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LETTER

Combining multiple tactics over time for cost-effective eradication of invading insect populations

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Abstract

Because of the profound ecological and economic impacts of many non-native insect species, early detection and eradication of newly founded, isolated populations is a high priority for preventing damages. Though successful eradication is often challenging, the effectiveness of several treatment methods/tactics is enhanced by the existence of Allee dynamics in target populations. Historically, successful eradication has often relied on the application of two or more tactics. Here, we examine how to combine three treatment tactics in the most cost-effective manner, either simultaneously or sequentially in a multiple-annum process. We show that each tactic is most efficient across a specific range of population densities. Furthermore, we show that certain tactics inhibit the efficiency of other tactics and should therefore not be used simultaneously; but since each tactic is effective at specific densities, different combinations of tactics should be applied sequentially through time when a multiple-annum eradication programme is needed.

Keywords

Bioeconomic, extinction, gypsy moth, insecticide, invasion, management, mating disruption, model, optimisation, sterile male.

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INTRODUCTION

Given the enormous ecological and economic costs of biological invasions, the management of invasions is an important priority in all world regions. Several studies have shown that preventing initial arrivals of new species is an economically preferable approach (Leung *et al.* 2002; Finnoff *et al.* 2007). But some invasion pathways are difficult to manage, and it may not be possible to prevent arrivals and establishments of all species (Perrings *et al.* 2005). Therefore, the strategy of detecting and eradicating localised, newly founded populations is a key component of biosecurity programmes in place in various countries (Simberloff 2003; Liebhold *et al.* 2016). Eradication, which refers to the suppression of a population to local extinction, has been recognised as a challenging goal, given the difficulty of finding and eliminating every individual in a population (Genovesi 2008). However, many different types of organisms exhibit Allee effects, in which their population grows slower or declines at low densities, and this can be exploited to facilitate eradication with reduced effort (Tobin *et al.* 2011; Liebhold *et al.* 2016). In the presence of a strong Allee effect, eradication can be achieved by reducing a population below a threshold level, after which it is likely to decline naturally to extinction; in some cases, the strength of an Allee effect can be manipulated to achieve extinction.

For insects, there has been increasing success at developing and applying effective tools/tactics for eradicating invading populations (Pluess *et al.* 2012; Tobin *et al.* 2014), including pesticide application, habitat removal, mass-trapping, the sterile male technique and mating disruption (Suckling *et al.* 2014; Liebhold and Kean 2019). A feature seen in several successful insect eradication programmes has been the application of several of these tactics for targeting a single species during an eradication programme. For example the successful eradication of the painted apple moth, *Teia anartoides*, from Auckland, New Zealand employed three different tactics between 1999 and 2002; initial efforts were limited to mechanical removal of host plants, but then aerial spraying of microbial pesticides was implemented and finally sterile male releases were used during the final year of the programme (Suckling *et al.* 2007).

Studies have investigated how various treatment tactics interact with Allee effects to achieve eradication. These studies have focused on pesticide treatments (Liebhold and Bascompte 2003), host removal (Barron *et al.* 2020), release of *Wolbachia* bacteria (Blackwood *et al.* 2018), mating disruption, mass-trapping and the sterile insect technique (Yamanaka and Liebhold 2009), but less is known about how these treatments interact with each other. Suckling *et al.*(2012) reviewed various possible biological interactions between different eradication tactics and speculated on how these combinations might perform. Blackwood *et al.*(2012, 2018) used a modelling approach to evaluate interactions between different eradication tactics when applied simultaneously and to identify economically optimal combinations of tactics for eradication. Lampert and Hastings (2019) examined how to combine

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tactics to restore ecosystems and cross the Allee threshold. Suckling *et al.* (2016) conducted field trials to evaluate the existence of synergistic vs. antagonistic interactions between insecticide and mating disruption treatments. However, these previous investigations have evaluated combinations of treatment tactics only when these tactics are applied simultaneously, and they have not considered sequences of eradication tactics during a multiple annum eradication programme. These sequences are potentially critical because eradication programmes typically target larger populations at the beginning, and populations are successively reduced to smaller levels. As the target population size decreases, certain tactics may become more effective than others, and consequently, managers may need to vary their tactics during different phases (years) of the eradication project.

