Pest persistence and eradication conditions in a deterministic model for sterile insect release

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The release of sterile insects is an environment friendly pest control method used in integrated pest management programmes. Difference or differential equations based on Knipling’s model often provide satisfactory qualitative descriptions of pest populations subject to sterile release at relatively high densities with large mating encounter rates, but fail otherwise. In this paper, I derive and explore numerically deterministic population models that include sterile release together with scarce mating encounters in the particular case of species with long lifespan and multiple matings. The differential equations account separately the effects of mating failure due to sterile male release and the frequency of mating encounters. When insects spatial spread is incorporated through diffusion terms, computations reveal the possibility of steady pest persistence in finite size patches. In the presence of density dependence regulation, it is observed that sterile release might contribute to induce sudden suppression of the pest population.

Keywords: pest control; spatial invasions; integrated pest management

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1. Introduction

The core idea in the sterile insect technique (SIT) consists in releasing a large number of sterile male insects into a wild population, where they mate with females and prevent reproduction. As a consequence, the pest population growth rate is reduced, and if the number of sterile males introduced is large enough, a mate-finding Allee effect might emerge [7,26,32]. This technique (and its first numerical model) was originally proposed by Knipling [19] and has been used since then due to clear advantages over insecticide application: it does not contaminate the environment, does not target other insect populations and is safe for farmer’s health [17].

Knipling’s model and its extensions have been extensively used as a framework in further analysis of a large number of biological control scenarios [2,17]. Its essential assumption is that the probability with which a wild female has a mating encounter with a fertile male is equal to $M_f / (M_f + S_f)$, where $M_f$ is the number of fertile males and $S_f$ is the number of artificially introduced sterile males at time $t$ (scaled to generations). Consequently, only this fraction of the female population would be able to reproduce, increasing at a constant population growth rate...
If the number of wild females at time $t$ is denoted with $N_t$, then basic model just described is written as follows:

$$N_{t+1} = \beta N_t \frac{M_t}{M_t + S_t}.$$  \hspace{1cm} (1)

Under the assumption that the sex ratio is 1:1, which is equivalent to say that $N_t = M_t$, the previous equation is rewritten as follows:

$$N_{t+1} = \frac{\beta N_t^2}{N_t + S_t}.$$  \hspace{1cm} (2)

This simple model has been successful describing the dynamics in populations with high densities and where almost every individual is able to find a mate. In contrast, for instance, pest populations that are likely to be more sparse might have an increased difficulty of mate finding, as it is observed at the beginning stages of some invasions [26]. In this case, Knipling’s paradigm fails to give an adequate qualitative description, as pointed out in [34].

A continuous time model analogue to Equation (1) is given by

$$N' = \beta N \frac{M}{M + S} - \mu N,$$  \hspace{1cm} (3)

where $'$ represents the derivative with respect to time and the variables $N, M, S$ are the number of fertile females, males and the sterile insects, respectively. Natural mortality is introduced with average per capita rate $\mu$. This model, which describes exponential growth when $S = 0$ and $\beta > \mu$, has been extended to include density dependence [3] and also spatial spread [25].

The crucial aspect in Kniplings’ model potential failure is that it lacks a detailed description of the mate encounter processes, which also explain the possibility reproductive Allee effects due to mating failure [7,8]. In particular cases, however, simple deterministic population models that include mate encounter rates can be derived [31], with adult females classified into two different stages, those ready to mate and those already fertilized. Differential equations can then be used to model the transitions between these stages. In this paper, we extend the model in [31] to incorporate sterile insect release, introducing a new class of females that contains those fooled by mating with sterile males. This allows to consider reproduction failure either by sterile release or by reduction in mate encounters. The model’s tractability improves for the case of species with long lifespan and short reproductive periods, like beetles, where it is possible to reduce the number of equations.

If spatial spread within a patch is taken into account, the model exhibits nontrivial steady solutions for certain patch sizes, even if the sterile population released is higher than the threshold necessary to eradicate a pest population in the non-spatial scenario. This result highlights the importance of considering the spatial component in applications and might add an insight into instances where SIT has been used in combination with other pest control methods that target mate encounters.

