

Models for Mating Disruption by Means of Pheromone for Insect Pest Control

Hugh J. BARCLAY and Gary J. R. JUDD*

Pacific Forestry Centre, 506 West Burnside Rd., Victoria B.C., Canada V8Z 1M5 and Department of Biology, University of Victoria, Victoria, B.C., Canada V8W 2Y2

**Agriculture Canada, Research Station, Summerland, B.C. Canada V0H 1Z0*

Abstract. Models are presented to investigate the population dynamic behavior of a pest population with the release of pheromone for mating disruption. Three mechanisms of mating disruption are considered: (i) confusion of males, (ii) competition with female pheromone trails yielding false trail following, (iii) emigration of males prior to mating. In addition, several refinements to confusion are considered. Confusion and emigration of males were found to be very similar both quantitatively and dynamically; also, a combination of both mechanisms was very little more efficient than either one separately. False trail following is difficult to compare with the other two, since competition with wild females is involved and thus the total population size enters the equations. Density dependence of the action of pheromones results in some cases in which mating disruption cannot control the pest population. Similarly, aggregation of the pest population decreases the efficiency of the method unless the pheromone action is density independent. Delayed mating of females makes control easier, and may constitute one mechanism for mating disruption.

Key Words: pheromone, mating disruption, model, pest control.

Introduction

The use of sex pheromone for mating disruption has proven a potentially effective means for controlling certain species. Among those potentially amenable to such control are Ponderosa pine tip moth (Niwa et al. 1988), tobacco budworm (Hendricks et al. 1982), Egyptian cotton leafworm (Ellis et al. 1980), pink bollworm (Critchley et al. 1983), western pine shoot borer (Sartwell et al. 1983), gypsy moth (Schwalbe et al. 1983), tomato pinworm (Van Steenwyk and Oatman 1983), spruce budworm (Palaniswamy et al. 1982) and Douglas-fir tussock moth (Sower et al. 1990).

The lack of an understanding of the mechanisms behind mating disruption has mitigated against any sophisticated approach to this pest control method, although considerable success has already been achieved in spite of this. Bartell (1982) reviewed five possible mechanisms for mating disruption using semiochemicals and later Carde and Minks (1995) reviewed nine possible mechanisms. These nine mechanisms are as follows: (i) diminution in responsiveness of males to pheromone via either sensory

adaptation or habituation; (ii) arrestment of upwind flight at high pheromone concentrations; (iii) shifting the timing of male response by the continuous presence of pheromone; (iv) disarrangement of the fine-scale structure of the natural pheromone plume causing disorientation; (v) camouflage of the plumes from calling females; (vi) competition between calling females and point sources of pheromone in traps; (vii) imbalance of sensory inputs by using ratios of pheromone components that diminish attractiveness to males; (viii) combinations of pheromone and insecticides that either kill male responders or render them non-responsive to pheromone; (ix) the use of pheromone analogues that would render the males non-responsive. Some of these potential mechanisms may not be distinguishable in a population model and may have similar population dynamic consequences. For example, diminution in male responsiveness (Carde and Minks 1995) may appear the same at the population level regardless of whether it is caused by sensory adaptation or by habituation within the central nervous system. Thus a population model addressing mating disruption should examine those mechanisms capable of being discerned at

the population level.

Nakasuji and Fujita (1980) constructed an intra-generational model to investigate the population dynamics of mating disruption. They modelled mating disruption by reducing the search area of males in the presence of excess pheromone from traps, thus reducing the chance of finding females. We use a somewhat different approach and in addition we use an inter-generational density-independent population model. We also investigate some possible mechanisms for generating disruption of mating and assess the efficiency and population dynamic characteristics of each mechanism.

The models

Assumptions and equations

The model developed here is a modification of a model developed earlier (Barclay and van den Driessche 1983). This model represents an insect species with three adult states: virgin females (V), fertilized females (F), and males (M). The assumed order of daily events is: overnight mortality, morning emergence of adults, oviposition by mated females, and then mating. Females are assumed to mate only once, or if they mate more than once they only produce pheromone as virgins; virgins mate on the day after eclosion and then join the mated females group. The sex ratio is one-to-one throughout the life cycle. The equations for the model with no pheromone release are:

$$\begin{aligned} F_{i+1} &= s F_i + s V_i, \\ V_{i+1} &= a F_{i-k}, \\ M_{i+1} &= a F_{i-k} + s M_i. \end{aligned} \quad (1)$$

The subscripts in equations (1) denote time in days; a is the recruitment rate per fertilized adult female; s is the daily adult survivorship and is assumed constant; k is the developmental period until eclosion. Eliminating the subscripts and solving for equilibrium, we see that for positive growth in the model above, it is required that:

$$as > (1-s), \quad (2)$$

i.e., that recruitment exceeds mortality. Males are assumed to attempt mating once each day.

