

Spatially implicit approaches to understand the manipulation of mating success for insect invasion management

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Abstract Recent work indicates that Allee effects (the positive relationship between population size and per capita growth rate) are critical in determining the successful establishment of invading species. Allee effects may create population thresholds, and failure to establish is likely if invading populations fall below these thresholds. There are many mechanisms that may contribute to Allee effects, but mate-location failure is a common cause in sexually reproducing insects. Consequently, mate-location failure represents a type of “weak link” that may be enhanced in order to achieve eradication of insect populations during the early stages of invasion. In this paper, spatially implicit models that account for mating behavior of both sexes are used to explore the enhancement of mate-location failure in pest eradication programs. Distinct from the previous studies, the Allee effect emerges from a mechanistic representation of mate-location failure in our model. Three specific eradication strategies, sterile insect release, mass-trapping, and mating disruption, are incorporated into the model and tested for their ability to depress population growth during the early stages of invasions. We conducted simulations with the model parameterized to represent two types of insects: Coleopteran-like insects which are long-lived and capable of multiple matings, but

have low daily reproductive rates, and Lepidopteran-like insects which are capable of mating only once per generation, have an ephemeral reproductive stage, and have high reproductive rates. Simulations indicated that: (1) many insect pests are more likely to be eradicated than had been previously predicted by classic models which do not account for mate-finding difficulties, (2) for Lepidopteran-like insects, mass-trapping has the greatest potential for eradication among the three methods when a large number of traps can be installed, although mating-disruption will be the most effective if we can anticipate confusion or trail-masking mechanisms of disruption, and (3) populations of Coleopteran-like insects may be most effectively eradicated using the sterile male release method. Though more detailed models should be tailored for individual species, we expect that the spatially implicit approaches outlined in this paper can be widely adapted to study the efficiency of various eradication approaches in sparse conditions.

Keywords Allee effect · Male annihilation · Mating-disruption · Mass-trapping · Random mating model · Sterile insect release

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Introduction

Invasions by non-indigenous insect species are recurring around the world and causing tremendous impacts on natural ecosystems, crop production, and human health. For example, the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae), accidentally introduced from Asia to North America in the 1950s, is causing extensive mortality of host hemlocks, ultimately leading to drastic changes in ecosystem processes (Stadler et al. 2006). An agricultural example is provided by the rice

water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae) which, following an introduction from North America, now infests >20% of the total paddy fields in Japan and causes an enormous reduction of rice yields (Saito et al. 2005). The tiger mosquito, *Aedes albopictus* (Skuse) (Diptera: Culicidae), which carries several lethal human diseases including dengue fever, is presumed to have been introduced to North America in used tires from northeastern Asia in the mid-1980s (Hawley et al. 1987).

Identifying and shutting-down invasion pathways are important approaches to reduce the number of new introductions, but given trends of ever-increasing levels of global trade, many of these pathways cannot be completely stopped (Levine and D'Antonio 2003). In these cases, early detection and eradication may be the best approach to prevent the impact and management costs once an invader is established (Sharov and Liebhold 1998). Eradication, which refers to the total extirpation of a species from an area, may be expensive and not always successful, especially if the invading population has already established over a large area (Myers et al. 2000; Liebhold and Tobin 2008).

Despite technical difficulties, there are several examples of successful eradication projects. Eradication of the screwworm, *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae), from portions of the southwestern USA in the 1960s is a classic success story. This was achieved by application of the sterile insect release (SIR) method in which millions of males were reared, sterilized, and released; females, which mated with sterilized males, could not produce viable offspring resulting in a decline of the population (Myers et al. 1998). A different method, male annihilation, was used to eradicate another fly species, the oriental fruit fly (*Bactrocera dorsalis* Hendel, Diptera: Tephritidae), from the island Rota in the Marianas in 1963 (Steiner et al. 1965). Vast numbers of sticky sheets baited with the male attractant, methyl eugenol, and impregnated with a chemical insecticide, naled, were distributed from airplanes throughout the island. This male removal led to a heavily female-biased sex ratio and mating success was consequently suppressed. Both SIR and male annihilation have been successfully applied in other cases, such as the eradication of the oriental fruit fly from the island of Okinawa via the male annihilation technique (Koyama et al. 1984), and the melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) via SIR also from Okinawa (Koyama et al. 2004).

Male annihilation and SIR are not the only methods applied for eradicating insect populations. Mass-trapping (a male annihilation method typically utilizing semiochemicals) and mating disruption (another method utilizing semiochemicals in which dense sex-pheromone permeates

an area to suppress mating success) are two other methods sometimes employed in local eradication or in suppression along an invasion front (e.g., Tobin et al. 2004; El-Sayed et al. 2006). There are also several trials for eradication carried out via application of pesticides, most notably microbial insecticide (Smitley and Davis 1993; Kean and Suckling 2005). In addition, introduction of alien parasitoids has a long history and can sometimes control invasive alien pests at very low densities (e.g., Caltagirone and Douth 1988; Moriya et al. 1989) though complete eradication has rarely been reported.

One of the reasons that methods controlling mating systems (SIR, male annihilation, and mating-disruption) are often preferred tactics is that they are extremely species-specific and generally considered to be less harmful to human health, to non-target animals, and to endemic ecosystems (McNeely et al. 2001). However, these methods do act in an indirect manner; they seldom show complete effectiveness over a short period and are generally less effective in moderate- to high-density populations (e.g., Miller and Weidhaas 1974; Cardé and Minks 1995).

Fortunately, most insect populations exist at low densities during the early stages of invasion. Such situations represent favorable conditions for the application of methods to control mating success. Several theoretical and empirical studies indicate that the growth of these colonizing populations are severely constrained by Allee effects arising from mate location failure (e.g., Berec et al. 2001; Liebhold and Bascompte 2003; Tobin et al. 2007). Mate-location thus represents a 'weak link' for the persistence of invading insect populations and consequently methods that exploit or enhance mate-location failure may be particularly effective for eradicating invading populations (Liebhold and Tobin 2008).

In this paper, we develop a general model in which the mating behaviors of both sexes are mechanistically described so that Allee effects arise in sparse populations as a result of mate-location failure. Three eradication methods, SIR, male annihilation (i.e., mass-trapping in our study), and mating disruption, are incorporated in the model. Using this general and mechanistic approach, we can evaluate and compare these methods in conjunction with the Allee effect in the early phases of invasions. Though it is not possible to fully analyze all the life histories of all important invasive alien insects, two representative types of insect pests are considered: Coleopteran-like insects which are long-lived and capable of multiple matings, but have low daily reproductive rates, and Lepidopteran-like ones which are ephemeral, only capable of mating once per generation, and have high reproductive rates. We will explore which method will be effective against the two insect types.

Eradication models and mate-location failure

Classic models of eradication

Though several mathematical models of eradication have previously been proposed, most of these models inherited their basic structure from the influential models developed by Knipling (1955) and Knipling and McGuire (1966). If the numbers of males and females at day d are M_d and F_d , then the total number of successful matings (C_d) can be calculated from Knipling's models as,

$$C_d = \frac{F_d}{D + F_d} \cdot M_d. \quad (1)$$

D represents a disruption effect, such as mass-trapping of males or mating disruption accomplished via many competing pheromone sources, calculated as an equivalent number of virgin females. This model assumes that all males will either mate with females or will be disturbed by the disruptants. Knipling and coauthors applied this model over multiple generations of disruption to calculate the time required before eradication is achieved (Knipling 1955; Knipling and McGuire 1966). This model, however, does not account for males that unsuccessfully search for mates during the entire mating period. In the case of SIR, a similar formulation can be derived from the perspective of females (Knipling 1955),

$$C_d = \frac{M_d}{S_d + M_d} \cdot F_d. \quad (2)$$

S_d is the number of sterile males that compete with wild males for females. All females are also assumed to mate with either sterile or wild males. Therefore, Eqs. 1 and 2 can be viewed as mating competition models because wild females (or males in SIR) engage in scramble competition for males (for females in SIR). Knipling's models were merely numerical simulations, but later studies extended Knipling's models incorporating additional processes/mechanisms and explored the stability of the system (e.g., Barclay and Mackauer 1980; Barclay and Van den Driessche 1983; Barclay 1987).

Despite the simple assumption of the mating competition models expressed in Eqs. 1 and 2, they capture the fundamental mechanisms of certain pest management programs and have been successfully applied for the evaluation of actual eradication programs (e.g., Roelofs et al. 1970; Ishii et al. 1985). These successes can largely be attributed to the fact that, under moderate to high pest densities, nearly all individuals are able to mate. However, this is not the case during the early phase of alien insect invasions where densities are sparse and individuals have difficulty finding their mates (Liebhold and Tobin 2008).