The objective of this study was to apply a bioeconomic model to identify optimal sequences for applying different tactics to achieve eradication. As a case study, we consider pesticide applications, mating disruption and sterile male release applied to eradicate isolated populations of invading insects. We focus on the gypsy moth, *Lymantria dispar,* though we expect that our analysis is generalisable to most univoltine insects. We analyse a mechanistic model to evaluate various sequences in which different tactics are applied in order to identify the most cost-effective strategies.

METHODS

Mathematical model

We consider an isolated population of a newly arrived non-native insect species, where the density of adult individuals in year t is given by $N(t)$. We consider a manager who can use various tactics to suppress populations of the species (Fig. 1) and can combine different tactics in different years with an ultimate intent of eradication. The objective of the manager is to minimise the total cost due to both treatment and damages over time, while promoting the eradication of the species locally in a given area. Below we describe which tactics are available to the manager in our model, how the target population responds to the various tactics over time and what the objective function of the manager is.

Tactics of the manager

Our goal is to determine how the manager should invest in each tactic over time (Fig. 1). Specifically, the manager can use any of the following three tactics, and s/he can decide how much to invest in each tactic each year, depending on the population density in that year: (1) Insecticide application, $R(t)$, which kills some fraction of larvae and thereby reduces the proportion of eggs that become adults; (2) mating disruption, $F(t)$, which inhibits the ability of males to find a female, thereby increasing the chances that a female is not fertile by the end of the mating season, and (3) release of sterile males, $S(t)$, that compete with the wild, feral males for mating with females, but mating events with sterile males do not produce viable offspring.

Dynamics of the insect population

We consider the dynamics of a univoltine insect species, which follows the following life stages: females lay eggs (in a single egg mass), which develop into larvae, which pupate and develop into adults. Each year, a new generation replaces the previous generation. In turn, the probability that a female lays a viable egg mass is given by the probability that the female finds a mate, P, times the probability that a female that found a mate lays viable eggs, Q. Note that both P and Q depend on the number of feral males (depends on N) and the number of sterile males (depends on S), and P also depends on the probability that a given male finds a female (depends on F): $P = P(N, F, S)$, and $Q = Q(N, S)$.

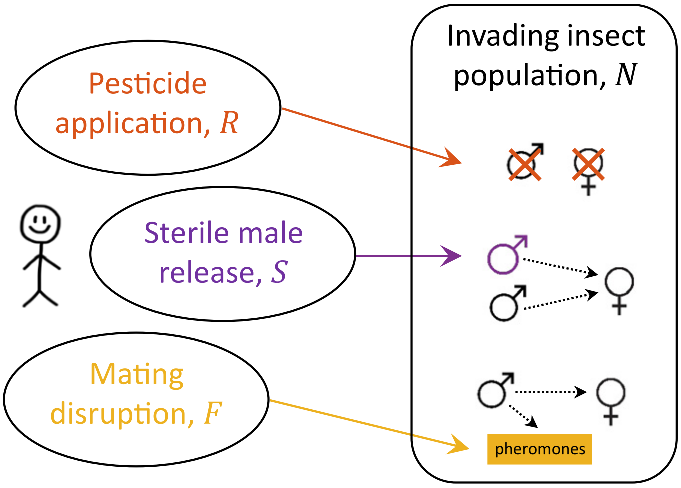

Figure 1 Illustration of the three tactics. Each year, the manager can use three different tactics to manage the invasive insect: (1) pesticide application, which is typically applied at the larval stage and kills both males and females; (2) the release of sterile males that compete with the wild males for the females, but result in females laying non-viable eggs and (3) mating disruption, accomplished via distribution of large numbers of pheromone sources that compete with females for the attraction of males.

In the second stage, we assume that, if the density is low and no pesticides are used, the number of eggs in a given egg mass that survive and ultimately become adult females is given by r. At higher densities, however, the larvae might compete for tree foliage (food resources), and the number of female adults produced by an egg mass is given by $r(1 - N/K)$, where K is the population's carrying capacity. Also, only a fraction $\exp(-\gamma R)$ of larvae survives the use of pesticides, where γ is the probability that an egg does not develop into a pupa due to each dollar invested in pesticide application.

It follows that the following formula characterises the density of adult individuals during the mating season in year $t + 1$ as a function of the density of adults in the former generation in year t:

$$N(t+1) = rN(1 - N/K)\exp(-\gamma R(N))P(N, F(N), S(N))Q(N, S(N)), \tag{1}$$

where N stands for $N(t)$ for simplicity of the notations. In turn, $R(N)$, $F(N)$ and $S(N)$ are the numbers of dollars invested in a given year on insecticides, mating disruption and sterile male release, respectively, in a year in which the density of adult individuals is $N(t)$. Note that $R(N)$, $F(N)$ and $S(N)$ are functions of N, and they can also be written as functions of time since $N(t)$ is a function of time.