Three possible ways in which pheromone may result in disruption of mating and which may have differing population consequences are: (A) males may become confused (i.e. habituated) by the concentration of pheromone to the extent that they simply cannot find the females and thus mating occurs at a reduced level (Carde and Minks 1995); (B) males may follow the scent from the traps and thus be diverted from mating for a while (i.e. false trail following); (C) males may be repelled by the high level of pheromone

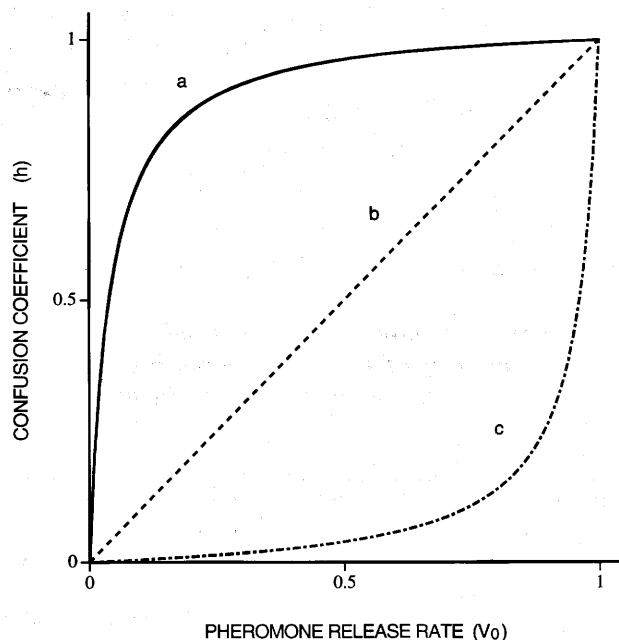


Fig. 1. Hypothetical curves used as possible functions relating the confusion coefficient (h) and the normalized pheromone release level (V_0). (a) convex, (b) linear, and (c) concave.

and emigrate from the control area and thus be unavailable for mating by their physical absence (Shepherd pers. comm.).

Cases (A) and (C) below assume that the relationship between disruption (quantified by the parameter h) and pheromone release level (V_0) is known. This relationship must be determined empirically, since it is likely to be unique for every species. Three possibilities are shown in Fig. 1 and these are probably sufficiently extreme to cover the range of many actual relationships. The horizontal axes are scaled from $V_0=0$ (where there is no confusion; i.e. $h=0$) to 1, where $V_0=1$ is the level of pheromone resulting in complete confusion (i.e. $h=1$). Each of the three curves in Fig. 1 are used together with those in Fig. 2 to generate critical values (h^*) (Fig. 3) in terms of pheromone release rate (V_0^*) (i.e. the minimum value of V_0 that results in eradication). To obtain quantitatively useful results, the form of the relationship between h and V_0 would have to be determined empirically.

(A) Mating confusion.

(i) Mating confusion independent of host density

In the case where disruption is caused by simple confusion (i.e. habituation), we can define a confusion coefficient, h , as the proportional reduction in fertilization of virgin females resulting from pheromone release. It is

assumed that those females that have already mated will store sufficient sperm to continue laying fertile eggs even with the reduced level of mating. If this action is independent of host density, the adult equations become:

$$\begin{aligned} F_{i+1} &= s(1-h)V_i + sF_i, \\ V_{i+1} &= aF_{i-k} + s h V_i, \\ M_{i+1} &= aF_{i-k} + sM_i. \end{aligned} \quad (3)$$

In these equations a value of h of 0.0 represents no disruption while 1.0 represents complete disruption (i.e. no mating). The value of h is expected to be affected by two separate features of the system: (a) the quantitative effect of the pheromone on the mating propensity of the males, and (b) the extent to which the males outnumber the virgin females. There is a value of h which will just reduce the population growth to zero, called the critical value (h^*), and this is associated with a value of V_0 termed V_0^* (the critical pheromone release rate). This value of h is:

$$h^* = \frac{as - 1 + s}{s[a - (1-s)]}, \quad (4)$$

and it depends only on survivorship and fertility. Values of h^* have been graphed for values of a and s that span the range from only just large enough to allow the species to persist in the absence of control (see inequality 2) to relatively large values (Fig. 2). The critical confusion

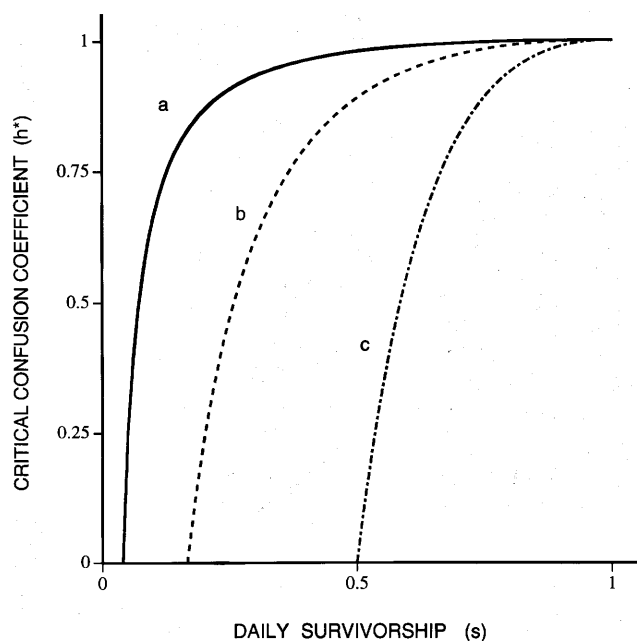


Fig. 2. The critical value of h (h^*), the confusion coefficient, in eq. (4) shown as a function of host survivorship for values of host survivorship between 0 and 1. The values of the daily oviposition rate, a , are: (a) 25, (b) 5 and (c) 1.

coefficient, h^* , increases with both a and s .

Using the middle curve in Fig. 2 and the three curves in Fig. 1, values of V_0 corresponding to these values of h^* are shown in Fig. 3. V_0^* increases very quickly with both s and a (jumping from curve to curve), indicating that pest species with high recruitment and survivorship are very difficult to control by this method.

