EFFECTS OF ATTRACTION RADIUS AND FLIGHT PATHS ON CATCH OF SCOLYTID BEETLES DISPERSING OUTWARD THROUGH RINGS OF PHEROMONE TRAPS

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Abstract—Results were analyzed from six previous studies in which marked bark and ambrosia beetles, *Ips typographus, I. paraconfusus,* and *Trypodendron lineatum* (Coleoptera: Scolytidae), were released at the center of concentric rings of pheromone traps. Assuming nearly straight flight paths, a "filtering" equation model predicts recapture percentages on several trap rings of specified radii, trap numbers, and effective attraction radius (EAR) of a pheromone trap. Equations were used to calculate recapture percentages on concentric trap rings as a function of increasing EAR and gave polynomial relationships for each ring with terms equal to the number of inner rings plus one. Results were confirmed by computer simulations. Filtering equations were iterated with increasing EAR values to find one that gave a recapture percentage for the innermost trap ring that matched the field results. The estimated EAR for a synthetic pheromone bait of *I. typographus* was similar in five tests (range 1.39–1.78 m), but in two other tests was larger (3.27 and 15.9 m). The EAR for pheromone of 75 male *I. paraconfusus* in ponderosa pine logs ranged from 0.35 to 34.5 m (mean of 4.7 m) and was generally larger for previously pheromone-responding beetles than for freshly emerged ones. For *T. lineatum,* the EAR of lineatin-baited traps at 100-m radius was 2.43 m. Recaptures of *I. typographus* were reasonably predicted by the estimated EARs in the filtering model. To obtain perfect fits, another model assumed the EAR could vary with ring radius (dispersal distance) and found that the EAR for *I. typographus* decreased with dispersal distance in four experiments, but increased or was variable in two others. However, in *I. paraconfusus* and *T. lineatum,* the EAR increased with dispersal distance. Simulations that varied combinations of the EAR and random angles of maximum turning (AMT) of beetles stepwise showed that a nearly straight flight path for *I. typographus* explained observed catches on trap rings best, while a higher AMT of 36° was better to explain catches of *T. lineatum.* Simulations show that catch per trap ring in relation to radial distance can be influenced by the beetle's AMT (still

unobserved in the field). A conceptual model of dispersal and host selection in "aggressive" bark beetles with regard to pioneer and joiner colonization strategies is presented.

Key Words—Effective attraction radius, dispersion, dispersal, host finding, host selection, Scolytidae, Coleoptera, *Ips typographus*, *I. paraconfusus*, *Trypodendron lineatum*, computer simulation model.

INTRODUCTION

In California, Gara (1963) released marked bark beetles, *Ips paraconfusus*, at the center of one ring of five traps containing ponderosa pine logs infested with 75 males each. The ring radius varied in individual tests from 3 to 2000 m. Since then, several studies in Europe have released marked spruce bark beetles, *Ips typographus*, at the center of several concentric rings of traps releasing pheromone components (Botterweg, 1982; Zumr, 1992; Zolubas and Byers, 1995; Duelli et al., 1997). The striped ambrosia beetle, *Trypodendron lineatum*, also was released from the center of three trap rings baited with the synthetic pheromone lineatin (Salom and McLean, 1989). Duelli et al. (1997) marked 6898 *I. typographus* termed "unflown" (freshly emerged) and 5123 considered "flown" (collected in pheromone traps) and released them at the center of three rings of pheromone-baited traps in a nonhost Scots pine forest (Table 1). Zolubas and Byers (1995) and Zumr (1992) released marked *I. typographus* at the center of four lines of pheromone traps in cardinal directions, which can be considered as concentric rings (only the first four or five rings considered here) in a spruce forest (Table 1). Botterweg (1982) also released marked spruce bark beetles at the center of pheromone trap rings in an area of meadow and Scots pine forest (Table 1). Among the purposes of these studies were to describe how far bark beetles disperse and whether flight behavior or responses to pheromone traps varies with distance from the release point. The authors concluded, based on trap catches, that bark beetles fly away from a release site in all directions when wind speeds are below 1 m/sec.

The "effective attraction radius" (EAR) was proposed as an index of attractive strength for a trap releasing semiochemicals (Byers et al., 1989). Given a population density that is proportional to the unbaited (passive) trap catch, the EAR is the radius that a spherical passive trap would need to be in order to catch, merely by interception, as many dispersing insects as were actually caught on the baited trap. Comparison of catches on passive and pheromone-baited traps gave an EAR of 1.9 m for *I. typographus* response to a release of pheromone components, 50 mg 2-methyl-3-buten-2-ol (MB) and 1 mg (S)-*cis*-verbenol (cV) per day (Byers et al., 1989). Similar amounts of MB+cV were also released in

TABLE 1. TRAP RING RADII AND NUMBER OF SYNTHETIC PHEROMONE-BAITED TRAPS
PER CONCENTRIC RING IN PREVIOUS STUDIES IN WHICH *Ips typographus* WERE RELEASED
AT CENTER OF THE RINGS AND A PORTION RECAPTURED ON PHEROMONE TRAPS

	Ring 1	Ring 2	Ring 3	Ring 4	Ring 5
Duelli et al. (1997)					
Ring radius (m)	5	200	500		
Number traps	4	80	80		
Catch unflown (6898)[a]	2445	650	195		
Catch flown (5123)	2070	95	38		
Zolubas and Byers (1995)					
Ring radius (m)	10 or 30[b]	60	90	120	
Number traps	1 or 4[b]	4	4	4	
Catch (5030 or 5920)[b]	284 or 384[b]	208	64	7	
Zumr (1992)					
Ring radius (m)	50	100	200	300	400
Number traps	4	4	4	4	4
Catch (6600)[c]	2673	1254	719	317	290
Botterweg (1982)					
Ring radius (m)	50	100	200	350	500
Number traps	4	8	16	28	40
Catch (1500 and 7000)[d]	125 or 198[d]	56 or 36	55 or 66	22 or 90	9 or 167

