

SIMULATION AND EQUATION MODELS OF INSECT POPULATION CONTROL BY PHEROMONE-BAITED TRAPS

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Abstract—A spatial-temporal model for personal computers is developed that simulates trapping of an insect population based on trap and population parameters that can be varied independently. The model allows individual “insects” to move forward at any step size with right or left turns within any specified angle taken at random. The x and y axes of the area within which insects move can be varied as well as the number of insects, their flight speed, and the duration of the control period. In addition, the number of pheromone-baited traps, their placement in a grid or at random (with a variable degree of spacing), and their effective catch radius (proportional to pheromone release rate) can also be varied. Simulations showed that catch was similar regardless of whether traps were placed in a grid or practically at random (random placement but no traps were allowed to overlap in their effective catch radii). Iterative equations were developed for computer that can rapidly obtain values that correspond to the mean results from the slower simulation model. Based on a set of input parameters, the equations determine the percentage of the population that should be caught during a specified time, the time required to catch a specified proportion of the insects, and the number of traps necessary to catch the population proportion in the time period. The effects of varying the number of insects, flight speed, trap radius, and number of traps on the percent control or time to catch all insects are presented. Population control of the bark beetle *Ips typographus* was simulated using realistic pheromone trap and population parameters. A discussion of insect and bark beetle (Coleoptera: Scolytidae) population control using pheromone traps is presented.

Key Words—Semiachemical, pheromone, pest, biological control, insect trap, personal computer program, Scolytidae, Coleoptera, mass trapping.

INTRODUCTION

Basic research in chemical ecology begins with the observation of natural phenomena regarding an organism's movements (behavior) in response to chemical stimuli released by other organisms of the same or other species (or different phylogeny). The natural phenomena are often utilized in a bioassay for isolation and identification of the chemical stimuli (semiochemicals). These semiochemical mechanisms are not only of inherent interest but also important from economic and applied viewpoints. In fact, much of the impetus for research on pheromones, allomones, and kairomones is due to their promise for use in an integrated system of pest management and control (Silverstein, 1981). The synthetic semiochemicals can be used for monitoring populations of insects and in direct control (by interfering with natural information-bearing chemicals leading to reduced ecological fitness and reproduction).

Pheromones have been used in the field to disrupt mate finding in moths (Hodges et al., 1984; Zvirgzdins et al., 1984; Flint and Merkle, 1984; Campion et al., 1989), beetles (Villavaso and McGovern, 1981; Villavaso, 1982), and flies (Jones et al., 1982). In most cases, relatively large quantities of pheromone (consisting of several pheromone components) are more or less evenly distributed throughout the field to adapt sensory receptors or habituate behavioral response (confusion) or to exhaust the individuals in orientation attempts (wild-goose chases). The best successes so far have involved straight-chain hydrocarbons of moths.

Bark beetles that colonize forest trees may present problems for disruption techniques for several reasons; one is that their pheromone components, usually oxygenated monoterpenes, are more volatile than moth straight-chain hydrocarbons (Byers, 1989). More important perhaps is that compared to moths even larger quantities are expected to be required for disruption of bark beetles since these individuals generally release higher rates (nanograms to milligrams per hour) of pheromone components than moths (picograms to nanograms per hour) (Browne et al., 1979; Schlyter et al., 1987; Birgersson and Bergström, 1989; Byers et al., 1990a,b; Ramaswamy and Cardé, 1984; Du et al., 1987). Furthermore, even higher quantities of synthetic pheromone are required to compete with pest bark beetles that typically call in large aggregations on their host tree. Possibly because of these reasons, as well as that both sexes are attracted by pheromone, several attempts to control bark beetles have used the mass trapping method. This method employs traps, either sticky-screen (Browne, 1978) or cylinder with holes or barriers (Bakke, 1989), baited with synthetic pheromone components to catch adults. Traps releasing pheromone components have been used in control programs to lure other pest insects such as moths to their death (Haniotakis et al., 1991; Sternlicht et al., 1990).

Previous theoretical attempts at determining the effectiveness of pheromone

mass trapping have used population dynamic models (Knipling and McGuire, 1966; Roelofs et al., 1970; Beroza and Knipling, 1972; Nakasuji and Fujita, 1980; Nakamura, 1982; Barclay, 1984, 1988; Fisher et al., 1985; Barclay and Li, 1991). These models are mathematically complex and make several assumptions about population survival and mating rates as well as attraction rates to pheromone traps, which limits their application. There have been no models where "insects" are moved in "real" time and space in relation to traps of specific dimensions and positions.

The first objective of the present study was to develop a simulation model where any number of individual insects can move within any size area at any specific speed and duration. Traps of any size radius, number, and placement may "catch" the individuals by intercepting them during flight. By varying these parameters, one can determine the number of traps required for effective control based on realistic assumptions or actual data about the insect species, its pheromone, and population level. The simulation model led to the development of iterative equations that rapidly derive the same results as the simulation model, although without indicating the statistical variation. The second objective was to use the model and the iterative equations to estimate the trapping efficiency of pheromone-baited traps during control of the bark beetle *Ips typographus*.

METHODS AND MATERIALS

A computer program for personal computers that simulates insect movement and their catch on traps was developed with the QuickBASIC programming language (version 4.5, Microsoft). The source code (TRAP-SIM.BAS) was compiled to a binary, machine-coded, executable file, by the Microsoft compiler version 4.50 and overlay linker version 3.69 to obtain maximum speed for simulations. IBM-compatible personal computers with EGA/VGA graphics can execute the simulation program (a math coprocessor is recommended). The operation of TRAP-SIM.BAS is diagrammed in Figure 1 and the arrows between boxes indicate program flow.