In Section 2, the model formulation is made without consideration of the carrying capacity, assuming abundant resources in favour of pest growth. Spatial spread is then modelled introducing a diffusion term and conditions for persistence through steady solutions are found. In Section 3, density growth regulation is included into the model, and the effects of spatial spread are analysed numerically.

2. Pest insects in the presence of abundant resources

Initially, let us assume that pest insects can access to an abundance of resources to survive. This is a reasonable assumption for the first stages of a pest invasion that, if successful, would be expected
to follow exponential growth at first. Notice that, at the beginning of an invasion process, low population densities may provoke a decrease in the probability of finding a mate, and consequently pest eradication or suppression is more likely to be successful due to the appearance of Allee effects [11,26,33].

We proceed to derive a continuous time model under the following initial group of reasonable assumptions [3]: (i) females and males are homogeneously mixed; (ii) sterile males and wild males are fully competitive; (iii) female mating is random and proportional to the number of males (sterile and wild); (iv) the release of sterile males is done in such a way that their density is constant all the time; (v) sterile insects mix homogeneously within the whole population immediately after they are released.

2.1. Model description

We model a sexually mature female pest population for the case where the average lifespan is considerably larger than the average time spent at the reproductive stage, understood here as an immediate post-copulatory stage where females are not sexually receptive. This is in agreement with the sharp loss of receptiveness that generally appears as a physiological response to male materials passed during copulation [24]. Let us denote the density of females at time $t$ by $N = N(t)$ and divide the female population in three groups:

- $N_1$: females at reproductive stage, after mating with wild males,
- $N_2$: females ready for mating,
- $N_3$: females at reproductive stage, after mating with a sterile male.

Females ready for mating, i.e. those in class $N_2$, might encounter a wild male to mate, and then move to compartment $N_1$, or encounter a sterile male and move to compartment $N_3$. The average time they remain either in $N_1$ or $N_3$ is the same. The difference is that those females in $N_1$ will successfully produce offspring. After oviposition, a female either in $N_1$ or $N_3$ returns to the class $N_2$. A scheme for the transitions between female stages is depicted in Figure 1. In the context of this paper, a sexually mature female is understood as a female that had at least one successful mating encounter (one that led to reproduction) with a wild male, and it is included in the adult female population when that first contact occurs. Thus, new sexually mature females are introduced to the class $N_1$ at a rate $\beta$ and notice that females which (i) only contact sterile males during their whole life, or (ii) get lost and do not have contact at all with any kind of male, are excluded from the dynamics. Thinking in the contact process between females and wild males as a Poisson process, and if $\xi$ denotes the average per capita rate of mating encounters, it comes clear that

![Figure 1. Females are classified in three groups: those that had a mating encounter with a wild male ($N_1$), females searching for a mating encounter ($N_2$) and females that had a mating encounter with a sterile male ($N_3$). The average rate of contacts of a female with wild and sterile males is $\xi M$ and $\xi S$, respectively. The time a female spends in the reproductive stage is $1/\sigma$, the average lifespan is $1/\mu$. New mature adult females are introduced at rate $\beta$. Additional mortality, while at the searching stage, is represented by $\lambda$.](image)
the probability for a female to have at least one contact with a wild male in her lifetime would be \( p = 1 - e^{-\xi M} \), where \( M \) is the number of wild males. Therefore, assuming that no juveniles die, this will be the fraction of the (per capita) offspring that would contact a wild male later on, \( \beta = (\text{birth rate}) \times p \). In the worst case scenario, the value of \( p \) is close to one and \( \beta \) could then be approximated with the birth rate, which is the approach taken here. As a result of this assumption, there is a slight overestimation that, for practical application, is preferred in trying to achieve pest extinction. Notice additionally that if the mortality in young females is small and the sex ratio is close to one, then \( \beta \) would be approximately equal to the birth rate divided by two. Let \( \mu \) be the per capita mortality rate, satisfying \( \beta > \mu \), and define \( \lambda \) as an additional mortality term that represents the possibility of a female being exposed to a higher risk of death resulting from leaving its well-sheltered home range while ready for mating. Also, let \( 1/\sigma \) be the average time that females expend carrying eggs and denote the (constant) density of sterile males released by \( S \), then set of equations proposed to include SIT then reads:

\[
\begin{align*}
N_1' &= (\beta - \mu)N_1 - \sigma N_1 + \xi MN_2, \quad (4) \\
N_2' &= -(\mu + \lambda)N_2 + \sigma (N_1 + N_3) - \xi (M + S)N_2, \quad (5) \\
N_3' &= -\mu N_3 - \sigma N_3 + \xi SN_2, \quad (6)
\end{align*}
\]

where \( ' \) represents the derivative with respect to time. A biologically reasonable assumption usually added in SIT modelling is that the adult sex ratio in the wild population is close enough to one \([2,3]\), thus allowing to replace \( M \) with \( N \) in the equations. Under natural selection, this hypothesis can be justified by the widely accepted Fisher’s arguments \([10]\), which explain why the sex ratio approaches 1:1 in most animal species. If the average lifespan is considerably larger than the average time at the reproductive stage, it is possible to reduce this system to one equation of exponential growth plus a type-II functional, involving only the total female population \( N \) (see Appendix 1 for derivation details):

\[
N' = \phi N \left( 1 - \frac{\eta(1 + \theta S)}{1 + \gamma(N + S)} \right), \quad (7)
\]

where

\[
\phi = \beta - \mu, \quad \eta = \frac{\sigma(\beta + \lambda)}{(\beta - \mu)(\sigma + \lambda)}, \quad \gamma = \frac{\xi}{\sigma + \lambda}, \quad \theta = \frac{\beta \xi}{\sigma(\beta + \lambda)}.
\]

From Equation (7), the per capita reproduction rate can be expressed as follows:

\[
\frac{N'}{N} = \phi \frac{A + N}{B + N}, \quad (8)
\]

where \( A \) and \( B \) are combinations of the model parameters. This allows to quantify the impact of \( S, \xi \) or \( \lambda \) as control parameters, see Figure 2. Equivalent algebraic expressions to Equation (8) are typically used to adjust empirical descriptions of Allee effects in population models \([7]\), often without linking \( A \) and \( B \) to relevant biological parameter values.

In addition to the trivial stable state, Equation (7) has an unstable equilibrium \( N^* \) when \( S = S_c \), the critical sterile male density. They are related as follows:

\[
N^* = \frac{\eta - 1}{\gamma} + \left( \frac{\eta \theta}{\gamma} - 1 \right) S_c = \frac{\mu}{\beta - \mu} \left( \frac{\lambda (\sigma + \mu - \beta) + \mu \sigma}{\xi \mu} + S_c \right). \quad (9)
\]

Therefore, if the number of sterile males introduced, \( S \), is larger than the critical value \( S_c = N^*/(\beta - \mu)/\mu - (\lambda(\sigma + \mu - \beta) + \mu \sigma)/\xi \mu \) the pest population will decline. In the absence of sterile release, i.e. \( S = 0 \), Equation (7) models the invasion with possible failure in the establishment...
due to insufficient mating encounters, the nontrivial equilibrium $N^* = (\eta - 1)/\gamma$ is the threshold for a reproductive Allee effect. In contrast, the absence of sterile insects in Equation (2) reduces it to that of exponential growth. If $S > 0$, the nontrivial unstable equilibrium in Equation (3) is $N^{**} = \mu S/(\beta - \mu)$, which can be recovered from Equation (3) as the average number of mating encounters approaches infinity, i.e. $N^* \to N^{**}$ as $\xi \to \infty$.