Allee effects in eradication models

How can we incorporate the Allee effect caused by mate-location failure into an eradication model? Various formulations for mate-location failure have been proposed but they have seldom been applied to eradication models (see list in Boukal and Berec 2002). Probably, the simplest approach would be to add an Allee effect term in the denominator of Eq. 1 (Boukal and Berec 2009 in this issue).

$$C_d = \frac{F_d}{D + \text{Allee} + F_d} \cdot M_d. \quad (3)$$

Equation 3 is very tractable to draw analytical solutions in combination with other population processes, such as interactions with generalist predators. However, we usually cannot use it directly to evaluate and compare eradication strategies because it may lack sufficient detail on the mating behavior. In order to make detailed evaluations of invasiveness, we also need a model for many pest species in which the strength of the Allee effect can vary within a season due to fluctuations in disruptant densities.

The Allee effect caused by mate-location failure can be mechanistically explained by the mate encounter rate. If there are few individuals in a limited area, each individual has little chance to find mates. As densities increase, the encounter rate will increase until the limitation of male and female frequency is saturated (see Dennis 1989 for a detailed explanation). We have selected Kuno's random mating model (1978) in this study, since all three eradication methods (mass-trapping, mating-disruption, and SIR) can be logically incorporated into the framework of his model. His model can be viewed as spatially implicit, which will be explained in the next section.

Kuno's random mating model (1978)

Assume that there are f females in an isolated area of size A m^2 . Each female emits a sex pheromone over a zone of male attraction with area a_f m^2 (Fig. 1). The probability of a male detecting the pheromone and being attracted for mating will be $1 - (1 - a_f/A)^f$ in case females are randomly distributed. This can be derived as the complementary event to the binomial probability $[(1 - a_f/A)^f$: zero out of f , respectively], which represents the situation where males never detect any sex pheromone. One might suspect that there are insect species in which females do not emit chemical signals for attracting males but instead males search widely over an area in order to encounter and mate with females. In such cases, we can formulate the probability of a female (instead of a male) being found over m mating trials conducted by males as $1 - (1 - a_m/A)^m$ where the search area of a male is a_m m^2 (Fig. 1b). In the

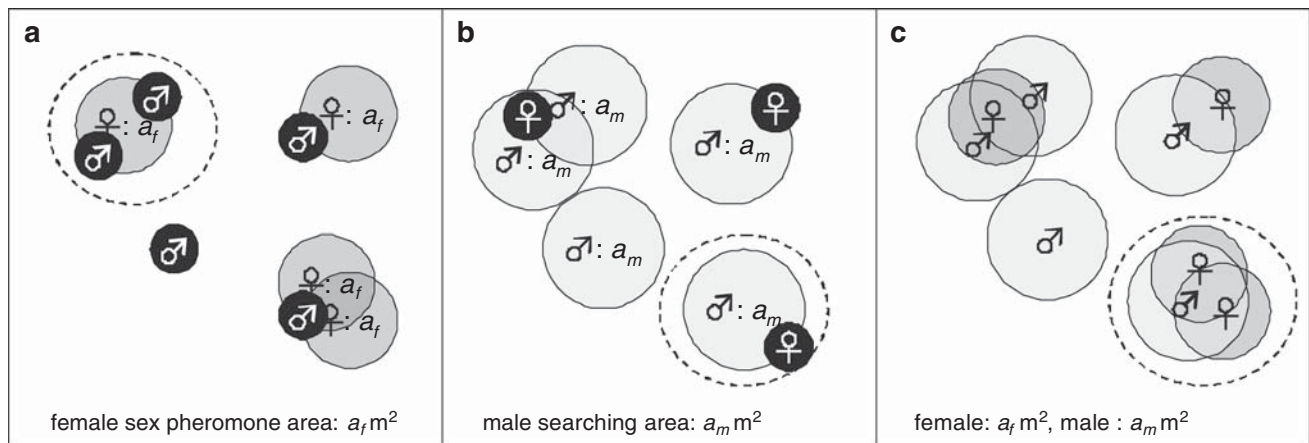


Fig. 1 Alternative random mating models. **a** Females emit sex-pheromone attracting males. **b** Males search intensively for females. **c** Females emit pheromone and males search for females. a_f Sex-pheromone area, a_m male searching area. For enclosed parts in the figures, see text

case where both males search for mates and females emit pheromone attractants, the probability that a female will mate is $1 - \{1 - (a_f + a_m)/A\}^m$ (Fig. 1c).

The problem with Fig. 1 is that there is no limit to the mating ability of females in Fig. 1a and of males in Fig. 1b and c. For example, the female enclosed by the dashed circle in Fig. 1a is expected to mate with two mates simultaneously, and in principle the number of matings she receives per day could become very large. Since copulation including pre- and post-copulative behavior can take many hours in many insects (e.g., Masaki 1975; Simmons 2001), we restrict the number of matings to one per day in our models.

Kuno (1978) recognized this problem and solved the differential equation for the number of mating success of the day (C_d) based on the number of males' mating behavior. Consider Fig. 1a again. When m males sequentially search for mates then copulate, one by one, the rate of decline of unmated females, $-df/dt$, is a product of the mating probability per male and the rate of change of available males, dm/dt , i.e.,

$$-\frac{df}{dt} = \left\{ 1 - (1 - a)^f \right\} \frac{dm}{dt}, \quad (4)$$

Given that the number of females changes from F_d to $F_d - C_d$ and the number of mating behavior of all males (m) also changes from 0 to M_d during the day, Eq. 4 can be rewritten as

$$M_d = \int_0^{M_d} dm = \int_{F_d}^{F_d - C_d} \frac{df}{1 - (1 - a)^f}. \quad (5)$$

Solving Eq. 5 for C_d , we get

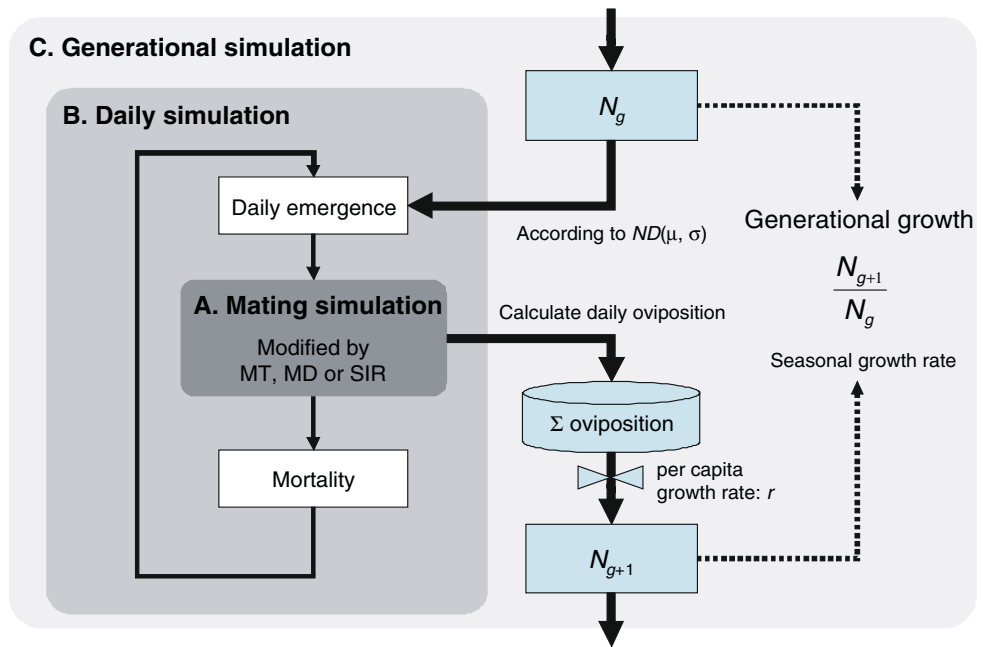
$$C_d = \frac{\ln[(1 - a)^{M_d} + (1 - a)^{F_d} - (1 - a)^{M_d + F_d}]}{\ln(1 - a)}. \quad (6)$$

Equation 6 is equivalent to model 2 in Kuno (1978) which assumes males and females are limited to mate once per night. It should be noted that the numbers of males (M_d) and females (F_d) at day d are symmetrical in Eq. 6 and this implies that the same form of the equation applies both to the situation in Fig. 1b where males search for females without attraction and to the situation in Fig. 1c where males search for females that emit an attractive pheromone. We constructed eradication models based upon the idea of Kuno's random mating model in the following sections.

