

# Nearest Neighbor Analysis and Simulation of Distribution Patterns Indicates an Attack Spacing Mechanism in the Bark Beetle, *Ips typographus* (Coleoptera: Scolytidae)

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**ABSTRACT** The attack sites of the bark beetle, *I. typographus*, on Norway spruce logs were observed to be more uniformly spaced than random using nearest neighbor analysis. A computer model which simulated various degrees of uniformity in spatial distribution was compared to the observed attack pattern. The model showed that a mechanism of spacing between attacks, in which beetles need to be greater than a minimum distance of about 2.5 cm away from the nearest neighbor before attacking, can explain the observed distributions in nature. In the model, the distribution of angular directions to the four nearest neighbors appeared random, regardless of the degree of uniformity in the spatial distribution. The model for the mechanism of spacing can be applied to other organisms that exhibit uniform distributions.

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MOST tree-killing bark beetle species use pheromones to locate mates upon hosts where they can feed and reproduce. Another vital function of these pheromones appears to be that in each species they cause a mass aggregation of individuals which collectively overpower the defenses of the tree. Thus a certain threshold number or density of beetles is required to kill a particular tree and insure the survival of the participating adults and their brood. However, after this density is reached during the aggregation sequence (concentration phase), further increases in density of attacking beetles result in increasingly detrimental effects on reproduction due to intraspecific competition between the larvae (Berryman 1974). The nature of the competition is probably a combination of interference competition (direct effects such as larvae being eaten) and exploitative competition (indirect effects such as eating the limited food resource). The adverse effects of competition become apparent even at very low densities when beetles colonize wind-thrown trees and broken tops that are less able to inhibit the beetles from feeding (Raffa and Berryman 1983).

There are reports of intraspecific competition in several bark beetle species in the genera *Ips*, *Dendroctonus*, *Scolytus*, and *Tomiscus* (= *Blastophagus*). These reports have shown that brood output per female decreases at higher attack densities (Miller and Keen 1960, McMullen and Atkins 1961, Ogibin 1973, Beaver 1974, Berryman 1974, Mayyasi et al. 1976). According to ecological theory, it is always advantageous for either party in a competitive interaction to avoid the other whenever possible. Bark beetles arriving at a host tree under colonization may avoid competition in at least four ways: avoiding landing in areas of high

density (inhibitors/allomones); leaving these areas after having landed (inhibitors/allomones/other mechanisms?); avoiding initiating an attack near others (chemical/acoustic/other?); and reemerging from under the bark sooner when at high densities.

In most species where it has been investigated, bark beetles will reemerge earlier at high attack densities compared with lower densities (Ogibin 1973, Coulson et al. 1978), presumably in order to establish a second brood in a more favorable location. This second host-seeking flight undoubtedly involves high mortality risks and should only be undertaken when conditions and competition are even more unfavorable under the bark, according to optimality theory. It appears that avoiding high density areas on the tree before landing can yield reproductive benefits for relatively little energy and time expended. Thus, several species have apparently evolved olfactory mechanisms such as inhibition of attraction response to pheromones in order to avoid intraspecific competition (Renwick and Vité 1970, Byers and Wood 1980, Byers 1983a,b, Byers et al. 1984) and interspecific competition before landing (Byers and Wood 1980, Byers et al. 1984). A beetle should be able to make a more precise determination of the likelihood of competition after landing; and some of these olfactory mechanisms have been also shown to operate after landing (Byers 1983a,b).

Another way of avoiding competition, with relatively little cost, would be for an individual to avoid initiating an attack within a given minimum distance from other established attacks. That this may occur is indicated from two lines of evidence. Miller and Keen (1960) summarized many reports of natural densities of attacking *Dendroctonus*

*brevicomis* and found them to vary from 5.9 to 23.2 per 0.1 m<sup>2</sup> but "always within certain limits." They further stated that "beetles seem instinctively to distribute their attacks so that overcrowding does not occur in any particular bark area." Others have analyzed the attack patterns of *D. ponderosae* (Shepard 1965, Safranyik and Vithayasai 1971), *D. frontalis* (Mayyasi et al. 1976), and *D. pseudotsugae* (Hedden and Gara 1976) and found them to be more uniformly, regularly spaced than would be expected if the pattern were random. Nilssen (1978) used nearest neighbor analysis and determined that the attack pattern of *Tomicus pini-perda* was uniformly distributed. The mechanisms that produce these attack distributions are virtually unknown, although acoustic/stridulatory (Rudinsky and Michael 1973), olfactory (Byers 1983a,b, Byers et al. 1984) or a combination of mechanisms may be involved (Rudinsky et al. 1976, Hedden and Gara 1976).

