rm_\kappa}{Rm_\kappa + 1 + m_\kappa}$$

then the linear term is positive. The constant is always negative. Under these conditions Eq. (29b) will have either one or three real positive roots. Also, using the recursion (27) it can be proved that if there is one equilibrium it will be stable, while if there are three, the middle one is unstable and the other two are stable. The discriminant of (29) in principle, provides the conditions for there to be one or three positive real roots (given the conditions above). Unfortunately, the discriminant is a complicated and uninterpretable function of the three parameters of (29b). However, it is possible to obtain an interpretable and instructive sufficient condition for there to be just one real root. If the function of $\hat{P}$ on the left of (29b) is monotonic, there will be one real root; a sufficient condition for this to be true is,

$$m_\kappa(3a_\kappa - 1) + (3a_\kappa/R) - 1 > 0. \tag{30}$$

This inequality says that if a_κ is large enough there will be only one root, or given that $a_\kappa > \frac{1}{3}$, then large m_κ will result in just one root. However, these do not supply necessary conditions, and a numerical example will be presented later showing how increasing m_κ ($m_\kappa < 1$, still) results in only one root regardless of a_κ. (In fact, if $m_\kappa \to 1$ it can be proved that there will be only one root, regardless of release numbers, a_κ.)

These results, as far as they go, can be made understandable from dynamical considerations.

First, the hard release case of the previous section already provided the possibility that the introduction of migration could create three nonzero equilibriums. It should be recalled that the equilibrium equation resulting from (16) is cubic with one root, $\hat{N} = 0$ which represents a stable equilibrium. Thus, if the release numbers A are such that two more equilibriums exist without migration, then the Karlin–McGregor (1972) small parameter theory guarantees the existence of a migration parameter small enough so there will be a stable nonzero equilibrium near $N = 0$, and also that there will be a stable equilibrium near the upper stable equilibrium which was present without migration. Continuity of the recursion (27) provides for the existence of the third unstable equilibrium lying between the two stable ones. Figure 4 contains some sketches of numerical cases involving ΔP as a function of P. Figures 4a and 4b show the creation of the third nonzero equilibrium by the introduction of migration. More important are Figs. 4c and 4d which show how increasing release numbers a_κ, or increasing migration, m_κ can bring about the reduction of equilibriums from three to one (stable).
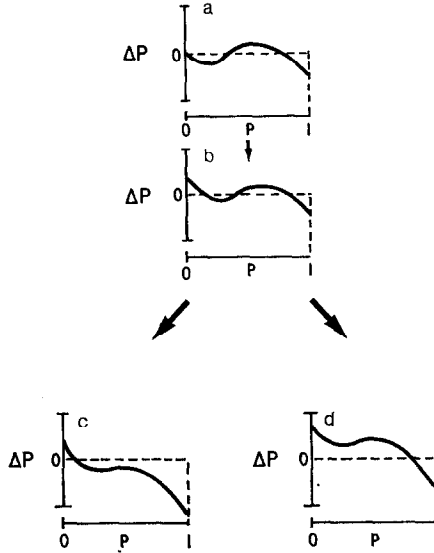
FIG. 4. ΔP as a function of P for the hard release model. (a) No migration and hard release such that three equilibriums result at $\Delta P = 0$. One of these is at the equilibrium, $\hat{P} = 0$. (b) Same as (a) except that small migration is introduced creating three nonzero equilibriums. The $\hat{P} = 0$ equilibrium in (a) is now at $\hat{P} > 0$ and is stable. (c) Same as (b) except that release is increased driving the upper equilibrium (b) in the $\hat{P} = 0$ direction and out of existence resulting in one stable equilibrium. (d) Same as (b) except migration is increased driving the lower equilibrium (b) in the $\hat{P} = 1$ direction and out of existence leaving one stable equilibrium.

We now turn to the case of migration with soft release. At equilibrium, Eq. (28) yields a quadratic equation with only one positive root (always real) which is as follows:

$$\hat{N} = K \left(\frac{(R - 1 - a) - \dfrac{M}{K}(R - 1)(1 + a) + \left([R-1-a) - \dfrac{M}{K}(R-1)(1 + a)]^2 + \dfrac{4MR(R - 1)(1 + a)}{K}\right)^{1/2}}{2(R - 1)} \right)$$

(31a)

or

$$\hat{P} = \frac{\left\{(R - (1 + a) - m_\kappa(R - 1)(1 + a) + ([R - (1 + a) - m_\kappa(R - 1)(1 + a)]^2 + 4m_\kappa R(R - 1)(1 + a))^{1/2}\right\}}{2(R - 1)}.$$

(31b)

It can be proved that this equilibrium is stable, assuming, of course, that the release *ratio* a is held constant.

The difficulty with this result is that there is no way known to this writer for determining which of the three hard release equilibriums, if they exist, is given by the solution (31). However, if it is known that the parameters are such that the hard release model will give only one equilibrium—if for instance condition (30) is satisfied—then that equilibrium value is given by the soft release solution (31). Furthermore, we would know that equilibrium (31) would be stable if hard release were employed. This is as far as this writer has been able to carry the formal analysis. So, for further characterization of the system some numerical studies of the test Populations I and II will be displayed.

