

## Simulation of the mate-finding behaviour of pine shoot beetles, *Tomicus piniperda*

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**Abstract.** An algorithm for animal searching behaviour was constructed that allows independent variation at random of movement parameters such as speed, duration, step size, and maximum right or left turn angle. The area, radius of the object searched for, and number of objects and searchers can also be varied. A capture algorithm is presented that can determine whether a searching animal intercepts a circle (object) irrespective of the step size. These two algorithms were incorporated into a computer simulation model of mate finding for walking male bark beetles, *Tomicus piniperda*, in search of females that remained stationary when boring into the bark of Scots pine, *Pinus sylvestris*. The model showed that, for realistically chosen parameters, males were able to find 'females' at apparently natural rates without the need to enlarge the radius of the 'female' beyond the size of an actual female. This indicates that there may be little, if any, advantage in the evolution of a long-range pheromone, for which no chemical and behavioural evidence has yet been found.

Simulation of animal movement is useful for understanding such areas of animal behaviour as kinesis (Rohlf & Davenport 1969; Doucet & Drost 1985; Benhamou & Bovet 1989), dispersal (Skellam 1973) and optimal searching for mates, prey, food or oviposition sites (Jones 1976, 1977; Pyke 1978; Gries et al. 1989). Models of search behaviour have concerned random movement in four (Rohlf & Davenport 1969; Pyke 1978) or eight (Jones 1976, 1977; Gries et al. 1989) possible directions. A more realistic model of animal movement in all possible directions was outlined by Skellam (1973) for use in dispersal studies, but was not implemented by computer. A recent model allows random changes in path directions based on a normal distribution (Bovet & Benhamou 1988). In the majority of these models a more natural movement was achieved by not allowing a reversal of direction so that the 'animal' generally progressed forward. However, there have been few, if any, computer models that have simulated realistically the relationships of animal movements and mate (or prey) finding in bounded areas with respect to such parameters as speed, time, angle of turning, size of mate or prey, rate of turning and density.

The model animal for my simulation study is the larger pine shoot beetle, *Tomicus piniperda* (L.). This bark beetle (Coleoptera: Scolytidae) is a serious pest of Scots pine, *Pinus sylvestris* L., in

Europe and Asia. Its dispersal and host-seeking flight coincides with temperatures above 13°C in early spring (Byers et al. 1985; Lanne et al. 1987). Almost immediately at these temperatures, *T. piniperda* aggregates en masse on fallen Scots pine that have been damaged during winter storms. It is common to find several tens to hundreds of beetles of both sexes walking about on the trunk. Females soon locate suitable sites where they bore into the bark, but for several hours they are exposed to predators (clerid beetles, *Thanasimus formicarius*). Also at this time males wander in search of females that are boring into the bark. Upon encountering a female a male attempts to monopolize her by jousting with and displacing any resident male, during which time both males stridulate repeatedly (personal observations). These interactions between males usually occur for only a few seconds.

Bark beetles that aggregate en masse on host trees mostly use pheromones (Byers 1989). An earlier study purported to find evidence of a long-range pheromone in *T. piniperda* (Schönherr 1972) while another report was inconclusive (Kangas et al. 1967). My colleagues and I (Byers et al. 1985) have demonstrated that *T. piniperda* are attracted equally to traps containing either infested or uninfested host logs in the field indicating that (1) there is no long-range aggregation pheromone and (2) host compounds are responsible for aggregation.

We used chemical fractionation of odours collected from infested logs and bioassay to isolate three host monoterpenes, ( $\pm$ )- $\alpha$ -pinene, 3-carene and terpinolene, that were attractive when released at natural rates in the forest (Byers et al. 1985; Lanne et al. 1987). These monoterpenes are found in substantial amounts in Scots pine oleoresin, which exudes from broken limbs and wounds on fallen trees. Thus, this olfactory mechanism appears to account for the aggregation of beetles. However, some question still remains as to whether *T. pini-perda* uses a long-range aggregation pheromone, since the previous studies used artificially infested logs and thus may have confounded the natural behaviour. Also, a short-range pheromone, operating after landing, might aid males in finding females.

Here, I present a mate-finding model which is simple in that it does not rely on spatial memory or on long-range orientation of the animal. The searching sex (male) is 'captured' when an individual enters or intercepts the circular area of the female. The model allows males to move in any direction at random, but within limits, while other parameters, such as step size, remain constant during the search period. However, movement parameters can be varied to test for their effect on the efficiency of mate finding and the magnitude of encounters between males. The angular degree of turning, rate of turning, speed of walking, duration of walking, radius of female, number of animals and the  $X, Y$  dimensions of the area can be varied independently. By varying the radius of the female, for example, it is possible to determine the radius at which the probability of pairing during the time period is equivalent to natural pairing rates in nature. This radius should then be similar to the effective radius of a female in nature; if the simulated radius is significantly larger than the female then a long-range attraction (olfactory, acoustic or visual) is indicated.

## METHODS

### Search Algorithm

The operational features of the algorithm are shown in Fig. 1. One begins by entering values for the model variables such as the maximum right or left turn angle and a radius for the 'female' within which all 'males' are 'captured'. According to the model, after each step the male may 'choose' to take

the next step at any angle at random that is within the angle of maximum turn, either right or left from the previous direction. The step size is specified and remains the same throughout the simulation. Other parameters are the  $X$ - and  $Y$ -lengths of the area and the number of male-female pairs. The number of moves (steps) is calculated from the input variables of time (s), step length and speed (i.e. speed  $\times$  time/step size).