In the present study, I used nearest neighbor analysis to determine whether the attack pattern of *Ips typographus* tended toward a uniform spacing. Then a simulation model was constructed which could generate various types of "attack patterns"—from more random to more uniform than the natural distributions. A distribution tending to be uniform was simulated by randomly selecting, in sequence, 400 attack locations within a specified area such that each subsequent attack site was separated by at least a minimum distance (the minimum allowed distance) from all previously chosen attacks. The simulation model was then run at the same attack density as that for each of three natural densities at increasing levels of uniformity to obtain the average distances to the four nearest neighbors. The average distances for the natural densities then were compared to the simulation results (quadratic regression analysis) to determine the minimum allowed distance. This distance, according to the model, can explain the natural distributions and indicates a spacing mechanism for reducing competition.

#### Materials and Methods

**Attack Pattern of *Ips typographus*.** A Norway spruce tree, *Picea abies* (L.) Karst., was felled at 1900 hours on 7 June 1983 and sectioned. A log (1 m by 18–21 cm diam) was placed at each of six sites (each about 30 m apart) in a spruce forest clear-cut about 15 km NNE of Skien, Norway (8 June). Beetles were attracted to three of these logs by release of synthetic pheromone components (50 mg 2-methyl-3-butene-2-ol per day and 1 mg (*S*)-*cis*-verbenol per day, chemicals from Aldrich and Borregaard, respectively) from a point about 0.4 m from each log during the entire exposure period (8–13 June). To monitor the levels of beetles attracted, a flat wire mesh (6 mm) screen, 15 by 15 cm, coated with Stickem Special® adhesive was placed on a somewhat larger plastic tarpaulin on

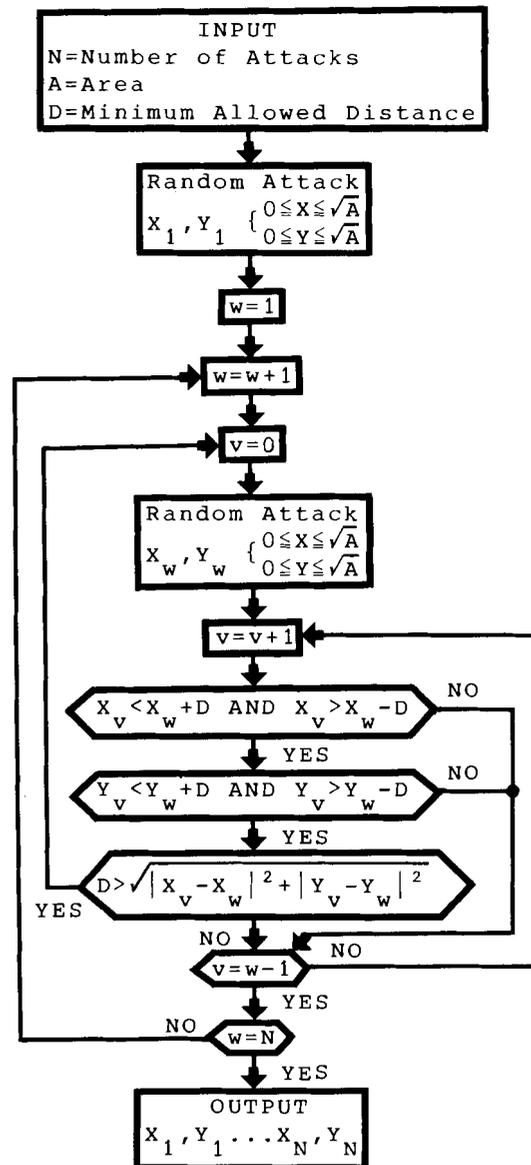


Fig. 1. Flow diagram of computer program used to simulate random or uniform attack distributions. The program determines the rectangular coordinates of all attacks within an area (any density).

the ground about 0.4 m from the pheromone and from the log. The three other control logs without pheromone were placed with similar sticky traps.

The number of attacks, within the bark area, that were >5 cm from the cut ends were counted. The distances between these attacks and their four nearest neighboring attacks, regardless of whether they were within the boundary area, were measured. These observed average distances were compared to expected distances (if the attacks had