The model is similar to a mate-finding model published earlier (Byers, 1991) except that each trap (formerly a female) can catch any number of insects. The user enters the x and y sides of the area, the number of insects, flight speed, trap radius, and duration of the control period. Realistic movement of insects is achieved by using polar coordinates in which the angle of directional movement is changed randomly at each step at most equal to the angle of maximum turn (AMT), which can be either right or left (chosen at random) from the previous direction (Figure 2). The step size and AMT can be varied in the model but have little effect on the results (Byers, 1991). When insects impact the area's

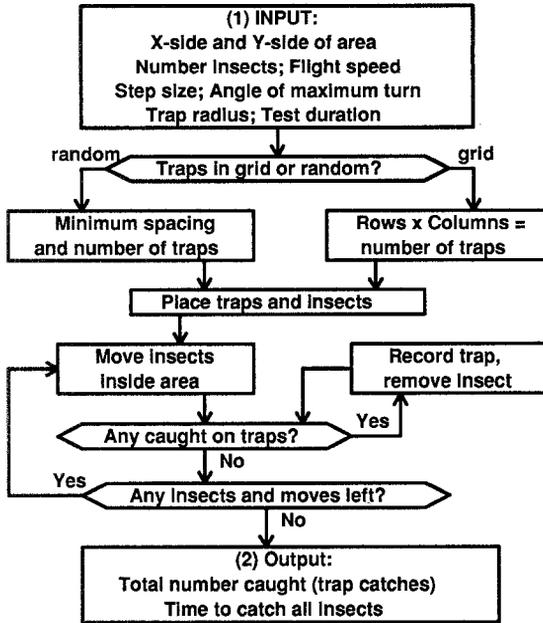


FIG. 1. Relationships of program parts of TRAP-SIM.EXE, a simulation model for insect movement inside a bounded area where any number of traps can intercept insects during the simulation period.

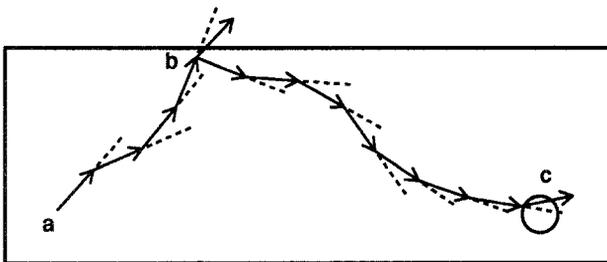


FIG. 2. Animal movement begins at (a) at a random angle for a uniform step (of any specified size). The next step is either to the left or right of the previous direction in an angular amount of less than the AMT (angle of maximum turn). The AMT is chosen by the user (0-180°), but the deviation (right or left) and magnitude (<AMT) are chosen at random. If an animal attempts to move outside the area's boundaries, e.g., at (b), then another angle of up to 360° is chosen at random. Animals are caught by circular traps when within the radius or even when intersecting the circle regardless of the step size (c).

boundaries, they rebound at a random angle (Figure 2). Initial angular directions and positions of individuals are also chosen at random.

Placement of a certain number of traps in the model can be done in a grid of any row \times column arrangement with automatic even spacing (Figure 1). Alternatively, traps can be placed in a random pattern with at least a specified amount of minimum spacing between traps (Byers, 1984, 1992). The "insects" move a step at a time (usually 5 m) up to the number of moves determined by the test duration and the speed of flight, or until caught by a trap. Insects are removed from the simulation if caught, and the percentage of the initial population caught at the end of the test, or the time observed to catch all the insects, is recorded at the end (Figure 1).

While the simulation model can be used with any insect where an average flight or walking speed can be determined, in this paper the focus will be on bark beetles (Coleoptera: Scolytidae), specifically *Ips typographus* L., the major pest of Norway spruce, *Picea abies* (L) Karst., in Europe (Austarå et al., 1984). In order to determine the effect of a model parameter on the catch, one can hold most other important parameters constant while varying the parameter of interest. It is more realistic and interesting to choose parameters that are as close to the expected natural values as possible. Byers et al. (1989) presented a method for comparing relative attraction distances of different insect species to pheromones called the "effective attraction radius" (*EAR*). The *EAR* for a pheromone-baited trap is the radius that would be needed by an imaginary spherical passive trap in order to intercept as many insects as that actually caught on the pheromone trap (Byers et al., 1989).

$$EAR = \sqrt{\frac{AL}{P\pi}} \quad (1)$$

The *EAR* is found by comparing the catches (*P*) on passive traps of known dimension (*L* is trap silhouette area) to the catch on pheromone-baited traps (*A*). For the synthetic two-component pheromone blend of *I. typographus* (2-methyl-3-buten-2-ol released at 50 mg/day and [1(*S*),4(*S*),5(*S*)-*cis*-verbenol at 1 mg/day], the *EAR* estimation was about 2 m (Byers et al., 1989). This three-dimensional theoretical distance was approximated as a two-dimensional (effective catch radius) in the model. The flight speed of *I. typographus* in nature was also estimated at about 2 m/sec (Byers et al., 1989).

The relationship between the number of moves and the cumulative catch for 200 beetles in a 1-km² area (a very low population density) was obtained by simulation. The model parameters are reported in Figure 3. The effects of increasing the number of insects, trap radius, flight speed, and number of traps also were determined on the percent control in 8 hr or the hours required to catch all insects. Based on the results from the simulation model, iterative

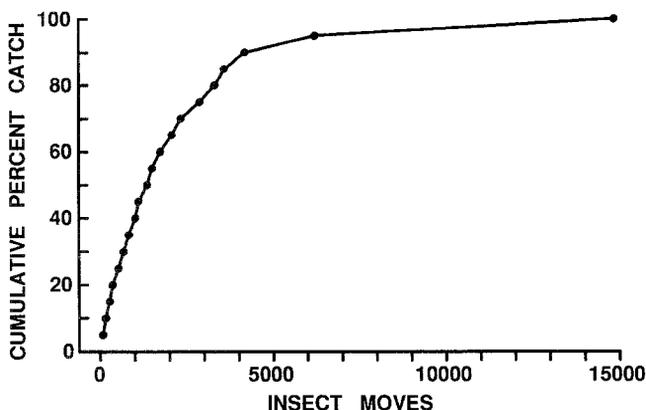


FIG. 3. Relationship between the number of insect moves and the cumulative percentage of catch obtained in the simulation model. Model parameters were: 1000×1000 -m (1-km^2) area, 200 insects, 2 m/sec flight speed, 5 m step size (move), 30° angle of maximum turn (AMT), 25 traps (5×5 grid, 142.8 m spacing), 2-m trap radius, and 8 hr test duration.

equations were derived that can construct the same relationships, but rapidly give theoretical mean results.