2.2. Spatial spread

We consider now the inclusion of one-dimensional insect dispersal and the possibility of persistence in patches of finite length. In an invaded patch of size $L$ surrounded by a lethal exterior, the boundary conditions

$$N\left(-\frac{L}{2}, t\right) = N\left(\frac{L}{2}, t\right) = 0$$

hold. This situation might correspond, for instance, to the use of insecticides outside the patch. We assume an approximate uniform release of sterile insects over the invaded zone, assuring with this that any female could find sterile males to mate, independently of the spatial location. The movement of females is modelled by introducing a diffusion term $D(\partial^2 N/\partial x^2)$ in Equation (7), with the parameter $D$ representing the diffusion constant. If we let $\hat{x} = \sqrt{\phi/D}$ and $\hat{t} = \phi t$ then, after dropping the hats, we obtain

$$\frac{\partial N}{\partial t} = N \left(1 - \frac{\eta (1 + \theta S)}{1 + \gamma (N + S)}\right) + \frac{\partial^2 N}{\partial x^2}.$$  

We can establish spatial persistence conditions through positive steady solutions of Equation (11), i.e.

$$\frac{\partial^2 N}{\partial x^2} + N \left(1 - \frac{\eta (1 + \theta S)}{1 + \gamma (N + S)}\right) = 0 \quad \text{if } |x| < \frac{L}{2},$$

with $N = 0$ if $|x| = L/2$. Introducing the variable $v = \partial N/\partial x$, we obtain a system of differential equations with the origin and

$$(N^*, v^*) = \left(\frac{\eta - 1}{\gamma} + \left(\frac{\eta \theta}{\gamma} - 1\right) S, 0\right)$$
as equilibrium points. Quick computations show that, for the linearized system, the origin and
\((N^*, 0)\) are a saddle and a centre, respectively, if \((\lambda (\beta - \mu - \sigma)/\mu - \sigma)/\xi < S\) holds. If the last
inequality is reversed, the origin turns into a centre and the nontrivial equilibrium, now a saddle,
moves to the left of the origin. After multiplying Equation (12) by \(\partial N/\partial x\) and integrating, we
obtain the relation
\[
\frac{1}{2} \left( \frac{\partial N}{\partial x} \right)^2 + F(N) = c,
\]
where \(c\) is constant and
\[
F(N) = \int_0^N u \left( 1 - \eta \frac{(1 + \theta S)}{1 + \gamma(u + S)} \right) du,
\]
which plays the role of a ‘potential’ function. Steady pest population distributions in space, with
corresponding maximum female density \(M\), can then be related to the size of the patch through
the formula
\[
L = L(M) = \sqrt{2} \int_0^1 \frac{M}{\sqrt{F(M) - F(Mw)}} \, dw
\]
obtained after some standard manipulation of Equation (14), see [5,9,22] or [27] for instance. This
formula can be evaluated (see Example below), and used to determine how the steady solutions
of Equation (11) depend on the length of the underlying patch size.

2.2.1. Example

Long lifespan with relatively low average reproductive periods and the capacity to have multiple
matings are characteristics commonly encountered among beetle species. Biological and eco-
nomic constrains, often related with relative long larval periods, have prevented the SIT to be a
feasible option to be used against Coleoptera. However, it has been successfully tested in pilot
programmes for the cases of cockchaferers (Melolontha vulgaris) [13], the boll weevil (Anthono-
mus grandis) [16,18,20] and sweetpotatoes weevils (Cylas formicarius) [21,23]. The latter case,
carried out at the Kume Island, Okinawa Prefecture in Japan, the eradication using sterile release
was complete. Following that success, new programmes have been designed against Euscepes
postfasciatus, another worldwide notorious pest of sweet potatoes, with new research focused on
overcoming rearing difficulties [28].