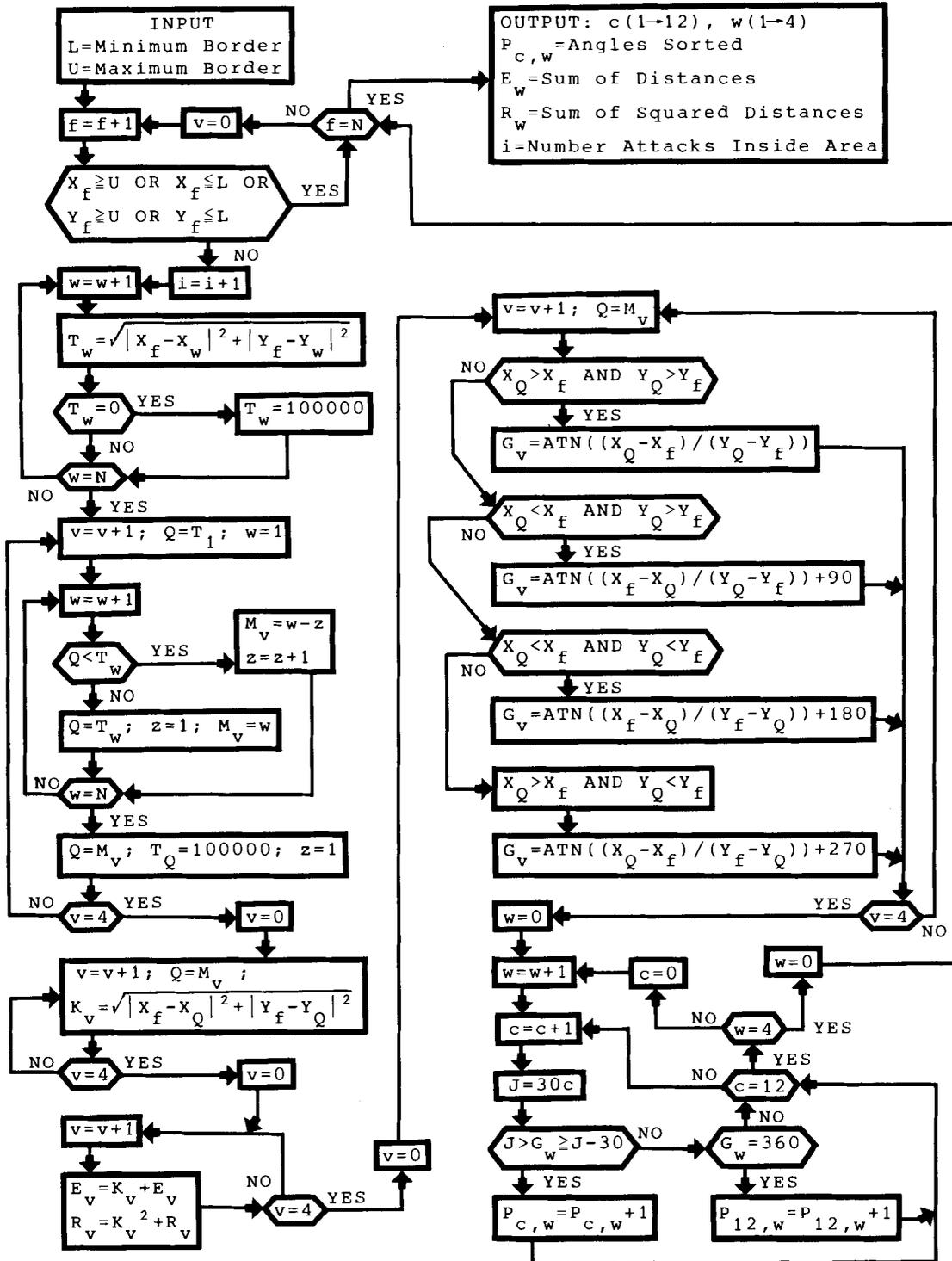


Fig. 2. Flow diagram of computer program used to analyze the pattern of attack simulated in Fig. 1. The program finds the average distances between attacks and their four nearest neighbors, and categorizes the corresponding angles, for all attacks within a specified boundary area.

**Table 1.** Nearest neighbor analysis of attack patterns of *Ips typographus* at three attack densities on Norway spruce logs (90 by 19 cm diam) in southern Norway (8-13 June 1983)

	Neighboring attacks			
	$N_1$	$N_2$	$N_3$	$N_4$
47 Attacks in log A (0.90 per dm <sup>2</sup> )				
Expected distance	5.26 ± 0.79 <sup>a</sup>	7.89 ± 0.82	9.87 ± 0.83	11.51 ± 0.84
Observed distance	5.69 ± 0.69	8.44 ± 0.73	10.23 ± 0.77	11.90 ± 0.82
$\chi^2$	47.1	35.1	32.6	32.1
P value for $\chi^2$	0.960 <sup>ab</sup>	0.975*	0.983*	0.984*
101 Attacks in log B (1.99 per dm <sup>2</sup> )				
Expected distance	3.54 ± 0.36	5.32 ± 0.38	6.64 ± 0.38	7.75 ± 0.38
Observed distance	4.22 ± 0.34	5.64 ± 0.31	6.95 ± 0.30	8.21 ± 0.32
$\chi^2$	70.5	44.5	34.6	32.4
P value for $\chi^2$	0.997*	>0.999**	>0.999**	>0.999**
179 Attacks in log C (3.17 per dm <sup>2</sup> )				
Expected distance	2.81 ± 0.22	4.22 ± 0.22	5.27 ± 0.23	6.15 ± 0.23
Observed distance	3.65 ± 0.20	4.82 ± 0.22	5.82 ± 0.23	6.66 ± 0.24
$\chi^2$	88.5	82.7	74.4	73.9
P value for $\chi^2$	>0.999**	>0.999**	>0.999**	>0.999**

<sup>a</sup> Mean values ±95% confidence limits.

<sup>b</sup> A P value of  $\chi^2 > 0.95$  or  $> 0.999$  indicates that the variation in the distribution of observed distances was smaller than expected assuming randomness (i.e., a uniform distribution) at  $\alpha = 0.05^*$  or  $0.001^{**}$ , respectively (Thompson 1956).

occurred at random) using  $\chi^2$  analysis (Table 1, Thompson 1956).

