

Simulation of Mating Disruption and Mass Trapping with Competitive Attraction and Camouflage

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ABSTRACT Simulation models of mass trapping and mating disruption were developed based on correlated random walks (CRW) of flying male moths searching for females. Males encountered pheromone plumes, transformed into a circular probability surface represented as an effective attraction radius (EAR), from females and from dispensers with or without traps. In simulations, parameters of dispenser EAR and density, female EAR and density, female stationary periods, male density, and male orienting times in EAR of dispensers or females were varied, whereas the male CRW parameters (speed, turning angle, and step size) remained constant to evaluate effects on the percentages of females mating. When male orienting time was constant regardless of EAR, the models indicated no difference in mating disruption efficacy between either a higher density of dispensers with smaller EAR or a lower density of dispensers with a compensating larger EAR. However, when the orienting time was increased in proportion to dispenser EAR, fewer dispensers with larger EAR were more effective in reducing female mating than were more numerous ones with smaller EAR. When costs of pheromone are substantial, however, more numerous dispensers of smaller EAR would be more economical because dose-response curves in previous studies indicate release rate must increase exponentially to achieve a linear increase in EAR. The models are useful in understanding the variables affecting the success of insect control programs. More precise measurements of the above parameters in the field are needed before the models can precisely predict outcomes of mating disruption and mass trapping.

KEY WORDS mating disruption, mass trapping, integrated pest management, pheromone plumes, computer simulation model

Mating disruption and mass trapping of insects have the goal of dispensing synthetic pheromones or other attractants in the field to reduce pest populations (Shorey 1977, Bartell 1982, Cardé 1990). The term mating disruption has traditionally been applied to methods using synthetic pheromone dispensers without traps to confuse and disrupt communication. Mating disruption using sex pheromones has had fair success in control of moths (Novak and Roelofs 1985, Rice and Kirsch 1990, Cardé and Minks 1995, Trimble et al. 2004, El-Sayed et al. 2006, Miller et al. 2006a, b). The mechanisms suggested to cause mating disruption include (1) false-plume (trail) following, (2) camouflage, (3) desensitization (adaptation and/or habituation), (4) sensory (or component) imbalance, and (5) combinations of these (Shorey 1977, Bartell 1982, Cardé 1990, Valeur and Löfstedt 1996, Cardé et al. 1998, Evenden et al. 2000, Gut et al. 2004, Miller et al. 2006a, b).

In false-plume following, male moths are competitively attracted either to calling (usually virgin) females or to pheromone dispensers; the latter decrease

the limited search time of males and reduce mating encounters (Daterman et al. 1982, Cardé 1990, Mani and Schwaller 1992, Stelinski et al. 2004, Miller et al. 2006a, b). In the mechanism of camouflage, calling females occur within larger plumes of dispensers so that males cannot distinguish female plumes and locate females for mating. Desensitization includes adaptation and habituation in which high concentrations of pheromone cause fatigue of neurons so the insect becomes unresponsive to pheromone for some time, again limiting effective search time and reducing chances of finding mates during the flight period (Bartell and Roelofs 1973, Shorey 1977, Kuenen and Baker 1981, Baker et al. 1989, Figueredo and Baker 1992, Rumbo and Vickers 1997, Stelinski et al. 2003, Judd et al. 2005). The suggested mechanism of sensory imbalance (Byers 1987a, Minks and Cardé 1988, Knight et al. 1998, Evenden et al. 1999) could occur when components are released from dispensers that mingle with female components or other dispensers to create unnatural pheromone component ratios in plumes that are unattractive or repellent to conspecific males. Noncompetitive mechanisms of mating disruption in-

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clude camouflage, desensitization, and sensory imbalance in which orientation behavior is interfered with.

Insects release semiochemicals from a point source of high concentration that diminishes as molecules are transported downwind in a plume that has a behaviorally active space (Bossert and Wilson 1963, Nakamura and Kawasaki 1977, Baker and Roelofs 1981, Byers 1996a). However, this generally means that an insect entering a pheromone plume would have a higher probability of reaching the source when closer rather than farther away (Elkinton et al. 1984). These source-finding probabilities at various distances within the plume are undoubtedly complex and in practice extremely difficult to delineate. However, they can be approximated by the effective attraction radius (EAR) method that is determined by the ratio of catch between an attractive pheromone trap and a passive (unbaited) trap of known dimensions (Byers et al. 1989, Byers 1999). In essence, all the various probabilities within the elongated active space of the plume are compressed into a circular area with a probability of $P = 1$ that insects entering the EAR will find the source and be trapped. Thus, the EAR does not represent plume structure or extent but rather the most compact representation of a plume's encounter rate and response probability surface in terms of catch or influence on behavior.

The purpose of mass trapping of moths is to lure males into traps, thereby reducing their numbers and potential mating with calling females (El-Sayed et al. 2006). In mass trapping and mating disruption, dispensers are competitive with females, but females might be camouflaged in both methods. The EAR of either females or dispensers can vary independently depending on response and release characteristics of the species and dispenser release rates. In addition, the period of male search interruption after encountering a dispenser or female plume could vary independently (because of any of the four suggested mechanisms above, and in the case of females, a delay spent mating). In mass trapping, as modeled here, only the delays caused by mating with females are meaningful because males encountering the EAR of a baited trap are killed. In both mass trapping and mating disruption, there is no general agreement whether it is better to spread throughout a crop many pheromone dispensers each at a low release rate, similar to an insect (Vickers and Rothschild 1991, Suckling and Angerilli 1996, Epstein et al. 2006, Miller et al. 2006a), or whether far fewer pheromone dispensers should be used each at a much higher release rate (Farkas et al. 1974, Daterman et al. 1982, Alford and Silk 1983, Shorey et al. 1994, 1996). There is a general agreement that mass trapping and mating disruption are less likely to succeed the higher the population density of the target pest (Knippling and McGuire 1966, Daterman et al. 1982, Sternlicht 1982, Barclay and van den Driessche 1983, 1984, Barclay 1987, 1992, El-Sayed et al. 2006, Miller et al. 2006a, b).