Objective of the manager

The objective of the manager is to minimise the net cost due to both treatment and damages over time until eradication is approached (Taylor and Hastings 2004; Born *et al.* 2005; Clark 2010; Epanchin-Niell and Hastings 2010; Wilson *et al.* 2011; Lampert and Hastings 2014). Namely, the objective is to choose the control functions $R(N)$, $F(N)$ and $S(N)$ that minimise the net present cost (NPC), given by

$$NPC = \sum_{t=1}^{\infty} [C_n(N) + R(N) + F(N) + S(N)]\theta^t, \tag{2}$$

under the constraint that eradication must occur ($N(t) \to 0$ for some value of t or as $t \to \infty$), where $C_n(N)$ is the annual cost imposed due to the presence of the invasive species, and $0 \le \theta \le 1$ is the economic discount factor. (Note that the cost and control functions depend on the time t as $N = N(t)$ depends on t.) Since we consider eradication programmes that typically span only a few years, economic discounting does not play a significant role, and we consider no discounting, that is $\theta = 1$.

Parameterisation

The model that we develop here is general and can be used to describe the dynamics of populations of most univoltine insect species. However, we parameterise the model using data for the gypsy moth, *Lymantria dispar*, because of the availability of an exceptional amount of information about the demographics of mating and effects of management tactics (Tobin *et al.* 2009, Blackwood *et al.* 2012, Barron *et al.* 2020). Because of the propensity of this insect to invade new regions, it is also a frequent target of eradication projects (Liebhold and Bascompte 2003; Hajek and Tobin 2010). Although we parametrise our model based on models of gypsy moth population dynamics and treatments, we consider a wide range of parameters for two reasons. First, our goal in this paper was to develop a general framework to analyse how optimal eradication strategies depend on various parameters and how the framework could apply to other invasive insect eradication projects. Second, even for the gypsy moth, there are large uncertainties about certain parameter values, and moreover, these values vary significantly across habitats and locations. Therefore, it is necessary to perform sensitivity analysis across larger parameter ranges.

Growth rates

We consider an annual life-cycle with non-overlapping generations. Without treatment and without larval competition, r adult females replace each fertilised female each year. In turn, Barron *et al.* (2020) estimated $r = 10$/year as a higher bound of r (20 adult individuals per egg mass, or 10 adult females as the sex ration is 1:1), and we used this value to generate our figures. Note that the actual number may be lower due to predation, particularly at lower densities (Elkinton *et al.* 1996).

Furthermore, since we model the local eradication of a newly invaded, isolated population, we assume that the initial population size is much smaller than the carrying capacity of the population (Liebhold and Bascompte 2003). Larval competition for foliage can be significant in outbreak gypsy moth populations, after the insect population has been established for many years and grown to extremely high levels; but during the initial stages of the local invasion, populations are not constrained by the availability of foliage (Sharov *et al.* 1996; Liebhold and Tobin 2006).

Cost and efficiency of pesticide use

We assume that pesticides can be applied either 0, 1 or 2 times in a given year, as additional applications are ineffective (Blackwood *et al.* 2012). We assume that each appliance costs 54 USD per hectare and kills 80% of the population (i.e. two applications cost 108 USD and kill 96% of the population) (Blackwood *et al.* 2012). (This implies that $\gamma = -\ln(0.2)/54 = 0.03\ \mathrm{USD}^{-1}$.)

Cost of damage, $C_n(N)$

Most of the damages caused by the gypsy moth are related to the defoliation of trees caused by high densities of larvae. When the population density is low, defoliation does not occur and the gypsy moth has no significant impacts (Epanchin-Niell *et al.* 2012). Accordingly, as in Epanchin-Niell *et al.*(2012), we assume that $C_n(N) = 0$ if N is below a threshold. This threshold is close to the population's carrying capacity, and in our simulations, we considered populations subject to eradication with sizes that are below that threshold.

However, if the population size becomes large, the cost of damages can reach millions of dollars (Aukema *et al.* 2011; Epanchin-Niell and Liebhold 2015). This cost affects the optimal treatment even when N is small: It implies that the optimal strategy is to eradicate the population and not to abandon the system untreated. This cost can be incorporated directly in the function $C_n(N)$ (e.g. $C_n(N) = 0$ if $N < N_c$ and $C_n(N)$ is large otherwise), or it can be incorporated indirectly as a constraint that implies that $N(t)$ has to approach zero. The results that we obtain from both approaches are identical.