The program then places the females and males at random within the area and sets the initial directions of males at random. The females remain stationary. The males are then moved forward to new cartesian coordinates at each move based on their previous direction plus an angle within the angle of maximum turn. If the new coordinates are outside the area then a new direction is chosen at random ( $\pm 360^\circ$ ) until the new coordinates are within the area. Then for each female, all males are checked to determine if any have ventured into, or through, the effective attraction radius of the female. Males that have been captured remain with the particular female throughout the rest of the simulation and any later arriving males are not allowed to stay with the pair, although a record of the encounters is kept.

### Capture Algorithm

The algorithm for determining whether a male has been captured begins on line 270 of the program (Fig. 2). In the interest of execution speed, the position of the male in question is compared first to the female's position to see if the  $X$ - or  $Y$ -distance between them is greater than the sum of the female's radius and the male's step size; if so, the male cannot be caught. The law of cosines is then used to calculate the angle between the line  $A$ , from the previous coordinates ( $X, Y$ ) to the female ( $J, K$ ), and the line  $B$ , from ( $X, Y$ ) to the new coordinates ( $P, Q$ ; Fig. 3). If this angle is equal to or greater than  $90^\circ$  then the male is moving away from the female and cannot be caught. Obviously if the distance between the male and female is less than the radius of the female then he is caught. However, if the step size is large relative to the radius then one must be able to determine whether the male could have intercepted the female.

In Fig. 3a, the circle has been intercepted by a male with a step from ( $X, Y$ ) to ( $P, Q$ ). The angle calculated above (with the law of cosines) and side  $A$  are used with the right triangle of sides  $A, G$  and

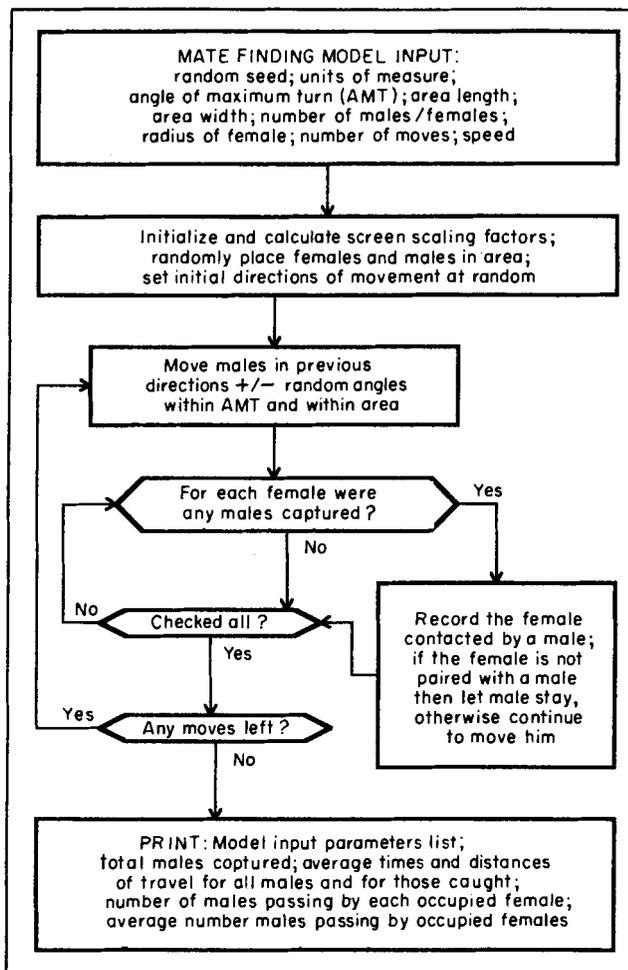


Figure 1. Flow diagram of the computer program for the simulation model of mate finding by *Tomiscus piniperda*.

$F$  to determine the length of  $G$  and  $F$  (line 360 in Fig. 2). If  $G$  is less than or equal to the radius  $R$ , and  $F$  is less than the step size  $B$ , then the male is captured. A special case arises when  $G$  is less than  $R$ , but  $F$  is greater than the step size  $B$ , as in Fig. 3b. Here the male moves towards the female but does not intercept her.

#### Speed of Walking on Scots Pine

I determined appropriate speeds of walking for use in the simulation model from experimental observations. I collected both sexes of *T. piniperda* as they walked on Scots pine trunks (18 April 1986, Sjöbo, southern Sweden). They were separated by sex and stored at 2°C for 3 days and then allowed to

warm for 1 h before I tested their walking speed at constant temperatures of 10, 17.9, 23.4 and 28.8°C ( $\pm 0.2^\circ\text{C}$ ) at 700 lx and  $65 \pm 5\%$  relative humidity in an environmental chamber (12.6 m<sup>3</sup>, Karl Weiss). Several males or females were released on a large freshly cut Scots pine log (24 cm diameter  $\times$  80 cm) with relatively smooth bark (bark flakes but no deep crevices). I used a stop watch to time a beetle as it walked from 3 to 6 cm while moving continuously. After timing, the beetle was removed from the log.