But before doing this, some important broad conclusions concerning the effects of migration will be presented by considering two limiting cases: the effects of migration alone without release of sterile males, and, the other extreme, of considering the maximum possible effects of the release of sterile males with migration. That is, we consider the cases where A (or a) $= 0$, and where A (or a)$\rightarrow \infty$.

(b) Consequences

(i) *The effect of migration alone.* The effect of migration amone is obtained by letting $a = 0$ in (31). This gives

$$\hat{N} = \frac{1}{2}\left(K - M_K + \left((K - M)^2 + \frac{4RMK}{(R - 1)}\right)^{1/2}\right) \qquad (32a)$$

or,

$$\hat{P} = \frac{1}{2}\left(1 - m_\kappa + \left((1 - m_\kappa)^2 + \frac{4Rm_\kappa}{R - 1}\right)^{1/2}\right). \qquad (32b)$$

One important characteristic is revealed immediately: the effect of migration alone on the numbers of emerging adults is negligible. This is because if R is somewhat greater than 1, then $R - 1 \simeq R$ in which case (32a) becomes $\hat{N} \simeq K$, or (32b), $\hat{P} \simeq 1$. For example, with migration as high as $m_\kappa = 0.10$, (32b) gives, for Population I, $\hat{P} = 1.010$ and Population II, $\hat{P} = 1.002$.

This result adds considerable value to normalizing adult equilibrium numbers to K as in Eq. (29b) and (31b), because this is nearly equivalent to normalizing to the population size without release but migration included. The larval numbers are more effected by migration. With migration alone,

$$n = F(N + M)$$

dividing by

$$k = FK,$$

$$p = (P + m_\kappa),$$

Letting

$$\hat{P} \simeq 1,$$
$$\hat{p} = (1 + m_\kappa).$$

For example, with $m_\kappa = 0.10$, $\hat{p} = 1.10$ for any population. In the numerical cases discussed below, larval numbers will be normalized to the population size with migration effects included.

(ii) *Maximum possible effect of release.* We now consider the other limiting case of the maximum possible reduction due to the release of sterile males.

Formally this case is obtained with $a \to \infty$ or $A \to \infty$; i.e., all emerging females are rendered sterile each generation. Returning to recursions (27) or (28) and letting $A \to \infty$ or $a \to \infty$, in either case the same result is obtained, namely,

$$\tilde{N} = \frac{RKM}{K + (R - 1)\, M}, \tag{33a}$$

$$\tilde{P} = \frac{Rm_\kappa}{1 + (R - 1)\, m_\kappa}, \tag{33b}$$

where

$$\tilde{N} \equiv \text{equilibrium population size if } A \text{ or } a \to \infty,$$
$$\tilde{P} \equiv \tilde{N}/K.$$

Note that $\tilde{P}$, as just pointed out; essentially compares the reduced population to the untreated population including migration, since with migration and no release $\hat{N} \simeq K$.

Equations (33) say that the only producing females are immigrants which gives an equilibrium by simply substituting the constant M for N in the basic recursion (2).

The number of larvae each generation is simply

$$\tilde{n} = FM.$$

The number of larvae with migration alone, using K to approximate adult numbers, is,

$$\hat{n} = F(K + M).$$

So, letting $\tilde{p} = \tilde{n}/\hat{n}$, we have

$$\tilde{p} = m_\kappa/(1 + m_\kappa) \simeq m_\kappa \qquad \text{when } m_\kappa \text{ is small.}$$

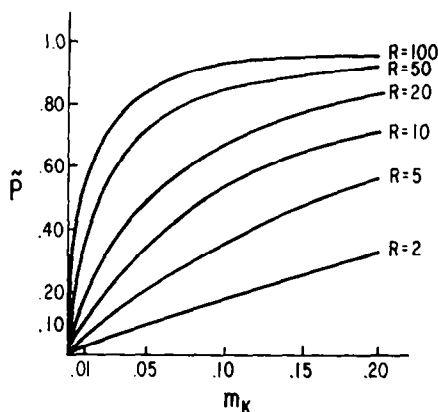The normalized numbers of larvae are a function of m_κ only and are approximately equal to it.

FIG. 5. Maximum possible effect of sterile male release with immigration. $\tilde{P} \equiv$ population size (normalized to K) resulting from complete sterilization of all native females. $m_\kappa \equiv$ immigration/generation of fertilized females normalized to K. $R =$ reproductive potential.

From a practical standpoint this simple result arising from considering the maximum possible effect of release with migration is, perhaps, the most important result of this study. For this reason (33b) is graphed in Fig. 5 over a wide range of reproduction potentials, R. It is clear that unless R is unusually slow—less than $R = 5$, say—then m_κ must be much less than $m_\kappa = 0.10$ in order for adult numbers to be substantially effected. For $m_\kappa = 0.10$ Population I adults could not possibly be reduced below $\tilde{P} = 0.526$ nor Population II below $\tilde{P} = 0.847$. It would seem that virtual isolation with $m_\kappa < 0.01$ is required in order for adult numbers to be substantially controllable. Even with $m_\kappa = 0.01$, if $R = 100$, which is not unreasonable, $\tilde{P} = 0.51$.