RESULTS

The simulation model (Figures 1 and 2) found that the cumulative percent catch of the beetles increased rapidly during the initial moves, but it took increasingly longer (more moves) to catch the last of the beetles (Figure 3). This result can be expected since initially there are many more beetles available to be caught by the 25 traps, but in the later part of the test period there are relatively few beetles (the density is much less) so the probability of catch by all the traps is much less. However, the probability of any particular insect being caught is constant over the whole period.

Surprisingly, the turn angle taken at random by each insect at each move (less than a maximum angle of turn = AMT) has very little effect on the rate of catch. An AMT of 30° simulates insect flight reasonably well, but use of 5° for a more straight flight produces almost the same effects on trap catch. For instance, using parameters as in Figure 3 but a trap radius of 0.25 m, the percent control for an AMT = 5° (nearly straight path) was $47.04 \pm 2.60\%$ ($\pm 95\%$ CL, $N = 12$), while it was $52.00 \pm 2.18\%$ for an AMT = 30° (used in most simulations) or $43.92 \pm 1.99\%$ for an AMT = 180° (purely random). The iterative equation (discussed later, Figure 8) predicts 51.5% control in 8 hr. The

step size also has little effect on the catch rate as shown earlier (Byers, 1991). Purely random path angles (Brownian motion) produce slightly less catch, since the insects cover relatively less new ground due to more likely back-stepping over areas they had just been in.

Another intriguing finding was that the placement of traps, whether distributed in a highly regular grid arrangement or at random (but not overlapping), had no apparent effect on the rate of catch. Using the same parameters as above, 49 traps of 2-m radius were placed in either a 7×7 grid (125-m spacing) or at random with a spacing of at least 4 m between centers (minimum allowed distance was 4 m). It was found that the average time to catch all insects was not significantly different between the two placements, 3.97 ± 0.36 hr and 4.03 ± 0.68 hr ($\pm 95\%$ CL, $N = 10$), respectively. The iterative equations (Figure 8) predict a time of 4.17 hr for 100% control.

Increasing the numbers (and densities) of insects in the initial population has a logarithmic effect on the number of hours needed to catch all the insects (Figure 4). Thus, for 25, 2-m radius traps in a 1-km² area, the time required to catch all beetles changes relatively little as the number of beetles is increased beyond several hundred. Increasing the radius of the trap or the flight speed has the same effect on the catch (percent control) of 200 beetles in a period of 8 hr and parameters as above (Figure 5A and B). Again, increases in flight speed or trap radius have greater effects on catch at lower speeds and smaller radii. As the flight speed or trap radius is increased still more, it has proportionally less

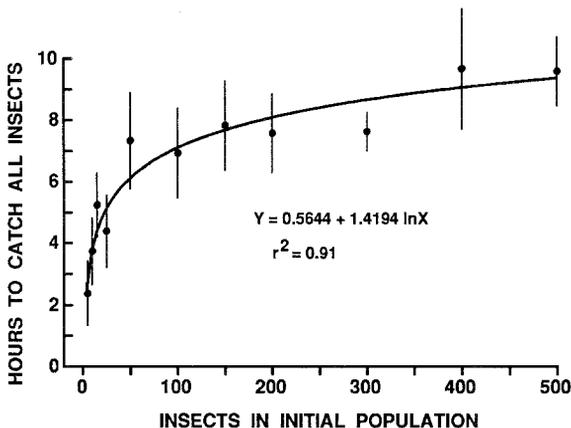


FIG. 4. Relationship between the number of insects in the initial population before control and the number of hours to catch all these insects as found with the simulation model. Model parameters were as in Figure 3 except that the number of insects was varied and the test duration was made long enough to catch all insects. Vertical bars represent 95% confidence limits ($N = 4$).

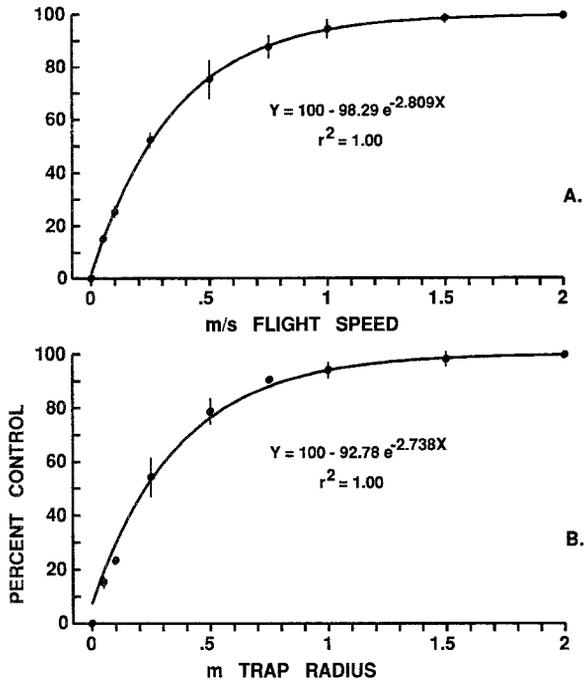


FIG. 5. (A) Relationship between flight speed (m/s) and percent control of the insect population as found with the simulation model. Model parameters were as in Figure 3 except for variation of flight speed. (B) Effect of trap radius (m) on percent control of the population as found with the simulation model, model parameters as in Figure 3 except for variation of trap radius. Vertical bars represent 95% confidence limits ($N = 4$).

effect on the time to catch all insects, even though less time is needed to catch them at these larger speeds or radii (Figure 6A and B). In the model, the number of traps of 2-m radius can be increased from 1 to 25 (Figure 7A), causing the percent control or catch to increase less and less rapidly as the trap number is increased. When the number of traps is increased still further, from 25 to 400/km², then the time to catch all insects decreases but less and less rapidly with an increase in number of traps (Figure 7B).