#### Simulations

A simulation model was constructed from the two algorithms and implemented as a computer

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10 DIM X(400): DIM Y(400): DIM J(400): DIM K(400): DIM P(400): DIM Q(400): DIM D(400): DIM U(400): DIM E(400)
20 SCREEN 9: CLS : PI = 3.14159265358920: DG = .017453292519940: DEFINT H, M-M, V
30 PRINT : PRINT "MATE FINDING MODEL": PRINT : INPUT "INPUT RANDOM SEED 1-100+": SEED: SEED = RND(-SEED)
40 INPUT "INPUT UNITS OF MEASUREMENT (cm or m etc.):": CH$: INPUT "INPUT ANGLE OF MAXIMUM TURNING (DEGREES)": AMT
50 PRINT "INPUT AREA LENGTH IN ": CH$: : INPUT L: PRINT "INPUT AREA WIDTH IN ": CH$: : INPUT W
60 INPUT "INPUT NUMBER OF FEMALES = MALES": M: PRINT "INPUT RADIUS OF FEMALE/PREY IN ": CH$: : INPUT R
70 INPUT "INPUT SECONDS OF WALKING": TT: PRINT "INPUT SPEED (": CH$: "/SEC.):": : INPUT CS
80 PRINT "INPUT STEP SIZE IN ": CH$: : INPUT S: INPUT "INPUT 1 FOR RESULT PRINTOUT": PR1
90 T = TT * CS / S: D = S + R: CLS : LOCATE 15, 70: PRINT "MOVES:": LOCATE 16, 70: PRINT T
100 XA = L: YA = W: BP = 26: XL = 540: YL = 350
110 IF YA = XA THEN XC = XL / XA: YC = YL / YA: XS = XL - 1: YS = YL - 1
120 IF YA > XA THEN YC = YL / YA: XS = XL * XA / YA: YS = YL - 1: XC = XL / YA
130 IF XA > YA THEN XC = XL / XA: XS = XL - 1: YS = YL * YA / XA: YC = YL / XA
140 FOR X = 0 TO XS + .1 STEP XS: LINE (X, YL - YS - 1)-(X, YL - 1), 15: NEXT: FOR Y = 0 TO YS + .1 STEP YS
150 LINE (0, YL - (YS - Y + 1))-(XS, YL - (YS - Y + 1)), 15: NEXT: PAINT (XS + 1, YL - 1), 1, 15
160 LOCATE 1, 70: PRINT "MATING": : LOCATE 2, 70: PRINT "Tomticus":
170 FOR H = 1 TO M: J(H) = RND * (L - 1) + 1
180 K(H) = RND * (W - 1) + 1: CIRCLE (J(H) * XC, YL - K(H) * YC), R * XC, 12: NEXT
190 FOR H = 1 TO M: X(H) = RND * (L - 1) + 1: Y(H) = RND * (W - 1) + 1
200 PSET (X(H) * XC, YL - Y(H) * YC), 15: E(H) = RND * 360: NEXT
210 REM - MOVE SEARCHERS (MALES) WITHIN BOUNDARIES OF AREA
220 FOR H = 1 TO M - M: RL = RND * 2 - 1: E(H) = E(H) + RL * AMT: IF E(H) > 360 THEN E(H) = E(H) - 360
230 IF E(H) < 0 THEN E(H) = E(H) + 360
240 P(H) = S * COS(E(H) * DG) + X(H): IF P(H) > L OR P(H) < 0 THEN E(H) = RND * 360: GOTO 240
250 Q(H) = S * SIN(E(H) * DG) + Y(H): IF Q(H) > W OR Q(H) < 0 THEN E(H) = RND * 360: GOTO 240
260 PSET (X(H) * XC, YL - Y(H) * YC), 0: PSET (P(H) * XC, YL - Q(H) * YC), 15: NEXT: GOTO 270
270 V = 0: REM - CHECK TO SEE IF ANY SEARCHERS (MALES) ARE CAPTURED
280 V = V + 1
290 FOR H = 1 TO M: IF J(H) < P(V) - D OR J(H) > P(V) + D OR K(H) < Q(V) - D OR K(H) > Q(V) + D THEN 370
300 A = SQR((X(V) - J(H)) ^ 2 + (Y(V) - K(H)) ^ 2): B = SQR((X(V) - P(V)) ^ 2 + (Y(V) - Q(V)) ^ 2)
310 C = SQR((P(V) - J(H)) ^ 2 + (Q(V) - K(H)) ^ 2): IF A = 0 THEN A = .00001 ELSE IF B = 0 THEN B = .00001
320 ZZ = ((A ^ 2) + (B ^ 2) - (C ^ 2)) / (2 * A * B)
330 IF ZZ > .99999 THEN ZZ = .99999 ELSE IF ZZ < -.99999 THEN ZZ = -.99999
340 Z = (-ATN(ZZ / SQR(1 - ZZ * ZZ)) + PI / 2): IF Z >= PI / 2 THEN 370: REM 90 degrees
350 IF C <= R THEN 410
360 G = A * SIN(Z): FF = A * COS(Z): IF G <= R AND FF < B THEN 410
370 NEXT
380 IF V < M - M THEN 280 ELSE IF M = M THEN 460
390 FOR H = 1 TO M - M: X(H) = P(H): Y(H) = Q(H): NEXT: I = I + 1: IF I >= T THEN 460
400 LOCATE 5, 72: PRINT I + 1: : GOTO 220
410 IF U(M) > 0 THEN 450
420 P(V) = P(M - M): Q(V) = Q(M - M): X(V) = X(M - M): Y(V) = Y(M - M): D(H) = I + 1: IF V = M - M THEN 440
430 V = V - 1
440 M = M + 1

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Figure 2. Computer program in QuickBASIC 4-0 for the stimulation model of mate finding in walking bark beetles.