The maximum effect of release on larval numbers is quite another matter. The effect is approximately equal to m_κ (see above). In the last example with $R = 100$, whereas $\tilde{P} = 0.51$ the larval numbers could be reduced to $m_\kappa = 0.01$.

Thus, this limiting case of $A \rightarrow \infty$, is very informative concerning the joint effects of release and migration on adult numbers, while, on the other hand, it holds out some hope but is quite ambiguous on the question of whether larval numbers can be substantially reduced with less than complete sterilization of females, as would occur with the release of finite numbers of males ($A < \infty$).

It is principally for this reason that the following numerical study was done.

(iii) *Some numerical results with finite release numbers.* Figures 6a and 7a present a study of the solution of the cubic equation (29b). Each of these two figures shows $\tilde{P}$ as a function of a_κ for different values of migration, m_κ with $R = 10$ (Population I) for Fig. 6a and $R = 50$ (Population II) for Fig. 7a. The second scale on the abscissa, denoted by a_κ', shows a_κ normalized to a_κ^*, the
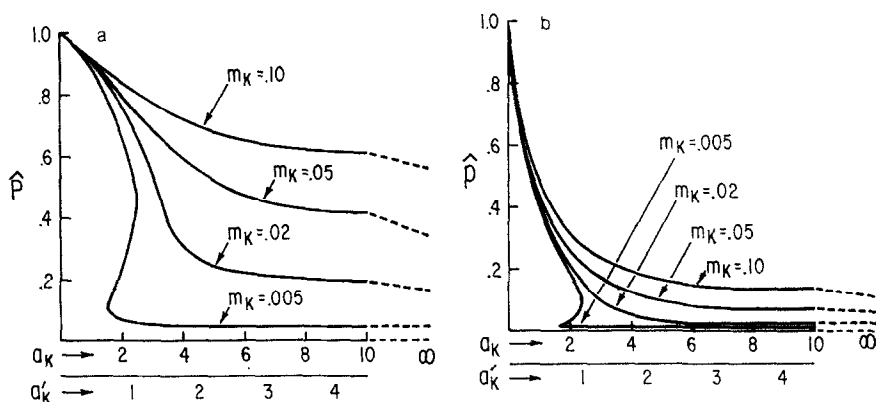
FIG. 6.   (a) The relation between equilibrium value, $\hat{P}$, and numbers of sterile males released, a_κ, for different amounts of migration, m_κ. $\hat{P}$ and the two parameters are normalized to K. $R = 10$ for all cases. a_κ' is the ratio of a_κ to a_κ^*, the release required to just bring about eradication in the absence of migration. For this case of $R = 10$, $a_\kappa^* = 2.25$. (b) The same as (a) except that the ordinate represents larval numbers, $\hat{p}$, rather than adults.
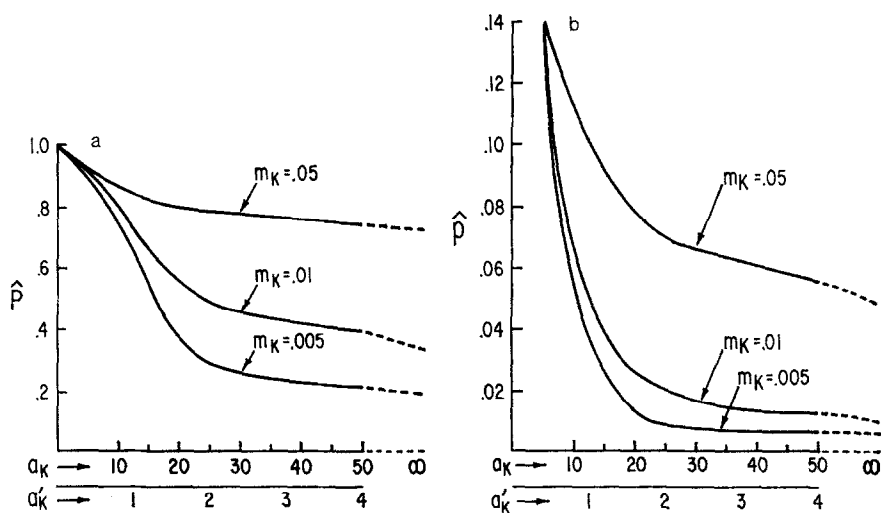

FIG. 7.   (a) The same as (a) except that $R = 50$ and $a_\kappa^* = 12.25$. (b) The same as (a) except that the ordinate represents larval numbers, $\hat{p}$, rather than adult numbers.

value which would just bring about eradication if there were no migration ($a_\kappa{}^* = 2.25$ for Population I and 12.25 for Population II).

Figures 6b and 7b translate $\hat{P}$ to $\hat{p}$, the effect on larval numbers. Using procedures analogous to those already shown for obtaining larval effects, the relationship of $\hat{p}$ to $\hat{P}$ works out to be

$$\hat{p} = \frac{\hat{P}^2}{(\hat{P} + a_\kappa)(1 + m_\kappa)} + \frac{m_\kappa}{1 + m_\kappa}.$$

$\hat{p}$ in this case is normalized to the size of untreated larval populations with the effects of migration included, while for reasons explained earlier the adults $\hat{P}$ are normalized to K.