Mating simulation (with eradication models)

The basic structure of our model is shown in Fig. 2 as a schematic flow chart. The simulation procedure can be decomposed into three parts: (1) mating simulation during day d in which three eradication methods are incorporated based on Kuno's (1978) model; (2) daily simulation of day d (including emergence, mating, oviposition, and survival) where two representative types of insects were parameterized instead executing full sensitivity analyses for all the parameters; and (3) generational simulation over generation g and evaluation of invasiveness with three methods to determine whether they can prevent the invading population from establishing. Mating simulations (Fig. 2a) will be described in this section. Daily simulations (Fig. 2b), generational simulations and the evaluation to determine whether the invading species can establish with eradication methods (Fig. 2c) will be explained in the next section. All the subscripts and parameters with canonical values are enumerated in Table 1. Simulations were executed in R (Version 2.6.1; R Development Core Team 2005) and source code is

Fig. 2 Schematic flow chart of the simulation. The simulation procedure can be decomposed into the three parts. *A* Mating simulation in which three pest management methods are incorporated. *B* Daily simulation where pest biology (Lepidopteran and Coleopteran) is described. *C* Generational simulation and evaluation of the methods. If and only if $N_{g+1}/N_g > 1$, then the alien pest can establish



available in Appendix A in Electronic Supplementary Material, ESM.

We assume that an invading species is initially distributed over an isolated area of A ($=10,000$ ha) which is comparable in size to several islands where eradication programs have previously been conducted (e.g., the ca 12,500-ha island Rota in the Marianas and, the ca 5,570-ha island Kume in Okinawa). For canonical simulations (executed with canonical parameters in Table 1), 10,000 individual eggs ($N_0 = 10,000$) were initially assumed to be introduced into the area. M_d males and F_d females attempted mating on day d and the resulting number of successful matings C_d should be formulated in terms of M_d and F_d .

Mass-trapping (MT, male annihilation in a broad sense)

Recently, Yamanaka (2007) developed a spatially implicit model that expresses mate-location failure based on Kuno’s model and we follow his derivation. Assume that there are T traps (in canonical simulations we assumed 500 traps) and f females. The canonical value of a_f is a 50-m radius circle ($=7,854$ m² over which the female sex-pheromone attracts males). The instantaneous probability that a male detects sex-pheromones emitted by females is $PF = 1 - (1 - a)^f$ and the probability that a male detects pheromones emitted by traps is $PT = 1 - (1 - c)^T$. The canonical value of parameter c was set at a value such that a trap had an attraction area

four times larger than that of a female (ca. a 100-m radius circle for a trap). In this situation, each male has four possibilities: detect female-produced pheromone alone ($PF - PF \cdot PT$), detect the pheromone emanating from traps alone ($PT - PF \cdot PT$), detect both ($PF \cdot PT$), or detect neither of them ($1 - PT - PF + PF \cdot PT$). Two additional parameters, b and k , are defined here. The parameter b is defined as the males’ preference for synthetic pheromones emanating from traps relative to female-produced pheromones. Thus, the proportion $1 - b$ of males detecting both ($PF \cdot PT$) is attracted to females. The parameter k is the capture efficiency of a trap. A proportion k of males attracted to traps will be captured. Then, instantaneous rate of decline of unmated females, $-df/dt$, and instantaneous rate of increase of captured males, dq/dt , can be related to the rate of increase of sequential mating behaviors of males dm/dt as

$$\begin{cases} -\frac{df}{dt} = \{PF - PF \cdot PT + (1 - b) \cdot PF \cdot PT\} \frac{dm}{dt} \\ \frac{dq}{dt} = k\{PT - PF \cdot PT + b \cdot PF \cdot PT\} \frac{dm}{dt} \end{cases} \quad (7)$$

When males (m) start their mate-searching sequentially (from 0 to M_d), the number of males captured (q) changes from 0 to TR_d and the number of females unmated similarly changes from F_d to $F_d - C_d$. Separating variables in Eq. 7 and integrating both sides of equations, we arrive at analytical solutions for C_d and TR_d ,

Table 1 Descriptions of variables and parameters

Parameter	Description	Canonical value	Unit
Variables			
N_g	Population size at generation g	Dynamic	Individuals
F_d	Number of females at day d	Dynamic	Individuals
M_d	Number of males at day d	Dynamic	Individuals
C_d	Number of matings at day d	Dynamic	Frequency
W_d	Number of wild males at day d	Dynamic	Individuals
S_d	Number of sterile males at day d	Dynamic	Individuals
CS_d	Number of matings by sterile males at day d	Dynamic	Frequency
CW_d	Number of matings by wild males at day d	Dynamic	Frequency
TR_d	Number of males captured by traps at day d	Dynamic	Individuals
F	Instantaneous number of females (unmated) during mating periods	Dynamic	Individuals
m	Instantaneous number of males during mating periods	Dynamic	Individuals
s	Instantaneous number of sterile males during mating periods	Dynamic	Individuals
w	Instantaneous number of wild males during mating periods	Dynamic	Individuals
q	Instantaneous number of males captured by traps during mating periods	Dynamic	Individuals
Parameters			
N_0	Initial size of the population	10,000	Individuals
μ	Peak date of adult emergence	50	Day
σ	Standard deviation of emergence	4.0 (Type-L) 12.0 (Type-C)	Day
Λ	Survival rate per day	0.75 (Type-L) 0.95 (Type-C)	–
r	Daily reproductive rate (including mortality from egg to pupa)	10.0 (Type-L) 0.5 (Type-C)	1/day
A	Total area of the simulation arena	10,000	ha
T	Number of traps (lures) installed in the simulation area	500 (mass-trap) 10,000 (disruption)	–
$S_{input, d}$	Number of sterile males inoculated on a given day	5,000	Individuals
a_f	Pheromone permeating area of females (a is used after transforming $a = a_f/A$)	7,854	m ²
a_m	Searching area of males for females (a is used after transforming $a = a_m/A$)	7,854	m ²
b	Competitive ability of sex-pheromone traps (lures for MD)	0.5	–
c	Pheromone permeating area of traps divided by the total area	31,416/A	–
k	Capture efficiency of traps	0.5	–
l	Competitive ability of sterile males	0.5	–
Probabilites			
PS	Instantaneous probability of female to be found by sterile males	Dynamic	–
PW	Instantaneous probability of a female to be found by wild males	Dynamic	–
PF	Instantaneous probability of a male to detect female pheromone	Dynamic	–
PT	Instantaneous probability of a male to detect synthetic pheromone in traps	Constant	–

$$\left\{ \begin{array}{l} C_d = \frac{\ln \left[(1-a)^{(1-b \cdot PT)M_d} \cdot \{1 - (1-a)^{F_d}\} + (1-a)^{F_d} \right]}{\ln(1-a)} \\ TR_d = k \cdot PT \left(M_d - \frac{(1-b) \cdot F_d \cdot \ln(1-a) + \ln \left[1 - (1-a)^{(1-b \cdot PT)M_d} \cdot \{1 - (1-a)^{-F_d}\} \right]}{(1-b \cdot PT) \cdot \ln(1-a)} \right) \end{array} \right. \quad (8)$$

where $PT (=1 - (1 - c)^T)$ is a constant since the number of traps will not change during the mating period.

Mating disruption

Mating-disruption (MD) is a method in which synthetic sex-pheromones (or their analogues) are emitted from multiple, widely spaced point sources in order to suppress mate-location behavior (Jones 1998). Despite the proven effectiveness of this method and its wide implementation for pest management, the precise mechanism responsible for the interruption of mate-location behavior remains uncertain. At least three mechanisms have been proposed: confusion, trail-masking, and false-trail following (Ridgway et al. 1990; Jones 1998). Confusion is the mechanism by which constant exposure to a high dose of sex-pheromone leads males to become inactive either because of sensory adaptation or habituation. Trail-masking describes the inability of males to locate females due to extensive dispersion of synthetic sex pheromone at background levels that masks the fine structure of pheromone plumes emanating from females. Under the false-trail following hypothesis, males waste time and energy locating point sources of synthetic pheromone instead of females.

Yamanaka (2007) found that Eq. 8 is also applicable to MD if parameter k , the capture efficiency, is set to zero, because Eq. 8 (with $k = 0$) reflects the situation of false-trail following; synthetic lures attract males which may otherwise have been attracted to females but they do not kill them. The model assumption may also hold some representation of trail-masking because the large areas of attraction to synthetic pheromone lures overlap with those of females. Consequently, some proportion of males that would have been attracted to females became inactive in the areas around lures. However, confusion was difficult to incorporate into our modeling framework since it would require individual histories of pheromone detection. In our study, the mechanism of confusion will be considered in the simulation analyses (below) by increasing the value of the parameter b , the competitive ability of lures. As b increases (maximum of 1.0), males in the area of attraction to pheromone lures become less attracted to females. Consequently, mechanisms of confusion (and also trail-masking) can be partly simulated with high b value.

For MD, TR_d in Eq. 8 is always zero but C_d is the same as in Eq. 8. Then, the model for MD is

$$C_d = \frac{\ln \left[(1 - a)^{(1-b \cdot PT)M_d} \cdot \{1 - (1 - a)^{F_d}\} + (1 - a)^{F_d} \right]}{\ln(1 - a)} \tag{9}$$

The canonical values of a and c are the same as in MT. Much larger numbers of lures can be deployed in MD (e.g., via aerial application) than in MT, since MD does not require deploying and maintaining a trapping device. The canonical number of lures (T) was thus set to 10,000.