**Simulation Model of Attack Distributions.** The simulation model (Fig. 1 and 2) was performed in BASIC on both a Sinclair ZX-81 home computer with 16K memory (up to 200 attacks) and a Sperry Univac 1100/80 system with 1,024K memory (up to 400 attacks). The goal of the model was to place a certain number of attacks,  $N$ , in an area,  $A$ , such that each attack is separated by at least a minimum distance,  $D$ , from all other attacks. The first attack location is created at random by selecting a uniform random number between 0 and  $\sqrt{\text{area}}$  for  $X_1$  and  $Y_1$  coordinates (Fig. 1). The coordinates of all subsequent attacks (for example  $n_{42}$ ) are obtained by again selecting random-number coordinates and then searching all previously chosen pairs of coordinates (in memory) for those that are located within the "box,"  $X_{42} \pm D$  and  $Y_{42} \pm D$ . The distance between  $n_{42}$  and each of the other attacks within this box are then calculated by the Pythagorean theorem (Fig. 1). If any of these distances are less than  $D$ , then another pair of coordinates for  $n_{42}$  is selected and the process repeated until a location is found where there are no other attacks closer than the minimum distance  $D$ .

In Fig. 2, the program analyzes the distribution of attacks that was created above. Since attacks near the periphery of the area have less chance for attacks to occur nearby than do attacks centrally located, only attacks within a specific inner area were analyzed. This inner area is delineated by specifying a minimum border  $L$  and a maximum border  $U$  for  $X$  and  $Y$ . Beginning with the first pair of coordinates selected in Fig. 1, the program finds the first pair of coordinates that are

within the inner area (e.g.,  $n_6$ ). It then proceeds to calculate distances between this attack and all others in the entire area (Pythagorean theorem). Then using a sort routine, the four lowest distances are determined and the selection positions (e.g., 44, 81, 16, 191) of these corresponding four nearest neighbors are saved in  $M_{1-4}$ . The computer keeps a running total of the distances to the respective neighbors,  $E_{1-4}$ , and sum of squared distances,  $R_{1-4}$  (for calculating ±95% CL). Next the angles between the attack and its four nearest neighbors are calculated trigonometrically (Fig. 2) using the coordinates of the attacks (positions saved above). Finally these four angles are sorted into one of 12 angle categories (0-30°, 30-60°, etc.) for each of the four neighbors (Berryman and Pienaar 1973). This was done to determine whether nonrandom distributions of angles occur between neighbors when they are distributed in semiuniform patterns. The process is repeated for all attacks ( $i$ ) occurring inside the bounded inner area.

Using the simulation model, the average distances to the four nearest neighbors (400 attacks in an area 140 by 140 cm) were calculated (Fig. 3) from about 248 attacks within an inner border area of  $L = 15$  and  $U = 125$  at each of several values of  $D$ . These average distances were compared to the values expected from an equal number had they been randomly distributed (Thompson 1956). Quadratic regression lines were constructed from average distances plotted against minimum allowed distances (Fig. 3).

Frequencies of occurrence of angles between attacks and their four nearest neighbors at differing degrees of uniform pattern ( $D = 0, 1, 2, 3, 4, 5$  cm) as determined from the simulation model (Fig.

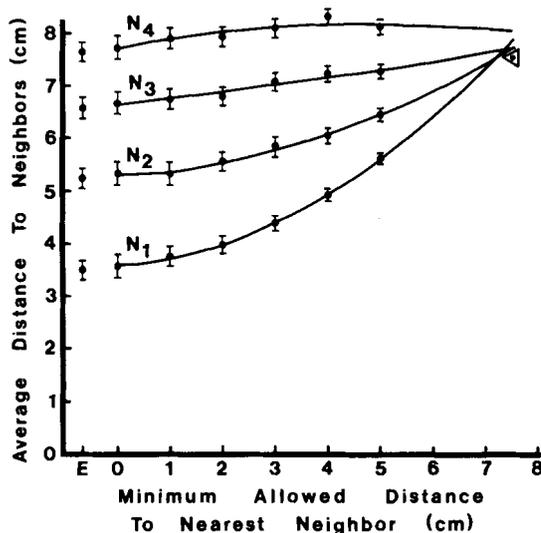


Fig. 3. Relationship between average distance to four nearest neighboring attacks ( $Y$ ) and the minimum allowed distance between attacks ( $X$ ) based on 400 simulated attack sites in a 19,600  $\text{cm}^2$  area (2.04 per  $\text{dm}^2$ ). Each point represents the average of about 248 simulated attacks that were within an inner boundary area (60% of total area) in order to avoid errors from analyzing sites on the area's periphery. Attack patterns are more uniform as the minimum allowed distance between attacks is increased. Points above E on abscissa are expected values for a random distribution, as determined from nearest neighbor mathematics (Thompson 1956).  $N_1$ - $N_4$  represent the simulated distances to the four nearest neighbors, respectively. The point inside the triangle represents the theoretical intersection of all quadratic regression lines based on the maximum hexagonal spacing of attacks at the same density but for an unlimited area. Brackets represent 95% C.I.