To estimate a lower bound on the cost imposed by large populations, note that eradication, if still achievable, is known to be desirable (Epanchin-Niell *et al.* 2012). In turn, without treatment, the population can be anticipated to start causing damages when it grows to ~10^{10} individuals, in which case it may cost ~10^7 USD to eradicate it (Epanchin-Niell *et al.* 2012). This implies that a lower bound of the cost per-individual moth is of the order of 10^{-3} USD.

Probability that a mated female lays viable eggs (i.e. her mate is not sterile), $Q(N, S)$

To derive a higher bound on the probability that a mated female lays viable eggs, we assume that each female can mate only once during the mating season: She lays viable eggs only if she mated with a wild, feral male (Sawyer *et al.* 2014). This is generally the case with the gypsy moth, in which females typically mate once except at high densities (Doane 1968; Cardé and Hagaman 1984; Proshold and Bernon 1994). We assume that, per dollar, β_1 sterile males can be produced and released in a given area. We assume that the probability of a sterile male to mate may be lower by a factor $\beta_2 \le 1$ compared to a feral male (β_2 is the 'relative competitiveness' of the sterile males) (Sawyer *et al.* 2014). In turn, the number of males per hectare in nature is $N/2$ (we assume a 1:1 sex ratio). Therefore, the probability that a mated female lays viable eggs is

$$Q(N, S) = \frac{N}{N + 2\beta S} \tag{3}$$

where $\beta = \beta_1\beta_2$ (Knipling 1959; Knipling 1970; Sawyer *et al.* 2014).

It has been estimated for some insects that $2 \times 10^4 \leq \beta_1 \leq 6.6. \times 10^4$ USD^{-1} (Mumford 2005). However, this only gives some higher bound on β for several reasons. First, β_2 is generally smaller than one. Second, in some other insects, including the gypsy moth, the use of sterile males was found empirically to be inefficient in many cases (Mastro 1993). Third, in some insect species, females often mate multiple times, and this generally reduces the effectivity of sterile male releases (Berryman 1967; Knipling 1979). Therefore, we consider as a reasonable estimate any value in the range $0 \leq \beta \leq 6.6. \times 10^4$ USD^{-1}.

Probability that a female finds a mate, P(N, F, S)

Typically, mating disruption treatments consist of the synthetic female-produced sex pheromone that is packaged in slow-release devices such as plastic dispensers or millions of emulsion droplets that are distributed by an aircraft (Miller and Gut 2015). In turn, these false pheromone sources compete with females for male attraction. To estimate the probability that a female is found by a male during the mating season, $P(N, F, S)$, some previous studies have used agent-based simulation models (Yamanaka and Liebhold 2009). Here, we consider a simpler model that incorporates key aspects of the searching process and incorporates the effect of the false pheromone sources.

We assume that the population is well-mixed and the probability that a given male finds a mate is independent of whether the other males succeeded. We denote the probability that a given male finds a particular female during the mating season as m and the number of males (feral and sterile) as $\hat{N}$. It follows that, the probability that a female is found by n males follows a binomial distribution, which can be approximated by a Poisson distribution with a mean of $m\hat{N}$. In particular, the probability that a given female is not found by any of the $\hat{N}$ males declines exponentially with $\hat{N}$ and is given by

$$P = 1 - \exp\left(-m\hat{N}\right). \tag{4}$$

(More precisely, $P = 1 - (1 - m)^{\hat{N}}$, but eqn 4 is a good approximation.) Specifically, without human intervention ($F = 0$ and $S = 0$), $\hat{N} = N/2$ (we assume 1:1 sex ratio), and $m = m_0$ can be estimated empirically based on the value of the Allee threshold, N_0. Specifically, where $N = N_0$, the population size in the next generation equals that in the present generation, which implies that $r(1 - \exp(-m_0N_0/2)) = 1$, or, equivalently,

$$m_0 = \frac{2}{N_0}\ln\left(\frac{r}{r-1}\right) \tag{5}$$

Empirical estimates show that the Allee threshold for the gypsy moth is about 2–4 egg masses (Robinet *et al.* 2008), which implies that N_0 is in the range of $4r$ to $8r$ because each egg mass results in $2r$ adults (or r adult females).