[a]Values in parentheses in first column are number of released *I. typographus*.
[b]Values for experiments 1 and 2, respectively; single values for experiment 2.
[c]1989 and 1990 results pooled.
[d]Experiments 1 (1980) and 3 (1981), respectively.

trap ring studies using Pheroprax baits (Zumr, 1992; Duelli et al., 1997) and
Ipslure baits (Botterweg, 1982; Zolubas and Byers, 1995). For simulation stud-
ies, the EAR can be considered more simply in two dimensions rather than three
because at large EARs the ground and beetle's flight height essentially flatten
the theoretical sphere into a cylinder.

In the dispersal studies above, catches on pheromone traps decreased as
a function of distance from the release point as described by power and expo-
nential regressions (Zolubas and Byers, 1995). This is expected based on the
movement of beetles outward into increasingly greater areas. However, the rela-
tionships can be greatly affected by several factors; for example, the EAR of
a trap could change with flight distance (proportional to distance from release
site). Another factor, previously ignored, is that there is a "filtering" effect such
that some beetles would be caught on the first rings of traps while those remain-
ing would pass through possibly to be caught on outer rings. There could also
be a selective catch of pheromone-responding beetles on the inner rings while
unresponsive beetles would pass through to be caught on traps of the outer rings
by chance interception. Bark beetles might even change their angle of turning
(or frequency of turning) with flight distance from the source, which ought to

affect catch rates. The previous studies were done in spruce, pine, or Douglas-fir forests so interceptions by trees, expected every 67 m for a 70-year-old Norway spruce forest of 30-cm-diameter trees (Byers, 1996a), might affect the dispersal directions when beetles that had landed took flight again in random directions.

My first objective was to develop equations that can calculate the theoretical filtering effect of any arrangement of concentric trap rings of specified dimensions, numbers of traps, and attractive power (EAR) in order to predict the catch of insects dispersing outward from a central release site. A second objective was to determine the influence of trap EAR and the beetle's angle of maximum turning at random (AMT) on catches of scolytid beetles in various trap ring arrangements in computer simulations. The comparison of predicted catches by using equations and simulations with those catches observed in the field in the previous studies may provide insights concerning the behavior of bark and ambrosia beetles during the initial dispersal from brood trees and overwintering sites. Finally, I develop a theory that during dispersal and host seeking, a beetle exhibits either a "pioneer" or a "joiner" strategy of colonization behavior that is based on competition, host resistance, presence of aggregation pheromone, and the bark beetle's fat reserves.

METHODS AND MATERIALS

Sequential Equations to Predict Catches. A general series of equations can predict the catch on any number of concentric rings of traps depending on the respective ring radii, number of traps per ring, and radii of the traps (assumed to be equal). Considering three rings as in Duelli et al. (1997), the number caught on rings 1–3, C_1–C_3, and the number escaping each ring, E_1–E_3, can be calculated by three successive pairs of equations, assuming a nearly straight flight path (no beetles can come back once they have left a ring):

$$C_1 = N \frac{T_1(EAR)}{R_1\pi} \qquad E_1 = N \frac{R_1\pi - T_1(EAR)}{R_1\pi} \qquad (1)$$

$$C_2 = E_1 \frac{T_2(EAR)}{R_2\pi} \qquad E_2 = E_1 \frac{R_2\pi - T_2(EAR)}{R_2\pi} \qquad (2)$$

$$C_3 = E_2 \frac{T_3(EAR)}{R_3\pi} \qquad E_3 = E_2 \frac{R_3\pi - T_3(EAR)}{R_3\pi} \qquad (3)$$

where N is the initial number of insects released, T_1–T_3 are the number of traps in rings 1–3, EAR is the effective attraction radius of the pheromone trap, and R_1–R_3 are the radii of trap rings 1–3, respectively. The catch on a fourth

ring, or more, can be considered by adding a fourth equation, or more, as indicated.

The sequential equations were used repeatedly by computer to graph the effect of changing the EAR on the percentage of released beetles caught on each trap row. The best-fitting EARs to the data of four studies and various experiments were found by incrementing the EAR from 0 to the maximum possible without overlap (MAX) in steps of MAX/10,000 m using sequential equation 1 by computer to find the least difference in the actual percent catch on ring 1 compared with the predicted catch. This EAR was then used to calculate the predicted catches on the outer rings for comparison to observed catches. Assuming, however, that the EAR can vary with distance from the center, an optimal EAR was found for each ring based on the maximum number that could have passed through the inner rings (by subtracting the catches from the number released) and again on the dimensions and trap numbers of the ring (as calculated for the first ring above).

Simulations to Predict Catches. Insect flight movement can be simulated in two dimensions by taking steps in a forward direction with possible random deviations up to an angle of maximum turn (AMT), either right or left at random (Skellam, 1973; Byers, 1991, 1993a, 1996a,b). An insect is caught when intercepting a trap, no matter how large the step size, according to the algorithm in Byers (1991). A computer model was made to simulate the trapping designs used in previous studies, e.g., by Duelli et al. (1997). The input parameters of the program are dispersal time, number of released insects, average insect speed, step size, AMT, number of trap rings, number of traps per ring, radii of trap rings, and the EAR of a trap. The release site is centered on the screen, and coordinates of the traps are calculated and traps drawn. Insects are given random initial directions (random number 0–360°).