First, it should be noted that for the case of $R = 10$, a value of m_κ was chosen, $m_\kappa = 0.005$, which permits the display of three real solutions of (29b). This is done for Fig. 6 only. In this case of $R = 10$, when $m_\kappa = 0.005$ there is a *region* between $a_\kappa = 1.56$ and $a_\kappa = 2.44$ where three equilibriums exist with stability characteristics as described earlier. This illustrates one aspect of inequality (30), namely, that if a_κ is large enough ($a_\kappa > 2.44$ in this case) only one equilibrium exists. However, this case also shows in two ways that condition (30), for there to be only one equilibrium, is not necessary. If $a_\kappa < 1.56$ there is only one equilibrium, and, more important, numerical study with $R = 10$ shows that if $m_\kappa > 0.0105$, there will be only one equilibrium regardless of the value of a_κ. The remaining curves, with larger m_κ, illustrate such single equilibriums.
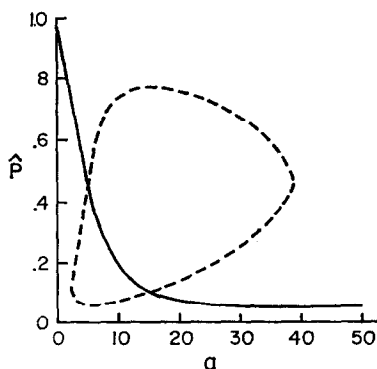

FIG. 8.   Relationship between single soft release equilibrium, $\hat{P}$, produced by a given release ratio, a, and the three possible equilibriums produced by a hard release of $\hat{A} = a\hat{N}$. Solid line is soft release equilibrium. Dashed lines are the other two equilibriums which would result by releasing $\hat{A}$ in a hard release model. For this case $m_\kappa = 0.005$ and $R = 10$.

Figure 8 was computed simply to illustrate the potential pitfalls of using a soft release model. Here the same parameter values of $R = 10$ and $m_\kappa = 0.005$ were substituted into the soft release equilibrium equation (31b). The dashed

lines show the other two hard release equilibriums which exist between $2 < a < 39.2$ but are not detected by the soft release model. Furthermore, the dashed lines show that when $2 < a < 5.2$ the soft equilibrium represents the upper stable hard equilibrium; when $5.2 < a < 15$, it represents the middle unstable hard equilibrium; and only when $15 < a < 39.2$ does it represent the equilibrium of interest, namely, the lowest one, which is stable.

From a practical point of view graphs 6a and 7a showing adult suppression do not add much to the previous discussion of the case where $A_K \to \infty$. For the case where $R = 10$, when migration is extremely small, $m_\kappa = 0.005$, substantial reduction can be obtained and this can be accomplished with release numbers no larger than $a_K{}' = 1$, that is the numbers released to achieve essentially maximum reduction need not be greater than the numbers required for eradication in the absence of migration. However, if migration is $m_\kappa = 0.05$ or higher then, as concluded in the previous section, when $R = 10$ adult numbers cannot be substantially reduced. What these graphs add is the fact that the asymptotic value, when $a_K \to \infty$, starts to be approached when $a_K{}'$ is 3 or 4. That is, little is accomplished by a major effort. For the case of $R = 50$, the critical migration for there to be only one equilibrium is extremely small, namely, $m_\kappa > 0.0025$ (values not graphed). With such an infinitesimal migration rate, substantial adult reduction could be obtained, but in this case of $R = 50$ if m_κ is much larger than $m_\kappa = 0.005$, adult numbers are not substantially affected.

Graphs 6b and 7b show effects of the same parameter values as in 6a and 7a, but on larval numbers, $\hat{p}$. These results are much more optimistic. Substantial reduction can occur, and this can be accomplished without a major effort since the maximum reduction, $\tilde{p}$ (when $a_\kappa \to \infty$) is approached at $a_K{}' = 3$ or 4. Whether or not this last conclusion is a robust result, or peculiar to the particular growth model used, is not known. The difference between the effects on adults and larvae is greater in the case of $R = 50$ than when $R = 10$. The change of the scale of the ordinate from Fig. 7a to 7b should be noted. However, a population with a larger R might be expected to have more young larvas in the first place as suggested by the numerical values in Table I.

4. COMPARISON WITH THE KNIPLING MODEL AND OTHER RESULTS

It was stated in the Introduction that Knipling introduced into the sterile male literature a model with exponential growth for the study of the effects of sterile male release and that this model enjoys extensive use. His population grows as stated by Eq. (1) and is truncated at the stipulated $\hat{K}$. Dietz (1976) used this model for evaluating migration effects. We now make a comparison between the foregoing results and behavior of the Knipling model.