(ii) Density-dependent mating confusion

The previous section assumed that the confusing effect of pheromone was independent of pest density (unless it involves false trail following, in which case the point sources of pheromone compete with the virgin female population). It may be that the effect of this confusion declines as pest density increases due to the greater probability of chance encounters at higher densities. To explore this possibility we let the degree of confusion be a negative function of density. Thus, at high density one can assume that the insects may find each other in spite of the existence of a confusing blanket of pheromone since they will come into close contact simply by means of random flight patterns; in contrast, at low density chance encounters would be rare and pheromone-mediated mate location would be essential, making a confusing blanket of pheromone effective in blocking mating. This could be modelled by making h in eqs. (3) density-dependent. A convenient formulation would be:

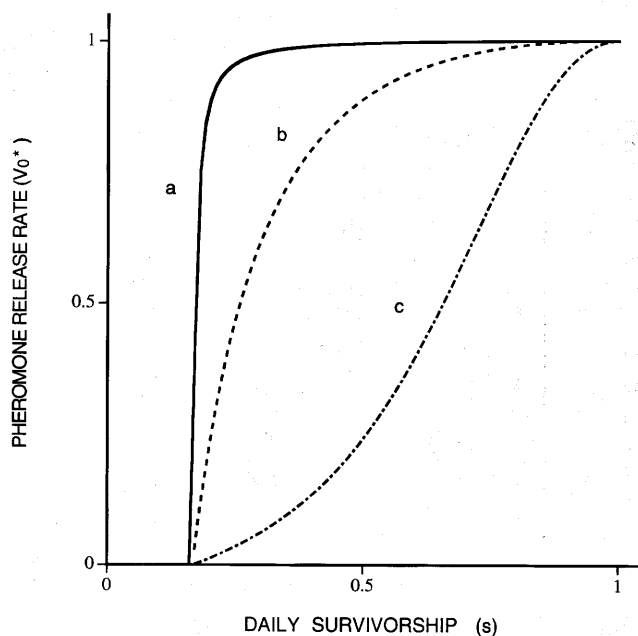


Fig. 3. Graphs of pheromone release rate versus host survivorship for the middle curve in Fig. 2 above ($a=5$), formed by combining the information from Figs. 1 and 2. The three curves derive from the three curves in Fig. 1 relating V_0 and h : (a) convex, (b) linear, and (c) concave.

$$h = h_0 \exp(-cT_i), \quad (5)$$

where h_0 is the value of h in the absence of density-dependent effects (see eqs. 3), c is a scaling constant and T_i is the size of the total population at time i (and in this case, twice the male or female population). At very high population densities, h approaches 0 (no confusion), while at very low densities h approaches h_0 . Substituting eq. (4) into eq. (5) we get:

$$h_0^* = (as - 1 + s) / [s(a - 1 + s) \exp(-cT)]. \quad (6)$$

Figure 4 shows values of h_0 required to achieve the critical value of h (h^*) for various population densities. Since c and T are simply multiplied together in eq. (5), varying T is equivalent to varying c . This formulation assumes a uniform spatial distribution of individuals. It is evident for the parameters chosen that the density-dependent effect is nearly linear and thus an upper limit of T exists that will effectively prevent the method from working at all. Indeed, for high values of fertility and survivorship, this control method becomes ineffective at moderately low pest densities using the parameters in Fig. 4 curve (c).

(iii) Delayed mating of females

Another possible outcome of mating confusion is simply to delay the mating of females due to a reduced search efficiency of the males. This could have the effect of

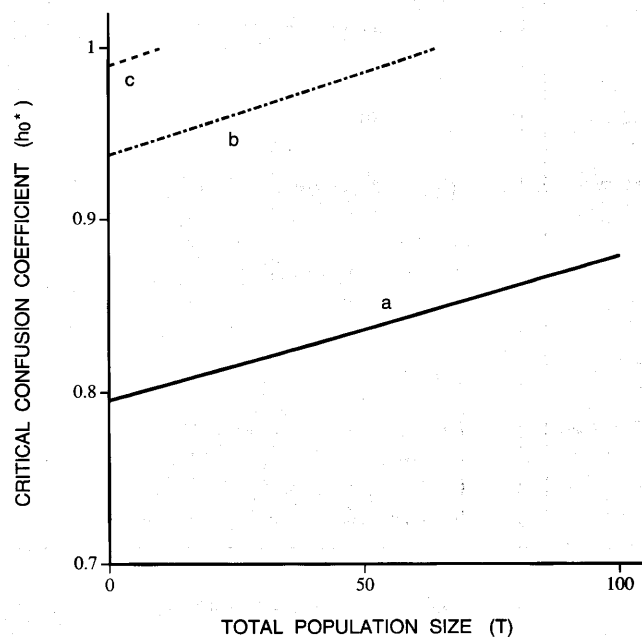


Fig. 4. Variation of the confusion coefficient, h , with pest population density when the effectiveness of mating confusion is density-dependent. The three cases are: (a) $a=5$, $s=0.4$; (b) $a=25$, $s=0.4$; (c) $a=25$, $s=0.8$. The value of c was 0.001.

slowing population growth due to both (i) delaying the time until the first egg laying, and (ii) allowing some added natural mortality of females to occur due to the delay.