In all simulations, flight speed was 2 m/sec, which is about what large bark beetles such as *Ips typographus* can maintain in still air (Byers, 1996a). Simulated dispersal periods were limited to 1 hr when AMT was varied, although a few beetles on flight mills have flow up to 6 hr (Forsse and Solbreck, 1985; Forsse, 1991; Gries et al., 1990). The AMT was varied from 0° to 45°, and steps were 2 m (possible turn every second). Catch was recorded for each trap ring. The "flown" bark beetles had a catch distribution on the three rings that was different from the "unflown" (Duelli et al., 1997) and did not fit well to the predicted based on the best-fitting EAR calculated for ring 1. Therefore, the EAR and the AMT were varied two-dimensionally (AMT varied at each varied EAR) in an attempt to find an EAR–AMT combination of simulated results that could predict the field data. The EAR was the same for all traps in the rings. Other catch distributions (Zolubas and Byers, 1995, *I. typographus;* Salom and McLean, 1989, experiment 1, *T. lineatum*) were modeled similarly.

The expected catch per trap with an EAR of 1.9 m at increasing distances

from the release point of 1000 insects was estimated by simulation when only one trap was present (no filtering effect). Insects had either an AMT of 5° or 20° and flew for 30 min. In another series of related simulations, competing traps were placed in 10 concentric rings of 20, 10, and then 4 traps each, respectively, every 25 m, with the same EAR and an AMT of 5°. Nonlinear regressions were fitted to the data when appropriate.

RESULTS

Sequential Equations to Predict Catches. The computer-iterated equations 1–3 found that increasing the effective attraction radius (EAR) of a trap from 0 to the maximum, without overlap between traps, linearly increases the recapture percentage (of those released) on trap ring 1 [for the trap configuration of Duelli et al. (1997), $Y = 25.465X$, $r^2 = 1$, Figure 1]. The innermost trap ring always will have a linear increase in recapture percentage as a function of EAR, regardless of the ring radius or number of traps in the ring. The recapture percentage on the second ring of traps has a quadratic relationship to EAR, first increasing then decreasing (Figure 1), again regardless of the ring radii or number of traps. For the trap configuration of Duelli et al. (1997), the relation follows $Y = -3.242X^2$
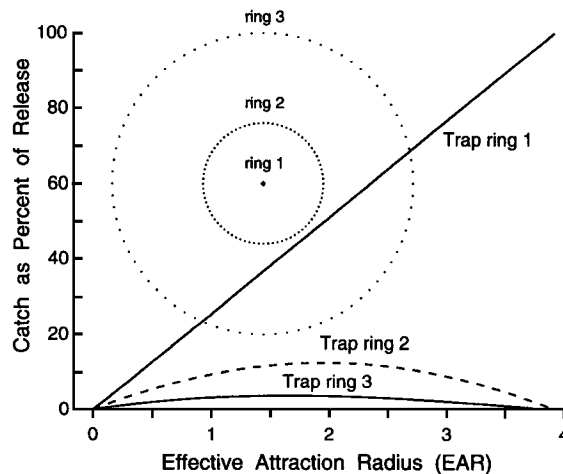

FIG. 1. Percentage caught on each trap ring of the number of insects released in relation to the effective attraction radius (EAR) of the trap. The curves are based on equations 1–3 for four traps in ring 1 (5 m radius), 80 traps in ring 2 (200 m radius), and 80 traps in ring 3 (500 m radius). The maximum trap radius of 3.927 m is based on four nonoverlapping traps in ring 1. Concentric rings of dots represent trap ring dimensions and number of traps (3 m radius).

TABLE 2. PERCENTAGES OF RECAPTURED *Ips typographus* IN PREVIOUS STUDIES COMPARED WITH PREDICTED PERCENTAGES CALCULATED FROM FILTERING MODEL WITH AN EFFECTIVE ATTRACTION RADIUS (EAR) OF PHEROMONE TRAPS BEST FITTING THE OBSERVED PERCENTAGE FOR TRAP RING 1

	Percentage recaptured				
	Ring 1	Ring 2	Ring 3	Ring 4	Ring 5
Duelli et al. (1997)					
Catch unflown (6898)	35.45	9.42	2.83		
Predicted (1.39 m EAR)	35.45	11.44	3.77		
Catch flown (5123)	40.41	1.85	0.74		
Predicted (1.59 m EAR)	40.41	12.04	3.84		
Zolubas and Byers (1995)					
Catch (5030 or 5920)[a]	5.65 or 6.49[a]	3.51	1.08	0.12	
Predicted (1.78 or 1.53 m EAR)[a]	5.65 or 6.49[a]	3.03	1.96	1.44	
Zumr (1992)					
Catch (6600)	40.5	19.0	10.89	4.8	4.39
Predicted (15.9 m)	40.5	12.05	4.8	2.88	2.01
Botterweg (1982)					
Catch (1500 or 7000)[b]	8.33 or 2.83[b]	3.73 or 0.51	3.67 or 0.94	1.47 or 1.29	0.6 or 2.39
Predicted (3.27 or 1.11 m EAR)[b]	8.33 or 2.83[b]	7.64 or 2.75	7.0 or 2.67	6.42 or 2.6	5.88 or 2.52

[a]Values for experiments 1 and 2, respectively; single values for experiment 2.
[b]Experiments 1 (1980) and 3 (1981), respectively.