Sterile male release

Sterile male release (SIR) can also be formulated in the framework of Kuno’s (1978) random mating model. Consider the situation shown in Fig. 1b but with the existence of two types of males: sterile (s) and wild (w) individuals. The instantaneous probability of a female being found by sterile males is $PS = 1 - (1 - a)^s$ and the probability of being found by wild males is $PW = 1 - (1 - a)^w$ (a_m/A was replaced by a for simplicity). In this situation, the fate of each female can be categorized into four possibilities: either she is found solely by sterile males ($PS - PS \cdot PW$), she is found solely by wild males ($PW - PS \cdot PW$), she is found by both ($PS \cdot PW$), or she is not found by either of them ($1 - PS - PW + PS \cdot PW$). Now we need to quantify the competitive ability of sterile males; l proportion of females, among those simultaneously found by the both types of males, will mate with the sterile males. Thus, the instantaneous probability that a female will mate with sterile males is $PS - (1 - l)PS \cdot PW$ and the probability that she will mate with wild males is $PW - l \cdot PS \cdot PW$. Then, instantaneous rate of decline of unmated sterile males ($-ds/dt$) and that of unmated wild males ($-dw/dt$) can be related to the rate of increase of sequential mating behaviors of females (df/dt) as

$$\begin{cases} -\frac{ds}{dt} = \{PS - (1 - l) \cdot PS \cdot PW\} \frac{df}{dt} \\ \quad = \{1 - (1 - a)^s\} \cdot \{(1 - l) \cdot (1 - a)^w + l\} \frac{df}{dt} \\ -\frac{dw}{dt} = (PW - l \cdot PS \cdot PW) \frac{df}{dt} \\ \quad = \{1 - (1 - a)^w\} \cdot \{l \cdot (1 - a)^s + 1 - l\} \frac{df}{dt} \end{cases} \tag{10}$$

Equation 10 can be rearranged after eliminating df/dt as

$$\left(l - \frac{1}{1 - (1 - a)^s} \right) ds = \left(1 - l - \frac{1}{1 - (1 - a)^w} \right) dw \tag{11}$$

Here, we define CS_d as the number of sterile males mated and CW_d as the number of wild males mated (where $CS_d + CW_d = C_d$). Then, the number of sterile males (s) will change from S_d to $S_d - CS_d$ while the number of wild males (w) will change from W_d to $W_d - CW_d$. Both sides of Eq. 11 can be integrated according to the change in each variable.

$$\int_{S_d}^{S_d - CS_d} \left(l - \frac{1}{1 - (1 - a)^s} \right) ds$$

$$= \int_{W_d}^{W_d - CW_d} \left(1 - l - \frac{1}{1 - (1 - a)^w} \right) dw. \tag{12}$$

Simplifying Eq. 12 and replacing M_d in Eq. 6 by $W_d + S_d$ for the SIR, we get a set of equations,

$$\begin{cases} \frac{(1 - a)^{W_d - (1 - l) \cdot CW_d} - (1 - a)^{l \cdot CW_d}}{1 - (1 - a)^{W_d}} \\ = \frac{(1 - a)^{S_d - l \cdot CS_d} - (1 - a)^{(1 - l) \cdot CS_d}}{1 - (1 - a)^{S_d}} \\ C_d = CW_d + CS_d \\ = \frac{(1 - a)^{W_d + S_d} + (1 - a)^{F_d} - (1 - a)^{W_d + S_d + F_d}}{\ln(1 - a)}. \end{cases} \tag{13}$$

Because it is impossible to solve Eq. 13 analytically, the roots of CS_d and CW_d were obtained numerically using the uniroot-function in R.

Daily simulation (two insect types)

In this section, daily and generational events are described (Fig. 2b, c). It is also explained how to evaluate the effect of each eradication strategy on the establishment of invasive insect pests. A total of N_g individuals are assumed to emerge during generation g . Emergence follows a Gaussian temporal distribution (denoted as ND with mean: μ , SD: σ) and a sex ratio of 1:1 is assumed. The population exhibits neither protandry (i.e., more rapid sexual maturation in males than in females) nor protogyny (the opposite pattern) in the sense of Wiklund and Fagerström (1977). Intra-specific competition or other factors limiting growth at high population densities are not assumed since we are only focusing on growth under low-density conditions. A generational simulation (g) is executed daily from $d = 1$ to 150 which corresponds to one growing season.

Because our models have many parameters and because daily simulation procedures must be formulated differently depending on the specialized oviposition behavior of the various insect species, we performed simulations with the canonical parameters of two representative types of insects, type-C (Coleopteran-like insects) and type-L (Lepidopteran-like ones). Though a full sensitivity analyses was not conducted here, the effects of some extra life history parameters in the two insect types were evaluated in Appendix B in ESM.

Type-L (Lepidopteran-like insects)

Type-L insects are assumed to have non-overlapping generations, an ephemeral reproductive stage but high reproductive rates such as in *Hyphantria cunea* Drury (Lepidoptera: Arctiidae) or *Lymantria dispar* (Linnaeus) (Lepidoptera: Lymantriidae). The survival rate per day is defined as $\Lambda = 0.75$ (50% of the individuals will die within 2.4 days), since *H. cunea* and *L. dispar* live only a few days (Masaki 1975; Elkinton and Cardé 1980). The daily reproductive rate (r) was difficult to set in part because it incorporates not only the number of eggs produced by a female but also mortality from egg to pupa. Life table analyses revealed that r ranges from 1.5 to 50.0 for *H. cunea* (Itô and Miyashita 1968; Itô et al. 1970) and is about 20.0 for *L. dispar* (Campbell 1976). Therefore, r was arbitrary set to 10.0 (per day) as a representative value for Lepidopteran pests. The temporal distribution of emergence was made compact [normal distribution ND (μ , σ) with $\mu = 50$ days and $\sigma = 4$] compared to that of type-C insects. These parameters were set base upon previous simulation models of *H. cunea* (Yamanaka et al. 2008) and of *L. dispar* (Robinet et al. 2007). Females mate only once during their lives while males can mate with several females though they can only mate once per day, which is concordant with *H. cunea* (Masaki 1975). The daily model of MT is formulated as

$$\begin{cases} M_{d+1} = \Lambda \cdot (M_d - TR_d) + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt \\ F_{d+1} = \Lambda \cdot (F_d - C_d) + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt. \end{cases} \tag{14}$$

C_d and TR_d are the number of successful matings and the number of males captured by traps, respectively, defined in Eq. 8. Numbers of males and females newly emerging daily are the product of the fraction of ND from d to $d + 1$ and the total number of individuals in the generation (N_g) divided by 2 (assuming a 1:1 sex ratio). Females which mate in day d will lay their eggs and die but unmated females will survive and join the mating behaviors the next day. Males which are not captured in traps will survive and join the next day’s trial. For MD, we can reuse Eq. 14 but TR_d is set to zero.

The canonical simulations of MT and MD ($N_0 = 10,000$) are shown in Fig. 3a and b, respectively. The reduction in mating success (C_d) caused by MT (lower panel of Fig. 3a) was much lower than reduction under MD (lower panel of Fig. 3b). The total number of males captured was quite small (1,159 out of 5,000 emerged males: upper panel in Fig. 3a) since the number of traps installed

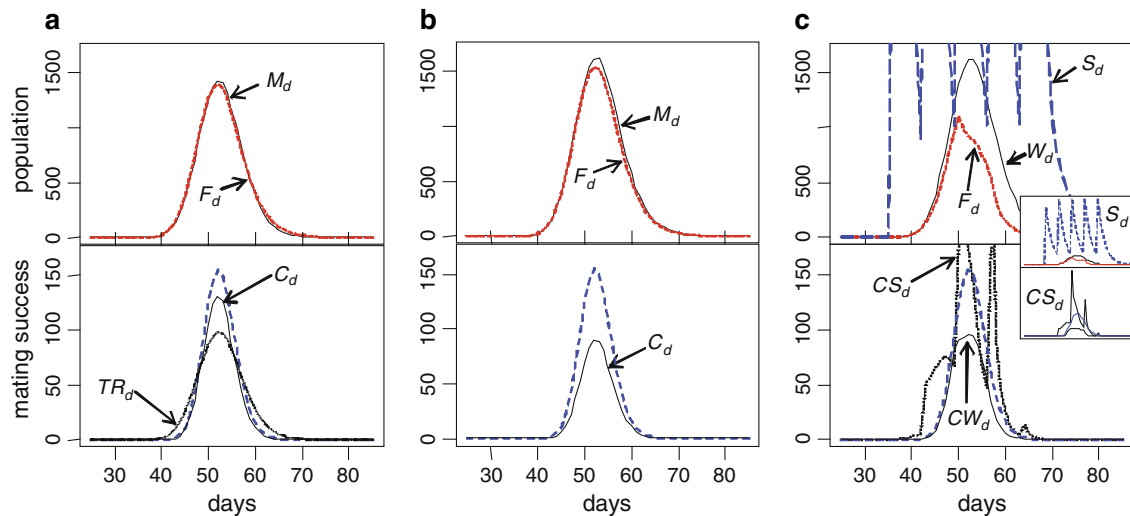


Fig. 3 Type-L (Lepidopteran pests) generational dynamics of each eradication program. **a** Mass-trapping, **b** mating-disruption and **c** sterile insect release (small window shows entire range of the dynamics). Parameters are canonical values in Table 1. M_d number of males on day d , F_d number of females on day d , W_d number of wild males on day d and S_d number of sterile males on day d . Also those in

lower panel represent, C_d number of successful matings, CW_d number of matings with wild males, and CS_d number of matings with sterile males. The dashed lines in the lower panels represent mating success when no pest control was installed. The two dotted lines represent the number of males captured (TR_d in **a**) and the number of matings with sterile males (CS_d in **c**)

in the area was sparse (500 corresponds to 0.05 trap/ha). The effectiveness of MD was better than that of MT (Fig. 3b). MD prevented more than 40% of matings. This was largely because the number of lures installed in MD was 20 times larger than that in MT. Though the lures cover 95% of the area ($1 - (1 - c)^{10,000}$) in MD, addition of more lures will do little to improve its effect since 0.5 of males (proportion b) still can mate with females within the effective area of lures, as assumed by our model.