The results of the simulations above gave insight for the development of iterative formulas that calculate the expected time required to catch a given proportion of the insects in a certain area based on trap radius, number of traps, number of insects, and average speed of flight. Intuitively, the time between catches of insect on traps would be inversely proportional to trap diameter, i.e., a larger trap would likely intercept insects sooner than a smaller trap. Further-

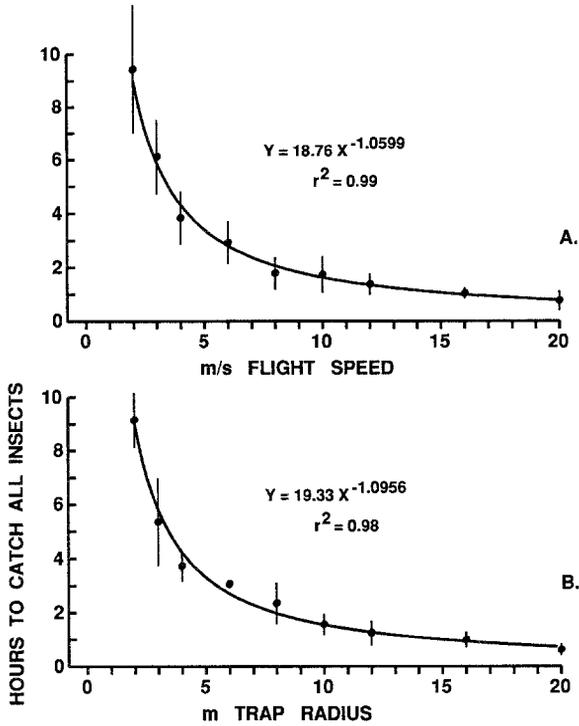


FIG. 6. (A) Relationship between flight speed (m/s) and the number of hours to catch all insects in the area as found with the simulation model. Model parameters were as in Figure 3 except for variation of flight speed and test duration was indefinite. (B) Effect of trap radius (m) on time required to catch all insects in the area as found with the simulation model, model parameters as in Figure 3 except for variation of trap radius and indefinite test duration. Vertical bars represent 95% confidence limits ($N = 4$).

more, a greater insect flight speed, greater number of traps, or greater density of insects would decrease the expected time between catches. Therefore, let R = radius of the trap in meters, K = number of traps, T = time in seconds, S = flight speed in meters per second, N = number of initial insects, and A = area in square meters, then the time needed to catch the first insect is: $T = A/(2RSKN)$. The total time to catch any proportion P of insects is given by the equation:

$$T = \sum_{C=0}^{NP-1} \frac{A}{2RSK(N - C)} \tag{2}$$

Thus, if $A = 1,000,000 \text{ m}^2$ (i.e., 1 km^2), there are 25 traps each of 2-m radius, beetles fly at 2 m/s, and there are 70,000 beetles initially, then the expected

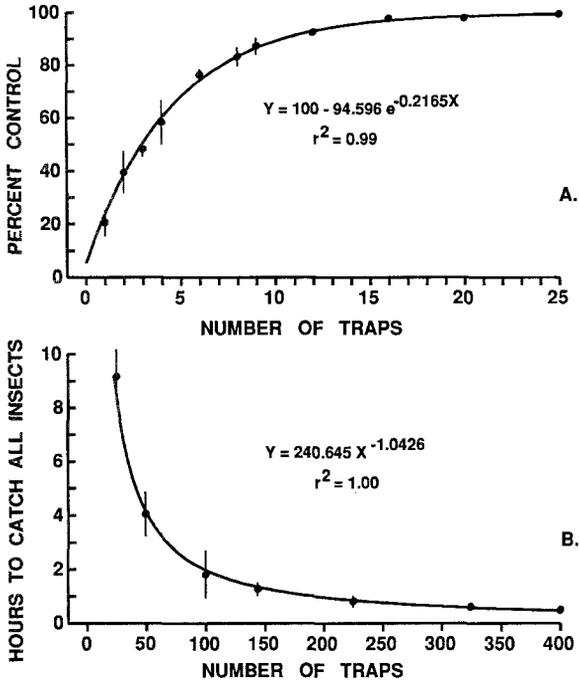


FIG. 7. (A) Relationship between number of traps and percent control of the insect population as found with the simulation model. Model parameters were as in Figure 3 except for variation of number of traps and grid rows and columns. (B) Effect of number of traps on time required to catch all insects in the area as found with the simulation model, model parameters as in Figure 3 except for variation of trap number, rows and columns. Vertical bars represent 95% confidence limits ($N = 4$).

time to catch 95% ($P = 0.95$) of the beetles is equal to 14,978 s (4.16 hr). A BASIC program that calculates the expected time from equation 2 and others below is shown in Figure 8.

When one wants to determine the expected proportion of the population that will be caught (percent control) in a specified time period based on the above parameters, then a repetitive calculation is done. Here the expected times (from equation 2) to catch successive insects are subtracted sequentially from the specified time until no time is left. The number of insects caught divided by the initial population estimate multiplied by 100 is then the percent control expected in the specified time period. The BASIC program in Figure 8 demonstrates the algorithm (lines 140–170). For example, Byers et al. (1989) used sticky trap screens to estimate that 9000 *I. typographus* were flying during a few hours in a 1-km² area. If control of *I. typographus* at this density is imple-