+ 12.732X, r^2 = 1 (Figure 1). The third ring of traps catches insects similarly (Figure 1) but even less according to a cubic relationship, $Y = 0.165X^3 - 1.945X^2$ + 5.09X, r^2 = 1. Trap placements with four or more rings are related as polynomials of four or more terms; however, the specific coefficients depend on the actual EAR, ring radii, and number of traps per ring.

The EAR of pheromone-baited traps in previous studies can be estimated using sequential equation 1 and incrementing the EAR until the predicted catch percentage matches the observed catch. Trap ring 1 is the only reliable one to use since the relation is monotonic, while rings 2 and 3 are unimodal with two values of X for each Y (Figure 1). In the study by Duelli et al. (1997), the pheromone traps would need to have an EAR for "unflown" *I. typographus* of 1.39 m to account for the observed catch of 35.45% recaptures on ring 1 (Table 2). This value also predicts recapture percentages on rings 2 and 3 that are quite close

to observed values. The best-fitting EAR for the "flown" beetles was 1.59 m yielding 40.41% catch on ring 1 as observed, but the predicted catches on rings 2 and 3 of 12.04 and 3.84% are much larger than the observed values of 1.85 and 0.74%, respectively (Table 2). The sequential equations predict a similar EAR of 1.78 or 1.53 m in the studies by Zolubas and Byers (1995) and 3.27 or 1.11 m in two studies by Botterweg (1982), and even the recapture rates on rings 2–5 are similar to predicted catches with some exceptions (Table 2). The EAR calculated for traps used by Zumr (1992), however, is much larger at 15.9 m, but the predicted catch rates are reasonably similar to those observed, again with some unexplained deviations (Table 2).

In contrast to a constant EAR assumed above, it is possible that bark beetles change their responsiveness to pheromone as they fly away from the release site (or as a function of flight time), thereby resulting in a variable EAR. The same result could occur if bark beetles varied inherently in their responsiveness to pheromone so that more pheromone-sensitive individuals would be filtered out by the inner rings of traps. The best-fitting EAR can be predicted based on the number expected to pass through each succeeding ring. The EAR for *I. typographus* appears to decline significantly with distance of dispersal from the release (Table 3), for example, from 1.59 to 0.15 m (Duelli et al., 1997) and from 1.53 to 0.11 m (Zolubas and Byers, 1995) or from 3.27 to 0.24 m in experiment 1 of Botterweg (1982). However, the EAR was consistently large (11–17 m) in Zumr (1992), but went down and then increased again with trap ring distance in experiment 2 of Botterweg (1982).

TABLE 3. ESTIMATED EFFECTIVE ATTRACTION RADII OF SYNTHETIC PHEROMONE TRAPS FOR EACH CONCENTRIC TRAP RING OF PREVIOUS STUDIES IN ORDER TO OBTAIN OBSERVED CATCHES OF *Ips typographus* WITH FILTERING MODEL

	Effective attraction radius (EAR) (m)				
	Ring 1	Ring 2	Ring 3	Ring 4	Ring 5
Duelli et al. (1997)					
Unflown	1.39	1.15	1.01		
Flown	1.59	0.24	0.25		
Zolubas and Byers (1995)					
Experiment 1 or 2[a]	1.78 or 1.53[a]	1.77	0.85	0.12	
Zumr (1992)					
Pooled release	15.9	25.1	42.3	38.2	55.7
Botterweg (1982)					
Experiment 1 or 3[b]	3.27 or 1.11[b]	1.6 or 0.21	1.64 or 0.38	0.68 or 0.53	0.28 or 0.99

[a]Values for experiments 1 and 2, respectively; single values for experiment 2.
[b]Experiments 1 (1980) and 3 (1981), respectively.

TABLE 4. ESTIMATED EFFECTIVE ATTRACTION RADII (EAR) OF TRAPS WITH
NATURAL PHEROMONE OF *Ips paraconfusus* (75 MALES IN LOGS) FOR NINE
EXPERIMENTS OF VARIOUS TRAP RING RADIUS TO OBTAIN OBSERVED CATCHES
(GARA, 1963)[a]

Ring radius (m)[a]	Emerging beetles		Responding beetles	
	Recapture %	EAR [m (95% CL)][b]	Recapture %	EAR [m (95% CL)]
3	18.58	0.35 (0.31–0.40)	19.05	0.36 (0.32–0.41)
5	28.18	0.89 (0.80–0.97)	26.73	0.84 (0.77–0.92)
10	20.62	1.30 (1.14–1.47)	25.92	1.63 (1.35–1.95)
25	15.74	2.47 (2.22–2.74)	16.96	2.66 (2.44–2.91)
50	5.97	1.88 (1.31–2.67)	16.39	5.15 (4.45–5.93)
100	2.31	1.45 (0.57–3.64)	11.89	7.47 (5.22–10.52)
500	1.45	4.56 (2.20–9.27)	10.98	34.49 (29.72–39.93)
1000	0.70	4.40 (1.19–15.71)	1.27	7.98 (4.21–15.08)
2000	0	—	0.13	1.68 (0.25–9.30)

[a]Five traps equally spaced in ring.
[b]Confidence limits for proportions (from Gara, 1963) were used to calculate 95% confidence limits for EAR.