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450 U(H) = U(H) + 1: GOTO 380
460 CLS : A$ = "MATING "
470 A$ = A$ + "Tomicus model": GOSUB 620: GOTO 480
480 A$ = "Length =" + STR$(L) + " Width =" + STR$(W) + " No. Moves" + STR$(T) + " Ma/Fe =" + STR$(N)
490 GOSUB 620: A$ = "Radius Fe/Prey =" + STR$(R) + " No. Seconds =" + STR$(TT): GOSUB 620
500 A$ = "Step size =" + STR$(S) + " Speed =" + STR$(CS) + " Max. turn angle =" + STR$(AMT): GOSUB 620
510 A$ = "Dist. travelled up to" + STR$(T * S) + " " + CMS: GOSUB 620
520 FOR H = 1 TO N: IF U(H) > 0 THEN TOCH = TOCH + 1: TOMB = TOMB + U(H)
530 NEXT: FOR H = 1 TO N: AVET = AVET + D(H): NEXT: A$ = "Total males caught =" + STR$(TOCH): GOSUB 620
540 A$ = "Ave. No. males by female =" + STR$((TOMB - TOCH) / N): GOSUB 620: IF TOCH > 0 THEN 550 ELSE 590
550 A$ = "Ave. time to catch of those caught =" + STR$(AVET / TOCH * S / CS) + " s": GOSUB 620
560 A$ = "Ave. time to catch for all N =" + STR$(((AVET * S / CS) + (N - TOCH) * TT) / N) + " s": GOSUB 620
570 A$ = "Ave. distance of male travel of those caught =" + STR$(AVET / TOCH * S) + " " + CMS: GOSUB 620
580 A$ = "Ave. distance of male travel for all N =" + STR$(((AVET * S) + (N - TOCH) * T * S) / N) + " " + CMS
590 GOSUB 620: A$ = "Female no. No. males by Time of first male catch": GOSUB 620
600 FOR H = 1 TO N: A$ = STR$(H) + STRING$(12, 32) + STR$(U(H)) + STRING$(14, 32)
610 A$ = A$ + STR$(D(H) * S / CS): GOSUB 620: NEXT: END
620 PRINT A$: IF PRT = 1 THEN LPRINT A$: RETURN ELSE RETURN

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Figure 2. Continued.

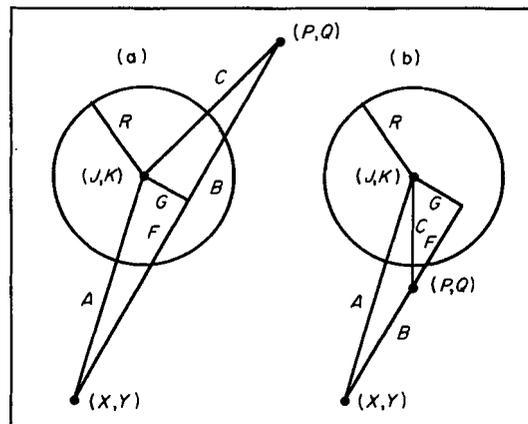


Figure 3. Geometric representation of the 'capture' algorithm for two cases. In (a) a male steps along (B) from (X, Y) to (P, Q) by passing through the female (J, K) with circle of radius R and thus is caught. In (b) a male takes a shorter step to (P, Q) in the same direction but is not caught since (P, Q) is outside the circle. See the text for more details.

program (Fig. 2) in QuickBASIC 4.0 (Microsoft) that works on any IBM-compatible personal computer. The program, with little modification, should run on other computers with Microsoft BASIC. An EGA (enhanced graphic) video display is currently supported but other graphic displays can be used by changing the variable YL on line 100 to appropriate values (e.g. 480 for VGA). The graphical display is important for confirming that the simulation is performing as desired.

The effects of increasing the male's speed, female's radius, duration of male's walking, step size, angle of maximum right or left turn and density of male-female pairs on the capture rate of males and the number of males passing per female were determined in an area of  $66 \times 500$  cm (a 'trunk' section 21 cm diameter by 5 m). The number of males passing per female does not include the count for the first male-female pairing, and is thus equal to the number of interactions between resident,

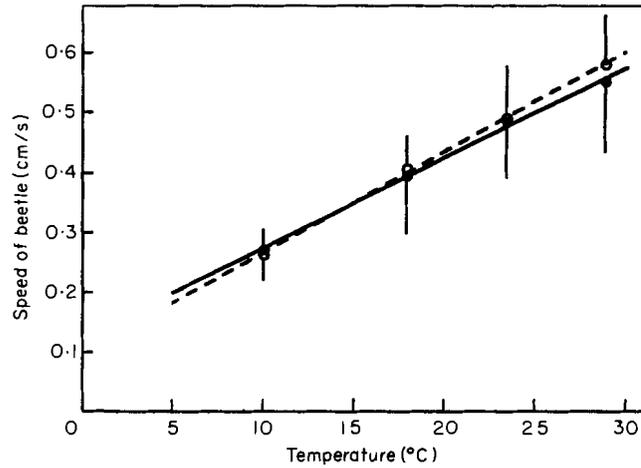


Figure 4. Effect of temperature on the speed of walking of male (●,  $Y=0.015X+0.125$ ) and female (○,  $Y=0.016X+0.099$ ) *Tomiscus piniperda* on the bark of Scots pine. The temperature coefficient,  $Q_{10}$ , (1.59) indicates the increase in walking speed over a 10°C temperature range. The bars represent 95% confidence intervals ( $N=9-18$ ).