Most models which incorporate intrinsic density regulation such as the one used in this article, will, when N is small, resemble the Knipling model by

growing exponentially (exceptions are those class of models which incorporate an Allee effect). Thus, the form of the Knipling model when it is subject to sterile male release and migration can be obtained directly from Eqs. (27) and (28) by simply letting N be small compared to K. Thus we have

$$\text{hard release,} \quad N' = \frac{RN^2}{N+A} + RM, \tag{34}$$

$$\text{soft release,} \quad N' = \frac{RN}{1+a} + RM. \tag{35}$$

Dietz studied the soft release case represented by recursion (35). (Dietz's variable includes the newly immigrant females, M, each generation.) Since N' is a linear function of N it can be seen by examining the coefficient of N that if $R > 1 + a$ the population grows exponentially until $\hat{K}$ is achieved.

On the other hand, if

$$R < 1 + a$$

which is the same as   (36)

$$a > R - 1$$

an equilibrium will result which is

$$\hat{N} = \frac{RM(1+a)}{(1+a)-R}. \tag{37}$$

Normalizing $\hat{N}$ and M to the stipulated $\hat{K}$,

$$\hat{P} = \frac{Rm_K(1+a)}{(1+a)-R} \tag{38}$$

where

$$\hat{P} = N/\hat{K},$$

$$m_\kappa = M/\hat{K}.$$

Assuming a constant release ratio, a, this equilibrium is stable.

However, a study of the hard release case, Eq. (34), reveals that equilibrium (27) may not be "truly" stable.

Without presenting the calculations, the Knipling models behave in the following way: With soft release alone and no migration there is no equilibrium; the population either grows exponentially (to $\hat{K}$) or contracts to zero depending on condition (36). With hard release and no migration, there is a single unstable equilibrium so that for a given release number, A, eradication is achieved only

if the initial population size is below the unstable point which is $\hat{N} = A/(R - 1)$. This condition on the initial population size is a well-known feature of the Knipling model (see, for example, Costello and Taylor, 1975). When migration is introduced into this Knipling model together with hard release (Eq. (34)) the situation becomes moderately involved. It turns out that if the following condition is satisfied.

$$A > MR(2R - 1 + 2(R(R - 1))^{1/2}), \tag{39}$$

there will be two equilibriums where the larger one is unstable and the lower one stable. If (39) is not satisfied there are no equilibriums and the population grows exponentially (to $\tilde{K}$). If there are two equilibriums, ((39) satisfied), then we have the condition again that initial population size must be below the unstable equilibrium in order for the population to be depressed to the lower stable one. These two equilibriums are

$$\hat{N}_{1,2} = \frac{A - RM \pm ((A - RM)^2 - 4MAR(R - 1))^{1/2}}{2(R - 1)}. \tag{40}$$

So, the unstable equilibrium of the primitive Knipling model continues to be present when migration is added to that model, and it would appear to be appropriate to identify this equilibrium with the unstable equilibrium which appeared in the analysis on the previous pages of a population with intrinsic density regulation. It would further seem appropriate and useful to call this unstable equilibrium, the "Knipling equilibrium."

Dietz's soft release equilibrium (37) gives the lower stable equilibrium only if

$$a > (R - 1) + (R(R - 1))^{1/2}. \tag{41}$$

This is roughly twice the size of, a, defined by condition (36). If (41) is not satisfied but (39) is, then Dietz's equilibrium (37) corresponds to the upper unstable Knipling equilibrium under a hard release procedure.

Thus, the Knipling model and the model incorporating intrinsic density regulation discussed in this article exhibit rather different characteristics.

A qualitative difference is that with intrinsic density regulation there is no condition on release numbers such as (36) or (39) in order for there to be any effect at all on population size (at $\tilde{K}$). Release of sterile males into the density regulated population will always have some effect.

Perhaps more important, is a quantitative difference between the two models: the density regulated population is more strongly affected by release of sterile males than is the Knipling model. Sample comparisons between the two models are made in Figs. 9 and 10. Figure 9a compares the Dietz equilibrium (38) with (29b) for soft release for Population I and fixed migration rate $m_\kappa = 0.05$. It can
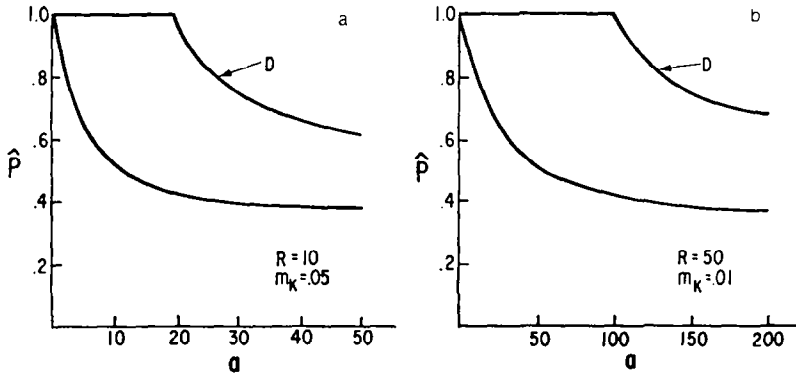
FIG. 9. Comparison of soft release equilibrium of this paper with Dietz's analysis of the Knipling model. Curve D ≡ Dietz's result. The other curve is obtained from the soft equilibrium solution, Eq. (31b). In (a), $R = 10$ and $m_\kappa = 0.05$ and in (b), $R = 50$ and $m_\kappa = 0.01$.
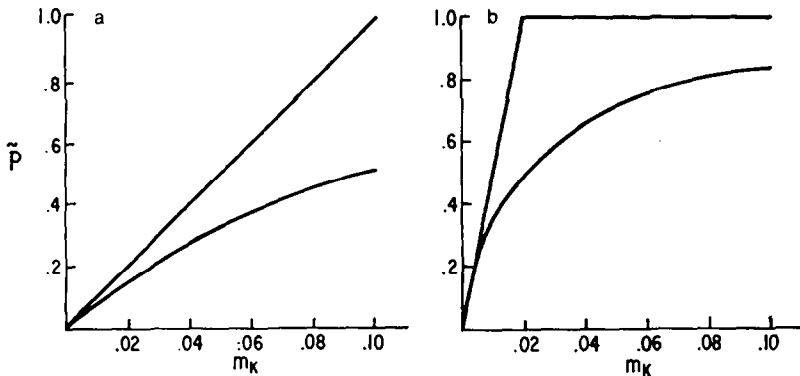