In the study with *I. paraconfusus* (Gara, 1963), nine experiments had a trap ring of radii from 3 to 2000 m (five traps in a ring) with EARs estimated to range from 0.35 to 34.5 m, average of 4.68 ± 4.13 m (95% CL, Table 4). Beetles that had freshly emerged were marked with one color of fluorescent powder, while another group that had responded previously to pheromone was colored differently, and both groups were released simultaneously. The EARs for both groups increased similarly as trap rings were enlarged from 3 to 25 m radius, then the EAR for the emerged group increased little with increases in ring radii while the EAR for the previously responding group continued to increase (Table 4). *T. lineatum* released in three concentric rings of traps (Salom and McLean, 1989) had EARs that increased from only 0.32 m close to the release to 1.72 m at 100 m radius (Table 5). In the one-ring tests, the EAR also seems to increase up to 7.1 m at 500 m radius (Table 5).

Simulations to Predict Catches. The catch of simulated insects dispersing outward through rings of traps (Figure 2) verified the sequential equations (Table 2, unflown) when the flight path was nearly straight, meaning that the angle of maximum turn at random (AMT) was only a few degrees. An extension of the AMT to 90° caused paths to twist wildly, and this caused the relationships between the AMT and the recaptured percentage on the various rings to be complicated (Figure 3). It was thought that simulations varying both the EAR and AMT could find values that would predict the percentages of catch of "flown" *I. typographus* on the various rings that were not fitted well by the equation model

TABLE 5. ESTIMATED EFFECTIVE ATTRACTION RADII OF LINEATIN-BAITED TRAPS FOR
EACH CONCENTRIC TRAP RING TO OBTAIN OBSERVED CATCHES OF *Trypodendron
lineatum* WITH FILTERING MODEL (SALOM AND McLEAN, 1989)

	Effective attraction radius (EAR, m)		
	Ring 1	Ring 2	Ring 3
Experiment 1[a]	0.32 (0.30–0.34)[b]	1.04 (0.98–1.10)	1.72 (1.61–1.84)
Experiment 2[c]	2.43 (2.29–2.59)		
Experiment 3[d]	7.07 (5.11–9.74)		

[a]Trap ring radii of 5, 25, and 100 m with 4, 8, and 16 traps for rings 1 to 3, respectively; and
recaptures of 8.1, 9.7, and 7.2% per trap ring, respectively, of 10,535 released in six replicates.
[b]Confidence limits for proportions were used to calculate 95% confidence limits for EAR.
[c]One trap ring of 16 traps in a radius of 100 m, and recapture of 12.5% of 6780 released in four
replicates.
[d]One trap ring of four traps in a radius of 500 m and recapture of 35 of 1985 released.

(Table 2). However, none of the stepwise values of EAR from 0 to 3.93 m (maximum without overlap) while varying AMT from 0 to 90° was able to predict the distribution of catch percentages of "flown" beetles on the three trap rings of Duelli et al. (1997). For example, using an EAR of 1.39 m and varying the AMT (0–90°) shows that no relative catch distributions on the three rings were
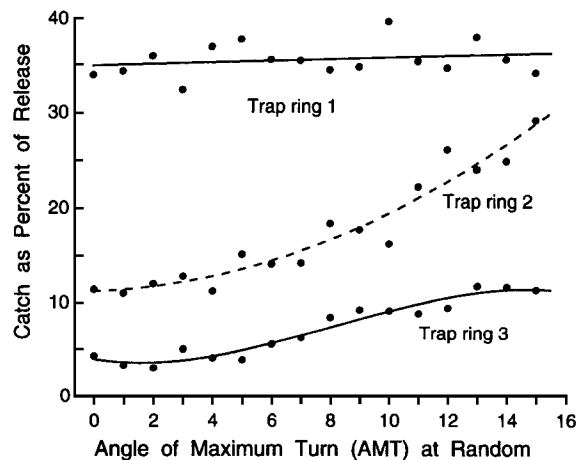

FIG. 2. Percentage caught on each trap ring of the number of insects released in relation to the insect's angle of maximum turn (AMT) at random, assuming a 1.39-m effective attraction radius (EAR) for a trap. The curves are based on release of 1000 simulated insects for each X value with trap arrangement as in Figure 1 (see text for details).
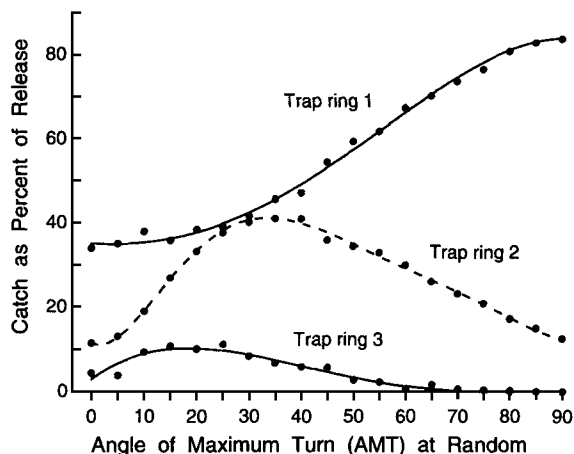
FIG. 3. Percentage caught on each trap ring of the number of insects released in relation to the insect's angle of maximum turn (AMT) at random, assuming a 1.39-m effective attraction radius (EAR) for a trap. The curves are based on release of 1000 simulated insects for each X value with trap arrangement as in Figure 1 (see text for details).

similar to those found in the field (Figure 3, Table 2). The "best" fit, although unsatisfactory, was an AMT of 0° or straight flight path.