We illustrate formula (16) for realistic parameter values, consistent with those often found in
beetles. Let \(1/\mu = 40\) (day), \(\beta = 0.3\) (day\(^{-1}\)) and an average reproductive time of \(1/\sigma = \frac{1}{2}\) (day).
We arbitrarily fix \(S = 300\) and \(\xi = 0.0001\) with no extra mortality, i.e. \(\lambda = 0\). Figure 3(a) shows
a sketch in the phase plane corresponding to the system \((N, v)\). Nontrivial steady solutions are
given by orbits that start and end at the \(v\)-axis \((\circ)\). There is an orbit \((\bigcirc)\) that separates the cycles
around the nontrivial equilibrium \((N^*, 0)\) and the steady-state solutions. The graph corresponding
to the ‘potential’ function \(F\) defined by expression (15) is given in Figure 3(b). The positive
root corresponds to the orbit \((\bigcirc)\), where the value of the integral (16) approaches infinity, see
Figure 3(c). If we follow the curve in the direction of decreasing \(L\), the values of \(M\) increase with
no bound, which is a biologically unreasonable scenario. Figure 3(b) explains this situation: the
function \(F\) is not bounded above and therefore cannot reach a maximum value. It is also possible
to show that the zero solution is stable, suggesting the unstability of the nontrivial solution. Thus,
under the current hypotheses, there would not be a critical patch length under which an invasion is
impossible, which is unreasonable. Therefore is the need to include mechanisms of growth
regulation, as addressed in the next section. Despite the limitations described, Equation (7) is still
useful to approximate the impact of SIT during the first stages of an invasion.
3. Inclusion of density dependence

We modify Equations (4)–(6) to incorporate an additional (constant) mortality rate $\nu$, corresponding to density regulation mechanisms that may include competition for limited resources. Density dependence might assist SIT in two ways [2]: (i) by increasing natural mortality at higher densities; (ii) by producing a sudden collapse of the pest population as the sterile release is increased above a critical value. The latter phenomena, resulting from the combination of overwhelming density regulation with a substantial Allee effect, has been observed, for instance, in experimental control programmes against melon fly [14] and is theoretically explained by the appearance of a bifurcation into the models [2].

3.1. Model description

We include the effects of density dependence under the same hypothesis used to derive models (4)–(6). The proposed equations linking $N_1, N_2$ and $N_3$ are as follows:

$$N_1' = \beta N_1 - (\mu + \nu(N + S))N_1 - \sigma N_1 + \xi NN_2,$$

(17)
An increment (decrement) in the value of $\eta$ represents an increment (decrement) of mortality in the population, caused, for instance, by a positive change in the additional mortality $\lambda$ in the cases when $\sigma > \beta$. The qualitative description of Equation (23) is simplified by observing that the last factor in the right-hand side of Equation (23) is a positive number less than one, which multiplies the quadratic $Q(w) = (M - w)(1 + w)/M$. In the particular case where sterile release is absent, i.e., if $s = 0$, the equation reduces to $\eta = Q(w)$, analysed in [31]. For $s > 0$ extinction occurs when $n = 0$, with a corresponding value of $\eta^* = (1 - s)(1 + Ms)/(\gamma + Ms(\rho + \theta))$, which is the point where a branch of positive equilibria bifurcates from the trivial equilibria.
Figure 4. The points on the curve are the nontrivial equilibria for Equation (21). The shadowed region represents the zone where the concurrent reproductive Allee effects take place. It is observed that the introduction of sterile insects enhances the Allee effect for lower values of $n$ and reduces the magnitude of the largest equilibrium due to competition for resources. Sudden extinction for sterile release values larger than $s^*$ is present.

![Figure 5](image)

Figure 5. Bifurcation curves in terms of the mortality $\eta$ for different values of sterile pressure release $s$. (a) If the mortality is large, individuals in low density populations are unable to replace themselves fast enough, giving rise to the appearance of an (unstable) Allee threshold at $\eta^*_s = 1$. (b) and (c) The introduction of sterile insects reduces the magnitude of the largest stable equilibria, due to the depressing effects of density regulation. As a consequence, as the value of $s$ increases, the minimum density required for sudden extinction decreases.