For SIR, the number of wild males and the sterile males should be formulated separately as,

$$\begin{cases} W_{d+1} = \Lambda \cdot W_d + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt \\ S_{d+1} = \Lambda \cdot S_d + S_{input,d} (d = 36, 43, 50, 57, 64) \text{ or} \\ S_{d+1} = \Lambda \cdot S_d, \\ F_{d+1} = \Lambda \cdot (F_d - CW_d - CS_d) + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt \end{cases} \quad (15)$$

where CW_{d-1} and CS_{d-1} are the number of matings with wild and sterilized males, respectively, and are the numerical solution of Eq. 13. The newly defined variable, $S_{input,d}$ denotes the number of males that are inoculated in the population in a given day. Weekly inoculations are scheduled in the SIR simulations at $d = 36$, $d = 43$, $d = 50$, $d = 57$, and $d = 64$. The canonical value, $S_{input,d}$, was set equal to 5,000 on these days.

The canonical simulation of SIR ($N_0 = 10,000$) is shown in Fig. 3c. The SIR method was slightly more effective than MD as the reduction of mating success (CW_d) was ca 50%. It should be noted that the daily number of females (F_d) was much smaller than in the other two methods (upper panel in Fig. 3c). This was because in type-L insects, females were assumed to lay eggs and die once they mated. This reduction of numbers of females reflects the removal of females caused by copulation with sterile males while MD suppresses mating success but does not impact the stock of unmated females (Fig. 3b, the upper panel).

The total number of offspring produced in generation g is the simple product of the total number of matings and the reproductive output of a female:

$$N_{g+1} = r \cdot \sum_{d=1}^{150} C_d. \quad (16)$$

In the case of SIR, C_d should be replaced by CW_d . To evaluate whether the invading population will collapse or establish, the generational growth rate (N_{g+1}/N_g) was plotted against various initial population sizes (N_g) in Fig. 4 (see also Fig. 2c). The effect of the eradication treatment can be evaluated by the value of the intersection with $N_{g+1}/N_g = 1.0$ (referred to N^* or the “Allee threshold”). N^* can be viewed as the unstable equilibrium point under which the population goes extinct. Therefore, we can conclude that an insect pest will be easily eradicated with a management method if the system has a large N^* .

Figure 4a represents the generational growth rate under MT. The Allee threshold, N^* , was calculated as 9,011.

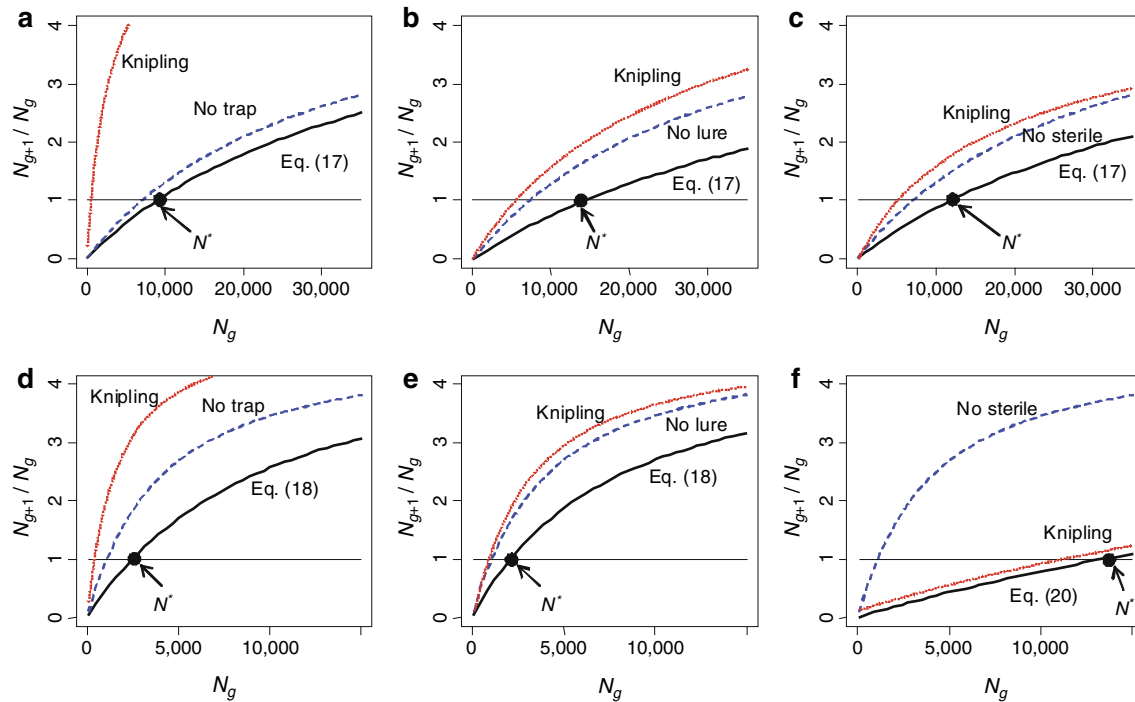


Fig. 4 Per capita generational growth in each eradication method. **a** Type-L (Lepidopteran pests) with mass-trapping, **b** type-L with mating-disruption, **c** type-L with SIR, **d** type-C (Coleopteran pests) with mass-trapping, **e** type-C with mating-disruption, and **f** type-C with SIR. *Dashed lines* indicate the simulation results without. *Dotted*

lines indicate the results of classic mating competition models in which parameter settings were adjusted to be compatible with our models (Knipling 1955; Knipling and McGuire 1966). N^* is the unstable equilibrium point below which populations decline

Because the canonical initial population size was set to $N_0 = 10,000$ which was larger than N^* , the population will gradually grow and consequently will establish in the invaded habitat. The value of N^* was just slightly larger than under natural conditions (Fig. 4a, dashed line). Obviously, MT would have to be improved in order to be effective under these conditions. For comparison, we also calculated generational growth rates for MT using the classic mating competition model of Knipling and McGuire (1966) and plotted these in Fig. 4a (dotted line) in which parameter settings were adjusted to be compatible with our canonical simulations (using the same number of traps, lures and sterile males). The Allee threshold of their model was far smaller than for our spatially implicit model (even smaller than for the simulation under natural conditions). The small Allee threshold of this classic mating competition model can be interpreted that even a small initial invading population would be sufficient to establish itself. Thus, the results of our models indicate that insect pests may be easier to eradicate (at low densities) than previously predicted by the classic MT models.

Figure 4b, and c represent generational growth rates under MD and SIR, respectively. The result of MD and SIR were similar; both methods would prevent the canonical type-L population from establishing because N^* was

calculated as 13,930 and 11,970 under MD and SIR, respectively (i.e., $N^* > N_0 = 10,000$). It should be noted that the classic mating competition models by Knipling and McGuire (1966) again predicted more susceptible situations for pest establishment than those predicted by our models.