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10 CLS : COLOR 15: PRINT "TRAPS NEEDED TO TRAPOUT PROPORTION OF INSECTS"
20 PRINT "IN TIME ALLOTTED - (C) 1992 by John A. Byers": PRINT : COLOR 11
30 INPUT "NUMBER OF INSECTS IN AREA"; N: N = INT(N): IF N <= 0 THEN 30
40 INPUT "RADIUS OF TRAP (In m)"; R: IF R <= 0 THEN 40
50 INPUT "SPEED OF INSECT (In m/s)"; S: IF S <= 0 THEN 50
60 INPUT "NUMBER OF TRAPS"; K: K = INT(K): IF K <= 0 THEN 60
70 INPUT "ENTER %CONTROL ( <=100% )"; P: IF P <= 0 OR P > 100 THEN 70
80 INPUT "ENTER DURATION OF TRAPOUT (In s)"; TIME: IF TIME <= 0 THEN 80
90 INPUT "AREA OF TEST (In m2)"; A: IF A <= 0 THEN 90
100 P = P / 100: TT = TIME: COLOR 15: PRINT
110 PRINT "WORKING...": PRINT : FOR C = 0 TO N * P - 1
120 T = T + A / (2 * R * S * K * (N - C)): NEXT: C = 0
130 PRINT "TIME TO CATCH"; P * 100; "% ="; T; "s OR"; T / 3600; "h"
140 IF C = N THEN K = 0: GOTO 170
150 TIME = TIME - (A / (2 * R * S * K * (N - C)))
160 C = C + 1: IF TIME > 0 THEN 140 ELSE K = 0
170 PRINT C / N * 100; "% CAUGHT IN TIME ="; TT; "s OR"; TT / 3600; "h"
180 FOR C = 0 TO N * P - 1: K = K + A / (2 * R * S * TT * (N - C)): NEXT
190 PRINT K; "TRAPS NEEDED TO CATCH"; P * 100; "% IN"; TT; "s ALLOTTED"

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FIG. 8. BASIC listing of program using iterative equations (see text) to predict (1) the time required to catch a specified percentage of the insect population, (2) the population percentage caught within a specified time period, and (3) the number of traps required to catch a specified percentage of the population within a specified time period. The predictions (1-3) are dependent on the number of insects in the initial population, the effective radius of the trap, the average flight speed of the insect, the number of traps, the desired level of control, the duration of the trapping period, and the size of the control area.

mented for 48 hr (172,800 s) using 10 pheromone traps with an effective radius of 2 m in a 4-km² area containing (4 × 9000) beetles flying at 2 m/s then 96.8% of the population would be trapped out.

Another calculation of interest is the expected number of traps of a certain dimension that are required to trap a certain percentage of the population in a given time period. Using the parameters described in equation 2, the number of traps can be found from the following equation:

$$K = \sum_{c=0}^{NP-1} \frac{A}{2RST(N-C)} \quad (3)$$

The BASIC program (Figure 8) calculated that in a trapping period of 20 hr five or six traps (actually 5.2 traps) each with a radius of 2 m would be needed to achieve 95% control of 9000 beetles (flying at 2 m/s) in an area of 1,000,000 m². Even if there were 100 times more beetles (900,000) flying in the area, only 5.2 traps would still be needed for 95% control in 20 hr (since the number of traps needed is logarithmically related to the number of insects). If 95% control is to be achieved in one tenth the time (2 hr) then 10 times the number of traps are needed (52 traps).

The iterative equations (Figure 8) also were used to validate the statistical regressions obtained from the simulation model. In Figure 4, a logarithmic relationship was found between population density and time to catch all insects ($r^2 = 0.91$), and the iterative equations also gave results that were a perfect logarithmic relation ($r^2 = 1.00$). The iterative equations also gave results that perfectly fit the asymptotic exponential form shown in Figures 5A and 5B and in Figure 7A. The negative power curves in Figures 6A, 6B, and 7B were validated with results from the iterative equations, which fit these curves perfectly.

DISCUSSION

The personal computer video monitor allows viewing of the individual "insects" as they wander about within the simulated area. Traps and their diameter are also represented on the screen and when insects are caught, they turn color from white to red and cease moving. The model is primarily useful for demonstrating the principles of insect mass trapping since the iterative equations yield essentially the same results and require much less computing time. The simulation model does allow an estimation of the statistical variation that could result in nature under similar conditions, while the iterative equations give exact-mean answers. The chemical ecologist and forest pest manager will find the iterative equations more useful in practice since several parameters of interest can be tried rapidly.

The simulation model revealed relationships that are not always intuitive. For example, it might seem that an increase in flight speed ought to cause a linear decrease in the time needed to catch all insects. The problem is that the entire population (or a specific proportion) must be caught, and this time decreases as a power function. Another example is that the percent of the population caught in a certain time period (percent control) with an increase in trap radius might seem to be linearly related, but this implies that more than 100% control could be achieved, which is impossible. Almost no matter how large the trap is made, there will always be some simulations where not all the beetles were caught in the time period due to pure chance.

Pheromone plumes are composed of packets of more concentrated pheromone molecules (cf. Baker, 1986). The precise dimensions of the packets are not known but it can be assumed that they differ under different wind and weather conditions. Gaussian surfaces can represent to some degree of accuracy the time-averaged dimensions of a pheromone plume (cf. Elkinton and Cardé, 1984; Byers, 1987). A plume extends indefinitely but its detection by the insect depends on a threshold concentration, and furthermore, the probability of orienting to the pheromone source (baited trap) depends on where the insect enters the plume.

These complications for use in models may be largely avoided with the concept of the effective attraction radius (*EAR*, see equation 1) of a semiochemical release rate for an insect. In order to use the *EAR* for the present models, one must determine it for the particular pest species. In *I. typographus*, as mentioned above, this radius was about 2 m for a specific release rate of synthetic pheromone components. This radius is three-dimensional, but for the model it was considered as two-dimensional (i.e., a cylinder). Thus, the *EAR* is probably a lower estimate of the effective catch radius that would be most appropriate for the simulation model. A review of these concepts of attraction radius is given by Schlyter (1992).

It should be stressed that the simulation model was instrumental in deriving the equations (2 and 3 and Figure 8) that iteratively calculate the same results as the simulation model. The simulation model can handle up to about 15,000 insects but becomes prohibitively slow. The iterative equations are much faster than the simulation, but the equations still must iterate once for each insect in the population. However, for populations of even one million insects, it takes only 1–2 min on IBM-compatible personal computers (486 or 386 + math coprocessor) to calculate expected catches or required traps (from Figure 8) for any set of model parameters.