### 3.2. Spatial spread

As the case in Section 2, we assume the invasion of a patch suitable for survival surrounded by a lethal exterior, i.e. the same boundary conditions (10) hold. After introducing spatial diffusion in Equation (20), normalizing and rescaling space and time to reduce the number of parameters we obtain

$$\frac{\partial n}{\partial \tau} = n \left(1 - (n + s) - \frac{\eta}{1 + K\gamma (n + s)} \left(1 + \frac{K\theta s}{1 + K\rho (n + s)}\right)\right) + \frac{\partial^2 n}{\partial x^2} \tag{24}$$

for which we look possible nontrivial steady solutions. Thus, considering the equation

$$\frac{\partial^2 n}{\partial x^2} + n \left(1 - (n + s) - \frac{\eta}{1 + K\gamma (n + s)} \left(1 + \frac{K\theta s}{1 + K\rho (n + s)}\right)\right) = 0 \text{ if } |x| < \frac{L}{2} \tag{25}$$
and defining \( v = \partial n / \partial x \), we obtain a system with the origin as equilibrium with possibly two additional positive equilibria. Repeating the procedure used in Section 2 to compute the patch size \( L \) required to sustain a maximum population \( M \), we arrive to an equation similar to Equation (16), but having

\[
F(n) = \int_0^n u \left( 1 - (u + s) - \frac{\eta}{1 + K\gamma(u + s)} \left( 1 + \frac{K\theta s}{1 + K\rho(u + s)} \right) \right) du
\]

instead. We can explore this expression as a ‘potential’ function: Figure 6 shows the graph of \( F \) for different values of sterile release \( s \), with parameter values as those used for Figure 4. The sequence of plots obtained evidences the disappearance of nontrivial steady solutions as the value of \( s \) increases. The maximum of \( F \) is pushed down and eventually collides with the positive root closer to the origin. A bifurcation diagram for the steady solutions in terms of the patch size is computed in Figure 7(c). It can be checked that the zero solution of Equation (25) is asymptotically stable [12], showing that under the minimum patch size \( L^* \) invasion is not possible. For patch sizes larger than \( L^* \), there are two additional steady nonzero solutions, the one with largest \( M \) associated to the introduction of carrying capacity and the other related to the presence of the Allee effect.

![Figure 6](image)

Figure 6. (a)–(c) The ‘potential’ function \( F \): as \( s \) increases the value of \( n \) at which \( F \) reaches its maximum and the middle positive root collapse and disappear, or equivalently, steady-state solutions cease to exist. (d) Zoom of the initial part in (a) (with \( s = 0 \)), showing the existence of a middle root close to zero.
4. Discussion

This paper presents new deterministic models that address the effects of sterile male release with parametrized mating encounter rates. The theoretical framework proposed incorporates long lifespan, low reproductive times and multiple matings. The model considers compartments in the sexually mature female population, as defined in Section 2, with individuals at two possible stages: those searching for a mate and those being in a sexually inhibited post-copulatory phase. The latter group is divided into two: females fertilized by sterile males and those by wild males. The release of sterile males in a pest population is then explored numerically when the population is subject to density dependence. Interesting results are obtained in the presence of spatial dispersal, which is included via random walks in invaded patches with lethal exterior: computations suggest plausible pest invasion for patch sizes larger than a critical value. In addition to suggesting that disregarding the spatial dimension could be misleading, numerical experimentation also provides new insight into the qualitative dynamics of sterile release, including the possibility of sudden pest extinction as a consequence of the combination of sterile insect overflow with density dependence [2,14]. Another relevant outcome from the spatial model is the establishment of a minimum patch size required for invasion that depends on the density of sterile males and the rate of mating encounters.

The models for SIT presented here capture important characteristics in the potential qualitative description of a large class of insects, like some species of beetles, and introduce mechanistically
the possibility of reproductive Allee effects. Thus, the model allows to observe the combined effects of simultaneous population reduction due to SIT and positive density dependence. In contrast, deterministic models that use Knipling’s paradigm as backbone only provide reasonable approximations for high density populations with large mating encounter rates and where females only mate once, as in the case of screwworm populations.

