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Mating-disruption or mass-trapping? -Numerical simulation analysis of control strategy for lepidopteran pests[†]

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Abstract

I constructed a simulation model applicable in both mass-trapping and mating-disruption for lepidopteran pest insects. The basic structure of the model is based on mass-trapping proposed by Knipling and McGuire (1966, Agric. Info. Bull. 308:1-20), but it is modified to include mechanistic competition among females and lures. Several new implications are derived from the model. 1) Long living pests are hard to control; 2) Protandry does not improve the control efficiency for pests with low survival rates; 3) Sexual communication occurring across large distances is more difficult to control than those across a short range; 4) There is an upper limit of improvement according to the increase of pheromone traps; 5) Catching efficiency of the traps does not improve mating suppression though improvements in lure efficiency greatly do. In particular, the last implication has practical importance. If an efficient lure attracts males or inhibits their ability to locate females and mate, then mating-disruption works equal to mass-trapping with the same number of lures. In such a case, mating-disruption is preferred over mass-trapping because the former does not incur the cost of the trapping devices. On the other hand, mass-trapping should be considered over mating disruption if the lure is not efficient enough and no other methods are available.

Keywords: *Mating-disruption, Mass-trapping, lepidopteran pest, random mating model, Population model*

Introduction

The use of sex pheromones has played an important role in insect pest management for decades (Howse et al., 1998; Ridgway et al., 1990; Silverstein, 1981). Lepidopteran pests, which cause some of the most harmful damages in crop fields, are often a primary target of this tactic. For simplicity, I will only focus on the mating system of lepidopteran pests in which males are generally attracted to the female sex-pheromone, though there are many insect pests whose females or both sexes are also attracted to sex-pheromones. There are three major methods of lepidopteran pest control that involve the use of sex pheromones: monitoring, mass-trapping, and mating-disruption (Silverstein, 1981). Monitoring is distinctive from the other two methods in that it does not kill or control pest populations but rather it informs decision makers about the abundance of the target insect and also guides in the timing of treatment applications. Though both mass-trapping and mating-disruption target the mating system of insect pests, their mechanisms are different. Conceptually, mass-trapping appears to be simple: place a high density of pheromone-baited traps in the target area and achieve a measure of protection through the trapping, and hence removal of a sufficiently high proportion of the males. It is, however, rarely that simple in practical applications. In fact, it seldom has been successful in lepidopteran pests. Even in the successful exceptions, it was still difficult to reduce the pest population below the economical injury threshold (Hathaway et al., 1985; Madsen et al., 1976; Nemoto et al., 1980; Trammel et al., 1974), or it remained uncertain if pest control was from the effects of mass-trapping or from mating-disruption due to the use of pheromones in the traps (Kitamura and Kobayashi, 1985; Taschenberg et al., 1974). On the other hand, mating-disruption, in which an area is covered with a high dose of sex-pheromone (or its analogues) to suppress mating behavior, seems to work well in practice. However, the mechanism behind mating-disruption is rather mysterious. Three hypotheses have been proposed: confusion, trail-masking, and false-trail following (Jones, 1998; Ridgway et al., 1990). Confusion is the mechanism in which constant exposure of a high dose of sex-pheromone makes males inactive because of adaptation in their antennal receptors or habituation in their central nervous system. Trail-masking describes the inability of males to locate females due to extensive scattering of synthetic sex pheromone, which in turn masks the fine structure of pheromones naturally emitted by females. False-trail following is a behavior in which males lock onto and follow a fake plume from a lure instead of a plume from a calling female. Consequently, they waste time and labor in the futile attempt to locate a female and mate. These three hypotheses are not at all entirely unconnected, and could in fact act synergistically to some degree (Cardé and Minks, 1995; Jones, 1998). There are many examples of successful applications of mating-disruption (Cardé and Minks, 1995; Jones, 1998; Ridgway et al., 1990), most notably in gypsy moth (Beroza et al., 1974; Leonhardt et al., 1996; Thorpe et al., 2000) and pink bollworm management (Kehat et al., 1999; Shorey et al., 1974; Staten et al., 1987).

As a companion to this paper, I have summarized a number of scientific papers published over the last 35 years on the use of pheromones in pest management from the portal website "Pherobase" (Figure 1; Leslie, 2005). In this database, it was quite apparent that the number of papers related to mating-disruption exceeded those published on mass-trapping. However, there is nevertheless a steady amount of work on the use of mass-trapping for various insect pests, especially for coleopteran pests in forest systems through the use of aggregation pheromones (Figure 1).

Because of the many examples in which mass-trapping has provided unsatisfactory results, its continued use motivates the question of why it is still used. One explanation could be that managers feel a degree of security and confidence in this tactic when large amounts of males are captured through mass-trapping, even though the desired biological effects are minimal. Also, there could be economic constraints in applying sufficient sex-pheromone lures in mating-disruption to be effective (Yamanaka et al., 2001). Indeed, mating-disruption ordinarily requires massive amounts of pheromone components, and the synthesis of the unique structure or the purification of the isomer is often a costly process (Ando

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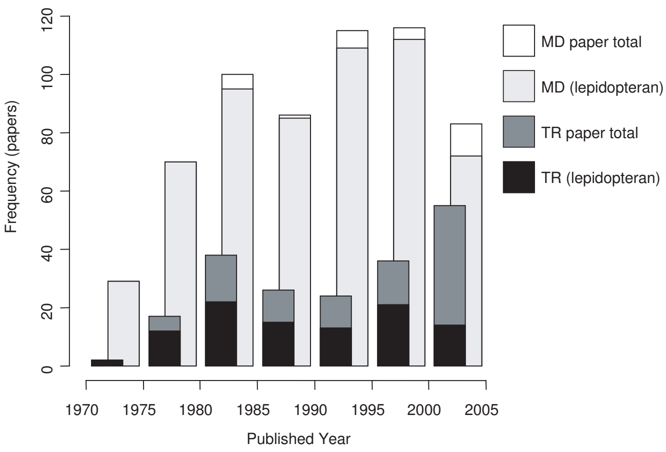