3) were compared with the expected frequencies of angles based on a random pattern using  $\chi^2$  analysis (Berryman and Pienaar 1973).

**Attack Spacing Mechanism.** The hypothetical minimum allowed distance that might be tolerated by individual beetles before attempting to excavate an entrance tunnel (attack) was determined by the comparison of observed distances at three attack densities to those distances generated by the simulation model. The natural attack density of 47 attacks per 5,207  $\text{cm}^2$  was converted to equivalent area parameters for the model, i.e., at 400 simulated attacks per 44,315  $\text{cm}^2$ , the coordinates must range from  $0 \leq X \leq 210.5$  cm and  $0 \leq Y \leq 210.5$  cm (in Fig. 1). Similarly, for 101 attacks per 5,073  $\text{cm}^2$  and 179 attacks per 5,655  $\text{cm}^2$ , the coordinates were allowed to vary randomly up to 141.74 cm and 112.41 cm, respectively. The simulation model was then performed at each of these densities and several minimum allowed distances in order to obtain the corresponding average distances to

the four nearest neighbors (Table 2). A comparison of the natural distances to the nearest neighbors with the simulated distances yields an approximation of the hypothetical minimum allowed distance respected by beetles in nature (Table 2). This distance was estimated more precisely by substituting the observed average distances into quadratic regression equations and solving for the minimum allowed distance (Table 3).

The minimum allowed distance ( $D$ ) calculated above for *I. typographus* (2.5 cm) was used to simulate an attack pattern for 100 and 200 beetles per 4,900  $\text{cm}^2$ . These patterns can be compared to simulated patterns at  $D = 0$  (random) and  $D = 5$  (uniform) at the 100-beetle density (Fig. 4).

## Results and Discussion

**Attack Pattern of *Ips typographus*.** *I. typographus* beetles were attracted by the synthetic pheromone components to the three logs at the different sites, as evidenced by both their attacks on logs and the catch on sticky traps. None of the logs without pheromone were attacked nor did beetles land on the sticky traps nearby. The final number attacking each log, 49 on log A, 105 on log B, and 186 on log C, was probably influenced by both the number of beetles landing and on the suitability of the bark surface for attack. Log A may have had fewer beetles attracted since 19 were caught on the sticky trap, while higher numbers were collected at sites with B (54) and C (42). Log C, from the base of the tree, had a rougher bark surface than the other logs, which were smoother with fewer knots. It seemed that beetles preferred to attack sites in rougher bark than in smooth areas so this may explain the higher attack rate on log C compared to B. Beetles were observed to wedge the head and body into the small bark crevices, probably as a means of leverage to exert more force when biting into the outer bark. However, many attacks were found in smooth bark where it would seem to be more difficult for beetles to penetrate.

More beetles may have landed on the logs than on a corresponding area of sticky trap because the logs protruded more into the flight space and may have provided an appropriate visual image. However, many beetles that arrived on the logs soon flew away and did not seem to return. For example, in 10 min of observation on log C (1400 hours, 10 June) at least 16 beetles landed while 11 of these flew away ( $>3$  m), each after at most a few minutes of continuous walking on the bark.

The nearest neighbor analyses of expected distances between attacks and their four nearest neighbors based on a random distribution compared with the observed average distances showed that *I. typographus* has a uniform spacing of attacks (Table 1). The uniformity of the natural attack pattern was more apparent at the higher at-

**Table 2.** Comparison of observed average distances to the four nearest neighbors ( $N_1$ - $N_4$ ) at three densities of *Ips typographus* attack with the corresponding values obtained from the simulation model in which the minimum allowed distance to  $N_1$  was controlled (from 0 to 4 cm)

Neighbor	Avg distance to neighbors (cm)						
	Observed distance	Theoretical distance (random)	Simulation of minimum allowed distance to $N_1^a$				
			0	1	2	3	4
47 Attacks in log A (0.90 per dm <sup>2</sup> )							
$N_1$	5.685	5.263	5.007	5.512	5.533*	5.971	6.477
$N_2$	8.442	7.894	7.725	8.088	8.073	8.201*	8.777
$N_3$	10.230	9.868	9.688	10.042	9.884	10.148*	10.519
$N_4$	11.896	11.512	11.452	11.733	11.492	11.852*	11.999
101 Attacks in log B (1.99 per dm <sup>2</sup> )							
$N_1$	4.223	3.544	3.480	3.696	3.935*	4.450	5.072
$N_2$	5.642	5.315	5.451	5.552	5.598*	5.796	6.209
$N_3$	6.953	6.644	6.874	6.675	6.901*	7.120	7.288
$N_4$	8.212	7.751	7.855	7.774	7.796	8.156*	8.229
179 Attacks in log C (3.17 per dm <sup>2</sup> )							
$N_1$	3.654	2.810	2.680	3.096	3.359*	3.976	4.522
$N_2$	4.815	4.216	4.195	4.556	4.583*	4.907	5.199
$N_3$	5.822	5.269	5.227	5.539	5.560	5.733*	5.931
$N_4$	6.658	6.147	6.087	6.462	6.342	6.542*	6.678

<sup>a</sup> Simulations (220-240 points within the boundary area) were performed at each minimum allowed distance at each of the respective attack densities.