One of the main drawbacks in applying SIT to insects like beetles is the excessive cost of rearing due to extensive larval periods, although other biological constrains might eventually play an important role too. However, under the hypothesis considered, the theoretical framework proposed here might help to provide a rationale for the design of improved control programmes that avoid the risk of expensive failures. For instance, combined with stochastic search techniques, Equations (4)–(6) have been used to address the optimal rearing of sterile males subject to production bounds, assuming that the release is not constant in time, but scheduled in periodic pulses [30], with sterile male population following an exponential decay.

The models can also be used to anticipate the effects of sterile release combined with simultaneous mating-failure techniques of pest control: the parameter $\xi$ in the equations might change in the case of using artificial pheromone sources intended to induce mating disruption through confusion, trail-masking and false-trail following Jones [15] and Yamanaka and Liebhold [34]. This is another advantage over deterministic models whose structure is based entirely on Knipling’s assumptions.

Within the SIT context, further questions arise that require modelling refinement combined with experimentation. For instance, in addition to the spatial distribution and polyandry considered in this paper, other factors might affect female mating failure at the pre-copulatory stage (age, diet, behavioural differences, size) or post-copulatory (inhibition of remating, failure in sperm transfer) [29]. In some cases, the impact of abiotic components could also be relevant, like decrements in ambient temperatures that may extend lifespan in some insect species [6]. In addition, the models presented here could offer new perspectives addressing the effects of residual fertility of sterile insects and a their loss of competitivity due to irradiation. Another aspect that requires further analysis concerns spatial boundaries. Here we only considered lethal boundaries, generally achieved in practice by insecticide application. However, permeable boundaries might potentially compromise the success of sterile release control programmes. For instance, USA and Mexico did not have a coordinated plan for the screwworm eradication programme in the mid-1960s. This unfortunate situation kept the USA vulnerable for some time to the influx of screwworms from Mexico and the original eradication plan became containment work [17].

It would also be of interest in further developments to determine the possible influence of larval stage times, included as a time lag $T$ in Equation (4) (through the term $\beta N(t - T)$), to study the models sensitivity with respect to the control parameters $S$ and $\xi$, and to determine optimal buffer zones for the spatial case [4]. Particular model applications require careful parameter estimates for each case, in particular that of $\xi$ if mating-failure techniques are used in conjunction with SIT, where it is worth to note potential interference.

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Appendix 1. Derivation of Equation (7)

Equations (7) and (20) are obtained following the arguments in [31], and have been included here for convenience.

We obtain an equation for the total female population adding Equations (4)–(6) and recalling that \( N = N_1 + N_2 + N_3 \):

\[
N' = (\beta - \mu)N - (\beta + \lambda)N_2 - \beta N_3. \tag{A.1}
\]

Rescaling time with \( s = \mu t \) and using \( \dot{\cdot} \) to denote the derivative with respect to the new time, the equations for \( N_2 \) and \( N_3 \) read

\[
\dot{N}_2 = -\left(1 + \frac{\lambda}{\mu}\right)N_2 + \frac{\sigma}{\mu} (N - N_2) - \frac{\xi}{\mu} (N + S)N_2, \tag{A.2}
\]

\[
\dot{N}_3 = -N_3 - \frac{\sigma}{\mu} N_3 + \frac{\xi}{\mu} SN_2. \tag{A.3}
\]

Let \( \epsilon = \mu/\sigma \), then

\[
\epsilon \dot{N}_2 = -\left(\epsilon + \frac{\lambda}{\sigma}\right)N_2 + N - N_2 - \frac{\xi}{\sigma} (N + S)N_2, \tag{A.4}
\]

\[
\epsilon \dot{N}_3 = -\epsilon N_3 - N_3 + \frac{\xi}{\sigma} SN_2. \tag{A.5}
\]

Assuming \( \epsilon \) to be small, we can approximate these equations as follows:

\[
N_2 = \frac{N}{1 + \lambda/\sigma + (\xi/\sigma)(N + S)}, \tag{A.6}
\]

\[
N_3 = \frac{\xi}{\sigma} S \left(\frac{N}{1 + \lambda/\sigma + (\xi/\sigma)(N + S)}\right). \tag{A.7}
\]