FIG. 10. Comparison of the maximum possible effect of release in the Knipling model and the density regulated model. Straight lines (truncated) are the Knipling model ($\tilde{P} = m_\kappa R$), and the curves are the same as in Fig. 5. In (a) $R = 10$ and in (b) $R = 50$.

be seen that in the Dietz model there is no effect until $a > 19$. In this particular case with $R = 10$, $a > 19$ satisfies (41), so the equilibrium values of $\hat{P} < 1$ are truly stable. A similar computation is made in Fig. 9b for Population II with $m_\kappa = 0.01$. It is quite clear that the density regulated population is more susceptible to the effects of sterile male release. Figures 10a, b show the maximum possible effect of release ($a \to \infty$) for the two models on Populations I and II. In the Dietz model

$$\tilde{P} = m_\kappa R.$$

Thus, one can be more optimistic about controlling a population with intrinsic density regulation than about one regulated by "truncation." In fact, the expres-

sion above is always greater than (33b) which gives the maximum effect of release with migration in the density regulated population.

Dietz (1975) also performed a realistic simulation study of the effect of migration and sterile male release thru continuous time on an age structured population. Although it is difficult to make a detailed comparison with that study, it appears that for the several parameter sets which he gives, his results are even more pessimistic than the results reported here. Also, for most of his results, his system also appears to be more susceptible to control when it is intrinsically density regulated, than when it is regulated by truncation.

DISCUSSION

The principle conclusion of this article is that the method of releasing sterile males for suppression of pest populations cannot be effective in the face of appreciable amounts of immigration.

As a qualitative conclusion this and Dietz's theoretical studies merely confirm intuition (Proverbs, 1974). What this study can add is a quantitative guess that for populations which this discrete generation model might approximate, migration rates cannot be tolerated much above $m_\kappa = 0.05$. This applies to a population with $R \simeq 10$, a value which seems very modest even when considering the fact that R not only includes fecundity but survival as well, under optimal conditions.

It seems reasonable that there should be many insect species which could increase by much more than $R = 10$-fold per generation when in low densities so that the maximum amount of migration is probably more like $m_\kappa = 0.01$ or $m_\kappa = 0.005$.

This kind of migration rate, m_κ, has clear meaning when applied to a geographically delineated target area—an island; however, it could be appropriately modified and applied to an arbitrary sector of a much larger area subject to diffusional migration (see, for example, Cavalli-Sforza and Bodmer, 1971, p. 429).

As already pointed out, the result of Dietz's study of migration in the Knipling model where there is no intrinsic density regulation is even more pessimistic about control by sterile male release in the face of migration. Here only infinitesimal migration is tolerable. Dietz's treatment, therefore, might be regarded as a study of a "worst case" situation, which is certainly desirable information to have.

All of this, of course, applies to suppression of adult numbers. The behavior of the numbers of immature stages is quite another matter. In this case it is by no means intuitively clear what levels of immigration a sterile male release program can tolerate. Most theoretical work has emphasized eradication rather than suppression to an acceptable equilibrium, which is the only possibility

with immigration, and it is perhaps for this reason that there has been only moderate emphasis on the considerable difference which can occur between reduction of adult numbers and reduction of immature stages. However, Berryman *et al.* (1973) have displayed the difference in a simulation study, and Proverbs *et al.* (1973), who study the codling moth, have been quite explicit about the importance of immatures *vs* adults when eradication is not achievable.

Mainly for illustrative purposes this study maximized this difference by comparing adult census with young larvae before any density dependent death set in. Perhaps for an agricultural pest it would be better to keep track of the total impact of immatures which might be measured by the integral of Eq. (5) over $t = (0, T)$) which is $(cb)^{-1} \ln (1 + P(R - 1))$ or, at equilibrium K simply $(cb)^{-1} \ln R$. Preliminary study of this "impact" function shows that it appears to behave as expected, being more responsive to sterile male release, than are adults, but not so responsive as young larvae.

Another situation which could moderate the effect of immigration might occur in species where egg laying is density regulated; i.e., where immigrant females compete for oviposition sites with females laying dominant lethal bearing eggs. A preliminary study of this situation suggests that somewhat higher migration rates would be tolerable.