Next, to incorporate the effect of the treatment, note that in the presence of sterile males, the effective number of males is given by $\hat{N} = N/2 + \beta S$. At the same time, false pheromone sources reduce the probability that a given male finds a female ($m < m_0$). Specifically, if a male is attracted to a false pheromone source, he loses a portion α_1 of the total time that he has for searching after the female. In turn, there is a probability α_2 that the male is attracted to a given false pheromone source during the mating season. Therefore, the probability that a male that would have otherwise found the female still finds her in the presence of the false pheromone source is reduced by a factor of $1 + \alpha_1\alpha_2\hat{F}$, where $\hat{F}$ is the number of false pheromone sources. In turn, by definition, $\hat{F} = \alpha_3 F$, where α_3 is the number of false pheromone sources released per dollar invested. It follows that

$$P(N, F, S) = 1 - \exp\left(-\frac{m\left(\frac{1}{2}N + \beta S\right)}{(1 + \alpha F)}\right), \tag{6}$$

where $\alpha = \alpha_1\alpha_2\alpha_3$. Note that the intuition behind this formula is simple: The portion of time that a male spends looking for actual females is $1/(1 + \alpha F)$, and the portion of time he spends looking after false pheromone sources is $\alpha F/(1 + \alpha F)$.

In turn, we use the same estimations of α_1, α_2 and α_3 that are used in Blackwood *et al.*(2012). A male that is attracted to a pheromone source spends approximately 3 hours, about 7% of the searching time in the season, before he leaves the false source and resume its search after the female ($\alpha_1 = 0.07$). The probability that a male is attracted to a false pheromone source is not precisely known, where Blackwood *et al.*(2012) estimated this number to be $\alpha_2 = 0.0015$: only 1 out of 100 release devices applied falls at the right range of heights, and among those, there is a 15% chance that a male will be attracted (which is taken assuming that the pheromone source attracts males in a fashion equivalent to a female). Finally, the cost per pheromone source is 0.0013 USD, which implies that, $\alpha_3 = (0.0013)^{-1}$ USD^{-1}. In summary, we get $\alpha = 0.07 \times 0.0015/0.0013 = 0.08$ USD^{-1}. However, note that Blackwood *et al.*(2012) emphasise that there is large uncertainty in these parameters, and accordingly, they performed sensitivity analyses to examine a much wider range of parameters. Accordingly, in our study, we consider any number in the range $0.008 \leq \alpha \leq 0.8$ to be a potentially realistic estimate.

Analysis

Our analysis incorporates three components: (1) analytic examination of the relative efficiencies of the tactics and how they depend on the population size (Appendix A and Fig. 2); (2) analytic examination of the interaction between the tactics, to determine whether these are synergetic or inhibitory (Appendix B) and (3) numerical solution of the optimal control problem to find the optimal solution (Appendix C and Fig. 3; Figs S1–S3).

Relative efficiencies of the tactics

We define the efficiency of a given tactic as the number of individuals removed per dollar invested in that tactic. In turn,