If confusion of the males results in a delay in mating of the females by an average of n days, then eqs. (3) become:

$$\begin{aligned} F_{i+1} &= s V_i + s F_i, \\ V_{i+1} &= s^n a F_{i-k-n}, \\ M_{i+1} &= s^n a F_{i-k-n} + s M_i. \end{aligned} \quad (7)$$

This results in the critical value of n becoming:

$$n^* = \frac{\ln((1-s)/as)}{\ln(s)}. \quad (8)$$

If in addition the fertility is age-dependent, then n^* is further modified. Three possible fertility curves are shown in Fig. 5. These represent (a) sharply decreasing fertility with age, (b) age-independent fertility, and (c) a naturally delayed peak in fertility. The three curves were constructed using the equations:

$$\text{fertility} = a_1 p^{x-1}, \quad (9)$$

$$\text{fertility} = a_2, \quad (10)$$

$$\text{fertility} = a_3 x \exp(-a_4 x). \quad (11)$$

where a_1, a_2, a_3, a_4, p are constants, $0 < p < 1$, and x is age.

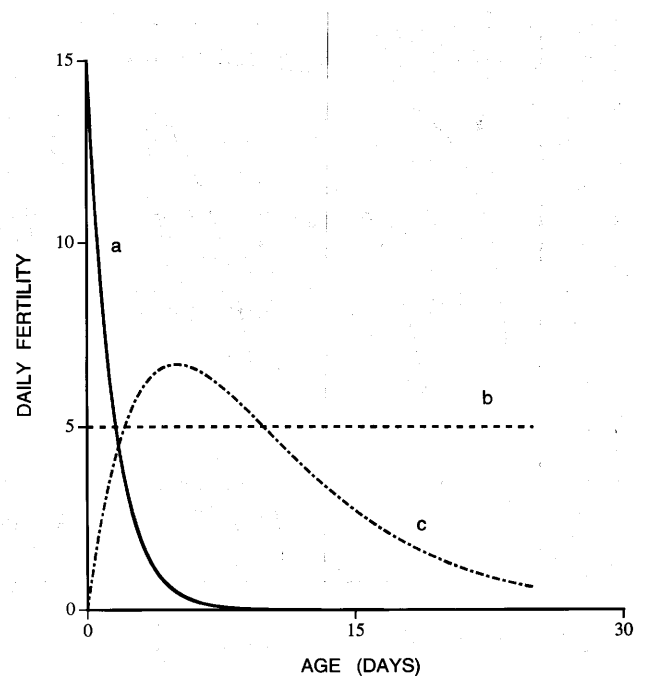


Fig. 5. Three possible fertility curves. (a) geometric decrease in fertility with age; (b) constant age-independent fertility; (c) delayed peak in fertility. In all cases the net reproductive rate, R_0 , was 25 assuming that oviposition began at adult eclosion.

The values of the parameters are: $a_1=15.0$, $a_2=5.0$, $a_3=3.64$, $a_4=0.2$, $p=0.5$. These values of the constants have been chosen to make the net reproductive rate, $R_0 = \sum l_x m_x$ (Lotka 1956), equal to a constant (in this case 25) in all three cases. The net reproductive rate, R_0 , was recalculated for each of several adult ages, assuming that oviposition did not begin until that age and that the rate of oviposition conformed to one of the three fertility curves above in left-truncated form. For example, using eq. (9) and assuming that mating was delayed until the fourth day, the fertility on the first day of oviposition would be $a_1 p^3$. Then, constructing adult age structure with constant survivorship, $s=0.8$, and applying eqs. (9)–(11) to that age structure, we obtain curves for R_0 shown in Fig. 6. There is a strong interaction between R_0 and the type of fertility curve. The first type of fertility (eq. 9) is reduced most by delayed mating; the second and third types (eqs. 10 and 11) are both reduced by about the same amount (Fig. 6).

(iv) *Effects of aggregated dispersion*

If the population has any significant degree of aggregation whereas the pheromone dispensers are relatively uniformly distributed, then areas with high pest density may be more difficult to control with pheromone if the effectiveness of confusion is a negative function of pest density, as in case (ii) above. If the attractiveness of the habitat varies according to the Gamma distribution and the number of pests in any small area varies according to the Poisson distribution with the mean being Gamma distributed over the entire area, then the numbers occurring in randomly placed quadrats in the control area will vary according to the Negative Binomial Distribution (NBD) (Boswell and Patil 1970), a commonly observed distribution in nature. When used as a distribution describing spatial dispersion (Pielou 1969), the NBD has the formula:

$$P(r) = (\Gamma(k+r)/r!\Gamma(k)) (\mu/k)^r (k/(k+\mu))^{k+r}, \quad (12)$$

where $P(r)$ is the probability of finding r individuals in a quadrat, $\Gamma(k)$ is the gamma function, k is an index describing the degree of aggregation and μ is the mean of the distribution. For purposes of computation (Barclay 1992a), eq. (12) can be rewritten as:

$$P(r) = ((k+r-1)(k+r-2)\dots(k)/r!) \times [(\mu/k)^r (k/(k+\mu))^{k+r}]. \quad (13)$$

A reduction in k , signifying a greater degree of aggregation, results in an increase in the relative frequency of the larger numbers. If the efficiency of mating disruption decreases with pest density, then an increase in aggregation would reduce the efficiency of pheromone in limiting population growth. In extreme cases of aggregation, pheromone might become virtually useless in causing mating disruption. In that case, the pest density would