The first part of this article dealing with an isolated target area is not likely to provide new insights involving this situation since here there already exists a substantial body of theory, mainly in the form of simulation work, to say nothing of actual experience (summaries in "Insect Pest Management and Control", 1969; Pal, 1974, La Chance *et al.*, 1967; Weidhaas, 1968). However, it may be of some value for the purposes of making first guesses, to have available a model which incorporates density regulation and is also susceptible to analytic study so that, unlike simulation models, its global behavior is understood.

This study, one again, demonstrates how sensitive conclusions can be to the assumptions made. It is quite clear when comparing the results of this study with those of the Knipling model how the whole behavior of the system and the important conclusions derived, depend in important ways on whether or not intrinsic density regulation is assumed. Most simulation models include density regulation in more realistic ways than done here, but some do not (e.g., Bogyo *et al.*, 1971). Also, there are the differences resulting from whether soft or hard release is assumed; specifically the soft release assumption can be quite misleading.

The appearance of two or three equilibriums, one being the unstable Knipling equilibrium, is probably a robust conclusion for any sort of density regulated system and is not dependent on the specific form of the regulation stated by Eq. (2). This conjecture arises from the dynamical considerations illustrated in Figs. 4a and 4b. This conjecture might be useful for realistic simulation studies where the existence of more than one equilibrium could easily go undetected. Also, the existence of more than one equilibrium could conceivably have

practical significance, suggesting that a population which appears to be holding its own against sterile male release could be eradicted or strongly depressed by a major effort. In fact, this describes quite well the sequence of events resulting in the eradication of the screw worm on Curacoa as described by Costello and Taylor (1975). However, they explain this experience in a very different way, namely, that it was the result of a threshold which appears when the stochastic effects are introduced into the primitive Knipling model.

Finally, there remains the problem of exactly how to interpret the numerous models in this field, including this one, which measure events in discrete generations. The virtue of these models is that important biological aspects can be easily incorporated as was done here, while in continuous time analytic models, such as the logistic, one is often hard put to identify the individuals being censused who comprise N. The discrete generation models are easily interpreted for organisms whose life stages are fairly synchronized by seasons, for instance, and have one or two generations a year. Discrete generation models are also fairly easily understood where a small number of cohorts are moving through their life history *en echelon* producing discrete age classes as illustrated by Riker's (1954) studies. However, it is not clear, to this writer at least, just how to interpret the relevant numbers such as N, A, M in this study for a population which has an essentially continuous age structure. N is in some way related to the rate of recruitment of adults from immature stages and to the cumulative numbers so recruited over a generation interval. The theoretical demography of age structure in exponentially expanding or contracting populations is well understood; while there appears to be a clear need for more theoretical demography of density regulated populations which achieve stable size.

REFERENCES

ASMUSSEN, M. A., AND FELDMAN, M. 1977. Density dependent selection. I. A stable, feasible equilibrium may not be attainable, *J. Theor. Biol.* **64**, 603–618.

AYALA, F. J., GILPIN, M. E., AND EHRENFELD, J. G. (1973). Competition between species: Theoretical models and experimental tests, *Theor. Pop. Biol.* **4**, 331–356.

BERRYMAN, A. A., BOGYO, T. P., AND DICKENSEN, L. C. 1973. Computer simulation of the population reduction by release of sterile insects II, *in* "Computer Models and Application of the Sterile Male Technique," pp. 31–43, International Atomic Energy Agency, STI/PUB 340, Vienna.

BOGYO, T. P., BERRYMAN, A. A., AND SWEENEY, T. A. 1971. Computer simulation of population reduction by release of sterile insects I, *in* "Application of Induced Sterility for Control of Lepidopteran Populations," pp. 19–26, International Atomic Energy Agency, STI/PUB 281, Vienna.

CAVALLI-SFORZA, L. L., AND BODMER, W. F. 1971. "The Genetics of Human Populations", pp. 428–430, Freeman, San Francisco.

CHRISTIANSEN, F. B., AND FENCHEL, T. M. 1977. "Theories of Populations in Biological Communities," Springer–Verlag, New York.

CLARK, B. 1972. Density-dependent selection, *Amer. Natur.* **106**, 1–13.

CLARK, L. R., GEIER, P. W., HUGHES, R. D., AND MORRIS, R. F. 1967. "The Ecology of Insect Populations," Methuen, London.

International Atomic Energy Agency, Vienna 1973. "Computer Models and Application of the Sterile Male Technique,'" STI/PUB 340.

COSTELLO, W. G., AND TAYLOR, H. M. 1975. Mathematical models of the sterile male technique of insect control, *in* "Mathematical Analysis of Decision Problems in Ecology" (A. Charnes and W. R. Lynn, Eds.), pp. 318–359, Lecture Notes in Biomathematics, Vol. 5, Springer–Verlag, Berlin.

CUELLAR, C. B., AND COOPER, A. 1973. "On the Net Reproductive Rate and Mean Generation Time of Mosquitoes in Reference to Sterile Male Release," WHO/VBC/73.460.

DAVIDSON, G. 1974. "Genetic Control of Insect Pests," Academic Press, New York.