Mating disruption and mass trapping can be studied with population models of discrete iterative equations based on estimated variables representing fecundity,

survival, and mating probability as affected by semiochemicals (Knippling and McGuire 1966, Barclay and van den Driessche 1983, 1984, Barclay 1987, 1992, Barclay and Judd 1995, Yamanaka 2007). Another approach is to use simulation models based on correlated random walks (CRW) of individual flying insects encountering various EARs of natural and synthetic attractants (Bovet and Benhamou 1988, Byers 1991, 1993). In one type of CRW, insects take a series of forward steps with a possible new direction after each step according to a normal distribution of possible angular turns (Turchin 1998). Computer algorithms of CRW and EAR were developed to simulate mate finding of pine shoot beetles, *Tomicus piniperda* L. (Byers 1991). This model was later modified for host-tree finding and mass trapping of bark beetles before trees were attacked (Byers 1993, 1996b). However, there are no models using CRW and EAR that describe mating disruption or mass trapping when there is competition with natural pheromone sources such as moth sex pheromones.

Worner (1991) suggested that goals of models are to define problems, organize thoughts, understand systems, identify areas to investigate, communicate understanding, make predictions, generate hypotheses, and act as standards for comparison. These goals are poorly achieved by overly complex models that are supposed to provide realistic predictions but may fail because of numerous assumptions. In contrast, my goal was to provide models that are simplified to their essential components to gain insights and understanding of mating disruption and mass trapping processes. My first objective was to design graphical simulations of male moth interactions with synthetic pheromone dispensers or trap dispensers as well as sex pheromone of calling females using CRW and EAR algorithms. The second objective was to develop equations to adjust male speed that give the same results in terms of mating rates as do models that have males spending (orienting) various periods inside pheromone plumes of females or dispensers. Such equations are needed to develop encounter rate equations modified from those of Rogers (1972) that should improve model performance speed. By varying parameters such as densities of moths and dispensers/traps, EAR of dispensers and females, and speeds and orienting periods of males interacting with dispensers or females, the effects of these parameters on mating disruption and mass trapping can be compared under the same conditions. The models will address the question whether control in an area is more efficient with either more numerous, but less potent sources, or fewer, but more potent dispensers. The simulations should be applicable not only to moths but also to other insect systems with attractive semiochemicals.

Materials and Methods

Simulation of Mating Disruption and Mass Trapping with Competitive Attraction and Camouflage. Two models were constructed: (1) competitive attraction of male moths to EAR plumes of virgin female

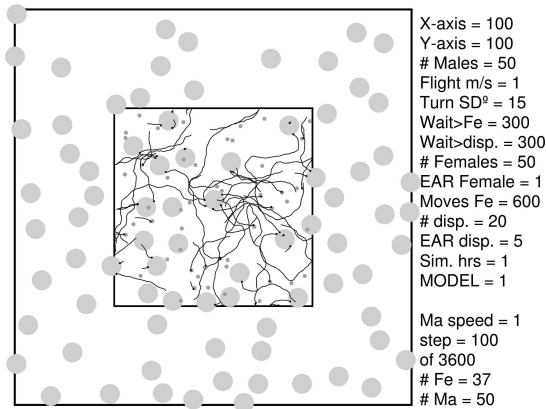


Fig. 1. Simulation area as generated by QuickBASIC program showing first 100 steps of CRW flight tracks of male moths in inner 1-ha area, females (smaller disk EAR), dispensers (larger disk EAR), and parameters of mating disruption model (see Materials and Methods for parameter details).

moths and synthetic pheromone dispensers without traps (mating disruption) and (2) the same model but with pheromone dispensers in traps (mass trapping). The simulation area with an x-axis (x_a) and y-axis (y_a) can be adjusted but was held in most simulations with sides of 100 m centered within a larger square area with sides of twice the inner side length (Fig. 1). Specific numbers of dispensers or traps were placed in the inner simulation area by choosing random coordinates, e.g., $x = \text{RND} \times x_a$ and $y = \text{RND} \times y_a$, where RND was a uniform random number ranging from 0 to <1. Then, three times more dispensers were placed outside the inner area at random to obtain the same density. If the specified density permitted, the dispensers were spaced apart in the entire area (Fig. 1) with a minimum allowed distance (MAD) method (Byers 1984). The MAD spacing was one half the maximum possible distance for a hexagonal pattern within an area, $\text{MAD} = 0.5 \times (1.0746 / \sqrt{n/x_a \times y_a})$, where n is the number of dispensers. If after 1,000 random tries, all dispensers could not be placed under the constraints, the MAD was set to zero for all remaining dispensers to be placed. Females and males were placed similarly and fully within the inner area but without a MAD constraint.