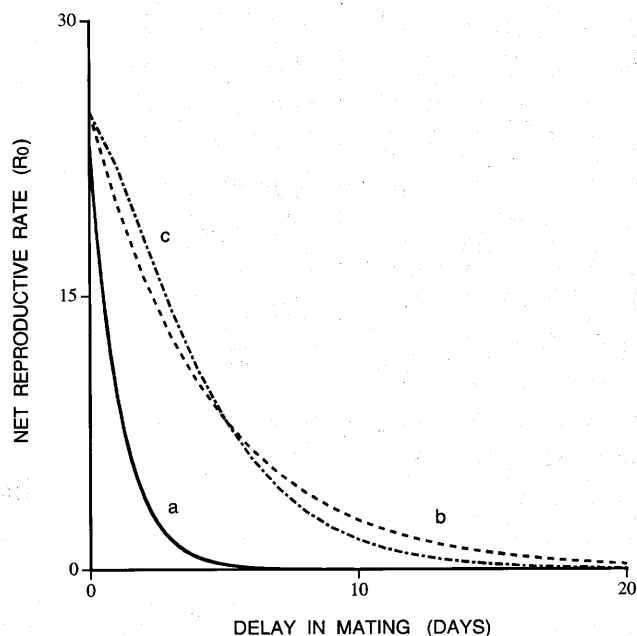


Fig. 6. Changes in net reproductive rate, R_0 , resulting from a delay in mating, for each of the three fertility curves in Fig. 5. Adult survivorship is geometric at 80% per day. The curves show the effects of delaying mating by n days, where n takes on all integral values between 0 and 20 inclusive. (a) geometric decrease in fertility with age; (b) constant fertility; (c) a humped fertility curve.

have to be reduced first by some other means before applying pheromone for mating disruption. One can calculate the proportion of the population that escapes suppression with various degrees of aggregation by applying eq. (6) to the NBD. In a population which has non-uniform spatial structure, some areas will have low density and will be easy to control, while others will have higher density and will be more difficult or impossible to control. Tabulating these areas over the entire population will allow calculation of the proportion of the population which will decrease with the application of pheromone as well as the proportion that will increase for a given level of pheromone release. Even a random dispersion will have a certain proportion of the population too dense for any given value of h to control, and this proportion increases as the degree of aggregation increases (Fig. 7). The proportion remaining after control increases with (i) the degree of aggregation, (ii) the recruitment rate, a , (iii) the survivorship rate, s , (iv) the strength of density-dependence (i.e. the scaling constant, c , of eq. 5), and (v) the proportion that h_0 is of h^* . Figure 7 only shows the first three effects above; the others were tested but are not shown. The effects above depend on a decreasing efficiency of mating disruption with increasing pest density; on the other hand, if mating disruption is

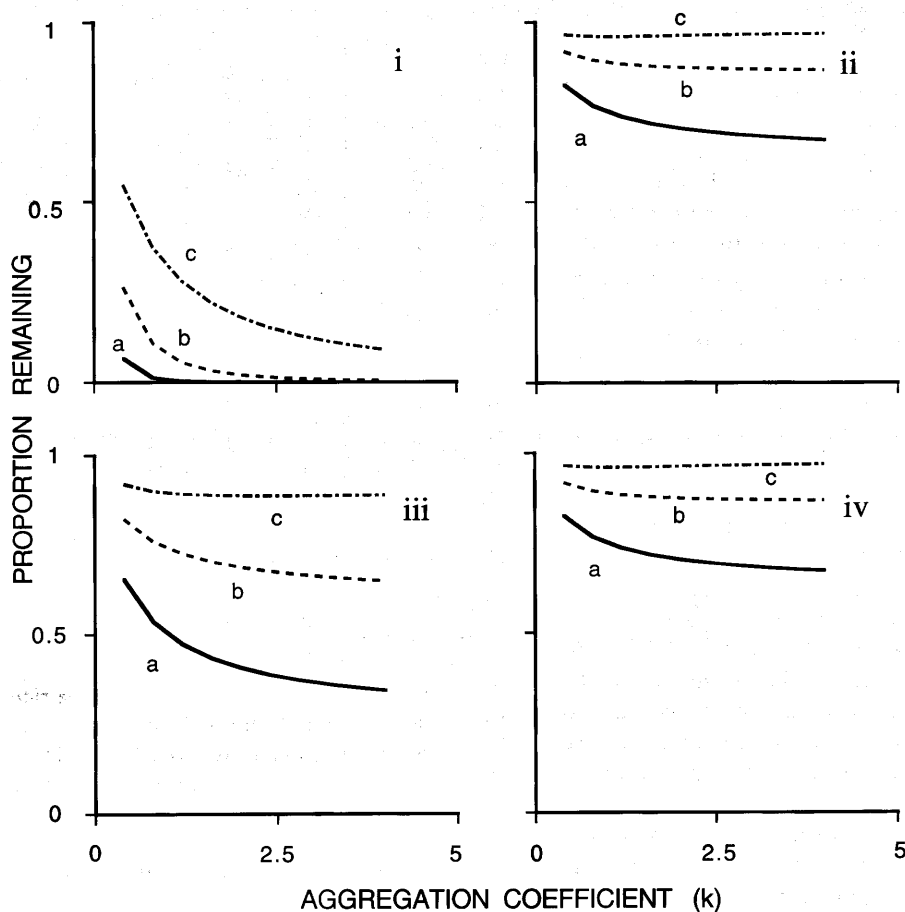


Fig. 7. Effects of pest aggregation on the efficiency of mating disruption for pest control when the efficiency of mating disruption decreases with increasing pest density. The curves represent the proportion of the population that exists in clumps too dense for mating disruption to be effective. The four frames represent: (i) $a=5$, $s=0.5$; (ii) $a=5$, $s=0.9$; (iii) $a=25$, $s=0.5$; (iv) $a=25$, $s=0.9$. The three curves in each graph represent values of the mean pest density, μ , of: 1 (a), 2 (b), and 3 (c) pests per unit area. The aggregation coefficient (k) varies between 0.4 and 4.0. For these curves $h_0=0.2h^*$ and $c=0.01$.

independent of pest density, then aggregation should not affect control by this method. Another possible factor is that the degree of aggregation may decrease with increasing density, as the clumps become intermingled, in which case the difficulty of control will tend to increase with increasing density but decrease with decreasing aggregation. The result will depend on the relative rates of change of density and aggregation, but the rate of change of control difficulty will change less than if only one feature was changing.