DIETZ, K. 1975. Simulation models for genetic control alternatives, *in* "Mathematical Analysis of Decision Problems in Ecology" (A. Charnes and W. R. Lynn, Eds.), pp. 299–317, Lecture Notes in Biomathematics, Vol. 5, Springer–Verlag, Berlin.

DIETZ, K. 1976. The effect of immigration on genetic control, *Theor. Pop. Biol.* **9**, 58–67.

HASSELL, M. P. 1975. Density-dependence in single-species populations, *J. Anim Ecol.* **44**, 283–295.

HENNEBERRY, T. J. 1971. Research on sterility methods for control of the cabbage looper, *Trichoplusia ni*, *in* "Application of Induced Sterility for Control of Lepidopterans Populations," pp.51–63, International Atomic Energy Agency, Vienna, STI/PUB 281.

Committee on Plant and Animal Pests 1969. Insect pest management and control, *in* "Principles of Plant and Animal Pest Control," Vol. 3, Nas. Res. Council, NAS Publ. 1695, Washington.

KARLIN, S., AND MCGREGOR, J. 1972. Polymorphisms for genetic and ecological systems with weak coupling, *Theor. Pop. Biol.* **3**, 210–238.

KLASSEN, W., AND CREECH, J. F., 1973. *In* "Computer Models and Applications of the Sterile Male Technique," p. 65, International Atomic Energy Agency, STI/PUB 340, Vienna.

KNIPLING, E. F. 1955. Possibilities of insect control or eradication through the use of secually sterile males, *J. Econ. Entomol.* **48**, 459–462.

KNIPLING, E. F. 1968. The potential role of sterility for pest control, *in* "Principles of Insect Chemosterilization" (G. C. Labrecque and C. N. Smith, Eds.), pp. 7–40, Appleton, New York.

KUNZ, S. E., AND J. L. ESCHLE 1971. Possible use of the sterile-male technique for the eradication of the horn fly, *in* "Sterility Principle for Insect Control or Eradication," pp. 145–156, International Atomic Energy Agency, STI/PUB/265, Vienna.

LA CHANCE, L. E., SCHMIDT, C. H., AND BUSHLAND, R. C. 1967. *In* "Pest Control" (W. W. Kilgore and R. L. Doutt, Eds.), Chap. 4, Academic Press, New York.

MAY, R. M. 1975. Biological population obeying difference equations: Stable points, stable cycle and chaos, *J. Theor. Biol.* **51**, 511–524.

MURDIE, G. 1973. Development of a population model of the cotton red bollworms as a basis for testing control strategies, pp. 119–128. *in* "Computer Models and Application of the Sterile-Male Technique," pp. 119–128, International Atomic Energy Agency, STI/PUB/340, Vienna.

PAL, R. 1974. WHO/ICMR program of genetic control of mosquitoes, *in* "The Use of Genetics in Insect Control" (R. Pal and M. J. Whitten, Eds.), Chap. 5, Elsevier/North–Holland, Amsterdam.

PIELOU, E. C. 1969. "An Introduction to Mathematical Ecology," Wiley, New York.

POULSEN, E. T. 1975. "A Mathematical Model for Population Regulation, I," Preprint Series 1975/76, No. 1, Matematisk Institut, Aarhus Universitet, Aarhus, Denmark.

PROVERBS, M. D. 1974. Ecology and sterile release programs, the measurements of relevant population processes, *in* "The Use of Genetics in Insect Control" (R. Pal and M. J. Whitten, Ed.), pp. 201–219, Elsevier/North–Holland, Amsterdam.

PROVERBS, M. D., LOGAN, D. M., AND CARTY, B. E. 1973. Some biological observations related to codling moth control by the sterility principle, *in* "Computer Models and Application of the Sterile Male Technique," pp. 149–165, International Atomic Energy Agency, Vienna STI/PUB 340.

RAJAGOPALAN, P. K., YASUNO, M., AND MENON, P. K. B. 1973. "Density Effect on Survival of Immature Stages of *Culex pipiens fatigans* in Breeding Sites in Delhi Villages," WHO/VBC/73.430.

RIKER, W. E. 1954. Effects of compensatory mortality upon population abundance, *J. Wildl. Manage* 18, 45.

SCHOENER, T. W. 1974. Competition and the form of habitat shift, *Theor. Pop. Biol.* 6, 265–307.

STALEY, D. H., CANNON, W. N., AND HOLD, W. R. 1971. A mathematical model of an insect population with overlapping generations. Where the females are polyandrous and the males are subject to auto-sterilization, *Ann. Entolog. Soc. Amer.* 64, 325.

TAYLOR 1976. *Environ. Entomol.* 5, 87–95.

VARLEY, G. C., GRADWELL, G. R., AND HASSEL, M. P. 1973. "Insect Population Ecology," Blackwell, Oxford.

WALLACE, B. 1967. "Topics in Population Genetics," Norton, New York.

WEIDHAAS, D. E. 1968. Field development and evaluation of chemosterilants, *in* "Principles of Insect Chemosterilization" (G. C. Labrecque and C. N. Smith, Eds.), pp. 275–314, Appleton, New York.