The algorithms for simulating animal movement in two dimensions as a CRW follow earlier descriptions for implementation on computers (Bovet and Benhamou 1988, Byers 1991, 1996b, 2001). Each male was given an initial position and direction at random. Thereafter, each male followed a CRW made of a series of steps, each calculated as a polar vector from the former position. The vector length was the average distance traveled per second, and the direction was the former direction plus a turning angle chosen at random from a normal distribution (15°SD°) centered on the former direction (Byers 2001). In the model flow (Fig. 2), males that either entered or crossed through an EAR during a step (Fig. 3 of Byers 1991)

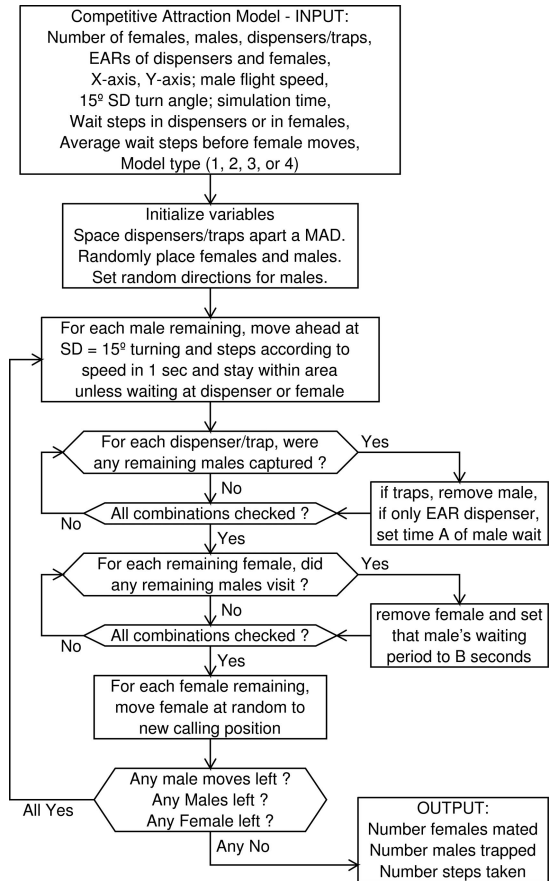


Fig. 2. Flow diagram of graphical CRW and EAR simulation.

were considered to be either (1) false-plume following, (2) trapped in the case of a dispenser plus trap, or (3) orienting to and mating with a female. For dispensers, these natural processes were simplified in the model so that the male simply stops moving (waits) a set time, termed the orientation time, and resumed searching unless a trap removed him. In the case of a male encountering a female EAR in the model, the male stopped moving a set period (orienting and mating), the female was removed (no longer calling), and the male resumed his search. Males could not encounter females inside the EAR of a dispenser/trap because of camouflage.

The above model (Fig. 2) was programmed in QuickBASIC 4.5 (Microsoft, Redmond, WA) for use in simulations, as well as Java 2.1 (Sun Microsystems, Santa Clara, CA) for web demonstrations (code available from author). Adobe PostScript code (Adobe Systems, San Jose, CA) was integrated with QuickBASIC code to print results of simulations as shown in the figures. The Java code was compiled into an applet and integrated into HTML and JavaScript code for use on the Internet with a web browser at <http://www.chemical-ecology.net/java2/compmoth.htm>.

Table 1. Effects of dispenser-trap diameter and dispenser-trap area on the percentages of females mating during 1 h of simulated search by males in a 1-ha area in mating disruption or mass trapping

Number	Dispenser			Percent females mating	
	EAR (m)	Σ EAR (m)	Σ EAR area (m ²)	Mating disruption ^a	Mass trapping ^b
Females move after mean of 600 ± 300 s					
10	12	120	4524	89.25 ± 4.97	17.75 ± 5.82
100	3.7948	379	4524	56.5 ± 5.84	6.5 ± 2.93
1,000	1.2	1200	4524	21 ± 5.06	1.75 ± 1.40
Females move after mean of 50 ± 25 s					
10	12	120	4524	96.50 ± 2.14	18.75 ± 5.51
100	3.7948	379	4524	70.50 ± 5.78	5.25 ± 2.67
1,000	1.2	1200	4524	44.25 ± 5.68	1.25 ± 1.24

^a Dispensers without traps in 1-ha inner area within a 4-ha area (Fig. 1) with 50 females and males initially (other parameters as in Figure 1 or as indicated). Error limits are ± 95% confidence limits (N = 8 simulations).

^b Dispensers inside traps, otherwise same parameters as above.

Unless otherwise stated, simulations were done in an inner 1-ha area (100 by 100 m) with 50 dispensers each of 5-m EAR. There were 50 individuals of each sex, females had a 1-m EAR, and males flew at 1 m/s within the inner area (Fig. 1). When a male contacted a dispenser EAR or a female EAR, he oriented/waited 300 s before continuing for up to 1 h of flight unless caught by a trap or until all females were mated. Females moved their positions after a mean period (FM) of 600 s that varied individually as $RND \times FM + FM/2$, where RND was as above. The effect of the frequency of female movement within the area in relation to dispenser plume EAR was modeled by changing the positions of females at random after various FMs ranging from 50 to 3,550 s at a dispenser EAR of 1, 3, 6, or 10 m. The simulations continued for 1 h of total male flight whereupon the percentage of females that had mated was recorded.

The effects of the diameter of an EAR plume versus the area of this plume on the rate that males find females was modeled using two mean stationary periods of females (50 and 600 s). Certain parameters were varied in simulations to determine the effects on the percentage of females that mated in a set time period of male flight. Simulations were ended when either all females were mated or all males were trapped (only in mass trapping). The following parameters were varied in a 1-ha area: (1) the EAR of dispensers from 0.5 to 12 m, (2) the EAR of females from 0.1 to 4 m, (3) the number of each sex from 10 to 200/ha (female with 0.5-m EAR), (4) the number of dispensers (10-m EAR) from 2 to 100, and (5) the orienting times of males on females and dispensers from 100 to 2,000 s. In (1) at an EAR of 6 m, the turning angle SD° for the male CRW was varied from 5 to 45°. In other simulations, two parameters were varied in a 9-ha area: (1) the number of each sex from 50 to 500/ha and the number of dispensers (or traps) from 50 to 500/ha and (2) the number of dispensers (or traps) from 10 to 100 and the EAR of the dispenser/trap from 4 to 40 m. In the above simulations, when males encountered a dispenser they spent 300 s regardless of the size of the dispenser EAR. This allowed the effects of varying the size of the EAR and thus the male encounter rates to be determined. However,

males may spend proportionately more time as the dispenser EAR is enlarged, so the last mentioned simulation above was repeated (but dispenser EAR varied from 2 to 20 m) with orienting times (Y) calculated as $Y = 100(EAR)$. The relatively large ranges of model parameters should produce results that encompass most natural systems.