(B) False trail following

In this case the pheromone in traps acts to attract the males temporarily away from the virgin females; thus pheromone in traps competes with that from wild females for the attention of the males. It is assumed here that males are removed from the mating population for one

day but are available for mating the following day. This case has been modelled previously in the context of trapping for male annihilation in a density-independent population (Barclay and van den Driessche 1983) and is presented here for completeness. The equations for the male deficit case are:

$$\begin{aligned} F_{i+1} &= s M_i V_i / (V_0 + V_i) + s F_i, \\ V_{i+1} &= a F_{i-k} + s V_i - s M_i V_i / (V_0 + V_i), \\ M_{i+1} &= a F_{i-k} + s M_i. \end{aligned} \quad (14)$$

These equations yield a single unstable equilibrium in which the required pheromone trapping rate, V_0^* , is a linear function of the population density. It is given by:

$$V_0^* = (a-1+s)(as - (1-s)^2)T / 2a(1-s)^2, \quad (15)$$

where T is the total population size ($T=F+V+M$). Here V_0^* depends only on pest fertility, survivorship and popula-

tion size. Control here is possible but not as easy as if the males were killed at traps rather than being free to return after being lured away temporarily; the value of V_0^* here is considerably greater than that with male annihilation (Barclay and van den Driessche 1983). Although this model is density-independent, the total population size, T , appears in eqn (15) since there is competition between the pheromone traps and the wild females.

(C) Emigration of males

In this case excess pheromone causes males to emigrate from the area, thus being unavailable for mating with the virgin females. It is assumed that emigration occurs before mating. It can be shown that emigration after mating is of no value in population control.

Let u be the proportion of males that emigrate each day. Here there are two sets of equations, depending on whether or not males outnumber virgin females. These are as follows:

(i) Male excess $((1-u)M > V)$:

$$\begin{aligned} F_{i+1} &= s V_i + s F_i, \\ V_{i+1} &= a F_{i-k} + s V_i, \\ M_{i+1} &= a F_{i-k} + s (1-u) M_i. \end{aligned} \tag{16}$$

In this case there are still sufficient males to fertilize all the virgin females, so that there is no value of u which will result in eradication of the population. The value of u which allows the males to fall below the number of virgin females in a growing population is not easy to determine as it depends on a , s and k . However, if $a \gg 1$, the required value of u will be close to $1/(a+1)$. Thus, for appreciable rates of emigration, the equations given below will usually apply.

(ii) Male deficit $((1-u)M < V)$:

$$\begin{aligned} F_{i+1} &= s (1-u) M_i + s F_i, \\ V_{i+1} &= a F_{i-k} + s V_i - s (1-u) M_i, \\ M_{i+1} &= a F_{i-k} + s (1-u) M_i. \end{aligned} \tag{18}$$

In this case, the total number of males available for mating is less than the number of virgin females, so some females remain unmated. The critical value of u is:

$$u^* = \frac{as - (1-s)^2}{s[a + 1 - s]} \tag{19}$$

This value of u^* is generally slightly less than h^* in eq. (4), especially if s is small. Also, as s approaches 1, then u^* approaches h^* . For example, if $a=10$ and $s=0.9$, $h^*=0.9989$ and $u^*=0.9890$. Thus, emigration is slightly more efficient than mating confusion in controlling the

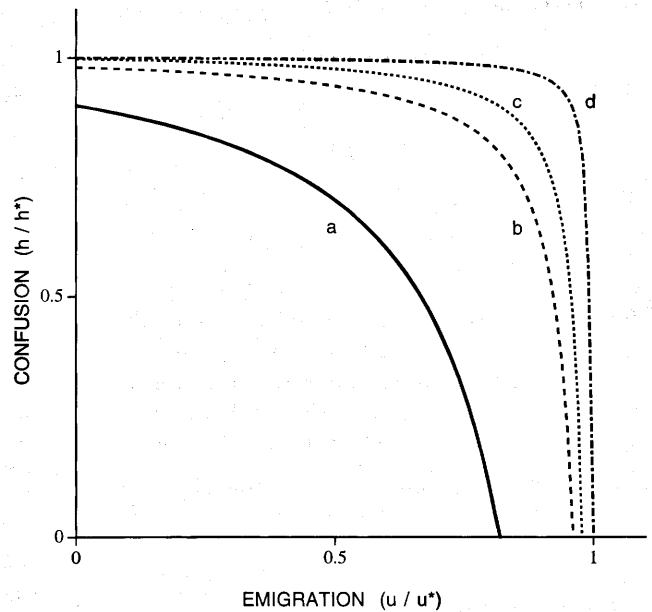


Fig. 8. Interaction of confusion (h) and emigration (u). The curves were normalized by dividing h and u by their respective critical values to illustrate the shape of the curves: (a) $a=5$, $s=0.5$; (b) $a=5$, $s=0.9$; (c) $a=25$, $s=0.5$; (d) $a=25$, $s=0.9$.

population, but both are quite inefficient with parameters in this range, since control requires almost complete cessation of mating.