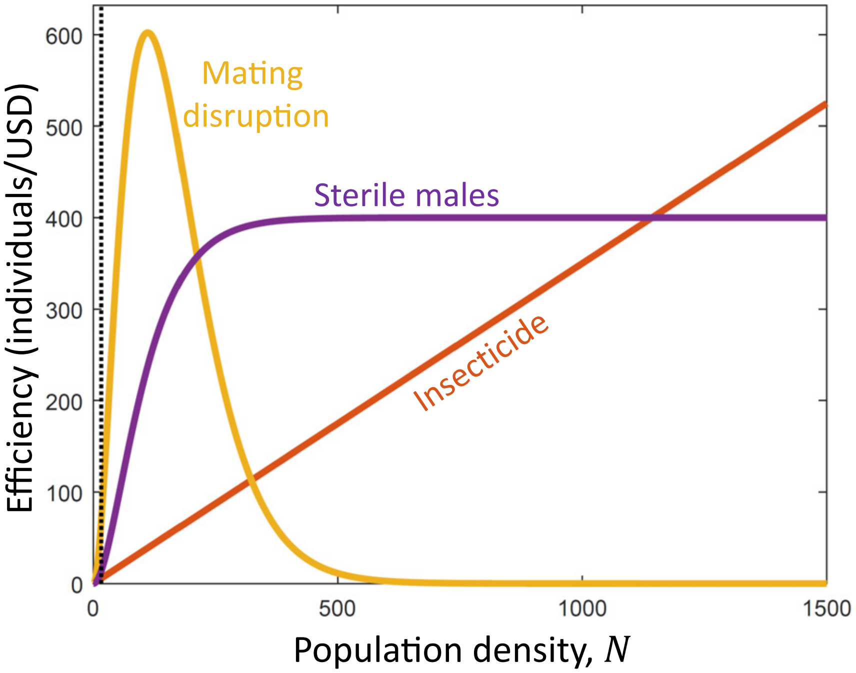

Figure 2 The efficiency of each tactic peaks at a different population density. We define efficiency as the number of individuals removed per dollar invested in treatment. The efficiency of mating disruption (yellow line) is the highest at relatively low population sizes. The efficiency of insecticides increases with the size of the population. In turn, relative to the two other tactics, the use of sterile males is most efficient at intermediate population sizes (purple line).

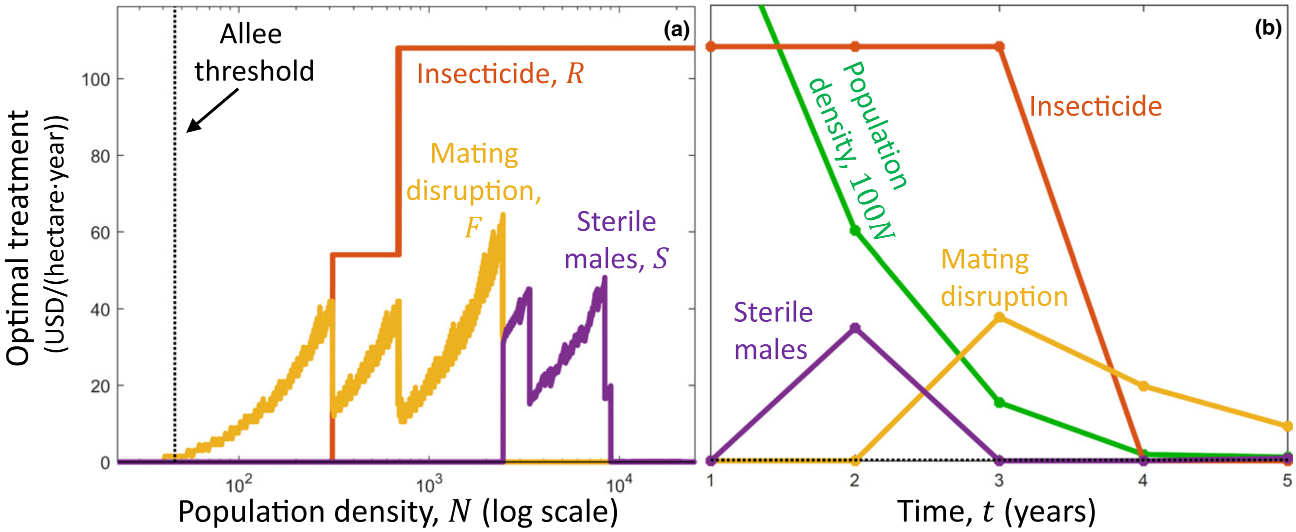

Figure 3 Managers may need to combine sterile males and mating disruption to achieve eradication, but they should use each of these tactics in distinct years, not simultaneously. Demonstrated are (a) the optimal treatment strategy as a function of N, and (b) its realisation over time for initial conditions of $15K$ individuals. The values on the y-axis are the annual dollar expenditures per hectare. Shown are the three tactics as they should be used optimally: insecticide application, R (red), mating disruption application, F (yellow) and sterile males release, S (purple). Also shown are the population size (green), and the Allee threshold assuming no treatment (dotted black). Following the optimal solution, insecticide application should be used alone if the population size is very large (e.g. first year), sterile males should be used together with insecticides for intermediate population sizes (e.g. second year) and mating disruption should be used together with insecticides when the population size is smaller (e.g. 3rd and 4th years). When the population size is very small and close to the Allee threshold, mating disruption alone is sufficient to ensure complete eradication (e.g. 5th year). Parameters: $r = 10$, $K = 10^6$, $C_n(N) = 0$, $\theta = 1$, $\alpha = 0.6$, $\beta = 50$, $\gamma = 0.03$. Figs S1 and S2 demonstrate the solution for other parameter values.

the efficiency depends on the density of the species. Mathematically, the efficiency of each tactic is given by minus the derivative of the growth function (incorporating the treatments), $f(N, R, S, F)$ (right-hand side of eqn 1), with respect to the investment in the tactic (Appendix A). We are particularly interested in the efficiencies when no other treatment is provided. The results are derived in Appendix A and are demonstrated in Fig. 2.