Figure 1. Number of papers published in *The Pherobase* from the 1970s to 2005, with permission by A.M. El-Sayed. MD papers are articles on mating-disruption methods and TR papers are those on mass trapping. The lepidopteran bars are those for lepidopteran pests

et al., 2004). In addition, there might be biological reasons (life history traits, population size and behavior) that may be decisive when choosing one strategy or the other. Small size of the pest population, the high mortality of adults, and the protandry had been though preferable especially for the mass-trapping (Roelofs et al., 1970; Beroza and Knipling, 1972). I will analyze these effects in this study. The disparity of success between mass-trapping and mating-disruption has been previously discussed. Jones (1998), for example, outlined some deficiencies of mass-trapping: 1) the lack of attraction of females to the trap lure , 2) the lack of highly efficient traps, 3) the problem of high insect populations and consequent trap saturation and 4) the need for a high density of traps per area, which in turn renders the technique too costly. Also, Nakasuji and Fujita (1980) and Barclay (1984) stressed in a theoretical context that mass-trapping was less effective against high target pest populations than mating-disruption. If we improve the efficiency of the traps to avoid trap saturation, and if we are not constrained by the cost of the traps, then is it possible to achieve satisfactory results from mass-trapping? Why do high populations vitiate the efficiency more so in mass-trapping than in mating-disruption? In this paper, I examined the use of mass-trapping and mating-disruption in a system of lepidopteran pest insects in which males search and trail the sex-pheromone emitted by female moths (Silverstein, 1981). I used an integrated simulation model applicable to both methods to identify ways of improving efficiency, and develop reasons why mating-disruption often works but mass-trapping does not.

Materials and methods

Model construction

The model is a discrete and deterministic type of numerical simulation. All simulations and analyses were executed in R (Ver2.01: CRAN). Because the main goal was to compare mass-trapping and mating-disruption, both of which target the mating period, I executed simulations during the course of one generation. A preliminary analysis using a simple mathematical model, however, will also be addressed briefly to explore the effect of the intra-specific competition processes connecting each generation. The implementation of the model is provided in Appendix S1.

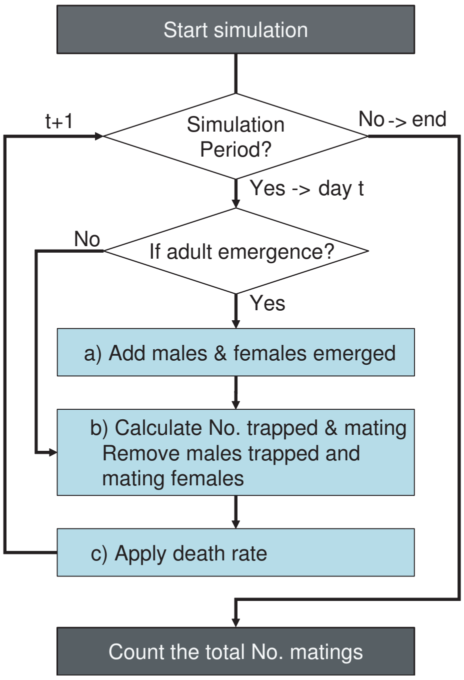

Figure 2. Schematic flow chart of the daily procedure in the model. The model is based on that of Knipling and McGuire Jr. (1966) for mass trapping. The second process "Calculate no. trapped and mating/remove males trapped and mating females" is totally. revised

The basic structure of the model was based on the mass-trapping model of Knipling and McGuire Jr. (1966). The schematic flow chart is depicted in Figure 2. Males are assumed to mate up to once a day as long as they are alive. Females, however, only mate once in their life, and they oviposit just after mating and then die. Therefore, all the females in the simulation are virgin. Two points were revised from Knipling and McGuire's model (1966). First, emergence of the adults is generated according to the Gaussian distribution (mean: μ, sd: σ) and there are several days of delay (lag) in female emergence (i.e., protandry, Figure 2a). When the total population to emerge in the simulation is Pop and the sex ratio is assumed to be 1:1, the males (EM_d) and females (EF_d) emerging at day-d will be

$$\begin{aligned} EM_d &= \frac{Pop}{2} \cdot \int_{d-1}^{d} \text{Normal}(\mu, \sigma)dx \\ EF_d &= \frac{Pop}{2} \cdot \int_{d-1}^{d} \text{Normal}(\mu + lag, \sigma)dx \end{aligned} \tag{1}$$

The second revision of Knipling and McGuire's model deals with mating and trapping mechanisms (Figure 2b). The calculation of mating success (MF_d) in Knipling and McGuire's model (1966) has been criticized (Barclay and van den Driessche, 1983; Nakamura, 1982; Nakamura and Oyama, 1978; Nakasuji and Fujita, 1980), mainly because their assumption of mating was presumably based on the harmonic mean of males and females, with males (M_d) and females (F_d) disrupted by sex-pheromone traps (T):

$$MF_d = \frac{2 \times F_d \times M_d}{F_d + M_d + T} \approx \frac{F_d \times M_d}{F_d + T} \quad \text{if}(F_d \approx M_d) \qquad (2)$$