The best fit for the data of Zolubas and Byers (1995) for each ring was better, giving an EAR of 1.6 m, an AMT of 0°, and recapture percents of 6.3, 3.5, 0, and 0% per ring, respectively (observed were 6.5, 3.5, 1.1, and 0.1%). By using the data of Salom and McLean (1989) for *T. lineatum*, an EAR–AMT combination was found that fit the observed catch percentages best with an AMT of 36° and EAR of 0.2 m, giving percentages of 8.5, 9.4, and 8.0% (compared to the observed 8.1, 9.7, and 7.2% recapture). A flight duration of only 10 min did not change the results much, as the best EAR was 0.3 m and AMT was 36°. This method does not work for experiments with only one ring. For example, in the second experiment, they recaptured 12.4% on the 16 traps in a ring of 100 m radius (Table 5), which in simulations was fit by many combinations of EAR–AMT, from an EAR of 0.2 m and AMT of 38° to an EAR of 2.5 m and AMT of 0°. In this case, the EAR and AMT vary inversely (in a negative logarithmic relation: EAR = 14.78 – 13.27 ln AMT, r^2 = 0.97), and thus no conclusions can be drawn about flight paths.

The catch per trap as a function of trap distance from the release site has been plotted in most earlier studies, as summarized by Zolubas and Byers (1995). Simulations which used an ideal situation of only one trap, so that competition among traps could not occur, showed a power relationship between catch and

Catch per Trap

50

40

30   20° AMT

20

5° AMT

10

0

0   50   100   150   200   250
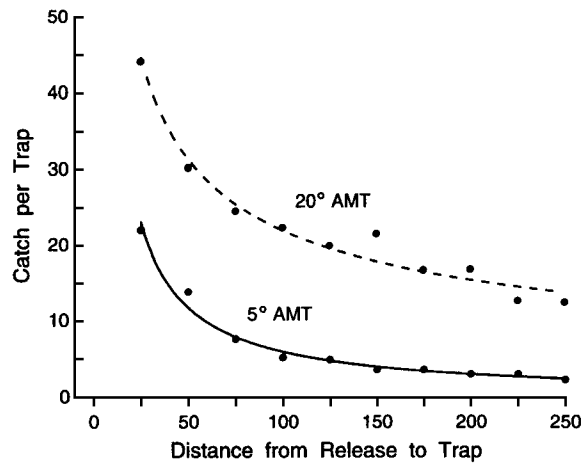
Distance from Release to Trap

Fig. 4. Catch on one trap as a function of distance from the point of insect release at two different random angles of maximum turn (AMT). Each point represents an average of 10 simulations of 1000 insects each that flew for 30 min. The effective attraction radius of the trap was 1.9 m.

distance ($Y = 540.19X^{-0.98}$, $r^2 = 0.98$) that depended on the AMT (Figure 4). For example, a more twisting AMT of 20° causes a higher catch on the trap at all distances, compared to a more straight path with an AMT of 5° (Figure 4). When traps were competing and filtering the beetles with flight paths of 5° AMT, the catch per trap was less, as expected, compared to the situation with only one trap (Figure 5). However, the first ring of traps filtered out many beetles, which biased the catch on the second ring so that it did not fit the general curve compared to the outer rings (Figure 5). This effect is evident in earlier studies where many beetles were caught on the first ring (Figure 7 of Botterweg, 1982; Figure 2 of Duelli et al., 1997) but is minimal in other studies where only four traps per ring were used at farther distances (Zumr, 1992; Zolubas and Byers, 1995). This effect tends to confound the regressions in a way that was not realized earlier (Zolubas and Byers, 1995).

DISCUSSION

The sequential equations used to filter out the dispersing insects on successive rings of traps were validated by simulation and, in some cases, by a good match with field catches. Usually, the traps in a ring, both in the simulations and in the field, are spaced equally apart. However, it does not matter whether the traps are placed at random or spaced about the ring as long as there is no
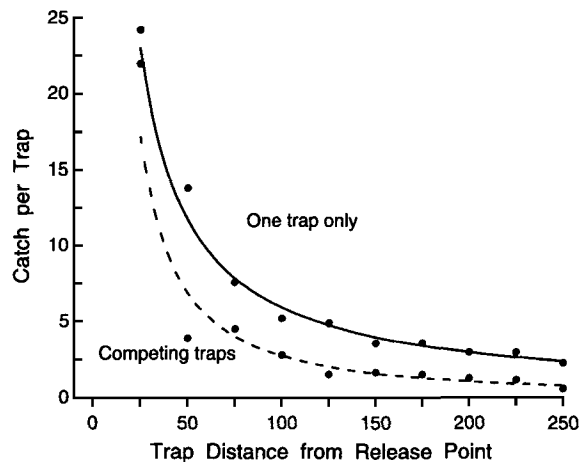
FIG. 5. Comparison of catch per trap in simulations with only one trap versus many competing traps in rings at indicated distances from the release site. The number of competing traps in each successive ring was 20, 10, and then constant at four traps per ring. Each point represents an average of 10 simulations of 1000 insects each, AMT of 5°, and EAR of 1.9 m, with flight for 30 min.

overlap of the EAR (or plume) and the beetles disperse in all directions equally at random. It also does not matter if beetles fly in one general direction (e.g., downwind) with random deviations; nonoverlapping EARs of traps theoretically would filter in the same proportions. In the simulations, on the other hand, if insects fly completely straight (0° AMT), then inner traps prohibit outer traps along the same trajectory from catching (which did not happen in any studies). Therefore, simulated traps must be offset or the insects must have some degree of random turning. However, too much random turning will cause them to turn back occasionally into a ring of traps they have already passed through, thereby possibly inflating the catch on that ring. The sequential equations do not consider the AMT or trap placement and, thus, give ideal results. The equations should not be used with an EAR that overlaps with other traps. In nature, the EAR could overlap but this should decrease catches as the traps directly compete and the insects could be confused by background levels of pheromone. Gara (1963) showed that bark beetles would fly past sources of natural pheromone when overlapped by pheromone from sources upwind.