Interactions between tactics

To analyse the nature of the interactions analytically, we find the second derivatives of the growth function *f* with respect to the various tactics (Appendix B). Specifically, f_{SF} characterises the relationships between the effects of mating disruption and sterile male release (Appendix B). If f_{SF} is positive, this indicates that the relationships are inhibitory (one tactic inhibits the other's efficiency), whereas if f_{SF} is negative, this indicates that the relationships are synergetic.

Finding the optimal solutions

The optimal strategy is given as a function of *N*, and it depends on the year *t* only via *N*(*t*) (i.e. the strategies are Markovian). Therefore, our objective is first to find the optimal tactics as a function of *N*, and then, for given initial conditions, we can translate them into functions of time. In turn, to find numerically the optimal solution, which is given by the functions *R*(*N*), *F*(*N*) and *S*(*N*) that minimise eqn 2 subject to the dynamics given in eqn 1, we implemented a stochastic programming algorithm (Bertsekas *et al.* 1995; Clark and Mangel 2000). We describe the algorithm in detail in Appendix C.

RESULTS AND DISCUSSION

Each tactic is efficient at different densities

A key result of our analysis is that the efficiency of each tactic varies with the population density; some tactics are more efficient at low densities and some at higher densities (Fig. 2). We define efficiency as the number of individuals removed per dollar invested in treatment. The efficiency of insecticide application is proportional to *N*, and therefore, it is most efficient at larger population sizes. In contrast, the efficiency of mating disruption reaches a maximum at a certain population size: it is efficient only sufficiently close to the Allee threshold (Fig. 2). Finally, the efficiency of sterile male release increases close to the Allee threshold, whereas at higher densities, it approaches a constant level. Therefore, as the population size increases, sterile male release becomes less efficient compared to insecticide application, but it becomes more efficient compared to mating disruption (Fig. 2).

This result is generally in agreement with historical experience in managing invading gypsy moth populations. Sharov *et al.*(2002a) analysed the historical success of treatments targeting low-density isolated gypsy moth populations using the bacterial insecticide *Bacillus thuringiensis* and mating disruption using Disrupt II applied operationally as part of the gypsy moth Slow the Spread programme (Sharov *et al.* 2002b). They found that mating disruption was generally more effective against low-density populations, whereas the microbial insecticide treatments were more effective against high-density populations. While their measures of effectiveness were not directly comparable to our measure of efficiency, their results are generally in agreement and support our conclusions.

The sterile male technique has been successfully applied for the purpose of eradicating several different species of invading insects (Dyck *et al.* 2006). Historical results from these programmes indicate that this method is the most practical when targeting small populations and that the method becomes less feasible against large populations because of the expense of producing large numbers of insects needed to achieve target overflooding ratios. These results generally support our finding that insecticide treatments are more efficient at high densities, but sterile male release is more efficient at lower densities. Note, however, that in the case of the gypsy moth, sterile male releases are rarely used in eradication programmes, in part due to problems of poor performance of mass-produced gypsy moths reared on artificial diet (Mastro 1993).

Some tactics should not be used simultaneously

Our results also show that mating disruption and sterile male release, if used simultaneously, mutually inhibit each other's efficiency. This result is demonstrated in two ways: (1) It is derived analytically in Appendix B (f_{FS} is always positive), and (2) Fig. 3 demonstrates that, although both tactics should be used throughout the progress, they should be used in distinct years rather than simultaneously. The reason for these inhibitory interactions is that the false pheromone sources disrupt the ability of sterile males to find females just like they disrupt the feral males. In addition, with the addition of sterile males, fewer feral males mate, and therefore, the benefit from disrupting the males with false pheromones is lower. (Note that these two effects can be seen from eqn B1 in Appendix B, as each effect corresponds to a different term in the equation.) These same potentially inhibitory/antagonistic interactions between the simultaneous use of the sterile male technique and mating disruption have previously been recognised (Suckling *et al.* 2012), whereas additive or synergistic interactions have been observed when they are applied sequentially to successive generations (Judd and Gardiner 2005).