'guarding', males and later arriving males. For all simulations, except for the variable of interest, the male step size was 5 cm, speed 0.4 cm/s, angle of maximum turn 30°, duration of walking 5 h and 50 male-female pairs (15 pairs/m<sup>2</sup>). These model parameters were chosen because they appear close to general observations of search movements of males in the field. For example, an approximate walking speed of 0.4 cm/s is expected on a 'warm' swarming day. I have observed densities of 50 males and 50 females, and often more, per 5-m trunk section (sex ratios are 1:1, Salonen et al. 1968). Each simulation was repeated at least four times. Best fit least squares regressions were performed on the simulated results to determine the mathematical relationships and data variation.

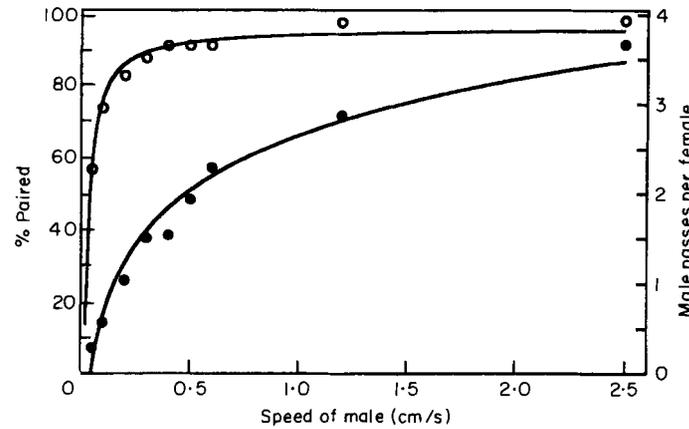
## RESULTS

The walking speeds of male and female *T. piniperda* increased linearly with temperature and were about the same at each temperature (Fig. 4). The  $Q_{10}$ , temperature coefficient, was about 1.6, i.e. for a 10°C rise in temperature the speed of walking increased 1.6 times. A speed of 0.4 cm/s, used in most simulations, corresponds to 17.9°C which is a normal temperature during the day of swarming flight. The effect of increasing the male's walking speed on the percentage of males pairing also followed an asymptotic (hyperbolic) relationship (Fig. 5). The relation indicates that even at speeds

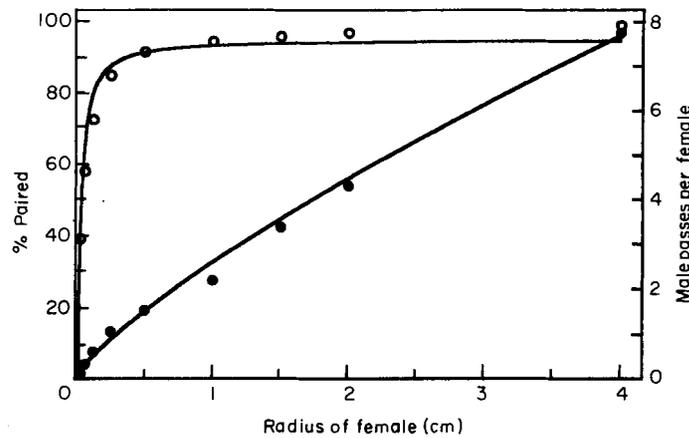
expected at cool temperatures (0.2 cm/s) a male would have a good chance of finding a female. At speeds that were higher than expected, or even not possible, there was little increase in pairing rates over the searching period. The rate of males interacting with male-female pairs (interactions between males) increased as a logarithmic function (Fig. 5). I use the term interactions between males only to describe the occasions when a male meets an 'occupied' female.

The effect of increasing the effective female radius from 0.03125 to 4 cm on the probability of pairing as well as the number of male passes per female (interactions between males) within the 5-h period of simulation is shown in Fig. 6. A hyperbolic function was evident for the percentage of males, or females, paired and indicates that under the model's assumptions, which attempted to simulate natural conditions, a radius of only 0.25 cm would capture 85% of the males (Fig. 6). This radius is about the physical size of a female and indicates that males could readily find females without the need for a long-range pheromone, simply by blundering into her. At radii much larger than a female there is little increase in the success rate of finding a female. On the other hand, the number of interactions between males increased as an exponential function that is approximately linear (Fig. 6).

As the duration of male searching was increased there was a rapid increase in success at finding a



**Figure 5.** Effect of varying the male's walking speed in the simulation model on the mate-finding success (% paired, ○,  $Y = -2.06/X + 96.36$ ,  $R^2 = 0.97$ ) and on the number of male passes per female (interactions between males, ●,  $Y = 0.8912 \ln X + 2.657$ ,  $R^2 = 0.97$ ). Model parameters were: 50 of each sex in an area of  $500 \times 66$  cm, 0.5 cm female radius,  $30^\circ$  maximum angle of male turning, 5 h of male walking, and 5 cm step size of male. Points represent average of four to eight simulations.