The EAR is expected to be smaller than an envisioned average distance of oriented flight toward a semiochemical source, which, in turn, is likely smaller than the average distance that bark beetles would first detect such a source (Byers et al., 1989; Schlyter, 1992). One can imagine a pheromone plume as globules

and filaments of higher and lower (or no) pheromone concentration snaking, splitting, or exploding into larger and more uniform clouds that dissipate below the threshold detection of the insect (of. Byers, 1996b). The probability that an insect will orient to the pheromone source after entering this plume depends in large part on the entry point in relation to the source. It is obvious that all these probabilities, behavioral variations, and differences in wind turbulence over time make the calculation of an average orientation distance virtually impossible. What the EAR attempts to do instead is reform the plume and all the orientation probabilities into a sphere (or cylinder) where 100% orient to the source (Byers et al., 1989; Byers, 1995, 1996a).

The EAR for a specific semiochemical release rate and insect species is, in theory, independent of the population density (or number released). Temperature and wind could have some effect by influencing orientation behavior, but this has not been studied. Most behavioral tests are done under similar weather conditions when insects can fly. The EAR can be estimated by comparison of a passive trap catch with the semiochemical trap catch and by using the dimensions of the passive trap (Byers et al., 1989). This method does not depend, in theory, on the trap efficiency, as a lower efficiency is like a lower population density. Neither should change the ratio of catches between the pair of traps. Alternatively, the EAR can be estimated with a second method by using the filtration model, as done here, by comparing the catches on semiochemical-baited traps with the number released from the center. However, in this case, the trap efficiency would affect the EAR.

Increasing the dosage of semiochemical release in traps should give increasing EARs, until inhibition at the highest rates. According to Schlyter et al. (1987), 1 m of Pheroprax tape one week old releases 50 mg MB and 1 mg cV per day (used by Duelli et al., 1997). Zolubas and Byers (1995) used Ipslure baits that released the same rates but also released ipsdienol (probably inactive; Schlyter et al., 1987). Botterweg (1982) used 0.25 m of Pheroprax and Zumr (1992) used some unspecified portion thereof. These studies all appear to have used comparable rates, so the much higher EARs of Zumr (1992) are probably not explained by release rate (Table 3). However, his was the only study that used a cluster of four traps as "the trap." This would both increase the trap surface area by four and broaden the spatial distribution. Byers et al. (1989) showed that enlargement of the sticky trap radius logarithmically increased trap catch of *I. typographus*. The EAR, as estimated with the filtering equations, depends on the trap efficiency, which probably differed in each study: Duelli et al. (1997) used Theysohn traps for ring 1 and a mixture of these and Olesnik traps in outer rings; Zolubas and Byers (1995) used cross-vane barrier traps, while Botterweg (1982) used drainpipe traps. There is no consistent effect of nonhost Scots pine or host Norway spruce forest on the recapture rates in the studies with *I. typographus*.

By using paired sticky traps, an EAR of 1.9 m was calculated for a MB+cV

release (Byers et al., 1989) that is similar to most of those estimated here for the inner trap ring (Tables 2 and 3). An effective catch radius (the same as the EAR) of about 2 m for a puddle trap, releasing the same MB+cV rate, in a grid of 49 (7 × 7) such traps at 6 m spacing was calculated for *I. typographus* (Byers, 1993b). The calculation was based on comparing the ratios of catch on the outer rectangular ring of 24 traps with the next inner ring of 16 traps with simulated results iterating larger EARs. The estimated EAR varied on different dates from 1.53 to 2.48 m (Byers, 1993b). All estimates of EAR which used different traps and methods were similar for the MB+cV release rate. However, in the experiments with multiple trap rings (*I. typographus*), the EAR appeared to decrease with distance (Table 3). This is probably due to a selective catch of responsive beetles on the inner trap rings, leaving less responsive ones caught less often on the outer rings (smaller EAR) rather than to changes in response with flight time.

In contrast, the EAR for *T. lineatum* attraction to lineatin (dose unspecified) in multiple funnel traps had the opposite trend, increasing from 0.32 to 1.72 m (Table 5). The low EAR value at 3 m from the release center may be the result of overlapping of plumes (or EARs) of the closely spaced traps, so that their locations were obscured. When single-ring tests were done at 100 and 500 m radius, the EAR still appeared to increase with radius or dispersal distance (Table 5). The EAR for *I. paraconfusus* to natural pheromone also increased with distance (Table 4). Since there was only one ring in each test, and thus no filtration, the increase in EAR would seem to be a function of dispersal flight distance. The initial increase in EAR close to the release center may result not only from overlapping plumes (or EARs) of the closely spaced traps but also from escape reactions as the beetles were ejected into flight mechanically (as opposed to the other studies where the beetles initiated flight at will). The EAR of 34.5 m seems to be an outlier. Both the "previously responding to pheromone" and "freshly emerged" groups of beetles behave similarly, at least out to 25 m, due to the "overlapping and fright" hypothesis. Then, the EARs enlarge for the previously responding beetles since they appear more willing to respond on average than the freshly emerged beetles that are in the dispersal stage with presumed higher fat reserves.