Equations Adjusting Male Speed to Increase Model Speed Performance. The average distance D that a male moth travels in the field between female plumes (R = EAR) can be determined (Byers 1996b) based on the number of female plumes (K) in an area (A):

$$D = \frac{A}{2 \times R \times K} \tag{1}$$

The average speed (S) that male moths travel through an area depends on how long (L) a male typically spends orienting inside the plume (Byers 1996b):

$$S = \frac{D}{\frac{D}{S_F} + L} \tag{2}$$

where S_F is the average male flight speed (e.g., 1 m/s). Using this flight speed, if 85 dispensers have plumes of R = 2 m each and males spend 120 s false-plume following when encountering a plume, males would effectively move more slowly through the area at a constant 0.197 m/s. The same formulas can be applied to female plumes.

The simulation model was modified to include a slower male flight speed (from equations 1 and 2 and also equations 3 and 4) to test whether results were equivalent to simulations with specific orienting periods by males in EAR plumes of females and dispensers.

Results

Simulation of Mating Disruption and Mass Trapping with Competitive Attraction and Camouflage. In mating disruption and mass trapping with competitive attraction, the time until all females are mated depends on the effective radius of the dispenser plume EAR multiplied by the number of dispensers rather

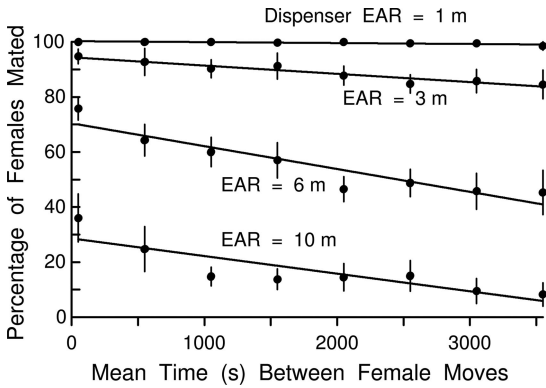


Fig. 3. Percentage of females mating in relation to mean time between female moves depending on dispenser EAR in a 1-ha area with mating disruption (unless indicated, parameters were as in Fig. 1 with 50 dispensers; each point represents a mean of eight simulations with ±95% CL).

than on the area of these combined plumes (Table 1). For example, if females move after a mean of 600 s, increasing the sum of the EAR of dispensers 10 times (the sum of areas remained constant) caused the percentage of females mating to decline from 89 to 21% in mating disruption and from 18 to 2% in mass trapping (Table 1). There was no effect on the percentage of females mating when the stationary time of females was lengthened between her moves if the dispenser plume EAR was about the same size or smaller than the female plume EAR (Fig. 3). However, as the EAR of dispenser plumes was enlarged, the likelihood of female plumes being camouflaged increased, and this caused a lower percentage of females to mate. Also, as the length of time between moves increased, a lower percentage of females mated because the females must move out of dispenser EAR to be exposed to males (Fig. 3).

An increase in the EAR of the dispenser caused the percentage of mated females to decline as a sigmoid curve in both mating disruption and mass trapping, although in mass trapping, the decline is more rapid and approximates an exponential decline as the dispenser EAR is further enlarged (Fig. 4A). There was little if any effect on mating disruption when male turning angle SD° was either 5, 15, 25, 35, or 45° because corresponding female mating percentages of 61.3 ± 5.4 , 67.5 ± 6.3 , 63.8 ± 3.8 , 67.5 ± 6.0 , or $63.3 \pm 6.0\%$ ($\pm 95\%$ C.L., $N = 8$) were similar. The same SD° values also had little effect on female mating percentages in mass trapping: 8.5 ± 2.8 , 7.3 ± 4.1 , 6.25 ± 4.2 , 6.25 ± 2.3 , and 6.5 ± 3.7 , respectively (parameters of Fig. 4A at 6-m dispenser EAR). Increasing the EAR of female plumes caused the percentage of females mating to initially increase linearly and curve logarithmically to fit the relationship $Y = 1 / (a + b/X)$ in both mating disruption and mass trapping models—with mass trapping being more efficient in preventing mating (Fig. 4B). An increase in number of females caused an increase in the percentage of mated females according to the same function in both mating disruption

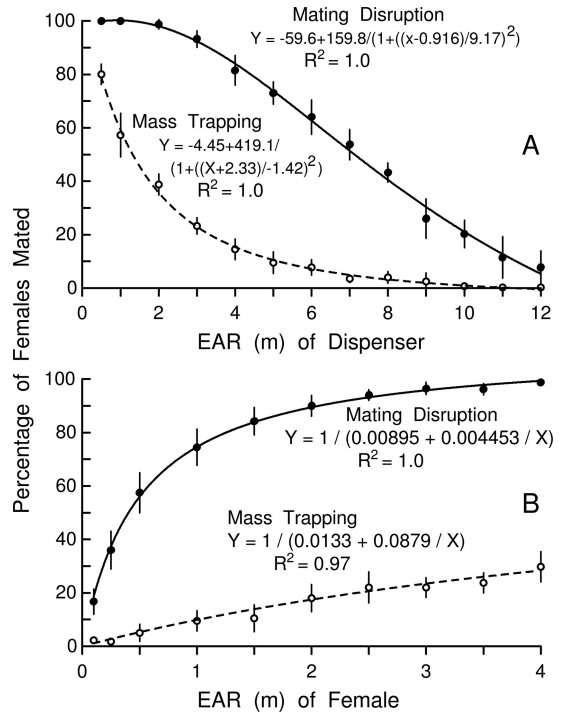


Fig. 4. Percentage of females mating in relation to EAR of dispenser plume (A) or female plume (B) in a 1-ha area with mating disruption or mass trapping (unless indicated, parameters were as in Fig. 1 with 50 dispensers with or without traps; each point represents a mean of eight simulations with ±95% CL).

and mass trapping, with far lower percentages of mating in mass trapping under the same conditions (Fig. 5A). Increasing the number of dispensers or traps per hectare in the two models caused mating percentages of females to decline as a sigmoid curve that was more steep in mass trapping, with both curves approximating an exponential decline at lower mating percentages when numbers of dispensers were increased further (Fig. 5B). The sigmoid effects were caused by asymptotic limits when approaching 100% of females mating.