(D) Confusion and emigration

Since both confusion and male emigration may operate simultaneously in field trials, the combination of these two is modelled below. A proportion, u , of the males emigrate prior to mating, leaving $(1-u)M$ for mating. The efficiency of these males is further reduced by pheromone to a factor $(1-h)$ of their normal efficiency.

(i) Male excess:

$$\begin{aligned} F_{i+1} &= s (1-h) V_i + s F_i, \\ V_{i+1} &= a F_{i-k} + s h V_i, \\ M_{i+1} &= a F_{i-k} + s (1-u) M_i. \end{aligned} \tag{20}$$

Here the assumption is made that a modest reduction in the number of males has no effect on the efficiency of the remaining males in finding mates. In this case the critical pheromone release rate is:

$$h = \frac{as - 1 + s}{s(a - 1 + s)} \tag{21}$$

which is exactly the same as without emigration.

(ii) *Male deficit:*

$$\begin{aligned} F_{i+1} &= s(1-h)(1-u)M_i + sF_i, \\ V_{i+1} &= aF_{i-k} + s h(1-u)M_i, \\ M_{i+1} &= aF_{i-k} + s(1-u)M_i, \end{aligned} \quad (22)$$

and then

$$h = \frac{[as + s(1-s)](1-u) - (1-s)}{as(1-u)}. \quad (23)$$

It is easy to show that $d^2h/du^2 < 0$ for all feasible values of the parameters, so that h is a convex function of u , and thus synergism is absent between confusion and emigration (Fig. 8). In fact, confusion and emigration together are only slightly more efficient than either alone.

Discussion

Major conclusions

All three mechanisms of mating disruption investigated are capable of yielding control. Confusion and male emigration are quantitatively comparable in their individual effects but when in combination they assist each other very little and the effect of the two together is very little better than with either singly (Fig. 8). This is not surprising, however, since both the parameters h and u relate to mortality (or at least to depressing reproduction), rather than to control effort, and two sources of mortality will generally not be synergistic even though the corresponding control efforts may be so (Barclay 1992b).

A comparison of the required pheromone release rate to achieve control by confusion or emigration with that for false trail following is difficult in generality, since neither the rates for confusion nor emigration depend on population size while that for false trail following does; this latter is due to the competition effect between pheromone release sites and wild females for the attention of the males. In a specific case in which parameter values and relationships such as those in Figs. 1 to 7 are known, then such a comparison could be made. Nakasuji and Fujita (1980) found mass trapping to be better than mating disruption for *Spodoptera litura* in their model, but that model involved killing the males which is not the case in our model.

The effect of density dependence in the action of pheromone is to put an upper limit on the possibility for control by this method. If the efficacy of pheromone for causing mating disruption decreases considerably at moderate pest densities, then control by this method may be impossible. For pests existing at naturally high densities, the use of mating disruption may suffer from this problem and the possibility of density-dependence should be investigated.

If mating is delayed after eclosion, the fertility of the pest is effectively reduced, and this assists the control program. This may mean that the dual action of confusion and false trail following may be synergistic, since both will tend to reduce fertility. However, this combination is probably not under the control of the pest manager.

A delay in the mating of females will both reduce the total fertile egg output per female and also reduce the number of females due to mortality prior to mating. This makes the control of a pest population easier and may be one mechanism of mating disruption, either being a consequence of, or separate from, confusion. Kiritani and Kanoh (1984) obtained experimental evidence that control was easier in *Homona magnanima* when females were deprived of mating for several days after eclosion, and their results will likely generalize to most pest species.

Most pests are aggregated to some extent in their spatial distribution. Aggregation produces clumps of higher than average density. If the disruptive action of pheromone does not depend on pest density, then aggregation has no effect on this control method. However, aggregation is likely to make mate finding easier due to physical proximity of potential mates and this allows mate finding by tactile or visual means (Carde and Minks 1995). In this case, aggregation makes control more difficult since some clumps will be above the density controllable by a blanket of pheromone. All the curves in Fig. 7 show a sharp increase as the aggregation coefficient, k , becomes small, making aggregation more extreme. The structure of Nakasuji and Fujita's 1980 model yielded density dependence with respect to pheromone action so that the efficacy of pheromone for mating disruption decreased with increasing pest density. Since that model was somewhat more mechanistic than those presented here, that may well be the general situation, in which case the results of equations 4, 8 and 19 above would need modification, while the results of equation 6 and Fig. 7 would likely be realistic.

Assumptions requiring testing

Any model makes assumptions about the situation being modelled. Some of these assumptions are due to the true nature of the processes being unknown; some are for reasons of generality and some are for simplification and mathematical tractability. Several assumptions in the models presented above require evaluation before the results of the models can be believed. Specifically, one should address the assumptions of:

- (i) Timing of mating and emigration of males; section (C) dealt with the case in which emigration precedes mating;
- (ii) Constancy of fertility and survivorship with changes of pest density and other conditions; this is almost certain-

ly not strictly true and the extent to which it is false will determine the extent to which the behavior of the model is wrong;

(iii) Single daily mating attempt of males; it was shown by Barclay (1984) that this assumption has a large effect on the behavior of a model for pheromone trapping for male annihilation. However, the effect on the models here may not be so large since one effect of mating disruption is to drastically reduce the frequency of mating;

(iv) Dependence of confusion effect on pest density would appear to be very important with pest aggregation (Fig. 7) and this assumption needs testing.