Type-C (Coleopteran-like insects)

We considered type-C insects to represent relatively long-lived insects which have low daily reproductive rates corresponding to some Coleopteran pests. We set parameters to represent invading beetles such as *Ophraella communa* LeSage (Coleoptera: Chrysomelidae) (Yamazaki et al. 2000) or *Melanotus tamusyensis* Bates (Coleoptera: Elateridae) (Nagamine and Kinjo 1981). Though laboratory studies indicate that adult *O. communa* and *M. tamusyensis* can survive more than 30 days in the laboratory, their mortality rate is likely to be higher in nature. Therefore, the survival rate per day was arbitrarily set as $\Lambda = 0.95$ (50% of the individuals will die within 13.5 days). We also execute additional simulations while varying the value of Λ in Appendix B in ESM. The canonical daily reproductive rate was set as $r = 0.5$ (per day). Though this value was small compared to that of the type-L insects ($r = 10.0$), it

was set to yield a net reproductive potential identical to that of type-L insects assuming that the type-C females can lay eggs every day while the type-L will mate and oviposit just the day after emergence. The type-C emergence period is more protracted [$\mu = 50$ and $\sigma = 12$ in ND (μ, σ)] compared to those of type-L considering that the prevalence of *O. communa* or *M. tamsuensis* continues for about a month (Watanabe 2000; Arakaki et al. 2008). Females and males can mate as long as they survive though they can mate only once per day as is known for many Coleopteran species (Simmons 2001). The type-C insect is not different from type-L insect in the way that mating success is calculated, but the number of eggs produced each day is not a simple product of the number of matings and the reproductive output of a female. That is, females that have mated previously produce eggs until their spermatheca are exhausted of sperm even if they are not able to mate on that day. In our simulations, a female that mated at least once was assumed to oviposit every day until she dies. Therefore, virgin and non-virgin females must be distinguished in type-C simulations and they are defined as FV_d and FC_d , respectively ($FV_d + FC_d = F_d$). Assuming that there is no behavioral difference between virgin and non-virgin females, the probability that a female will mate on day d will be C_d/F_d where C_d is the number of matings calculated by Eq. 8 for MT and Eq. 9 for MD. The number of non-virgin females on day d will be $FC_d + C_d \cdot FV_d/F_d$ and those still unmated will be $(F_d - C_d)FV_d/F_d$. Consequently, the daily model can be formulated for MT and MD as,

$$\begin{cases} M_{d+1} = \Lambda \cdot M_d + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt \\ FV_{d+1} = \Lambda \cdot \frac{(F_d - C_d)FV_d}{F_d} + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt \\ FC_{d+1} = \Lambda \cdot \left(FC_d + \frac{C_d \cdot FV_d}{F_d} \right) \end{cases} \quad (17)$$

The total number of the offspring for MT and MD will be

$$N_{g+1} = r \cdot \sum_{d=1}^{150} \left(FC_d + \frac{C_d \cdot FV_d}{F_d} \right). \quad (18)$$

Canonical simulations of MT and MD ($N_0 = 10,000$) are shown in Fig. 5. Numbers of ovipositing females (=number of non-virgins, FC_d) are shown in the lower panels of Fig. 5. In type-C simulations, there was little suppression of the number of ovipositing females for both MT and MD, with 26 and 22% reduction of mating frequency from levels in untreated populations, respectively. The MT treatment was slightly more effective than MD even though MT used 500

traps, which represented a 20-fold smaller number of pheromone point-sources than MD. This was because traps in MT removed males and this removal effect produced more substantial effects in type-C insects. Nevertheless, both methods were far from successful because N^* was 2,319 for MT and 2,116 for MD (Fig. 4d, e), both of which were much smaller than the canonical population size ($N_0 = 10,000$).

For type-C insects, the structure of daily model under SIR is more complex than those in MT and MD because there are several possible types of sperm utilizations in coleopteran pests. Many species are reported to utilize only the sperm last inseminated, some only use sperm from the first mating and others mix sperm from several mates (Simmons 2001). Consequently, the total number of fertile ovipositions by a female will also be affected by which type of male(s) she has mated with. In our simulations, we assumed that females only use sperm from the last insemination. The number of virgin females, the number last mated with wild males, and numbers last mated with sterile males are defined as FV_d , FW_d , and FS_d , respectively ($FV_d + FW_d + FS_d = F_d$). The probability that a female mates with wild and sterile male on day d will be CS_d/F_d , and CW_d/F_d , respectively. The probability that a female does not mate with any male is $(F_d - CS_d - CW_d)/F_d$. Then, the generational dynamics can be formulated for SIR as,

$$\begin{cases} W_{d+1} = \Lambda \cdot W_d + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt \\ S_{d+1} = \Lambda \cdot S_d + IS_d \\ FV_{d+1} = \Lambda \cdot \frac{(F_d - CW_d - CS_d) \cdot FV_d}{F_d} \\ + \frac{N_g}{2} \cdot \int_d^{d+1} ND(\mu, \sigma) dt \\ FW_{d+1} = \Lambda \cdot \left(CW_d + \frac{(F_d - CW_d - CS_d) \cdot FW_d}{F_d} \right) \\ FS_{d+1} = \Lambda \cdot \left(CS_d + \frac{(F_d - CW_d - CS_d) \cdot FS_d}{F_d} \right), \end{cases} \quad (19)$$

CS_d and CW_d in Eq. 19 are the numerical solution of the Eq. 13.

The total number of offspring in generation $g + 1$ under SIR will be

$$N_{g+1} = r \cdot \sum_{d=1}^{150} \left(CW_d + \frac{(F_d - CW_d - CS_d) \cdot FW_d}{F_d} \right). \quad (20)$$

The canonical simulation of SIR ($N_0 = 10,000$) is shown in Fig. 5c. The suppressive effect of SIR greatly exceeded that of either MT or MD; fertile mating was

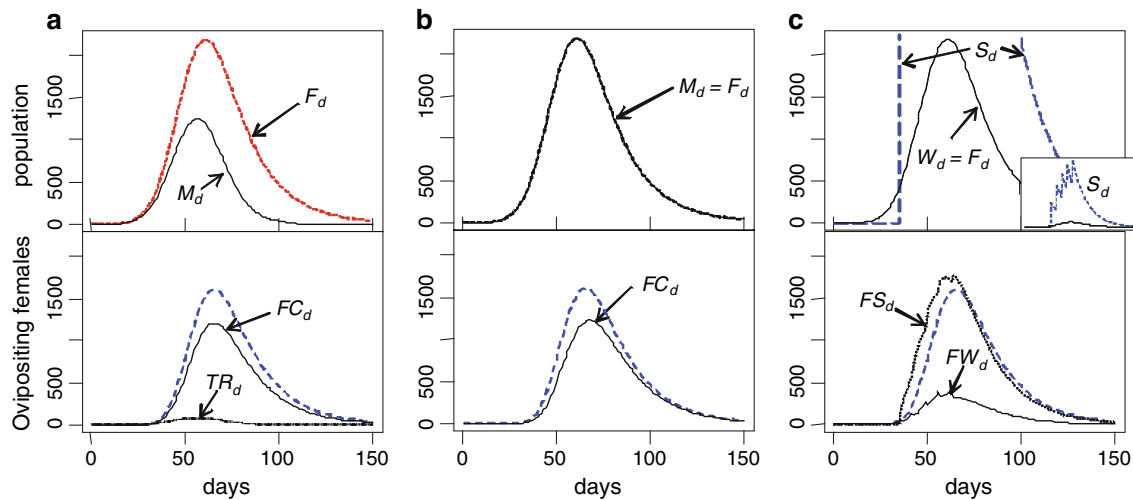


Fig. 5 Type-C (Coleopteran pests) generational dynamics of each eradication method. **a** Mass-trapping, **b** mating-disruption and **c** SIR (the *small window* shows whole range of the dynamics). Captions in the *upper panels* are as in Fig. 3 and those in the *lower panels*

suppressed by 77% from levels under natural conditions (the lower panel in Fig. 5c). Therefore, the population would be expected to collapse with application of SIR to the initial population of $N_0 = 10,000$ since N^* was calculated as 13,442 (Fig. 4f).

The classic mating competition model (Eq. 2) for type-C yielded more difficult conditions for control than our models (Fig. 4, dotted lines). However, it was not very different in SIR (Fig. 4f). This was because the SIR eradication effort had a much more drastic effect than the inherent Allee effect to reduce the generational growth rate because there is an after effect of females that have mated with sterile males even in the classic mating competition model.

Comparison of MT, MD and SIR methods

Parameters that might be manipulated in each of three methods (MT, MD, and SIR) were evaluated to explore the efficiency of control. These analyses provide critical information on designing management programs to maximize their effectiveness for the purpose of eradication. Though only two representative insect types were examined with canonical parameters here, key life-history parameters (Λ : survival rate per day, σ : standard deviation of emergence and r : daily reproductive rate) were tested in conjunction with the efficiency of eradication methods in Appendix B in ESM.

Mass trapping

To evaluate the effectiveness of mass trapping (MT), the number of traps (T) and the capture efficiency (k) were

represent, FC_d number of mated females, FW_d number of females mated with wild males, FS_d number of females finally mated with sterile males

manipulated. Allee thresholds (N^*), below which populations can be expected to collapse toward extinction, were plotted against T (Fig. 6). Large N^* indicated a highly effective control. Though the value of N^* in the canonical simulation of MT ($T = 500$) was the smallest among the three methods (Fig. 4a), values of N^* increased as the number of traps increases over $T = 10,000$ and then leveled off (not shown in Fig. 6a). This indicates that installing a large number of traps can enhance the efficiency of eradication. The leveling-off of N^* with larger numbers of traps occurred because almost the entire area will be covered by the area of attraction once a certain number of traps had been reached and additional traps will do little to increase this area. Increasing the capture efficiency (k) also enhanced the eradication efficiency but it had a secondary effect. Even if k was enlarged from 0.5 to 0.75 ($T = 500$, canonical), N^* slightly increased from 9,011 to 9,726. However, the subsidiary effect of k was magnified as the number of traps increased (Fig. 6a).