As the male's orienting time in the EAR of females and dispensers was increased from 100 to 2,000 s, there was an exponential decline in the percentage of females mating from 96% down to 21% in the mating disruption model (Fig. 6). In the trapping model, $\approx 10\%$ mated regardless of the orienting time in female plumes and dispenser/traps (Fig. 6). The slight decline (slope = -0.0005) in mating percentage of females as orienting time was increased was because of females that shortened average male search distance slightly rather than dispenser traps that can catch males.

The percentage of females mating decreased as the density of dispensers increased from 50 to 500, as well as when there were relatively fewer females per hectare (Fig. 7A). Again, the percentage of females mating was least when the density of females was least and the

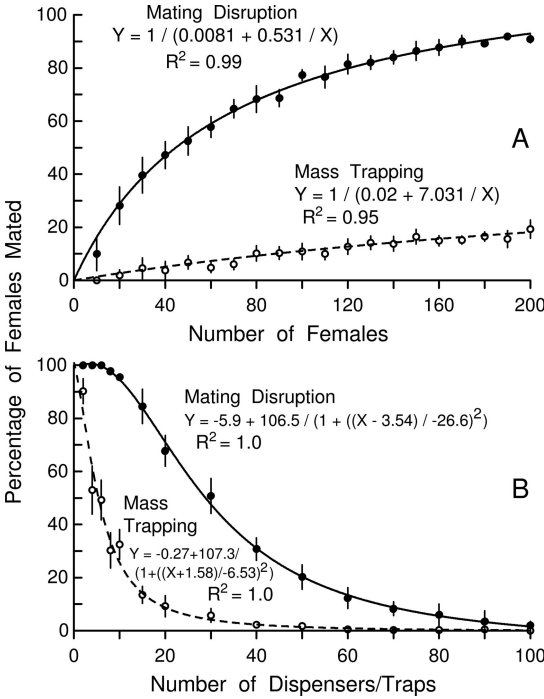


Fig. 5. Percentage of females mating in relation to number of females of 0.5 m EAR (A) or the number of dispensers of 10 m EAR (B) in 1-ha area with mating disruption or mass trapping (unless indicated, parameters were as in Fig. 1 with 50 dispensers with or without traps; each point represents a mean of eight simulations with $\pm 95\%$ CL).

density of traps was most (Fig. 7B). The least number of females mated when the density of dispensers was highest and the size of the EAR was greatest in mating disruption (Fig. 8A). Even more so, increases in the density of traps and the size of the trap dispenser EAR gave the lowest percentages of mated females in mass trapping (Fig. 8B). In both mating disruption and mass trapping, there seems to be little difference between

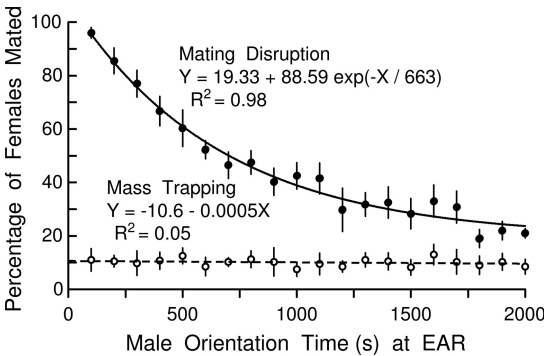


Fig. 6. Percentage of females mating in relation to the orientation time of males at EAR of females and dispensers in a 1-ha area with mating disruption or mass trapping (unless indicated, parameters were as in Fig. 1 with 50 dispensers; each point represents a mean of eight simulations with $\pm 95\%$ CL).

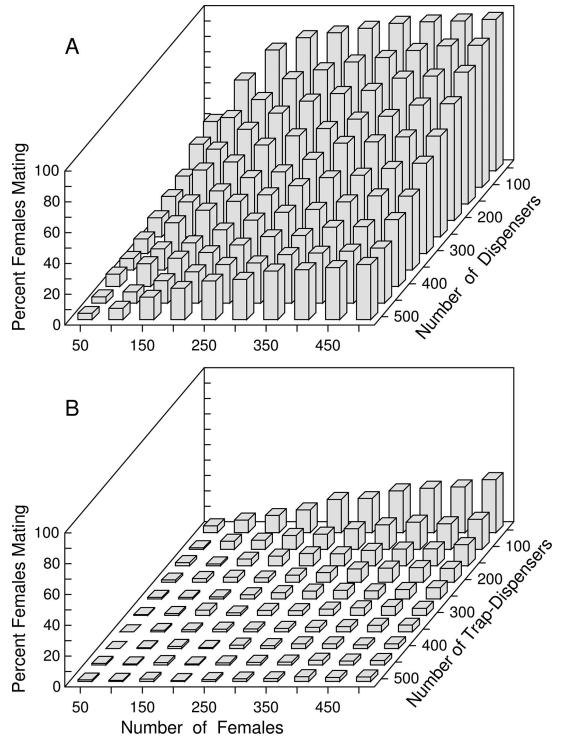


Fig. 7. (A) Percentage of females mating in relation to number of females and number of dispensers in a 9-ha area with mating disruption. (B) Percentage of females mating in relation to number of females and number of trap dispensers in a 9-ha area with mass trapping. Unless indicated, parameters were as in Fig. 1 but with 300 by 300 m and 8-m EAR of dispensers/traps; each point represents a mean of four simulations.

a higher density of dispensers with smaller EAR or a lower density of dispensers with a compensating larger EAR, when orienting time was constant regardless of EAR. In mass trapping, orienting times on dispensers have no effect because males are trapped. However, when the orienting time was proportional to the dispenser's EAR, fewer dispensers with larger EAR were slightly more effective in reducing mating than more numerous dispensers with smaller EAR (Fig. 9A). In the case of mass trapping, there was no effect of longer orienting periods on larger EAR because males never leave a trap (Fig. 9B).