\* The asterisks denote where the observed distance corresponds to the minimum allowed distance, and this indicates the closest distance beetles tolerated for their nearest neighbors, assuming the hypothesis of the model.

tack densities (higher  $\chi^2$  values, Table 1) which might be expected if due to a behavioral spacing mechanism that becomes constraining when beetles are crowded together. At even lower densities than observed here, the hypothetical behavioral spacing would be hard to detect since the beetles would have so little restraints on where they could attack that their distribution should appear random.

**Simulation Model of Attack Distributions.** The simulation model for creating a uniform attack distribution presumes that a beetle will decide to attack a particular site (selected at random) only if there are no other attacks in progress within a certain minimum distance (minimum allowed distance). When this distance ( $D$ ) was set at 0 or random, the simulated average distances to the four nearest neighbors did not differ significantly from the corresponding values expected from a random spacing (Fig. 3). The quadratic regression lines of increasing average distance to the respective neighbors as the uniformity is increased (Fig. 3) should converge at 7.52, the theoretical value of maximum hexagonal spacing ( $1.0746/\sqrt{N/\text{area}}$ ), Clark and Evans 1954). However, the lines converge at an average distance slightly greater than the theoretical value, which is based on an unlimited area. This is because the simulated attacks are chosen initially at random and so almost never can be "perfectly" arranged. Furthermore, the attacks can occur at the very edge of the area, but in an unlimited area there would be a pressure from attacks just outside the bordered area, proportional to the minimum allowed distance, which would

tend to compress all attack positions slightly toward the center. This error was minimized by simulating with 400 points so that the ratio of the points at the perimeter to the total was rather small.

The simulation program cannot calculate average distances using minimum allowed distances much beyond 5 cm at the density used in Fig. 3 because of the problem of finding the minute areas that are unoccupied. Once several points are established at the proper spacing it can be impossible to place the remaining points because all areas are utilized. This is analogous to what a beetle may face when trying to find an unoccupied area on an infested tree, and indicates that a specific upper density will be reached at a certain spacing condition (such as the minimum allowed distance).

Berryman and Pienaar (1973) found that the frequencies of angles between attacks and the three nearest neighbors obtained with their simulation model were not significantly different from those that would be expected from a random distribution. The question arises whether this procedure to describe "reality" might imply that a nonrandom (tending toward uniform) distribution of attacks would have a distribution of angles that was significantly different from random. In fact, a completely regular or uniform pattern such as a grid or hexagonal spacing does have a nonrandom distribution of angles to the four nearest neighbors. However, even at the most uniform spacings tested ( $D = 4$  or 5) in the simulation model, the probability that the differences observed between expected and simulated frequencies of angles were due to random errors was  $P > 0.99$  (cf. Berryman

Table 3. The quadratic regression of the simulated values in Table 2 and the observed average distances to neighbors in *Ips typographus* were used to determine the hypothetical minimum allowed distance to the nearest neighbor

Neighbor	Quadratic regression equation <sup>a</sup>	Calculated minimum allowed distance (X) <sup>b</sup> in cm
47 Attacks in log A (0.90 per dm <sup>2</sup> )		
N <sub>1</sub>	Y = 0.0299X <sup>2</sup> + 0.2202X + 5.080	2.13 (1.04-3.05) <sup>c</sup>
N <sub>2</sub>	Y = 0.0406X <sup>2</sup> + 0.0591X + 7.811	3.28 (1.93-4.28)
N <sub>3</sub>	Y = 0.0326X <sup>2</sup> + 0.0465X + 9.768	3.12 (0.98-4.43)
N <sub>4</sub>	Y = 0.0238X <sup>2</sup> + 0.0262X + 11.511	3.51 (0.31-5.25)
101 Attacks in log B (1.99 per dm <sup>2</sup> )		
N <sub>1</sub>	Y = 0.0777X <sup>2</sup> + 0.0829X + 3.494	2.58 (2.19-2.92)
N <sub>2</sub>	Y = 0.0554X <sup>2</sup> - 0.0457X + 5.480	2.17 (0.90-2.85)
N <sub>3</sub>	Y = 0.0519X <sup>2</sup> - 0.0804X + 6.821	2.55 (1.22-3.24)
N <sub>4</sub>	Y = 0.0461X <sup>2</sup> - 0.0716X + 7.828	3.77 (3.10-4.31)
179 Attacks in log C (3.17 per dm <sup>2</sup> )		
N <sub>1</sub>	Y = 0.0439X <sup>2</sup> + 0.2810X + 2.702	2.45 (2.24-2.65)
N <sub>2</sub>	Y = 0.0114X <sup>2</sup> + 0.1905X + 4.239	2.61 (2.16-3.05)
N <sub>3</sub>	Y = -0.0054X <sup>2</sup> + 0.1819X + 5.267	3.39 (2.61-4.22)
N <sub>4</sub>	Y = -0.0113X <sup>2</sup> + 0.1713X + 6.147	4.08 (2.78-6.38)

<sup>a</sup> Y = aX<sup>2</sup> + bX + c, where X = minimum allowed distance and Y = simulated distance to neighbor (data from Table 2).