The approximation of Eq. 2 is only valid if the sex ratio is 1:1, which seems unlikely since the number of virgin females must be smaller than male abundance because females constantly disappear from the simulated population after mating. In addition, mass-trapping changes the number of males intensively. Also, when there are a small number of females with a multitude of males, Eq. 2 generates an unrealistic overestimate of mating males (MF_d) compared to virgin females (F_d) (Nakamura and Oyama, 1978). In addition to the inequality between male and female abundance, adding the negative effect of pheromone traps in the numerator in Eq. 2 has no biological meaning. Therefore, I constructed a new competition equation among pheromone traps (or lures) and virgin females by referring to Kuno's random mating model (1978). Assume that there are T pheromone traps (or lures only) and v virgin females in an isolated area of size S. Every single pheromone lure (with or without trap), trA, and sex pheromone emitted by single virgin, fA, is saturating an area. Males are assumed to enter the area randomly. Then the probability of a male detecting the pheromone plume of either the lure (P_{InTrap}) or a female (P_{InFemale}) will be:

$$P_{\text{InTrap}} = 1 - \left(1 - \frac{trA}{S}\right)^T \quad \text{or}$$
$$P_{\text{InFemale}} = 1 - \left(1 - \frac{fa}{S}\right)^v$$

respectively. These two probabilities are derived as the complementary event to the binomial probability (zero out of T and v, respectively), which represents the situation males never mate or are never captured. These equations assume that wild females and traps are independent of each other i.e. there is no additive effect of their pheromone plumes on male behavior even if two pheromone sources (females or lures) are next to each other. As the density of lures and females increase, the overlapping area, $P_{\text{InTrap}} \times P_{\text{InFemale}}$, cannot be neglected because in this overlapping area, males may be attracted to both the females and lures. Two extra parameters, b and c, are thus added. The parameter b is the probability for a male within the zone of overlap to be attracted to a female, and consequently mate with her. Thus, $1 - b$ is the fraction of males that is attracted to lures or the degree of inhibition from mating. The parameter c is the catching probability of the trap, and its incorporation enables us to consider various trapping situations, such as when traps attract but do not capture males. For example, the mechanical structure of a trap greatly affects catching efficiency, and high pheromone dose or the lack of a lure component may repel males away even though it still attracts males to the area (Jones, 1998). Parameter c with small parameter b can also express mating-disruption without catching males. Thus, the probability of a male mating with a female (P_{Mate}), and a male being captured (P_{Captured}) is

$$\begin{aligned} P_{\text{Mate}} &= P_{\text{InFemale}} - (1-b)P_{\text{InFemale}}P_{\text{InTrap}}, \\ P_{\text{Captured}} &= c(P_{\text{InTrap}} - bP_{\text{InFemale}}P_{\text{InTrap}}). \end{aligned} \qquad (3)$$

Although these equations estimate the exact instantaneous probability of a male mating (the first equation in Eq.3) or being captured (the second equation in Eq.3), neither can be used to calculate the total number of matings or captures because the number of virgin females (v) will drastically change as the number of matings increase during the mating period. Consequently, Eq. 3 is dependent on the number of virgin females and may be rewritten as $P_{\text{Mate}}(v)$ and $P_{\text{Captured}}(v)$, respectively. It is, however, difficult to incorporate the concept of time in Eq. 3 to integrate along the time because mating duration differs daily, among species, and is dependent on environmental conditions. Therefore, a remedy is defined here, that is, males are assumed to start their mating one by one, sequentially. Though the number of males is an integer, its increment can be assumed as a differential particle when the number of males is large. Then the rate of change in female abundance equals the negative product of mating probability and each segment of males' trial. The rate of change in the number of males captured by traps (t) is the product of the probability of capture and each segment of males' trial.

$$\begin{aligned} \Delta v &= P_{\text{Mate}}(v) \cdot \Delta m \\ &= -\left\{P_{\text{InFemale}} - (1-b) \cdot P_{\text{InTrap}} \cdot P_{\text{InFemale}}\right\} \cdot \Delta m \\ \Delta t &= P_{\text{Captured}}(v) \cdot \Delta m \\ &= c\left(P_{\text{InFemale}} - b \cdot P_{\text{InTrap}} \cdot P_{\text{InFemale}}\right) \cdot \Delta m \end{aligned} \qquad (4)$$

Equation 4 can be integrated over the rate of change in male abundance (m) for those that have finished mating from 0 to M_d as $\Delta m \to 0$. The number of virgin females changes from F_d to $(F_d - MF_d)$ and those captured by traps from 0 to TM_d. Thus, Eq. 4 becomes

$$\begin{aligned} \int_{F_t}^{F_t - MF_t} \frac{-1}{P_{\text{Mate}}(v)} dv &= \int_0^{M_t} dm, \\ \int_{F_t}^{TM_t} dt &= \int_0^{M_t} P_{\text{Captured}}(v) dm. \end{aligned} \qquad (5)$$

The first equation in Eq.5 can integrated on each side based on the number of females and male trials, respectively. The second equation in Eq. 5 can also be integrated on each side over the number of captures and male trials, respectively, after substitution of v for a function of m derived the first equation in Eq. 5:

$$
\begin{aligned}
MF_d &= \frac{\ln\left\{h^{(1-P_{\text{InTrap}}+bP_{\text{InTrap}})M_d}\left(1-h^{F_d}\right)+H^{F_d}\right.}{\ln(h)}\\
TM_d &= cP_{\text{InTrap}}M_d - bcP_{\text{InTrap}}\\
&\quad\times\frac{F_d\ln(h)+\ln\left\{1-h^{(1-P_{\text{InTrap}}+bP_{\text{InTrap}})M_d}\left(1-h^{-F_d}\right)\right\}}{\left\{1-P_{\text{InTrap}}+bP_{\text{InTrap}}\right\}\ln(h)},\\
&\left(P_{\text{InTrap}} = 1-\left(1-\frac{trA}{S}\right)^{T} : \text{constant},\right.\\
&\left.h = (1-a) = 1-\frac{fA}{S} : \text{constant}\right). \qquad (6)
\end{aligned}
$$