Equations Adjusting Male Speed to Increase Model Speed Performance. Equations 1 and 2 refer to either female or dispenser plumes but not both at the same time unless they are equally attractive, which is usually not the case. Thus, a competitive situation requires a more complex equation:

$$D = \frac{A}{\sum_{c=1}^n 2 \times R_c \times K_c} \quad [3]$$

where n is the number of attractant types with various R_c and K_c values analogous to equation 1 and S is

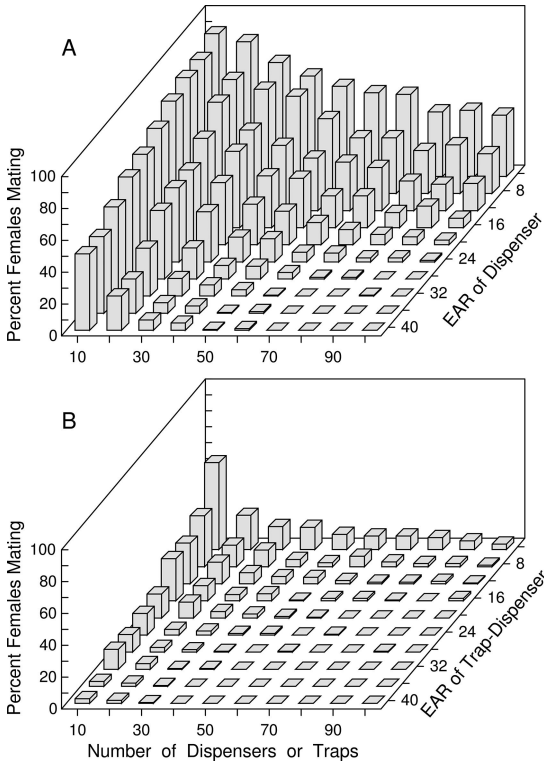


Fig. 8. (A) Percentage of females mating in relation to number of dispensers and the EAR of dispensers in a 9-ha area with mating disruption. (B) Percentage of females mating in relation to number of traps with dispensers and the EAR of trap dispensers in a 9-ha area with mass trapping. Unless indicated, parameters were as in Fig. 1 but with 300 by 300 area; each bar represents a mean of four simulations.

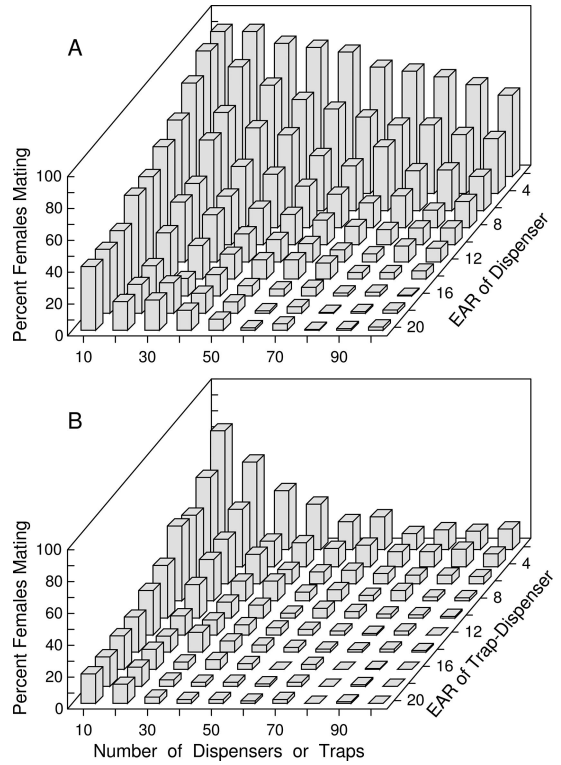


Fig. 9. (A) Percentage of females mating in relation to number of dispensers and the EAR of dispensers when male orienting time was proportional to EAR ($Y = 100 \times \text{EAR}$) in a 9-ha area with mating disruption. (B) Percentage of females mating in relation to number of trap dispensers and the EAR of trap dispensers when male orienting time was proportional to EAR in a 9-ha area with mass trapping. Unless indicated, parameters were as in Fig. 1 but with 300 by 300 area; each bar represents a mean of four simulations.

calculated by equation 2. This assumes that males spend the same time in any type of plume, which might be reasonably correct but perhaps the L could be different in a female plume versus that for a dispenser plume, especially if the EAR of one type is much larger than the other type.

In this case, the L in equation 2 would be weighted based on the numbers of each type of plume (K_c), their EAR sizes (R_c), and the average time spent in each type of plume (L_c):

$$L = \frac{\sum_{c=1}^n K_c \times R_c \times L_c}{\sum_{t=1}^n K_c \times R_c} \quad [4]$$

For example, if a 1-ha area has 10 female plumes each of $R = 1$ m that males spend 1,000 s in when encountered, and the area has 25 pheromone dispensers each of $R = 3$ that males spend 100 s in when encountered, $D = 58.8$ m (equation 3, $L = 205.9$ s; equation 4) and male travel speed is $S = 0.22$ m/s (equation 2 with $S_F = 1$ m/s).