<sup>b</sup> Solve for X = [-b + √(b<sup>2</sup> - 4a(c - Y))]/2a, at Y = observed distance (from Table 2).

<sup>c</sup> Values in parentheses obtained by substituting the ±SE for Y (Table 1) into the regression equations.

and Pienaar 1973). Therefore, it seems that measurements of angles to nearby neighbors would not provide information useful in describing natural patterns that differ from random.

**Attack Spacing Mechanism.** The simulation model will calculate the average distances to nearest neighbors at any density by adjusting the "area," or in other words, the limits of the X and Y coordinates. The model was used at the three natural densities, at increasing levels of uniform pattern, to generate average distances to the four nearest neighbors. The natural distances to the four neighboring attacks corresponded to a degree of spacing that could be simulated by using a minimum allowed distance of >2 or 3 cm (asterisks, Table 2). The minimum allowed distance that a beetle might tolerate for his nearest neighbor was estimated more precisely (about 2.5 cm) by comparing the natural values to quadratic regressions from the simulation data (Table 3). The average of N<sub>1</sub> and N<sub>2</sub> at the three densities was used to estimate this value because the regression lines have steeper slopes, so comparisons are more accurate.

Figure 4 shows a random attack pattern for 100 beetles per 4,900 cm<sup>2</sup> (2.04 per dm<sup>2</sup>) compared to a uniform pattern of equal density generated at a minimum allowed distance spacing of 5 cm. The 2.5-cm minimum allowed distance calculated above for *I. typographus* was used to create a uniform pattern at this density (similar to log B) and at twice this density (somewhat higher than log C). It can be seen that at the higher density (4.08 per dm<sup>2</sup>) the spacing is fairly regular. This density is similar to "heavy" final densities attained on successfully colonized trees, which attained an average of 3.9 per dm<sup>2</sup> and a maximum of about 6 per dm<sup>2</sup> (Martinek 1956).

It is interesting to note that the estimated minimum allowed distance did not differ appreciably at the three natural densities (Table 3). This may indicate that the minimum allowed distance is controlled behaviorally and that it is inherently fixed. This further implies that there may be an upper density which can never be exceeded because of the spacing requirement. This could have important consequences for terminating the aggregation and mass attack during colonization. It has been shown that several species of bark beetle diminish the production of various attractive pheromone components after mating (cf. Byers et al. 1984), including *I. paraconfusus* (Byers 1981). Thus, at an upper density a spacing mechanism would prevent new attacks from occurring, and then production and release of pheromones would begin to decline so that fewer and finally no beetles would be attracted to the infested tree.

The nature of the supposed behavioral spacing mechanism in *I. typographus* is unknown. It is possible that at least part of the mechanism could be avoidance of higher concentrations of male pheromone as shown for *I. paraconfusus* (Byers 1983b). Bakke (1981) has shown that ipsenol and verbenone, present in male *I. typographus* hindguts in the latter stages of colonization (Birgersson et al. 1984), can inhibit the response of beetles to the attractive pheromone components. Stridulation by beetles has also been suggested to play a role in spacing of attacks (Rudinsky and Michael 1973, Rudinsky et al. 1976, Hedden and Gara 1976). *I. typographus* is able to stridulate, according to Rudinsky (1979), but neither my colleagues nor I can hear stridulatory sounds by the beetle in the laboratory or field (while *D. brevicornis*, *T. pinterda*, and *I. paraconfusus* are easily heard).