I can then solve for the probability of mating success and the number of moth captures, which can then be used to deterministically calculate the mean result of the stochastic simulation. Though the mathematical expressions in Eq. 6 seem complicated, they are more tractable than Monte-Carlo simulations that are individually based. The procedure to derive Eq. 6 is similar to the Kuno's model (1978). Though the sequential mating behavior of males does not permit a female to attract multiple males at one time, it will not change the number of matings and captures in Eq. 6 because males' positions are implicitly assumed not to move all though the mating period in the model. It is important to note that the original use of the parameters b and c come from Nakasuji and Fujita (1980). Though their idea was scientifically sound, their formulation and assumptions were inadequate. For example, the number of males captured by a trap was not affected by the change in the number of virgin females though they calculated the number of successful matings according to Kuno's random mating model (1978). However, based on the assumption of Kuno (1978), it is quite likely that the probability of males being captured increases as the number of available virgin females decreases. For the death rate in Figure 2c, I used the formulation from (Knipling and McGuire Jr., 1966), since (Roelofs et al., 1970) predicted no biologically significant consequences between the sigmoidal and exponential decay functions when applied to death rate. The number of males at the next day -d+1 is the summation of males survived, $su \cdot (M_d - TM_d)$, and emergence at day-$d+1$. The number of females is the product of unmated females, $(F_d - MF_d)$, and su, and then added to the number that emerged at day $d+1$.

$$
\begin{aligned}
M_{d+1} &= su \cdot (M_d - TM_d) + EM_{d+1},\\
F_{d+1} &= su \cdot (F_d - MF_d) + EF_{d+1}. \qquad (7)
\end{aligned}
$$

Hereupon, the daily number of males, females, matings, and male captures can be calculated according to the relationship presented in Figure 2 and based upon Eqs (1), (6), and (7).

Simple numerical model for population processes

Some past theoretical work on mass-trapping and mating-disruption have modeled all stages of a generation (Barclay, 1984; Barclay and Judd, 1995; Barclay and van den Driessche, 1983; Fisher, 1985) and pointed out the importance of the population processes connecting each generation, such as intra- and inter- specific competition. However, those mechanisms may greatly differ among species and situations. Although studies on population dynamics have been a great issue in ecology, it is not at all tractable to make generalizations for various kinds of pest controls. Therefore, I tentatively incorporated the growth and intra-specific competition factors into the generic model using the logistic equation (function h in Eq. 8) proposed by Hassell et al. (1976). The parameters λ and K are the intrinsic growth rate and carrying capacity of the population, respectively, and f is a virtual function that yields the total number of matings in the whole generation. It can be computed from the numerical iteration of the procedures depicted in Figure 2.

$$
\begin{aligned}
N_{g+\Delta} &= f(N_g)\\
N_{g+1} &= h(N_g) = \frac{\lambda \cdot N_{g+\Delta}}{1+\frac{(\lambda-1)}{K}N_{g+\Delta}}. \qquad (8)
\end{aligned}
$$

N_g is the size of the population at generation g, $N_{g+\Delta}$ is that after the mating period, and N_{g+1} is that at generation $g+1$. Then, the equation $N_{g+1} = h(f(N_g))$ expresses the population dynamics generation by generation. The pest population stability based on the feature of stable points, nodes of the reproductive curve (expressed by the composed function $h \circ f$), and the line, $N_{g+1} = N_g$, will be discussed later (Figure 7).

Model insect and situation, parameter determinations

The model presented here was based on the dynamics of the fall webworm, *Hyphantria cunea* Drury (Lepidoptera: Arctiidae). *H. cunea* is a notorious non-indigenous pest in Europe and Asia that feeds on many species of shade, fruit, and ornamental host trees (Deseo et al., 1986; Masaki, 1975; Warren and Tadic, 1970). It is native to North America, and it was accidentally transported to Europe in the 1940s and has since spread over most of Europe and Asia. This model used 12 canonical parameters that were defined based on previous works (Table 1), and they were also dependent on a specific type of pheromone trap. Mass-trap settings and configuration of the target area ($T_{step} = 75$, $S = 80$ ha and $T = 80$) mimic those applied in Tokyo from 1994 to 1996 (Yamanaka et al. 2001). An area of 314 m^2 (10m in radius) was the canonical value of the permeating area of female-pheromone (fA) because the attraction area of H.cunea virgin females is < 10 m radius based on the analysis of diffusion equations (Hirooka and Suwanai, 1976) and by field observation (Hirooka, 1983). Pheromone permeating area of lures (trA) corresponds to the "effective sampling area" (**?**) from which all captured insect originate if the trap catches 100% of the insects within the area. Using the result of mark and recapture experiment conducted by Zhang and Schlyter (1996), trA was estimated as 68,978 m^2 (Radius :148.2 m). Survival rates per day (su) and the total number of H. cunea emergence (Pop) were determined by mark-recapture experiments (T. Yamanaka unpublished data) that were conducted concurrently with field trials of mass-trapping (Yamanaka et al., 2001). The parametric values based on mass-trapping trials for *H. cunea* were used as canonical. However, the survival rate per day (su), the delay in female emergence (lag), and the pheromone permeating area of females (fA) were changed by coupling each with

Table 1. Descriptions of model parameters and the canonical values used in the simulation model.

Parameter	Description	Canonical value	Unit	Citation
Simulation settings				
T_{step}	Simulation period in one generation	75	day	(Yamanaka et al., 2001)
S	Total simulation area	80	ha	
Pop	Total number of emergence	25000	individuals	mark–recapture experiment (T. Yamanaka, unpublished)
Characteristics of insect (H.cunea)				
μ	Peak date of male emergence	30	day	(Yamanaka et al., 2001); laboratory breeding data (T. Yamanaka, unpublished)
σ	Standard deviation of emergence	6	day	
lag	Delay of female emergence	2.5	day	
su	Survival rate per day	0.75	—	mark–recapture (T. Yamanaka, unpublished)
Characteristics for mass-trapping				
fA	Pheromone permeating area of females (radius: 10 m)	314	m^2	(Hirooka and Suwanai, 1976; Hirooka, 1983)
trA	Pheromone permeating area of lures (radius: 148.2 m)	68,978	m^2	(Zhang and Schlyter, 1996)
T	Number of traps	80	—	(Yamanaka et al., 2001)
b	Priority of female pheromone within an overlapped area	0.5	—	arbitrarily defined
c	Catching probability of the trap	0.5	—	arbitrarily defined

the total number of emerged adults (Pop) to elucidate the model ramifications in pests that have different life history traits. The number of traps (T) was altered from 5 to 80 to determine if mass-trapping efficiency could be increased relative to those results obtained by Yamanaka et al. (2001). Finally, stepwise simulations with b vs. c were executed from 0 to 1.0 in 0.025 increments for both parameters to explore differences between mass-trapping and mating-disruption and their respective efficiency. The effect of mass-trapping and mating-disruption as a management control tactic were evaluated according to:

$$\text{Control ratio} = 1 - \frac{\sum_d MF_d(\text{with treatments})}{\sum_d MF_d(\text{no trap})}. \quad (9)$$

This ratio expresses the degree towards which mating is suppressed through traps relative to an untreated control (i.e., no traps). It is the subtraction of the total number of matings (integration of Figure 3d: under the solid line, see Results for details) divided by those matings that occur in the absence of traps (Figure 3d; broken line, see Results for details).