The value of S becomes less appropriate in reality when females mate and cease calling so that male speed would effectively increase because of fewer encounters with calling females. In this case, a dynamic situation was modeled (Table 2) by recalculating S of males after each female was mated to give equivalent results to that of simulations using constant male orienting periods (300 s; parameters as in Fig. 1). These results further validate equations 1–4 that may prove useful in development of encounter rate equations (Rogers 1972, Byers 1996b) for mating disruption and mass trapping.

Discussion

The mating disruption model presented here is helpful in understanding the effects of various parameters on mating disruption in which success is indicated by the percentage of females mating. Simulations with traps show effects of the same parameters on the percentage of females mating before all males are caught (precluding further mating), with lower percentages being indicative of more efficient control.

Table 2. Percentage of females mating (mean \pm 95% CL, $N = 8$) in a 1-ha area with 50 dispensers (5-m EAR) in relation to the number of these females in mating disruption and mass trapping when males were arrested for 300 s at female or dispenser EAR (mating disruption only) or when male speed was adjusted to give equivalent results

Number of females = males ^a	Mating disruption		Mass trapping	
	Male arrested at EAR	Male speed adjusted ^b	Male arrested at EAR	Male speed adjusted ^b
25	53.0 \pm 8.0	50.5 \pm 9.5	10.5 \pm 5.6	8.5 \pm 5.8
50	77.3 \pm 5.7	70.0 \pm 4.5	13.0 \pm 3.6	19.5 \pm 5.8
100	89.0 \pm 3.2	87.4 \pm 2.8	24.0 \pm 3.7	23.8 \pm 3.3
200	98.1 \pm 0.6	97.1 \pm 0.6	42.4 \pm 5.2	45.9 \pm 5.6

^a Simulation parameters as in Fig. 1.

^b Male speed was dynamically adjusted according to equations 2, 3, and 4.

In all cases with a wide range of parameters (Figs. 4–9), mass trapping had lower percentages of females mating than in mating disruption under similar conditions. It is not surprising that mass trapping is more efficient because many males are removed before finding females. However, some of the densities of traps shown in Figs. 7–9 could be impractical compared with using dispensers alone. In noncompetitive mating disruption, several mechanisms such as camouflage, desensitization, and sensory imbalance may coexist to interfere with the male's search for mates. However, in mass trapping as modeled here, noncompetitive mechanisms would include only camouflage so that males ignore females within dispenser trap plumes but still orient to the source and are caught. The models have the potential to make accurate predictions about specific pest populations but require realistic parameters that are either difficult to obtain or poorly known as discussed subsequently. Thus, the main benefit of the models is a better understanding of the relative importance of various parameters in limiting the percentage of females mating within a set period.

Miller et al. (2006a) proposed that mating disruption by competitive attraction in the field can be revealed by use of Miller-Gut plots (dispenser number per hectare versus $1/[\text{male visits}/\text{dispenser}/\text{time}]$) that yield positive linear relationships. The results of simulated mating disruption (Fig. 5B) agree with analysis by the Miller-Gut plot (number of dispensers versus $1/[\text{male visits}/\text{dispenser}/\text{h}]$), yielding a positive linear equation: $Y = 0.0035 + 0.00163X$ ($R^2 > 0.999$). The simulation had males flying continuously for 1 h at 1 m/s or a total of 3.6-km distance. In nature, the male's flight would be interrupted by periods of rest and feeding as well as during inactive times of the circadian rhythm [e.g., turnip moths, *Agrotis segetum* (Schiff.)] (Byers 1987b). Insects searching for mates or host plants would be expected to move in a CRW as straight as possible to cover the most area; thus, the turning angle SD° of 15° seems to reasonably simulate insect search with a degree of randomness. In fact, simulations showed little or no effect of varying the SD° from 5°, for a rather straight path, to 45°, for a more sinuous track. Byers (1991) found that the turning angle distribution had little effect on encounter rates of bark beetles when distances between walking males

and stationary females were relatively small compared with the total distance of male travel.

The EAR was originally proposed as a spherical radius of a passive trap that would be required to intercept as many dispersing insects as were actually caught on the trap when baited with a lure. Comparison of catches on passive and pheromone-baited traps gave an EAR of 1.9 m for *Ips typographus* bark beetle response to a release rate of synthetic aggregation pheromone components (Byers et al. 1989). For simulation studies, the EAR can be considered more simply in two dimensions as a circle rather than as a sphere in three dimensions, because searching insects often fly within a height of a few meters over large areas. The EAR as an index of attractive strength is relatively easy to measure in the field and can be used to optimize the pheromone blend and release rate for maximal catch. Unfortunately, only a few studies have considered EAR and none on moths, so we know little about the relationships between semiochemical release rates and EAR for various insect species. A flow chart for development of successful mass trapping programs using the EAR was discussed recently by El-Sayed et al. (2006).

In simulations within a rectangular area, the EAR should be able to cover any part of the area. Thus, the centers of EAR circles were placed anywhere such that portions of some circles exceeded the area boundaries, but this caused another type of error because of decreasing slightly the probability of contact with males. This type of error increased as the radius of the dispenser or female was increased. Alternative approaches such as simulating in a circular area and fully containing the circles without overlap still allowed gaps of coverage in the periphery. The final simulation approach avoided these problems by centering an inner 1-ha area within a larger 4-ha square area populated with the same overall density—which required about four times as many comparisons at each male step to determine when males encountered dispensers.