The first major attempt to control bark beetle populations using pheromone-baited traps was done in 1970 in California (Bedard et al., 1979; Wood, 1980; DeMars et al., 1980). Large (1 × 2 m) sticky screens baited with *exo*-brevicommin and frontalin, pheromone components of the western pine beetle, *Dendroctonus brevicomis* (Silverstein et al., 1968; Kinzer et al., 1969), plus the host monoterpene, myrcene (Bedard et al., 1969), were placed in ponderosa pine forests at Bass Lake, California. In four plots of 1.3 km² each, 66 pheromone traps were deployed in a grid of about 161 m spacing. Over a million beetles were caught, and the test appeared to be successful since the number of trees killed by the beetle declined to 10% of the pretreatment level for several years (Bedard et al., 1979; Wood, 1980; DeMars et al., 1980).

Norway and Sweden have extensive forests, and in the 1970s a major outbreak of the European spruce engraver, *I. typographus*, devastated many areas (Austarå et al., 1984). Since the pheromone of this beetle had recently been identified as a mixture of 2-methyl-3-buten-2-ol and 1(*S*),4(*S*),5(*S*)-*cis*-verbenol (Bakke et al., 1977), an extensive mass-trapping control program was initiated in 1979 and may have led to the decline of the outbreak after 1980 (Bakke, 1985, 1988, 1989; Vité, 1989). Several other European studies have reported successful control of bark beetles with the intensive use of pheromone-baited traps (Vrkok, 1989; Richter, 1991).

These pioneering studies of mass trapping using pheromones did have some deficiencies. Many of these studies lacked appropriate controls or check plots, so it is not possible to determine the success of the control program. Further-

more, a combination of experience and intuition led to subjective estimates as to the level of trapping and the pheromone release rate most appropriate for control of the population. Certainly these questions are complex, and it is not surprising that they were not solved entirely successfully back then. However, the models presented here may help establish a rational basis for future control efforts using pheromone traps based on estimates of the population size (density), average flight speed, expected control duration, effective trap catch radius, and number of traps deployed.

Weber (1987) was critical of pheromone trapping of bark beetles for control since he calculated that enough beetles would remain untrapped to then colonize susceptible hosts and replenish the population due to an absence of competition. This assessment seems overly pessimistic since trapping experiments with different traps and pheromone dosages were not done. Furthermore, the complementary effects of other forest management practices, such as removal of slash and infested trees to reduce populations, were not considered. The consequences of population reduction to densities below the threshold required to overcome tree resistance by means of a mass attack were also not considered (Berryman and Stenseth, 1989; Berryman et al., 1989). In contrast, the present models indicate that insect populations can potentially be drastically reduced with a surprisingly small number of traps with an effective radius that seems smaller than that one might intuitively expect for pheromone baits. However, whether this population reduction is sufficient to affect natural matings and population levels over several generations is still an open question.

In many past control programs using pheromone trapping there has been the problem of finding control areas to determine whether the treatment has been effective. However, several monitor traps placed inside the control area (or even the control traps themselves) will indicate the population density and the progress of the control program. If no more insects are being caught, then obviously the control is a success, unless the flight period is over. This can be determined by monitor traps in untreated areas some distance away but still within the same general biotope and climatic regime. Usually only one beetle or pair of bark beetles begins attack of a tree, and at this time pheromone release is relatively low compared to a few days later when thousands of beetles participate in the mass attack. Thus, it seems advantageous to initiate mass trapping before beetles swarm in the spring and have time to build aggregations that can compete with traps for attraction of dispersing beetles. In moths, reproduction can occur despite the high trapping efficiency suggested by the model because male moths may mate with females before being trapped (Roelofs et al., 1970).

There are several variables that can influence the situation in nature so that trapping of the population does not follow the predictions based on the simulation model or iterative equations. For example, the "flight" speed used in the models (2 m/s; Byers et al., 1989) may be more than the speed observed for

flying or wind-blown insects since they often stop to rest or feed. Moreover, in the case of bark beetles, there can be host volatiles that attract the beetles during their swarming flight or trees under colonization where aggregation pheromones are released (Byers, 1989). Several studies have indicated that as the density of calling female moths increases, the catches on pheromone-baited traps increase relatively less or may decline, probably due to competition between the natural and synthetic sources (Raulston et al., 1979; Nakamura, 1982; Witz et al., 1992). Traps can also be overloaded with catch, and synthetic pheromone release rates can diminish, which will cause catches in nature to differ from model predictions. Pheromone release rates can decrease (and the effective pheromone trap radius) due to compound degradation and in other cases due to exponential decline from substrates (e.g., rubber septa). Methyl decadienoate, a pheromone component of the bark beetle *Pityogenes chalcographus*, is especially sensitive to sunlight and attraction rates can be halved in a few hours unless the compound is shaded. In the models, the shapes of pheromone plumes emanating from traps have been transformed to the *EAR*, which also reduces the correspondence between reality (some type of Gaussian time-averaged plume depending on the wind) and the models (a circle).

In spite of these assumptions, the iterative equations should prove useful to pest control managers in agriculture and forestry. Models are useful to define problems, organize thoughts, understand the system, identify areas to investigate, communicate understanding, make predictions, generate hypotheses, and act as standards for comparison (Worner, 1991). The model here allows one to balance resources (number of traps per area) with expected populations and parameters of the pest insect to obtain a cost-effective deployment of pheromone traps as a first approximation for experiments and control treatments.

The programs TRAP-SIM.EXE (Figure 1) and TRAPOUT.EXE (Figure 8) can be obtained from the author (send a formatted disk and mailer for IBM-compatible computers). Donations of \$5 or 35 Swedish Kronor for shipping would be appreciated.

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REFERENCES

- AUSTARÅ, O., ANNILA, E., BEJER, B., and EHNSTRÖM, B. 1984. Insect pests in forests of the Nordic countries 1977–1981. *Fauna Norv. Ser. B.* 31:8–15.
- BAKER, T.C. 1986. Pheromone-modulated movements of flying moths, pp. 39–48, in T.L. Payne, C.E. Kennedy, and M.C. Birch (eds.). *Mechanisms in Insect Olfaction*. Clarendon Press, Oxford.
- BAKKE, A. 1985. Methods and effects of suppressing bark beetle populations, pp. 169–174, in L.