Results

Basic simulation with canonical values

The simulation results of 80 traps (solid lines) and no traps (broken lines) are shown in Figure 3. The other parameters were canonical. More than 70% of the male population was removed through traps (Figure 3b) while females that were left unmated were largely accumulated (Figure 3c; solid line). The number of females in the absence of traps (Figure 3c; broken line) was less than the simulation results with traps because females constantly disappear from the simulated system under natural mating conditions (no trap).

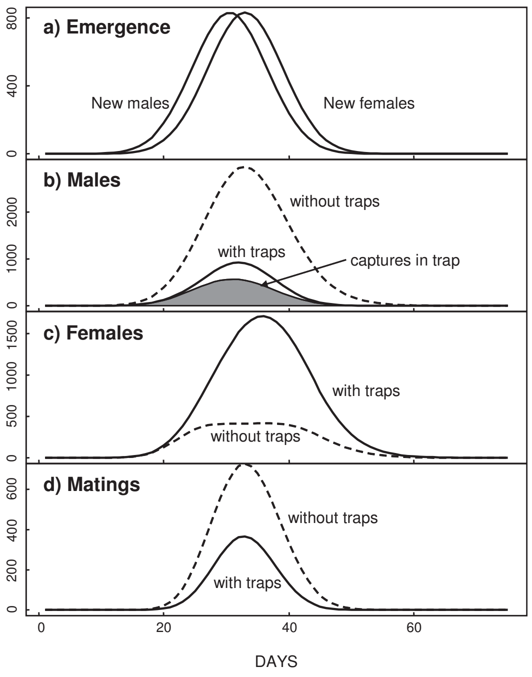

Figure 3. Simulation results with canonical values. Solid and broken lines in all figures indicate the simulation with 80 traps (T) and no traps, respectively. The shaded area in b represents the number of captures by traps in the simulation with 80 traps. a Number emerging (same in the no-trap simulation), b number of males on each day, c number of (virgin) females on each day, d number of matings on each day

Though 72.9% of males were captured in traps in the whole simulation period (in an 80 trap simulation), only ≈ 40% of the males were captured daily during peak emergence (25-40 days) (Figure 3b; shaded area). As a result, more than 45% of matings were observed (Figure 3d) overall, albeit the pheromone permeating area of 80 traps covers almost all of the simulation area ($P_{\mathrm{InTrap}} = 1 - (1 - \frac{trA}{S})^T \approx 1.0$). This was because parameter b permits some males to mate with females even if P_{InTrap} covers nearly entire area. In addition, males mated with females are protected from being captured in traps, and also can contribute to mating in subsequent days. The Control Ratio was calculated as 0.548 by Eq. 9 with the canonical parametric values (Figure 3d). It was a low result considering that a total of 72.9% of males were captured.

Effects of pest biology, survival rate (su), delay (lag) and number of traps (T)

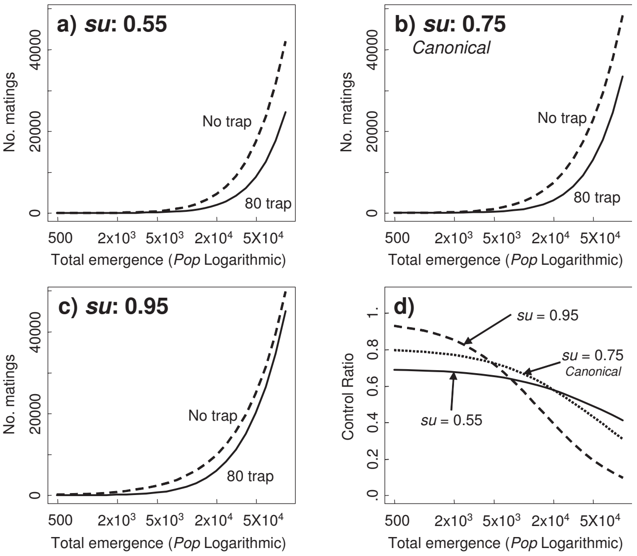

Figure 4. Simulations changing the survival rate per day (su) according to the change in the total number emerging (Pop). a, b, and c represent the number of matings in each scenario, su=0.55, 0.75, and 0.95, respectively, d shows the control ratio (determined by use of Eq. 9) for each survival rate.

The simulation results with three survival rates per day (su) are shown in Figure 4. When survival rate is low (su = 0.55), the difference in mating success between the 80 trap simulation (Figure 4a; solid line) and no trap simulation (Figure 4a broken line) diverges according to population size compared to the simulation with canonical values (su = 0.75; Figure 4b). Contrarily, the difference between traps and no traps diminishes in large populations with a high survival rate (su = 0.95; Figure 4c). When control ratios (Eq. 9) are compared concurrently, the pattern becomes clearer (Figure 4d). Long living pests (su = 0.95) are hard to control with mass-trapping during the outbreak period, but are more easily controlled during endemic levels. Insects with low survival rates (su = 0.55), however, are less susceptible to the population size than long living ones. The result can be explained by the reproductive value of a male. As males live longer, their reproductive value becomes more important since they can mate more often than short living ones. Therefore, killing males in a small population is critical to suppress mating and achieve adequate control. However, in a large population, even if a large proportion of males were captured by traps, the remaining males can disproportionately contribute to the total mating success in virtue of their longevity. On the other hand, killing males with low survival rates does not largely affect mating success even in small populations since males that have previously emerged have lower reproductive values than those males that have emerged more recently. Thus, in this case, the trapping rate of the day will only be a matter of efficiency.