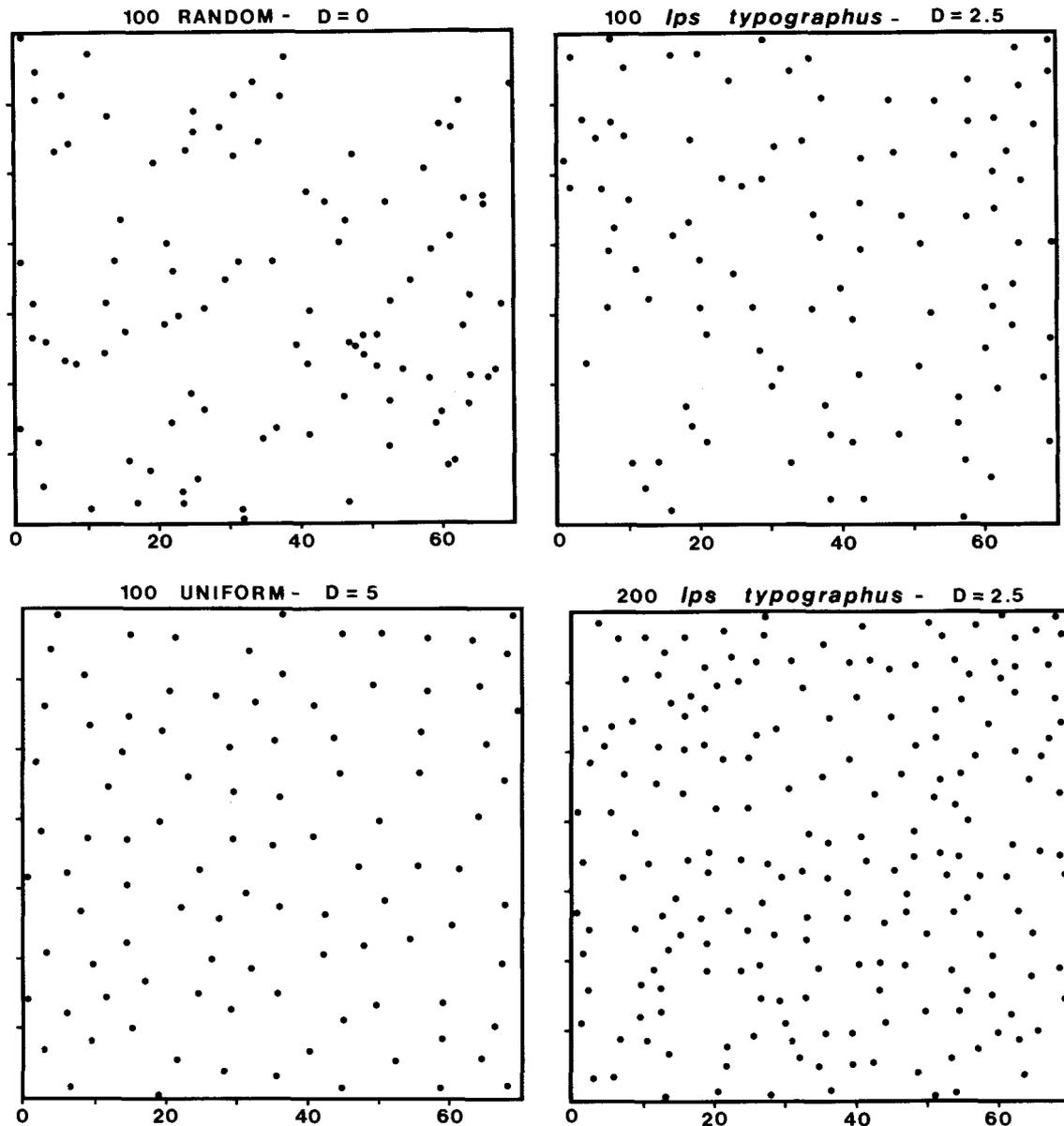


Fig. 4. Simulated patterns of attack in an area of 4,900 cm<sup>2</sup> at a minimum allowed distance of 0 cm (Random), 5 cm (Uniform), and 2.5 cm (corresponding to the value from the analysis of *Ips typographus*) at 100 attacks (density as in Fig. 3, 2.04 per dm<sup>2</sup>) and at 200 attacks (4.08 per dm<sup>2</sup>).

Other possible mechanisms are avoidance of frass piles or beetles by means of olfaction or simply by visual inspection. Finally, it could be possible that beetles simply prefer to attack certain bark surface structures that are uniformly distributed, as suggested by Shepard (1965) for *D. ponderosae* on lodgepole pine.

In an interesting experiment where closely spaced pairs of drilled holes in logs were offered to *D. ponderosae*, Safranyik and Vithayasai (1971)

found that attack initiation was not influenced by the spatial proximity of previously established attacks. They concluded that the regular attack pattern in nature is due to the regular pattern of suitable bark niches. However, their use of drilled holes may have provided an artificial inducement for beetles to initiate feeding and attack, and thus could counteract some beetle-induced spacing mechanism which operates under more natural conditions. This criticism is supported by one of their

experiments (Safranyik and Vithayasai 1971) in which all of 28 attacks were initiated in predrilled holes spaced in a 2.5-cm hexagonal pattern, while none were begun on the surrounding bark. Bark surface irregularities appear to influence the distribution and density of attacks (Safranyik and Vithayasai 1971) as modified by a given population, but bark niches do not seem limiting in a physical sense for it should be possible to concentrate many attacks in a particular bark crevice—something the beetles do not do (cf. Fig. 3 of Safranyik and Vithayasai 1971). It is probable that behavioral preferences for bark niches, light, and other abiotic factors (Safranyik and Vithayasai 1971), and nearness of neighboring attacks all influence whether a particular beetle decides to attack. However, further behavioral work is required to narrow the range of possibilities.

The simulation model for creating uniform distributions and the techniques for calculating the minimum allowed distance can in principle be applied to many plant and animal species. For instance, the model could be applied to plants that inhibit growth of neighboring plants with allelochemicals. Another example would be the model's use with territorial animals such as many nesting birds and some insects. The model should prove useful for analysis of most bark beetle attack distributions.

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