Different tactics should be used and combined in distinct years

We also show that the release of sterile males and the mating disruption tactics can be combined synergistically if they are used in distinct years (Fig. 3). Specifically, since each tactic is efficient at different values of *N*, and since *N* changes over time, different tactics could be more efficient in different years (Fig. 2); and using each tactic in those years when it is more efficient may be favourable. Therefore, the optimal strategy may be (Fig. 3) to use insecticides if the population size is large (e.g. in the first year of an eradication programme), to use sterile males combined with insecticides for intermediate population sizes (e.g. second year), and to use mating disruption combined with insecticides when the populations is closer to the Allee threshold (e.g. third and fourth years). Also, note that pesticides should be used simultaneously with the other tactics in some years, but when the density approaches the Allee threshold, pesticides are often not necessary to achieve eradication (Fig. 3). When the density falls sufficiently below the Allee threshold, the population is likely to decline naturally, and no further intervention is needed (see also Lampert and Hastings 2014). Similar results were obtained with a continuous-time version of the model (Appendix C and Fig. S3). Note, however, that there are parameter regimes in which mating disruption is more efficient than sterile male release even at larger population densities (Fig. S1), or in which sterile male release is more efficient than mating disruption for N (Fig. S2), in which case only the more efficient tactic should be combined with insecticides or be used alone in all years.

Although field tests by Suckling *et al.*(2016) indicated neither synergism nor antagonism between mating disruption and insecticide treatments applied in the same year, other empirical evidence shows that the combination of multiple tactics is sometimes more effective than the use of a single tactic (Suckling *et al.* 2012). For example Bloem *et al.*(2007) found that combining mating disruption with sterile male release could be more effective than using only one of these tactics. Simmons *et al.* (2007) found a similar result with mating disruption, sterile males and insecticides. Bloem *et al.*(1998) and Cossentine and Jensen (2000) found that combining parasitoids and sterile males is more effective than using either tactic alone. In turn, these empirical findings are backed by theoretical analysis (Carpenter *et al.* 2004; Blackwood *et al.* 2012). Furthermore, some of these papers considered the sequential use of the different tactics within the same year, as each tactic may be effective in different life stages of the invasive insect. However, there is no distinction in these papers between the use of all the tactics in the same year, and the use of each tactic in a different year. Also, to our knowledge, there has not been a serious attempt to compare the use of all tactics in the same year versus their use in different years. Our results suggest that, at least for the combination of mating disruption and sterile male release, this distinction is critical.

The results presented in Figs 2 and 3 provide guidance to managers in the selection of the optimal tactic(s) given various ranges of target insect densities. However, it should be noted that in operational eradication programmes, assessment of population density can be challenging given that populations typically exist at extremely low densities and measurement error may dominate estimates derived from surveys. For insects such as the gypsy moth, invading populations are typically assessed using pheromone traps and it may be possible to translate trap counts into absolute densities (Carter *et al.* 1994). However, one limitation of population assessment from pheromone trap counts is that mating disruption applications are likely to inhibit capture in pheromone traps (Thorpe *et al.* 2007), and therefore, they prevent population assessment during the course of the multi-year eradication programme. In these cases, it may be necessary to identify the optimal sequence of tactics (Fig. 3) at the start of the programme rather than continual assessment of populations. Also, note that one of the reasons why eradication programmes often continue over several years is that the effectiveness of treatments may vary spatially so that populations are eliminated in some areas but persist in others and must be retreated. This type of spatial heterogeneity has not been modelled explicitly in this study but potentially could be a useful theoretical exploration in the future.

The general conclusion that follows from the paper is that the efficiency of the different management tactics may depend on the density of the population, and therefore, in eradication programmes that span over multiple years, the optimal treatment may encompass different combinations of tactics in different years. From a scientific point of view, this implies that future studies can benefit from a more careful examination of how the efficiencies of various tactics, applied alone or in combination, depend on the population size (in contrast to only examining whether and how much a given tactic is effective). From a practical point of view, our study suggests that managers should not only determine which tactics to apply in an eradication programme, but rather, they should develop a plan that might include a sequence of tactics applied in distinct years.

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AUTHORS’ CONTRIBUTIONS

Adam Lampert designed research, developed model, performed simulations, wrote the paper; Andrew M. Liebhold designed research, developed model, wrote the paper.

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DATA AVAILABILITY STATEMENT

We have no new data reported in the manuscript. All the data needed to reproduce the results is given in the paper. In particular, the parameter values used for each figure are given in its legend. These parameter values are taken from the references that are cited in the Methods section.

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