The control ratio changed with a delay in female emergence (lag) (Figure 5). Surprisingly, there is little effect of lag on the control ratio, though some researchers illustrate positive effects of protandry (Barclay and van den Driessche, 1983; Fisher, 1985; Nakamura, 1982). As lag becomes larger, the total number of matings remarkably decreases, but there is little improvement in the control ratio (Figure 5a). The effect of removing males through traps does not contribute much to reduce mating success when su = 0.75. For example, more than 50 and 75% of males that emerged 2.5 or 5 days ago, respectively, were dead. Therefore, consistent with the previous analysis, the males that are currently emerging are more important in mating success in canonical simulations than older males, which exert little influence due to their higher cumulative death rates. The effect of the pheromone permeating area of females (fA) is shown in Figure 5b. Doubling of the attractive distance from the females makes the area four times larger than the original fA. It drastically diminishes the effect of control, especially when the population size is medium to large (Figure 5b; broken line). Halving of the distance makes quarter smaller than the original fA and it drastically strengthens the effect of control (Figure 5b; solid line). That is, lepidopteran pests with smaller ranges of sexual communication (i.e. smaller values of fA) would be more easily controlled through mass-trapping even during outbreaks, but population growth easily diminishes the control efficacy for those pests that can sexually communicate over larger ranges. The mating success of the pests directly depends on how much area females occupy in the target area, where the area of the pheromone lures (trA: canonical) covers almost all of the area. There was an upper limit of improvement when increasing the number of traps used in mass-trapping (Figure 5c). No additive or synergetic effects were included in the model for the multiple overlapping of the area with lures. Therefore, only the proportion of the area occupied by lures is critical. Even 20 traps could cover 83.5% of the total simulation area. Increasing beyond 80 traps did not result in any additional improvement of mating suppression in the level of control.

Effects of attracting and trapping mechanism

The stepwise simulation results of the two parameters b and c is shown in Figure 6. The parameter b is a measure of the degree of female attractiveness relative to lures. For example, if b = 0, all of the males follow lures while if b=1, they all locate females. The catching probability of the trap is represented by c. All of the males coming close to the trap will be captured when c=1, while no male will be captured when c = 0. Simulations when c = 0 with small parameter b can be regarded as the case of mating-disruption, because lures did not catch males at all but prevented males from mating in an areas saturated with pheromones. This can

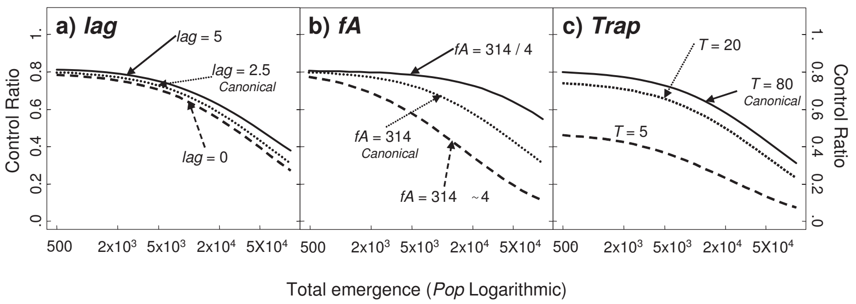

Figure 5. Effect of biological characteristics of the pest and the configuration of the treatment. a Duration of female delay for emergence: lag=0, 2.5 (canonical), and 5 according to the total number emerging (Pop). b Pheromone permeating area of (virgin) females: fA=314/4, 314 (canonical), and 314·4. c Number of traps: T=5, 10, and 80 (canonical). Effects are evaluated by control ratio as in Figure 4d.

be interpreted as trail-masking and/or false-trail following (Jones, 1998; Ridgway et al., 1990).

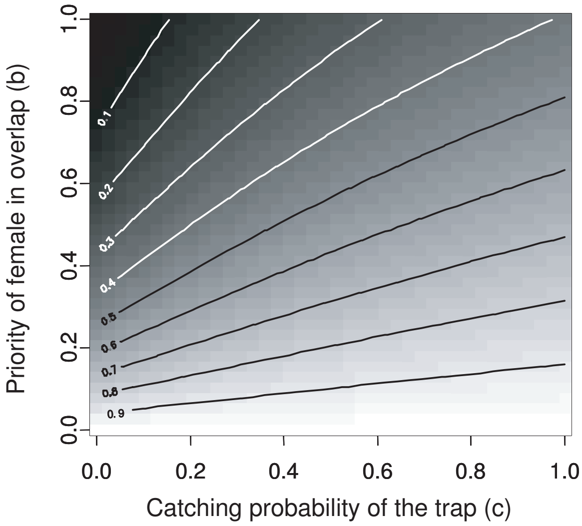

Figure 6. Effect of the priority of the female in overlapped area (b) and the catching probability of the trap (c). Simulations are executed with Pop=25,000 (canonical) and the other variables are also canonical. Control ratio is expressed by the gradient from complete white 1.0 (completely successful) to complete black 0.0 (no difference from no-trap simulation). When c=0, no male is captured by the traps, corresponding to matingdisruption trials revised.

Unsurprisingly, as the degree of female attractiveness (b) becomes smaller and the catching probability of the trap (c) becomes larger, mating success was more depressed. But the parameter b was the dominant one in achieving high control efficiency especially with small b values (lower (brighter) region in Figure 6). That is, if b is nearly 0 (all males in the overlapping area choose lures), then even if c = 0 (traps do not catch males at all), then substantial levels of control can be achieved. Contrarily, even if c = 1.0 (all males attracted to the lure will be captured) but b = 1.0, the ratio of control is only 0.4. This result suggests that pheromone traps need not catch males when the pheromone of the lure has a stronger attraction effect than pheromones emitted by females. Thus, catching males only acts as a subsidiary effect when b is not high. Though all the simulations used to construct the relationship presented in Figure 6 were executed with Pop = 25,000, there was no qualitative differences in these results when Pop was changed (results not shown). Thus, the results in Figure 6 could have a broad and general interpretation in the application of pheromones for insect pest control.