- Safranyik (ed.). The Role of the Host in the Population Dynamics of Forest Insects. Proceedings. IUFRO conference Banff Centre 1983. (Pacific Forest Research Centre, Victoria, B.C.).
- BAKKE, A. 1988. Potential use of semiochemicals for integrated control of bark beetles in Europe, pp. 257-261, in T.L. Payne, and H. Saarenmaa (eds.). Integrated Control of Scolytid Bark Beetles. Virginia Polytechnic Institute and State University, Blacksburg, Virginia. 356 pp.
- BAKKE, A. 1989. The recent *Ips typographus* outbreak in Norway: Experiences from a control program. *Holarct. Ecol.* 12:515-519.
- BAKKE, A., FRØYEN, P., and SKATTEBØL, L. 1977. Field response to a new pheromonal compound isolated from *Ips typographus*. *Naturwissenschaften* 64:98.
- 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. 1988. Models for combining methods of pest control: Food-baited and pheromone-baited traps containing either insecticide or chemosterilant. *Bull. Entomol. Res.* 78:573-590.
- BARCLAY, H.J., and LI, C. 1991. Combining methods of pest control: Minimizing cost during the control program. *Theor. Popul. Biol.* 40:105-123.
- BEDARD, W.D., TILDEN, P.E., WOOD, D.L., SILVERSTEIN, R.M., BROWNLEE, R.G., and RODIN, J.O. 1969. Western pine beetle: Field response to its sex pheromone and a synergistic host terpene, myrcene. *Science* 164:1284-1285.
- BEDARD, W.D., WOOD, D.L., and TILDEN, P.E. 1979. Using behavior modifying chemicals to reduce western pine beetle-caused tree mortality and protect trees, pp. 159-163, in W.E. Waters, (ed.). Current Topics in Forest Entomology. U.S. Forest Service General Technical Report WO-8.
- BEROZA, M., and KNIPLING, E.F. 1972. Gypsy moth control with the sex attractant pheromone. *Science* 177:19-27.
- BERRYMAN, A.A., and STENSETH, N.C. 1989. A theoretical basis for understanding and managing biological populations with particular reference to the spruce bark beetle. *Holarct Ecol.* 12:387-394.
- BERRYMAN, A.A., RAFFA, K.F., MILLSTEIN, J.A., and STENSETH, N.C. 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. *Oikos* 56:256-263.
- BIRGERSSON, G., and BERGSTRÖM, G. 1989. Volatiles released from individual spruce bark beetle entrance holes: Quantitative variations during the first week of attack. *J. Chem. Ecol.* 15:2465-2483.
- BROWNE, L.E. 1978. A trapping system for the western pine beetle using attractive pheromones. *J. Chem. Ecol.* 4:261-275.
- BROWNE, L.E., WOOD, D.L., BEDARD, W.D., SILVERSTEIN, R.M., and WEST, J.R. 1979. Quantitative estimates of the western pine beetle attractive pheromone components, *exo-brevicomin*, *frontalin*, and *myrcene* in nature. *J. Chem. Ecol.* 5:397-414.
- BYERS, J.A. 1984. Nearest neighbor analysis and simulation of distribution patterns indicates an attack spacing mechanism in the bark beetle, *Ips typographus* (Coleoptera: Scolytidae). *Environ. Entomol.* 13:1191-1200.
- BYERS, J.A. 1987. Interactions of pheromone component odor plumes of western pine beetle. *J. Chem. Ecol.* 13:2143-2157.
- BYERS, J.A. 1989. Chemical ecology of bark beetles. *Experientia* 45:271-283.
- BYERS, J.A. 1991. Simulation of mate-finding behaviour in pine shoot beetles, *Tomicus piniperda*. *Anim. Behav.* 41:649-660.
- BYERS, J.A. 1992. Dirichlet tessellation of bark beetle spatial attack points. *J. Anim. Ecol.* 61:759-768.
- BYERS, J.A., ANDERBRANT, O., and LÖFQVIST, J. 1989. Effective attraction radius: A method for comparing species attractants and determining densities of flying insects. *J. Chem. Ecol.* 15:749-765.