Relationships requiring measurement

In addition to the assumptions, several relationships need to be derived for any given species. These include:

(i) Dependence of fertility and survivorship on adult pest age;

(ii) Spatial distribution of the pest population;

(iii) Extent and timing of male emigration;

(iv) The relationship between confusion (h) and the pheromone level (V_0);

(v) The dependence of confusion on pest density.

This paper is largely heuristic as it attempts to outline the possibilities for pest control by mating disruption and at the same time identify those features of the biology which are important to measure. Clearly the large number of successful cases of control by mating disruption on at least an experimental level indicates optimism for the method as a useful tool in insect pest control. The unsuccessful cases point to the need to understand the mechanisms behind mating disruption as well as the population dynamic consequences of those mechanisms.

Acknowledgements: We would like to thank Roy Shepherd for discussions in the formative phase of this research. In addition, the paper has benefitted from the suggestions of two anonymous reviewers.

References

- Barclay, H. J. (1984) Pheromone trapping models for pest control: effects of mating patterns and immigration. *Res. Popul. Ecol.* **26**: 303–311.
- Barclay, H. J. (1992a) Modelling the effects of population aggregation on the efficiency of insect pest control. *Res. Popul. Ecol.* **34**: 131–141.
- Barclay, H. J. (1992b) Combining methods of insect pest control: partitioning mortality and predicting complementarity. *Res. Popul. Ecol.* **34**: 91–107.
- Barclay, H. J. and P. van den Driessche (1983) Pheromone trapping models for insect pest control. *Res. Popul. Ecol.* **25**: 105–115.
- Bartell, R. J. (1982) Mechanisms of communication disruption by pheromone in the control of Lepidoptera: a review. *Physiol. Entomol.* **7**: 353–364.
- Boswell, M. and G. P. Patil (1970) Chance mechanisms generating the negative binomial distributions. pp. 3–22 In G. P. Patil (ed.) *Random counts in models and structures*. The Penn. State Univ. Press, University Park, Penn.
- Carde, R. T. and A. K. Minks (1995) Control of moth pests by mating disruption: successes and constraints. *Annu. Rev. Entomol.* **40**: 559–585.
- Critchley, B. R., D. G. Champion, L. J. McVeigh, P. Hunter-Jones, D. R. Hall, A. Cork, B. F. Nesbitt, G. J. Marrs, A. R. Jutsum, M. M. Hosny, and E. S. A. Nasr (1983) Control of pink bollworm, *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae), in Egypt by mating disruption using an aerially applied microencapsulated pheromone formulation. *Bull. Entomol. Res.* **73**: 289–299.
- Ellis, P. E., L. C. Brimacombe, L. J. McVeigh and A. Dignan, (1980) Laboratory experiments on the disruption of mating in the Egyptian cotton leafworm *Spodoptera littoralis* (Biosduval) (Lepidoptera: Noctuidae) by excess of female pheromones. *Bull. Entomol. Res.* **70**: 673–684.
- Hendricks, D. E., C. T. Perez and R. J. Guerra (1982) Disruption of *Heliothis* spp. mating behavior with chemical sex attractant components. *Environ. Entomol.* **11**: 859–866.
- Kiritani, K. and M. Kanoh (1984) Influence of delay in mating on the reproduction of the oriental tea tortrix, *Homona magnanima diakonoff* (Lepidoptera: Tortricidae), with reference to pheromone-based control. *Prot. Ecol.* **6**: 137–144.
- Lotka, A. (1956) *Elements of mathematical biology*. Dover, New York.
- Nakasuji, F. and K. Fujita (1980) A population model to assess the effect of sex pheromones on population suppression. *Appl. Entomol. Zool.* **15**: 27–35.
- Niwa, C. G., G. E. Daterman, C. Sartwell and L. L. Sower (1988) Control of *Rhyacionia zozana* (Lepidoptera: Tortricidae) by mating disruption with synthetic sex pheromone. *Environ. Entomol.* **17**: 593–595.
- Palaniswamy, P., R. J. Ross, W. D. Seabrook, G. C. Lonergan, C. J. Wiesner, S. H. Tan and P. J. Silk. (1982) Mating suppression of caged Spruce Budworm (Lepidoptera: Tortricidae) moths in different pheromone atmospheres and high population densities. *J. Econ. Entomol.* **75**: 989–993.
- Pielou, E. C. (1969) *An introduction to mathematical ecology*. J. Wiley, New York.
- Sartwell, C., G. E. Daterman, D. L. Overhulser and L. L. Sower (1983) Mating disruption of western pine shoot borer (Lepidoptera: Tortricidae) with widely spaced releasers of synthetic pheromone. *J. Econ. Entomol.* **76**: 1148–1151.
- Schwalbe, C. P., E. C. Paszek, B. A. Bierl-Leonhardt and J. R. Plimmer (1983) Disruption of gypsy moth (Lepidoptera: Lymantriidae) mating with disparlure. *J. Econ. Entomol.* **76**: 841–844.
- Sower, L. L., J. M. Wenz, D. L. Dahlsten and G. E. Daterman (1990) Field testing of pheromone disruption on preoutbreak populations of Douglas-fir tussock moth (Lepidoptera: Lymantriidae). *J. Econ. Entomol.* **83**: 1487–1491.
- Van Steenwyk, R. A. and E. R. Oatman (1983) Mating disruption of tomato pinworm (Lepidoptera: Gelechiidae) as measured by pheromone trap, foliage, and fruit infestation. *J. Econ. Entomol.* **76**: 80–84.

Received 23 May 1995; Accepted 9 October 1995