Effects of population processes

An example of the reproductive curve ($h \circ f$) for total population processes is shown in Figure 7 (K = 104 and λ = 25). When the intrinsic growth rate, λ, and the carrying capacity, K, are high as in most cases of pests that are targeted for control, there are three equilibria in the system. Two points, S_2 and the origin, are the steady stable points but S_1 is an unstable equilibrium point (Figure 7).

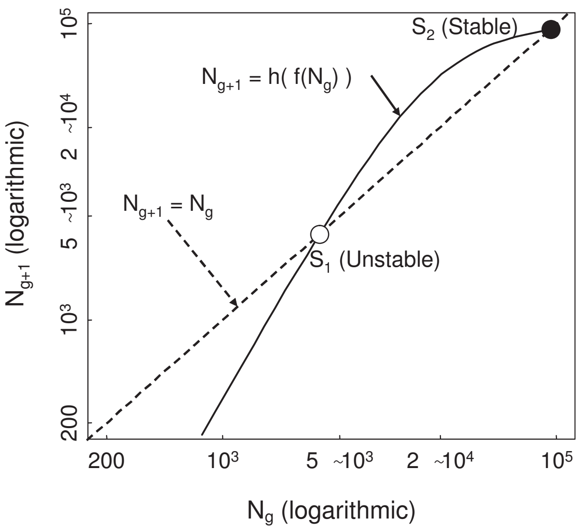

Figure 7. Example of the reproductive curve generated by composed function $h\ s\ f$. Large K (=104) and k (=25) make two stable points in the dynamics of the pest population. Other variables are canonical.

It should be noted here that the equilibrium at the origin is not shown in Figure 7 due to its logarithmic scales. S_2 is a carrying capacity mainly regulated by K in Eq. 8 and the unstable S_1 takes place as a result of the Allee effect generated by the density dependent mating success in Eq. 6. If the current population is larger than S_1, the population will converge at the steady stable point S_2 (Figure 7; the black dot). Contrarily, the population will go extinct under S_1 (Figure 7; the white dot). To consider the improvement of the pest control efficiency, three parameters can be changed, the number of traps (T), the priority of female pheromone (b), and the catching probability of the trap (c). The increase of T and c and the decrease of b move the unstable point S_1 to the larger state, in other word, the reproductive curve bows downward. The larger S_1 will be, the larger population can be acceptable for the starting population level to apply the pest eradication program with sex-pheromones. Only the parameter of priority of female pheromone (b) however, acts drastically against the population dynamics. When b becomes smaller than around 0.12, S_1 and S_2 disappear and the origin becomes the singular stable point. It means that any size of the population can be theoretically eliminated soon or later.

Discussion

The model presented here is unique among the other theoretical works of sex-pheromone control such as Nakasuji and Fujita (1980); Barclay and van den Driessche (1983); Barclay (1984); Fisher (1985), because it has the mechanistic structure of pheromone competition among and between virgin females and lures. For example, Nakasuji and Fujita (1980) decreased the area of female pheromones assuming that sexual communication would decrease in mating-disruption. Barclay and Judd (1995) kept a certain fraction of the females unmated to express the condition of the mating-disruption (habituation) trial a priori. Though the phenomenological assumptions for mating disruption made by the other authors are easy to incorporate and may draw some suggestive results for each method, it is biologically irrelevant when we compare the two different types of the pheromone control, mass- trapping and mating disruption. Several suggestions for the application of pheromone-based control tactics are derived from the model. 1) Long living pests are hard to control 2) Protandry does not greatly improve the control efficiency for pests with low survival rates. 3) Pests that are able to sexually communicate over a large distance relative to lures are more difficult to control than those that exhibit only short range communication abilities. 4) There is an upper limit of trap density (or lure density) beyond which no further improvement in control will be achieved. I conclude that these qualitative features of these results are applicable to both mass-trapping and mating-disruption because they are observed not only in canonical simulations but also in wide range of the parameters b and c. The most interesting result derived from the model was that an increase in trap efficiency (i.e., large c) did not improve mating suppression but the improvement of lure efficiency (i.e., small b) greatly does. When parameter b is small and $c = 0$, no male is captured by the trap yet the majority of the males do not respond to the females. This unresponsiveness by the males can be interpreted as "false-trail following" (males are arrested by the lures) and / or "trail-masking" (males are inhibited to orientate to the females). It is obvious from the result that there is no great difference in the effect between mass-trapping and mating-disruption when the pheromone of the lure can effectively prohibit males from mating with females. Though the model can represent "false-trail following" and / or "trail-masking", another important mechanism of mating-disruption, "confusion", could not be incorporated into the model. It is impossible to argue the rigorous contribution of "confusion" without the use of a highly complicated simulation, like individual based models, in which the high and frequent exposure of those lures dull the males sensitivity in locating females. Anyhow, confusion can be expected to act in a positive way, though we cannot easily quantify its effect. Though I believe the model is useful for qualitative predictions, it is still difficult to apply it for quantitative calculations in practice. There are three issues to consider. First, though the representation of circle area was essential in rigorous formulation, the pheromone area might not develop circularly in the field. In fact, pheromone plumes are thought to flow like smoke meandering intermittently or turbulently (Murlis et al., 1992; Wyatt, 1994). If the pheromone plumes had developed in spherical or Gaussian diffusion modes in the three dimensional space, the model could have predicted well qualitatively. However, snake like structure of the pheromone plumes may develop further down wind without overlapping each other. Previous works emphasize that the number of pheromone sources as well as the high dosage of the lures is important to mating suppression (Cardé et al., 1998; Kehat et al., 1999; Rothschild, 1975). The requirement for high source densities implies that the small number of traps cannot fill out the three-dimensional space. Therefore, they cannot achieve sufficient control effects even with a high dose of the pheromone effusion. In addition, the pheromone area of the lures used in the model (68,978 m^2 with a radius 148.2 m) may be an overestimate, since it cannot be possible that all males within 148.2m will be attracted to (or affected by) the lures. Therefore, even 80 traps would not cover the whole area in mass-trapping of *H. cunea* in Tokyo (Yamanaka et al., 2001). I recommend here that as many lures as possible should be used until the maximum upper limit can be revealed through field experiments. Second, the model neglected the effects of visual cues or other stimuli to aide males in finding females over short ranges. Visual cues are reported to play an important role for many lepidopteran pests (Baker and Kuenen, 1982; Cardé and Minks, 1995; Gross et al., 1983; Shorey and Gaston, 1970). When the pest population size is large, such as in outbreaks, the distances between males and females are probably quite small. Though males are affected by the pheromone emitted by the lure, they may still be able to locate and mate with females in such a situation by relying on visual cues. Consequently, high inhibition of mating by lures cannot be expected when the population size is extremely large as precedent field works have reported (Schwalbe et al., 1983; Webb et al., 1988). If pest control using sex-pheromones must be conducted in an outbreak period, then the mating behavior of males must be carefully considered before the trials. Third, the pest population may compensate for their abundance with strong reproductive power and with high carrying capacity in crop fields. Our tentative model predicted that there was an unstable point under which population can be eradicated. The result was consistent with previous theoretical studies (Barclay and van den Driessche, 1983; Fisher, 1985). In addition to these results, the importance of lure efficiency (i.e., parameter b) is, however, stressed even in the dynamics part of our model. It is important to note that I did not further elucidate the effect of model parameters on the total population dynamics because of ambiguity of the population processes in various species and under different situations. In spite of some caveats described above, the result of the simulations clearly shows the preference for mating-disruption. The effect of mating-disruption, such as false-trail following and / or trail-masking, appears more important than the effects of mass-trapping, even in the absence of a "confusion" effect. If excellent synthetic sex-pheromone lures that can effectively prevent males from locating females within a target area are available, then one should consider mating-disruption over mass-trapping. We should also choose mating-disruption particularly when the trap costs are high. On the other hand, mass-trapping still has important or at least a synergistic role in pest management when we can only use inferior lures that have little effect on limiting mating between males and females in close proximity, but still can attract them.