For those of type-C insects, the results in Fig. 6b were qualitatively the same as those of the type-L. Increasing the number of the traps caused the Allee threshold to increase but this effectiveness approached a maximum value near $T = 15,000$ (not shown in Fig. 6b). Improving trap efficiency (k) again only had a secondary effect but was more profound as the number of traps increased.

Mating disruption

For mating disruption (MD), the number of lures (T) and the competitive ability of lures (b) were examined. The results of simulations for type-L insects were striking (Fig. 7a). Though the Allee threshold, N^* , was the largest

Fig. 6 Sensitivity analyses for the number of traps (T) and trap catching efficiency (k) in mass-trapping (MT). **a** Type-L (Lepidopteran pests), **b** type-C (Coleopteran pests). Eradication effects are evaluated by the threshold (N^*) under which the population will collapse. The *black dot* is the value from simulation with canonical parameters in Table 1

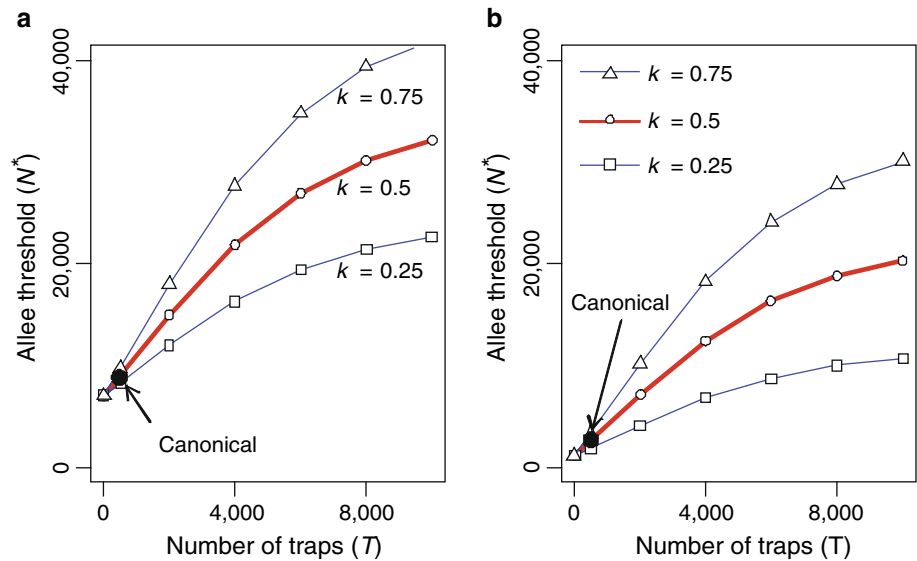
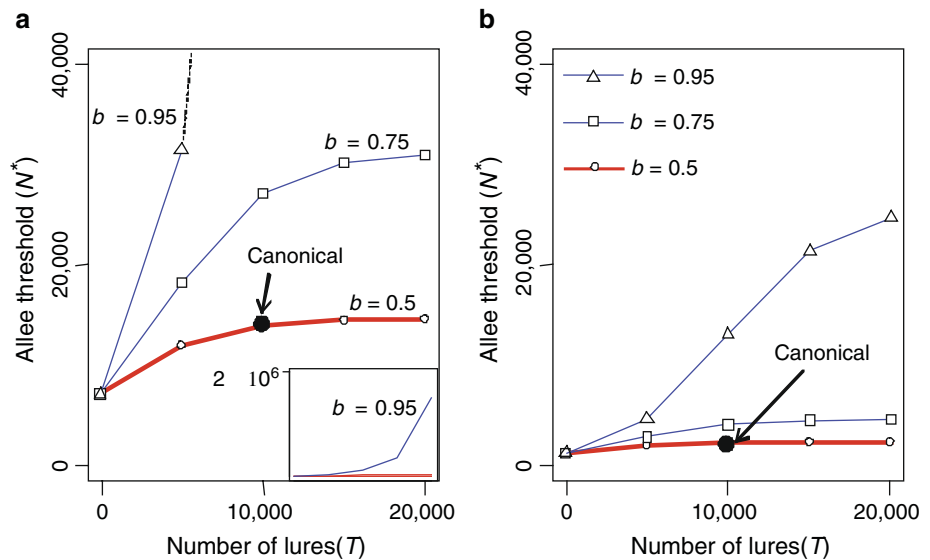


Fig. 7 Sensitivity analyses for the number of lures (T) and reduction effects on male searching behavior (b) in mating-disruption (MD) programs. **a** Type-L (Lepidopteran pests, the small window shows the entire range of results), **b** type-C (Coleopteran pests). Controlling effects are evaluated by the threshold (N^*) under which populations decline. The *black dot* is from simulation with canonical parameters in Table 1



among three methods in the canonical simulations (Fig. 4b which corresponds to the black dot in Fig. 7a), it was improved only marginally by adding more lures (Fig. 7a). In fact, N^* in MD canonical simulation was equal to that of the MT simulation with $T = 1,750$ (Fig. 6a). That is, with MT, it was possible to achieve the same level of control using less than 20% of pheromone sources as with MD. However, as b approached 1.0, the effectiveness of MD drastically and exponentially improved. As we mentioned in “Mating disruption”, large values for b would only be possible under either confusion or trail-masking mechanism driving mating disruption. Thus, as long as confusion or trail-masking mechanisms exist, we can expect that MD will work quite effectively for eradicating invading populations.

In contrast, the effectiveness of MD for type-C insects was much weaker (Fig. 7b). The effectiveness of MD (as measured by the Allee threshold, N^*) did not substantially improve with the addition of large numbers of lures even for $b = 0.75$. Though high lure competitiveness (b) enhanced the effectiveness in the presence of large numbers of lures (Fig. 7b), the effect was not as pronounced as in the type-L insects. Males of type-C insects are more likely to mate successfully because they can live for several days and MD lures do not kill them. Moreover, females can produce eggs every day once they mate. Unless MD completely prohibits mating every day, we conclude that a male can mate with females sooner or later. Once a female has mated, she can oviposit until she dies. Therefore, we can conclude that MD will not work well for species that

are long-lived and that are capable of mating multiple times.

Sterile insect release

The effectiveness of the sterile insect release (SIR) method was evaluated for varying numbers of sterile males released per inoculation ($S_{\text{input}, d}$) (Fig. 8). In addition to examining various values of $S_{\text{input}, d}$, we also explored responses to varying values of l , the competitive mating ability of sterile males, because it has been reported that irradiation for sterilization sometimes debilitates the competitiveness of males (e.g., Hamada 1980; Hendrichs et al. 2002). In simulations for type-L insects, the controlling effect linearly increased until approximately $S_{\text{input}, d} = 100,000$ (Fig. 8a) and then was saturated. Therefore, we can expect that the release of large numbers of sterile males would be effective for eradicating invading populations though the increment of the effect was not conspicuous compared to MT simulations (Fig. 6a).

In simulations for type-C insects (Fig. 8b), increasing values of $S_{\text{input}, d}$ had a more drastic effect than in type-L ones (Fig. 8a). The controlling effect increased linearly until $S_{\text{input}, d} = 30,000$ and then saturated. Parameter l represents the competitive ability of sterile males. If $l = 0.5$ (canonical), a female that is found both by wild males and sterile males has an equal chance to mate with either of them. Though the inferior competitive ability (small l) negatively affected the effectiveness of SIR for control, the reduction was not large especially when $S_{\text{input}, d}$ was small. This is because we assumed an identical searching area (a_m) for both wild and sterile males. When numbers of wild and sterile males are both small, the overlap in areas searched by the two types of males will be negligible. If we could have formulated a sterilization-

induced reduction of searching area, we would have observed a greater reduction of the control effect. We discuss this matter in *Future studies for field applications* in “Discussion”.