Using these in the equation for \( N \), we finally obtain

\[
N' = \phi N \left(1 - \frac{\eta(1 + \theta S)}{1 + \gamma(N + S)}\right), \tag{A.8}
\]

where

\[
\phi = \beta - \mu, \quad \eta = \frac{\sigma(\beta + \lambda)}{(\beta - \mu)(\sigma + \lambda)}, \quad \gamma = \frac{\xi}{\sigma + \lambda}, \quad \theta = \frac{\beta \xi}{\sigma(\beta + \lambda)}. \]

Appendix 2. Derivation of Equation (20)

With \( K = (\beta - \mu)/\nu \), adding Equations (17)–(19) gives

\[
N' = (\beta - \mu)N \left(1 - \frac{N + S}{K}\right) - (\beta + \lambda)N_2 - \beta N_3. \tag{A.9}
\]

Writing

\[
N = xK, \quad N_2 = yK, \quad N_3 = zK \quad \text{and} \quad S = sK,
\]

we obtain the following system

\[
x' = (\beta - \mu)x(1 - x - s) - (\beta + \lambda)y - \beta z, \tag{A.10}
\]

\[
y' = -(\mu + \lambda)y - (\nu + \xi)K(x + s)y + \sigma(x - y), \tag{A.11}
\]

\[
z' = -(\mu + \sigma)z - vK(x + s)z + \xi Ksy. \tag{A.12}
\]
Rescaling the time with $s = \mu t$ and using \( \dot{\cdot} \) to denote the derivative with respect to the new time, transform the system into

\[
\begin{align*}
\dot{x} &= \left( \frac{\beta}{\mu} - 1 \right) x (1 - x - s) - \frac{\beta + \lambda}{\mu} y - \frac{\beta}{\mu} z, \\
\dot{y} &= -\left( 1 + \frac{\lambda}{\mu} \right) y - \frac{\nu + \xi}{\mu} K(x + s)y + \frac{\sigma}{\mu} (x - y), \\
\dot{z} &= -\left( 1 + \frac{\sigma}{\mu} \right) z - \frac{\nu}{\mu} K(x + s)z + \frac{\xi}{\mu} Ksy.
\end{align*}
\] (A.13)

Define $\epsilon = \mu/\sigma$, then the last two equations read

\[
\begin{align*}
\epsilon \dot{y} &= -\epsilon y - \frac{\lambda}{\sigma} y - \frac{\nu + \xi}{\sigma} K(x + s)y + x - y, \\
\epsilon \dot{z} &= -\epsilon z - z - \frac{\nu}{\sigma} K(x + s)z + \frac{\xi}{\sigma} Ksy.
\end{align*}
\] (A.16)

Because $\epsilon$ is assumed to be small, we can approximate these equations as follows:

\[
\begin{align*}
0 &= -\frac{\lambda}{\sigma} y - \frac{\nu + \xi}{\sigma} K(x + s)y + x - y, \\
0 &= -z - \frac{\nu}{\sigma} K(x + s)z + \frac{\xi}{\sigma} Ksy.
\end{align*}
\] (A.18)

Solving for $y$ and $z$ from the last two equations and replacing in the expression for $\dot{x}$ we obtain, after going back to the original time,

\[
N' = \phi N \left( 1 - \frac{N + S}{K} - \frac{\eta}{1 + \gamma(N + S)} \left( 1 + \frac{\theta S}{1 + \rho(N + S)} \right) \right),
\] (A.20)

where

\[
\eta = \frac{\sigma (\beta + \lambda)}{(\beta - \mu)(\sigma + \lambda)}, \quad \rho = \frac{\nu}{\sigma}, \quad \gamma = \frac{\nu + \xi}{\sigma + \lambda}, \quad \theta = \frac{\beta \xi}{\sigma (\beta + \lambda)}.
\]