Data Accessibility

The R code underlying the simulation model is included in Appendix S1.

Competing Interests

The author declares no conflict of interest.

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Supporting Information:

Mating disruption or mass trapping? Numerical simulation analysis of a control strategy for lepidopteran pests

Takehiko Yamanaka

Appendix S1. Simulation code

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The final published version is available at: https://doi.org/10.1007/s10144-006-0018-0.

Appendix S1: Simulation code

```
# Parameter definition
tstep <- 75      # Simulation period in one generation
s <- 800000      # Total simulation area
pop <- 25000     # Total number of H. cunea emergence (males+females)
myu <- 30        # Peak date of male emergence
sigma <- 6       # Standard deviation of male emergence
lag <- 2.5       # Delay of female emergence
su <- 0.75       # Survival rate per day

female_radius <- 10
fa <- pi * female_radius^2
fas <- fa / s

trap_radius <- 148.2
tra <- pi * trap_radius^2
tas <- tra / s

trap <- 80       # Number of traps
b <- 0.5         # Priority of female pheromone
cr <- 0.5        # Capture rate

crit <- 700 / abs(log(h))  # Approx double precision storage

##### KUNO (1978)-based mating #####
kunoMate <- function(f, m, trap, fas, tas, b) {
  h <- 1 - fas
  st <- 1 - (1 - tas)^trap
  vr <- 1 - st + b * st
  if (f > crit || vr*m > crit) {
    return(min(f, vr * m))
  } else {
    numerator=log(h^(vr*m)-h^(vr*m+f)+h^f)
    denominator=log(h)
    return (numerator/denominator)
  }
  numerator / denominator
}

##### Male capture #####
kunoTrap <- function(f, m, trap, fas, tas, b, cr) {
  h <- 1 - fas
  st <- 1 - (1 - tas)^trap
  vr <- 1 - st + b * st
  temp1 <- cr * st * m
  temp2 <- f * log(h) + log(1 - h^(vr*m) * (1 - h^(-f)))
  temp3 <- vr * log(h)
  temp1 - b * cr * st * temp2 / temp3
}

##### Emergence #####
emergence <- function(pop, day, myu, sigma) {
  pop/2 * (pnorm(day, myu, sigma) - pnorm(day - 1, myu, sigma))
}

# Registry
emerMa <- numeric(tstep)
emerFe <- numeric(tstep)
male <- numeric(tstep)
female <- numeric(tstep)
mf <- numeric(tstep)
tm <- numeric(tstep)

##### Simulation #####
for (i in 2:tstep) {
  emerMa[i] <- emergence(pop, i, myu, sigma)
  emerFe[i] <- emergence(pop, i, myu + lag, sigma)

  male[i]   <- male[i-1] * su + emerMa[i]
  female[i] <- female[i-1] * su + emerFe[i]

  # mating
  mf[i] <- kunoMate(female[i], male[i], trap, fas, tas, b)

  # trapping
  tm[i] <- kunoTrap(female[i], male[i], trap, fas, tas, b, cr)
```

```

  # update populations
  male[i]   <- max(0, male[i] - tm[i])
  female[i] <- max(0, female[i] - mf[i])
}

##### Plot #####
par(mfrow=c(3,1))

# Emergence
plot(emerMa, type="l", main="Emergence", xlab="Days", ylab="")
lines(emerFe, lty=2)

# Population
plot(female, type="l", lty=2, main="Adults", xlab="Days")
lines(male)
```

Listing 1. R code for pheromone-based mating and trapping model