- BYERS, J.A., BIRGERSSON, G., LÖFQVIST, J., APPELGREN, M., and BERGSTRÖM, G. 1990a. Isolation of pheromone synergists of bark beetle, *Pityogenes chalcographus*, from complex insect-plant odors by fractionation and subtractive-combination bioassay. *J. Chem. Ecol.* 16:861-876.
- BYERS, J.A., SCHLYTER, F., BIRGERSSON, G., and FRANCKE, W. 1990b. E-Myrcenol in *Ips duplicatus*: An aggregation pheromone component new for bark beetles. *Experientia* 46:1209-1211.
- CAMPION, D.G., CRITCHLEY, B.R., and McVEIGH, L.J. 1989. Mating disruption, pp. 89-119, in A.R. Jutsum and R.F.S. Gordon (eds.). *Insect Pheromones in Plant Protection*, Wiley & Sons, New York.
- DEMARS, C.J., SLAUGHTER, G.W., BEDARD, W.D., NORICK, N.X., and ROETTGERING, B. 1980. Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. *J. Chem. Ecol.* 6:853-866.
- DU, J.W., LÖFSTEDT, C., and LÖFQVIST, J. 1987. Repeatability of pheromone emissions from individual female ermine moths *Yponomeuta padellus* and *Yponomeuta rorellus*. *J. Chem. Ecol.* 13:1431-1442.
- ELKINTON, J.S., and CARDÉ, R.T. 1984. Odor dispersion in chemical ecology of insects, pp. 73-91, in W.J. Bell and R.T. Cardé (eds.) Chapman and Hall, Ltd., New York.
- FISHER, M.E., VAN DEN DRIESSCHE, P., and BARCLAY, H.J. 1985. A density dependent model of pheromone trapping. *Theor. Popul. Biol.* 27:91-104.
- FLINT, H.M., and MERKLE, J.R. 1984. Studies on disruption of sexual communication in the pink bollworm, *Pectinophora gossypiella*, (Lepidoptera: Gelechiidae) with micro encapsulated gossyplure or its component Z, Z isomer. *Bull. Entomol. Res.* 74:25-32.
- HANIOTAKIS, G., KOZYRAKIS, M., FITSAKIS, T., and ANTONIDAKI, A. 1991. An effective mass trapping method for the control of *Dacus oleae* (Diptera: Tephritidae). *J. Econ. Entomol.* 84:564-569.
- HODGES, R.J., BENTON, F.P., HALL, D.R., and DOS, S.S.R. 1984. Control of *Ephestia caustella* (Lepidoptera: Phycitidae) by synthetic sex pheromones in the laboratory and store. *J. Stored Prod. Res.* 20:191-198.
- JONES, O.T., LISK, J.C., HOWSE, P.E., BAKER, R., BUENO, A.M., and RAMOS, P. 1982. Mating disruption of the olive fruit fly *Dacus oleae* with the major component of its sex pheromone, pp. 500-505, in R. Cavalloro (ed.). *Fruit Flies of Economic Importance*. Proceedings of the CEC/IOBC International Symposium, Athens, Greece.
- KINZER, G.W., FENTIMAN, A.F., JR., PAGE, T.F., FOLTZ, R.L., VITÉ, J.P., and PITMAN, G.B. 1969. Bark beetle attractants: Identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. *Nature* 211:475-476.
- KNIPLING, E.F., and MCGUIRE, J.U., JR. 1966. Population models to test theoretical effects of sex attractants used for insect control. *U.S. Dep. Agric. Inform. Bull.* 308:2-4.
- NAKAMURA, K. 1982. Competition between females and pheromone traps: Time lag between female mating activity and male trap captures. *Appl. Entomol. Zool.* 17:292-300.
- NAKASUI, F., and FUJITA, K. 1980. A population model to assess the effect of sex pheromones on population suppression. *Appl. Entomol. Zool.* 15:27-35.
- RAMASWAMY, S.B., and CARDÉ, R.T. 1984. Rate of release of spruce budworm *Choristoneura fumiferana* pheromone from virgin females and synthetic lures. *J. Chem. Ecol.* 10:1-8.
- RAULSTON, J.R., LINGREN, P.D., SPARKS, A.N., and MARTIN, D.F. 1979. Mating interaction between native tobacco budworms and released backcross adults. *Environ. Entomol.* 8:349-353.
- RICHTER, D. 1991. Control of bark beetles in the five new states of the Federal Republic of Germany, pp. 28-36, in A. Wulf and R. Kehr (eds.). *Bark Beetle Hazards following Storm Damage: Possibilities and Limits of Integrated Control*. Colloquium, Braunschweig, Germany. Communications from the Federal Biological Institute for Agriculture and Forestry, Berlin-Dahlem, No. 267.

- ROELOFS, W.L., GLASS, E.H., TETTE, J., and COMEAU, A. 1970. Sex pheromone trapping for red-banded leaf roller control: Theoretical and actual. *J. Econ. Entomol.* 63:1162-1167.
- SCHLYTER, F. 1992. Sampling range, attraction range, and effective attraction radius: Estimates of trap efficiency and communication distance in coleopteran pheromone and host attractant systems. *J. Appl. Entomol.* 114:439-454.
- SCHLYTER, F., BIRGERSSON, G., BYERS, J.A., LÖFQVIST, J., and BERGSTRÖM, G. 1987. Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates. *J. Chem. Ecol.* 13:701-716.
- SILVERSTEIN, R.M. 1981. Pheromones: Background and potential for use in insect pest control. *Science* 213:1326-1332.
- SILVERSTEIN, R.M., BROWNLEE, R.G., BELLAS, T.E., WOOD, D.L., and BROWNE, L.E. 1968. Brevicomin: Principal sex attractant in the frass of the female western pine beetle. *Science* 159:889-891.
- STERNLICHT, M., BARZAKAY, I., and TAMIM, M. 1990. Management of *Prays citri* in lemon orchards by mass trapping of males. *Entomol. Exp. Appl.* 55:59-68.
- VILLAVASO, E.J. 1982. Boll weevil, *Anthonomus grandis*, isolated field plot studies of disruption of pheromone communication. *J. Ga. Entomol. Soc.* 17:347-350.
- VILLAVASO, E.J., and MCGOVERN, W.L. 1981. Boll weevil, *Anthonomus grandis grandis*, disruption of pheromonal communication in the laboratory and small field plots. *J. Ga. Entomol. Soc.* 16:306-310.
- VITÉ, J.P. 1989. The European struggle to control *Ips typographus*: Past present and future. *Holarct. Ecol.* 12:520-525.
- VRKOC, J. 1989. Use of insect pheromone in integrated pest management examples from Czechoslovakia. *Chem. Scr.* 29:407-410.
- WEBER, T. 1987. Can bark beetles be controlled efficiently by application of pheromone traps. *Allg. Forstz.* 42:87-89.
- WITZ, J.A., LOPEZ, J.D., JR., and LATHEEF, M.A. 1992. Field density estimates of *Heliothis virescens* (Lepidoptera: Noctuidae) from catches in sex pheromone-baited traps. *Bull. Entomol. Res.* 82:281-286.
- WOOD, D.L. 1980. Approach to research and forest management for western pine beetle control, pp. 417-448, in C.B. Huffaker (ed.). *New Technology of Pest Control*. John Wiley & Sons, New York.
- WORNER, S.P. 1991. Use of models in applied entomology: The need for perspective. *Environ. Entomol.* 20:768-773.
- ZVIRGZDINS, A., LINGREN, P.D., HENNEBERRY, T.J., NOWELL, C.E., and GILLESPIE, J.M. 1984. Mating disruption of a wild population of tobacco budworm, *Heliothis virescens*, (Lepidoptera: Noctuidae) with virelure. *J. Econ. Entomol.* 77:1464-1469.