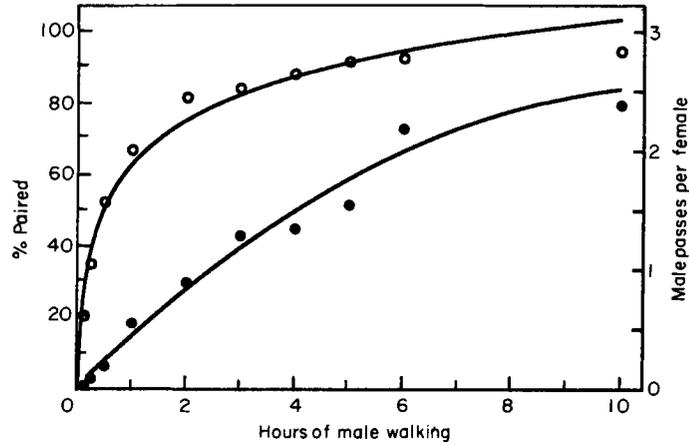


**Figure 6.** Effect of varying the female's radius in the simulation model on the mate-finding success (% paired, ○,  $Y = -1.9145/X + 95.09$ ,  $R^2 = 0.95$ ) and on the number of male passes per female (interactions between males, ●,  $Y = 2.591X^{0.7841}$ ,  $R^2 = 0.98$ ). Other model parameters as in Fig. 4 but with a 0.4 cm/s male walking speed.

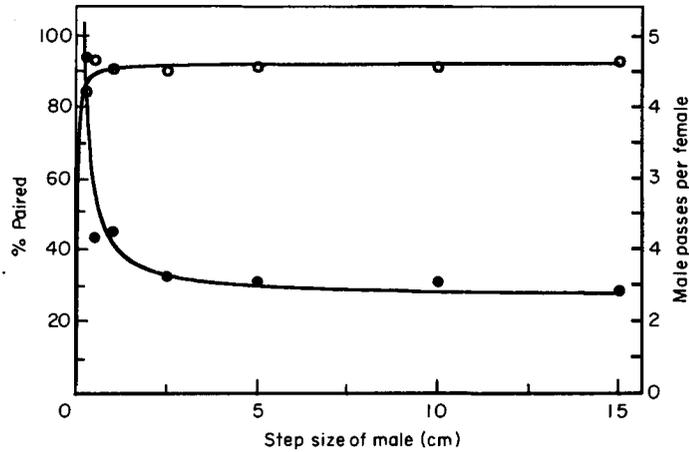
mate (Fig. 7). The majority of males were successful at finding a female after just a few hours using model parameters that were assumed to be natural. The rate of interactions between males was approximately linear with respect to time over the first 6 h. The step size had practically no effect on the percentage paired (Fig. 8). For example, at a small step of 0.25 cm, and consequently many turns, 84.5% of the males were captured and this remained relatively constant at any step size up to 15 cm where 93% were caught. The rates of male

interactions with male-female pairs (interactions between males) were also relatively constant at ranges of step size from 0.5 to 15 cm. Only at a very small step size of 0.25 cm was the rate high (Fig. 8).

The angle of maximum right or left turn had no significant effect on the male's ability to find females (Fig. 9). There was a small increase in interactions with paired beetles at the nearly random movement pattern ( $180^\circ$ ). The number of males and females per area was varied over expected natural densities (Fig. 10). A small increase in density



**Figure 7.** Effect of varying the male's walking duration in the simulation model on the mate-finding success (% paired, ○,  $Y = 17.66 \ln X + 62.77$ ,  $R^2 = 0.97$ ) and on the number of male passes per female (interactions between males, ●,  $Y = -0.0198X^2 + 0.4476X + 0.0164$ ,  $R^2 = 0.99$ ). Other model parameters as in Fig. 4 but with a 0.4 cm/s male walking speed.



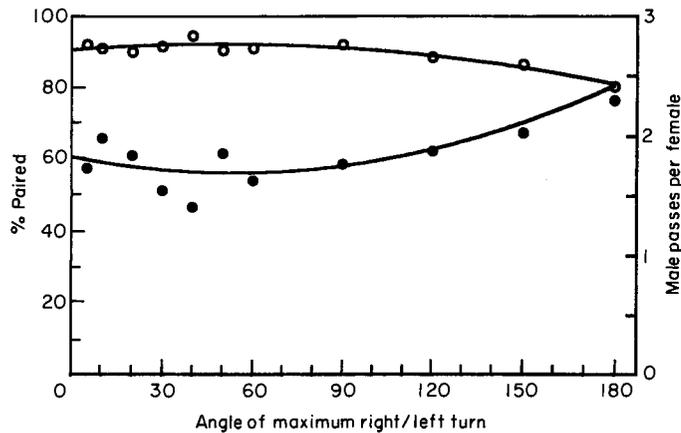
**Figure 8.** Effect of varying the male's step size in the simulation model on the mate-finding success (% paired, ○,  $Y = -1.528/X + 92.48$ ,  $R^2 = 0.55$ ) and on the number of male passes per female (interactions between males, ●,  $Y = 0.772/X + 1.327$ ,  $R^2 = 0.92$ ). Other model parameters as in Fig. 4 but with a 0.4 cm/s male walking speed.

caused a rapid increase in the ability of any particular male to find a female. At densities that are commonly observed, 25 or 50 pairs/area (7–15 pairs/m<sup>2</sup>), the success of pairing had reached 88.5% and 91.5%, respectively. The interaction rate between males increased approximately linearly over densities of 5–100 pairs per area (Fig. 10).