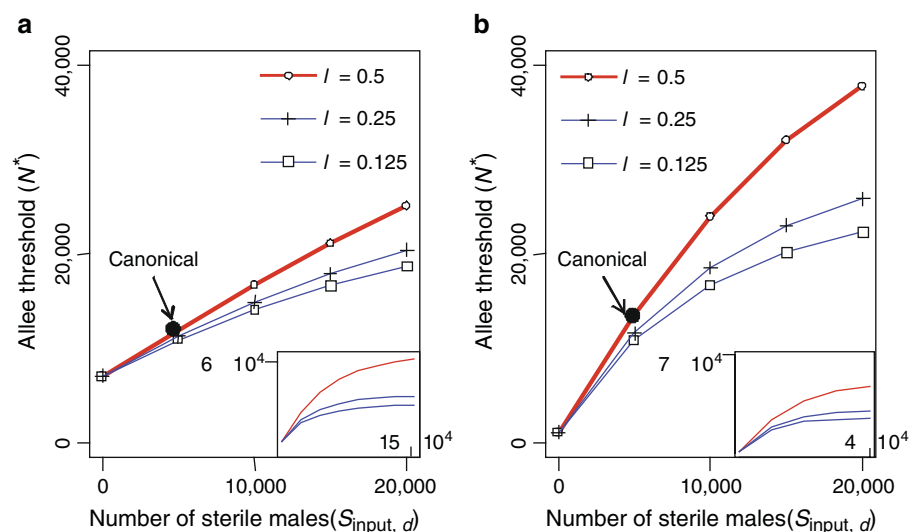
Discussion

General conclusion from our results

Because our models for the three eradication methods were based on a single structure derived from Kuno’s (1978) random mating model, it was possible to directly compare the effectiveness of each management strategy by simply changing parameter values and comparing the behavior of simulated populations. Furthermore, because reproductive potentials were carefully set to be equivalent between the type-L and type-C in the canonical simulations, we were also able to directly compare the efficiency of three controlling methods applied to both types of insects.

Our model predicted that the eradication can be achieved more easily than predicted by the previous eradication models in which no inherent Allee effect was incorporated (e.g., Knipling and McGuire 1966; Barclay and Mackauer 1980; Barclay and Van den Driessche 1983). These results thus support the hypothesis (Liebhold and Bascompte 2003) that Allee effects are of critical importance to successful eradication because they create population thresholds below which populations decline toward extinction. Liebhold and Tobin (2008) suggested that there are two approaches to achieve eradication. In the first approach, a pesticide or other killing techniques can be used to force the current population below the Allee threshold. In the second approach, the Allee threshold can be shifted up to a level that exceeds the current population

Fig. 8 Sensitivity analyses for the number of sterile males inoculated ($S_{\text{input}, d}$) and competitive ability of sterile males (l) in SIR. **a** Type-L (Lepidopteran pests, the *small window* shows the results extended $S_{\text{input}, d}$ up to 150,000), **b** type-C (Coleopteran pests, the *small window* shows the results extended $S_{\text{input}, d}$ up to 40,000). Eradication effectiveness is evaluated by the threshold (N^*) under which populations collapse. The *black dot* is from simulation with canonical parameters in Table 1



density. As illustrated in our study, the MT, MD, and SIR methods are all examples of strategies for achieving eradication through actively shifting the Allee threshold upward.

Our simulations also indicated that population of type-L insects can be eradicated most effectively using mass-trapping when a large number of traps can be installed. This result is concordant with the suggestion of El-Sayed et al. (2006), that is, mass-trapping has a great potential for controlling insect pests in low density and isolated conditions. Further improvement for eradication cannot be achieved in MD even with a large number of lures when false trail-following is assumed as the only disruption mechanism. On the other hand, it can be extremely effective when the major disruption mechanisms are confusion and/or trail-masking (high b value in Fig. 7b). This result is concordant with the findings by Yamanaka (2007). He concluded that efforts to shut-down mating behaviors (MD effects) will yield greater improvements to lepidopteran insect management than enhancing the capture effect (MT effects).

For type-C pests, SIR seemed generally more effective than MD or MT (Figs. 6b, 7b, 8b) because the negative effect of copulation with sterile males persists until females mate with wild males. Simulations using MD provided generally the worst effective control among the three treatments. This result most likely is a consequence of the ability of type-C insects to compensate for the low mate-finding probability (caused by the MD treatments) by searching for mates over many days.

Comparison to the other pest management models

The main difference between our models and classic mating competition models (e.g., Knipling 1955; Knipling and McGuire 1966) is that we assume that the attraction of wild females or traps (lures) is limited to males occurring in finite areas while the classic mating competition models of MT and MD assumed that females and traps (lures) would scramble to attract all males. In our SIR model, we assume that the searching ability of wild and sterile males is limited to finite areas while the classic mating competition models assumed that they could scramble to find all females. The critical difference here is thus that our model incorporated negative population growth caused by Allee effects arising from mate-location failure at low densities, but the classic models assumed that, in the absence of treatments, all females would be mated even in sparse conditions.

Barclay and his coworkers developed several differential and difference equation models to explore the dynamics behavior of the system under various pest management programs and also several insect types (e.g., Barclay and

Mackauer 1980; Barclay and Van den Driessche 1983; Barclay 1987). This work yielded some important conclusions regarding important features of pest management programs, e.g., the effectiveness of mating-disruption may be nearly equivalent to that of mass-trapping, a pest that has high survivorship and high reproductive rate is difficult to control, and a strong intra-specific competition assists the control. Many of their results agreed with the conclusions drawn from our simulations. However, their model cannot exactly predict the consequences in very sparse conditions and fell short for evaluation of the efficiency of the methods because their basic structure is based on the classic mating competition models of Knipling.

Boukal and Berec (2009) have analyzed simple models of pest control that incorporate a mate-finding Allee effect similar to Eq. 3. Their simple models can capture qualitatively similar dynamics to those derived from Eqs. 17, 19 and 21. However, their approach is based on differential equations, which cannot be used directly to evaluate and compare pest management programs if the population dynamics are seasonal and the strength of the Allee effect changes dynamically over the season. On the other hand, their models can provide a quick overview of interactions of mate-finding Allee effects with other mechanisms, such as introduction of predators or artificial culling, in context of the pest control strategies explored in this paper.

Future studies for field applications

Though our canonical simulations for two insect types were useful for comparing the effectiveness of various management methods, more detailed models should be tailored for specific insect species before field application. A limited exploration of varying parameters is provided in Appendix B in ESM. Some interesting features were obtained in Appendix B. The reproductive potential (r , the number of eggs per day) and the survival rate per day (Λ) had a large effect for pest management efficiency while the standard deviation of emergence (σ) had little effect. This suggests a need to carefully develop specialized strategies for managing populations of high reproductive insect species. However, the preliminary result in Appendix B also suggest that if reproductive/survival rates can be reduced by other means (e.g., via pesticide applications), then eradications may be more easily achieved using one of several methods that target reproductive behavior.

The models utilized here have limitations that should be recognized. For example, our model, which incorporates Allee effects arising from mate-location failure, may be particularly useful when applied to model sparse populations but have less applicability to more dense conditions. In dense conditions, average distances between males and females are quite small and mating probabilities can be

expected to be enhanced by visual or other cues (Gross et al. 1983). In such situations, scramble competition based on the Knipling's models (Eqs. 1, 2) might be more appropriate. Another limitation is the way the competitive mate searching ability of sterile males was incorporated using the parameter $l = 0.5$. Irradiation and mass-rearing may contribute to inferior competitive abilities; this may cause, for example, asymmetric searching areas between sterile and wild males (differing a_m), which was technically impossible to represent in Eq. 13. In fact, Hamada (1980) reported that high γ -irradiation diminished the dispersal ability of male melon fly and medfly, *Anastrepha obliqua* (Wiedemann) (Diptera: Tephritidae) (see also Toledo et al. 2004). Therefore, the effect of asymmetric searching areas should be explored in the future.

There remain other problems that need to be solved before directly applying our conclusions to specific field problems. Continuous or intermittent immigration into pest populations is a significant problem that threatens the efficiency of many eradication programs (Drake and Lodge 2006; Liebhold and Tobin 2008), but the effectiveness of various treatments under these situations could be explored via simulation. Another avenue worthy of attention is the use of elevated pheromone release rates and release of various behavioral chemicals for increasing the effectiveness of MD. Trap arrangement in MT and the inoculation schedule in SIR should be explored and optimized via simulation. Several practical constraints are also likely to limit the application of any of the three control strategies here. Obviously, if a sex-pheromone has not been identified and synthesized, neither MT nor MD can be implemented. The application of SIR is obviously limited by the practicality and cost of mass-rearing and the irradiation. Another important biological detail which should be addressed in the future is within population variation in the timing of sexual maturation (i.e., protandry or protogyny). Recent theoretical studies proposed that such differences will significantly affect mating success (Robinet et al. 2007; Calabrese and Fagan 2004). Differences in the timing of sexual maturation should be carefully considered for individual pest species that are the focus of eradication programs. Such differences can be easily represented by using different values of μ for males and females in Eqs. 14 and 17 in our simulation framework.

In spite of these deficiencies, our spatially implicit modeling approach is highly suited for adaptation to specific problems by incorporating the specifics of biology and management. Individual-based, spatially-explicit models (e.g., Robinet et al. 2007) may be slightly easier to modify for incorporation of specific biological attributes, but they tend to require more computer resources than our spatially-implicit simulations. We expect that the modeling framework presented here for comparison among methods under

sparse conditions may be widely adapted in the future to study the efficiency of various eradication approaches, targeting individual systems.

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