The models may camouflage females, as in nature, by placing them at random within EAR of dispensers and prevent contact with males. In nature, females probably take flight to feed on flowers between calling bouts as well as possibly to spread the risk of calling in areas of low male density or unfavorable plume con-

ditions. Thus, females in the models were moved usually after a mean of 600 s to another location at random to give all a chance to be exposed to searching males. The camouflage effect is reduced if females are moved more frequently after a mean of only 50 s. Encounter rate equations (Rogers 1972, Byers 1996b) give results closer to the 50-s female movement (J.A.B., unpublished data), but less frequent female movements as in the simulations here would be more natural. Little is known about female movement in the field.

The results of Table 1 show that encounters between males and females are directly related to the sum of the EARs of dispensers or traps (Holling 1959, Byers 1991, 1993) rather than the sum of the EAR areas. In most simulations, it was assumed that the male's orienting period on dispensers was the same regardless of size of the EAR. Thus, an increase in size of the EAR would increase the rate of orienting bouts but not the time spent per orientation bout. In the case of trapping, the orienting time is not relevant. The EAR size of dispensers in nature can be manipulated by increasing the release rate of semiochemicals or using a more complete blend of components (Byers et al. 1989).

Several investigators (Suckling and Angerilli 1996, Epstein et al. 2006, Miller et al. 2006a, b) have found better mating disruption using more numerous dispensers of smaller release than fewer with larger release. Others have suggested that widely spaced dispensers of large release are just as effective (Farkas et al. 1974, Shorey 1977, Daterman et al. 1982, Alford and Silk 1983, Shorey et al. 1994, 1996). Assuming orienting times are not affected by EAR, the simulations here (Fig. 8A) indicate there would be little difference in efficacy when deploying more dispensers of smaller EAR compared with fewer dispensers of larger EAR on an equivalent summed-radius basis. A close inspection of Fig. 8A, however, indicates that, at larger dispenser EAR and fewer dispensers, female mating was slightly lower than at the equivalent smaller dispenser EAR and higher density (Fig. 8A). This subtle effect is caused by some camouflage of females in the larger dispenser areas. For example, 30 dispensers of 40-m EAR yields a sum of 1,200 m (summed area of 5,026 m²) that allowed less mating compared with the equivalent 100 dispensers of 12-m EAR (sum of 1,200 m, but area of 452 m²).

In some studies above, mating disruption may have been greater with a higher density of low-release dispensers compared with the same overall release from fewer large-release dispensers because the low-release dispensers had a higher EAR sum than the large dispensers. For example, if a low-rate dispenser has an EAR of 1 m, it would not be expected that 10 of these combined at one point would have an EAR of 10 m. This is because a linear increase in pheromone release rate will produce a catch or EAR that increases logarithmically at a slower rate (Byers 1988, Byers et al. 1988). Thus, the 10 combined dispensers would have a smaller EAR than 10 m and would disrupt or catch less than when the dispensers were placed apart. If the cost of pheromone is considerable, more numerous dispensers of smaller EAR also should be more eco-

nomical than larger EAR of an equivalent effect. This is because the release rate must be increased exponentially to obtain a linear increase in EAR. For example, solving the dose-response relationship, $Y = 1,802 + 457.5 \ln X$, for attraction of a bark beetle to pheromone (Byers et al. 1988, Table 1, test 4), where $Y = \text{catch}$ and $X = \text{release}$, gives $X = \exp(0.00503Y - 9.07)$. Given that a release of 0.1 U/d catches 665 insects for an EAR of 2 m, to obtain an 8-m EAR, there must be four times more catch ($Y = 2,660$), which requires a 74-fold increase in release rate or 7.4 U/d. For mass trapping, pheromone costs are less when using four traps of smaller 2-m EAR (0.4 U/d) than to catch the same on one 8-m EAR trap that uses 7.4 U/d. However, in terms of materials, four traps cost more than one. For mating disruption, costs and benefits are similar but more difficult to judge given that the relationships between EAR and how long males are delayed are poorly known.

Another complicating possibility is that orienting times may increase with EAR, which was tested in simulations shown in Fig. 9. In this case, if males in larger EAR have proportionally longer orienting times, fewer dispensers of larger size should be more efficient than smaller ones. However, it may not be possible to increase the EAR sufficiently so that a few large EAR are as effective as many smaller EAR. In moths, as pheromone release rates are increased above the natural rate, there is a level beyond which no further enlargement of the EAR can be achieved, and the catches (and EAR) begin to decline (Roelofs and Cardé 1977). This interference would certainly place limits on the EAR in mass trapping. For mating disruption, at high release rates, competitive attraction could be obstructed, but these high rates may still reduce mating by noncompetitive disruption (camouflage, desensitization, sensory imbalance). Thus, the behavioral relationships between EAR, release rate, and orientation time need to be studied further before the models can aid in developing an optimal system of dispensers and release rates for mass trapping or mating disruption with a particular species and population level.

The models of mating disruption and mass trapping of individual insects were based on an average flight speed of males that interrupt their search for a period of time and orient to pheromone when encountering EAR of females or dispensers. An alternate approach was to calculate a slower effective speed (equations 3 and 4) that gives an equivalent encounter rate but without orientation bouts when encountering EAR. The two simulation approaches gave nearly identical mating rates (Table 2) and indicate that encounter rate equations proposed by Rogers (1972) perhaps can be developed into equations that predict mating disruption and mass trapping results instantly compared with much longer simulations. The models here are applicable to fairly short time periods where effects of population growth, emigration/immigration, and survival are likely to be insignificant. Alternatively, the mating disruption or mass trapping should be conducted synchronously on an areawide basis to prevent effects of dispersal from untreated areas (Byers and Castle 2005). It is also possible to combine aspects of

population dynamic models with CRW- and EAR-based simulations. The models show relative efficiencies of mating disruption and mass trapping over a range of moth and dispenser/trap densities based on various EAR. The models also reveal the need for better knowledge of various parameters to achieve successful mating disruption and mass trapping.

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