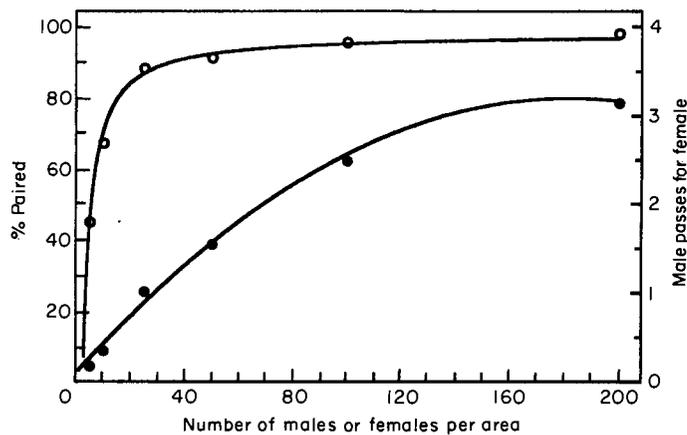
## DISCUSSION

The colonization of a tree usually occurs in a few afternoon flights that may not necessarily be on

successive days. Thus by the next morning after each aggregation on the trunk the female–male pairs have bored into the bark. The final attack density can range from about 50, or less, up to 300/m<sup>2</sup> (Nilssen 1978; Långström & Hellqvist 1988). The placement of males at random in the model is realistic but in nature females are actually somewhat over-dispersed in their spatial distribution (Nilssen 1978). However, this spatial pattern of female attacks should have little, if any, effect on the mate-finding success or rates of interactions between males compared with the random pattern used in the model.



**Figure 9.** Effect of varying the angle of maximum right or left turn of the male in the simulation model on the mate-finding success (% paired, ○,  $Y = -0.00064X^2 + 0.0634X + 90.53$ ,  $R^2 = 0.88$ ) and on the number of male passes per female (interactions between males, ●,  $Y = 0.000046X^2 - 0.005X + 1.84$ ,  $R^2 = 0.66$ ). Other model parameters as in Fig. 4 but with a 0.4 cm/s male walking speed.



**Figure 10.** Effect of varying the number of male-female pairs per area (density) in the simulation model on the mate-finding success (% paired, ○,  $Y = -272.56/X + 98.01$ ,  $R^2 = 0.99$ ) and on the number of male passes per female (interactions between males, ●,  $Y = -0.000094X^2 + 0.0342X + 0.09$ ,  $R^2 = 0.99$ ). Other model parameters as in Fig. 4 but with a 0.4 cm/s male walking speed.

The speed parameter of 0.4 m/s is expected for males walking at 18°C in the afternoon. The average speed of a male may actually be less as they probably stop occasionally and also take time contesting males that are guarding females. However, even at slower speeds in the model, 'males' had little difficulty finding females (Fig. 5). The 5-h period of searching used in the model is reasonable if the male landed in the afternoon and searched until dusk. However, in reality males may search even longer, such as through the night (although not observed) and during the next morning. I have seen beetles

walking in the morning when temperatures were well below 12° and thus precluded flight.

The angle of maximum right or left turning of 30° used in most simulations appears reasonable when one observes the tracks on the video display and compares these with walking beetles in nature. The natural turning angle probably has some normal distribution about the previous direction (Bovet & Benhamou 1988; Benhamou & Bovet 1989) instead of the uniform random distribution used here. The angular distribution would also probably be influenced by the 'roughness' of the bark, a rougher

bark causing more detours. Fine tuning of this parameter, however, may not improve our understanding of mate finding in the present model since the angle had practically no effect (Fig. 9) even when its distribution changed from  $\pm 5^\circ$  (nearly straight path) to  $\pm 180^\circ$  (completely random path). This is surprising until one considers that when males strike the boundaries of the area they change directions at random. There is a real border on the longer sides of the area since the fallen pine is lying on the ground and beetles prefer to remain on the exposed bark. The slight increase in interactions between males as the angle of maximum turn is increased to  $180^\circ$  may be due to repeated re-entries of males into pairs because of the possibility of reversing direction at  $180^\circ$  (Fig. 9). In nature, males do not appear to avoid areas previously visited.

The step size of an insect is not a discrete parameter, as has been discussed by Benhamou & Bovet (1989), but can be used, together with the angle of maximum turn, to simulate animal movement paths explicitly. The step size is inversely proportional to the frequency of turns. At very small step size, or very high turning frequency, the male essentially simulates Brownian motion and thus traverses only short spaces and pairing rates are consequently low. On the other hand, a male near a pair would probably collide several times during the short circling motions and consequently there would be many male passes per female (Fig. 8). Increases in step size rapidly allow efficient mate finding and further increases seem to have little effect under the model's constraints. A male appears to travel at least 1 cm before changing direction under natural conditions. In the model, even at steps of 0.25 cm, considered quite small, the males still found 84.5% of the females, while at 0.5 cm steps 93.5% were found. Larger steps produced no significant change in mate-finding efficiency (Fig. 8). The effects of aggregation density on mate-finding success were significant at low densities but by the time 25 pairs had landed the expected probability for a male to find a female in the 5-h period was up to 88.5% (Fig. 10).

The effective radius of the female is the radius within which a male is captured. This is similar to Smith's (1973) 'zone of danger' for prey items or the 'effective attraction radius' for a pheromone (Byers et al. 1989a). The circle catches 100% of the males so the natural radius would be somewhat larger and not necessarily circular. When *T. piniperda* males encounter females that are walking they make no

attempt to chase them and seem oblivious. When males encounter stationary females they appear to veer into them at a very short distance ( $< 0.5$  cm) and touch them and then may attempt to mate from behind or simply press the head against the female's elytral apex. It seems reasonable that radii of 0.5 cm in the model allowed 91.5% pairing or even 85% at only a 0.25 cm radius, the female size (Fig. 6).

At higher densities the pairing rate would be higher still (Fig. 10), while at lower densities the males would require more time to find a mate (Figs 7, 10). The results account for pairing rates observed in nature where in early afternoon the majority of beetles are single but by evening the majority have paired, although many beetles of both sexes are still walking about. The high mate-finding success rate in the model using a range of 'natural' parameters indicates that *T. piniperda* females do not require a long-range pheromone to attract males after they land. A long-range pheromone might increase slightly mate acquisition at low population levels; however, at most levels there would not be a significant selection pressure for evolution (or maintenance) of a pheromone system considering the significant attraction to host-tree odours (Byers et al. 1985, 1989b). The expected energy cost of maintaining a pheromone system and the possibility of increased apparency to predators, who might evolve a kairomone response to a long-range pheromone, argue against selection for pheromone-producing females.

Other bark beetles that aggregate en masse on their host tree mostly use long-range pheromones (Byers 1989). The western pine beetle, *Dendroctonus brevicomis*, of North America has a monogamous mating system in which the male joins the female in her gallery system but in this case the male responds to an aggregation pheromone (Silverstein et al. 1968). In this species, however, colonization of the tree begins with one female so initially densities are quite low in comparison with *T. piniperda*. Using model parameters as above but for *D. brevicomis* in an area 100 times greater (i.e. lower density) and a female radius of 0.5 cm, only 10% of the males find females while at a radius of 32 cm about 77% find females. Thus, at the densities expected during initial colonization for bark beetles using long-range pheromones it would be clearly advantageous for beetles to orient to an odour source (gallery entrance) while walking. That beetles may do this in nature has been observed with several species in the laboratory (Lanne et al. 1987; Byers

1989). However, the results of the present study indicate that at higher densities, when colonization has progressed and pheromone is emanating from many points with consequent sensory adaptation, beetles can find gallery systems simply by interception during directed random walks.

Optimal foraging theory is concerned with decision rules for staying and leaving and with movement between resource patches (Pyke 1984). Here male *T. piniperda* are searching for mates within a patch consisting of a fallen Scots pine that is susceptible to attack and releasing attractive monoterpenes (Byers et al. 1985). Standing trees are rarely attacked since the beetle is not able to cope with resin flow as readily as other more 'aggressive' bark beetles (Långström & Hellqvist 1988; Byers 1989) and because these trees do not have wounds that could release appreciable levels of monoterpenes. Window traps on dead trees fallen in previous years do not catch beetles compared with recently fallen, living trees (Byers et al. 1989b, J. Byers, unpublished data). The fallen tree patches would be expected to be randomly dispersed throughout the forest. A male's decision whether to fly away from a particular patch in search of another should depend on the density of unpaired females. A long search time without encountering any females would indicate that the probability of finding a female was low and it might be advantageous to seek another patch with a higher female density. A high rate of encountering male-female pairs by a searching male would indicate a high degree of potential competition among several larval broods of neighbouring pairs which may occur under the bark (Byers 1984; De Jong & Saarenmaa 1985). Thus it would be advantageous to fly to another patch.

Before a female chooses an attack site she is also seen to search as males do. However, upon encountering either a female boring alone or a pair she walks away from the area, most probably to avoid potential future competition for her larvae (De Jong & Saarenmaa 1985). This behaviour could be part of the mechanism that leads to a spacing of attacks on the bark as observed previously (Nilssen 1978; Byers 1984). A high rate of these interactions should cause her to decide to search for another patch, while a low rate should induce her to stay. At suitable temperatures during the aggregation beetles commonly both land and take flight. For example, I observed at least 14 beetles taking flight from an 8-m section of trunk in 5 min, and all but

two flew more than 10 m away before I lost sight of them. As the colonization progresses over several days, verbenone (a ketone of  $\alpha$ -pinene) is released and causes both sexes to avoid attacked areas since the beetles are less attracted to the monoterpenes when verbenone is present (Byers et al. 1989b). Thus, since the beetles contain verbenone (Lanne et al. 1987) it may function at close-range in the spacing of attacks and limiting competition while signalling later in the colonization, before landing and at long-range, that the host is becoming unsuitable for reproduction (Byers et al. 1989b).

The capture algorithm should prove useful in models of predator-prey interactions, host and mate finding, and trapping of insect or animal populations. The model can be used to explore many variations of the parameters discussed above to fit a wide variety of animal systems. The graphical display allows for immediate confirmation of the model's proper functioning and illustrates the principles to students and researchers alike.

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