At the beginning of a dispersal flight, bark beetles are considered rather unresponsive to pheromone or host volatiles. The theory is that fat reserves are higher in freshly emerged beetles so that they have the ability for extended flight and can gain adaptive benefits from dispersal before responding to hosts (Borden et al., 1986; Anderbrant et al., 1985; Gries et al., 1990). Graham (1959) showed that continued flight exercise by *T. lineatum* caused an increase in responsiveness to visual and olfactory stimuli of the host. Freshly emerged *T. lineatum* and *D. pseudotsugae* required 30 or 90 min of flight, respectively, before responding to pheromone from female frass (Bennett and Borden, 1971). Atkins (1966)

found that female *D. pseudotsugae* with more than 20% fat (dry weight) were usually not responsive to the host, while those under 20% fat were responsive and still could fly. Beetles with less than 10% fat had trouble flying since fat was required as an energy source (Atkins, 1969). The fat metabolized by *D. pseudotsugae* consists mainly of C_{16} and C_{18} fatty acids (Thompson and Bennett, 1971). Other studies have found that scolytid beetles in the genera *Trypodendron, Dendroctonus, Scolytus,* and *Ips* increase their responsiveness or upwind orientation to host and pheromone after continued flight exercise (Choudhury and Kennedy, 1980; and cf. Borden et al., 1986).

However, some bark beetles appear rather responsive to pheromone upon emergence. Lindelöw and Weslien (1986) found that overwintered *I. typographus,* taken from emergence tents in the field and marked, were caught in synthetic pheromone traps within minutes of release. Moreover, the majority of *I. paraconfusus* will respond to aggregation pheromone soon after emergence (Wood and Bushing, 1963; Gara, 1963; Hagen and Atkins, 1975). Botterweg (1982) also found that *I. typographus* can respond immediately to pheromone when beginning dispersal, and this is in accordance with his finding that beetles lost 40–50% of their fat over the winter. Possibly, second-generation beetles in southern Europe would have higher fat and disperse further.

Increasing competition among larvae due to increasing densities of parents laying broods was shown to reduce size and fat content of bark beetles (Atkins, 1975; Anderbrant et al., 1985). This seems in conflict, however, with the statement of Forsse (1991) that flying time of *I. typographus* on flight mills was "similar among populations and appeared unaffected by outbreak conditions." Earlier, Forsse and Solbreck (1985) could not find any affect of sex or body size on the duration of flight on mills. Botterweg (1982) also concluded that there was little, if any, effect of beetle size or fat content on dispersal distance, as monitored in field traps. However, he did find that fat content of beetles declined over the flight period. This was probably due to consumption of fat during host-seeking rather than later emergence of lower-fat beetles, since beetle's sizes (elytral weights) did not decrease over the spring season.

Newly emerged *D. pseudotsugae* fly on flight mills an average of 2 hr before resting (3 hr total) but some individuals can fly up to 8 hr uninterrupted (Atkins, 1961). Jactel and Gaillard (1991) flew *I. sexdentatus* on rotary flight mills and found that 50% of the beetles could fly more than 20 km and 10% more than 45 km based on about 50 interrupted flights. About 25% of *I. typographus* taken from litter in an outbreak area can fly for over 1 hr and 10% for more than 2.5 hr on flight mills, with a maximum flight of 6 hr and 20 min recorded (Forsse and Solbreck, 1985). At free-flying speeds of 1.9–2 m/sec (Gries et al., 1989; Byers, 1996a), a maximum range would be 41 to 45.6 km without wind transport. However, wing beat frequency declines with flight duration, which may affect flight range. In the only case studied, the wing beat frequency of *D. pseudotsugae*

of about 95 Hz declines 18% with flight time over 4 hr to about 75 Hz (Atkins, 1960). Speed on flight mills also declined from 1.11 to 0.99 m/sec (Atkins, 1961).

The view that bark beetles can fly some tens of kilometers is based less on mark–recapture studies and more on collections of beetles far from forests. Nilssen (1978) found two *I. typographus* in the stomach of a salmon 35 km from spruce forest. Miller and Keen (1960) report results of studies by the US Forest Service in California where the western pine beetle, *D. brevicomis*, infested "islands" of ponderosa pine, initially free of beetles, that were separated from the main forest by open sagebrush areas. They concluded that significant numbers of bark beetles must have flown a minimum of 3.2 km in one study, and 9.6 or even 20 km in another study, to reach the infested trees and kill them.

At some point during the flight, or throughout the flight, beetles respond to pheromone, avoid unsuitable trees, or land on trees and presumably determine their suitability. Encountering pheromone while flying, by definition, means that a suitable host is nearby. Other volatiles, notably ethanol (a diseased or decaying tree) and verbenone (signaling competition, fully colonized host, or decaying host), as well as green-leaf alcohols are avoided in flight and after landing (cf. Byers, 1995; Borden et al., 1997; Byers et al., 1998). Some bark beetles respond to host volatiles (e.g., *Tomicus;* Byers, 1995) but the aggressive, tree-killing bark beetles considered here are believed to find hosts by random landing without the aid of any long-range host volatiles (Raffa and Berryman, 1979; Moeck et al., 1981; Byers, 1995, 1996a). For example, *Scolytus ventralis* in one area made borings in 74% of the grand fir, but only 3.5% of the trees were colonized (Berryman and Ashraf, 1970). Hynum and Berryman (1980) also found no differences between landing rates on killed and nonkilled lodgepole pine or between host and nonhost trees for *D. ponderosae*. There was a direct relationship between the magnitude of the flying population (as measured by total catch) and the number of trees landed upon (catch in window traps), indicating a random landing pattern (Raffa and Berryman, 1979). Ponderosa pines that were injured by freezing were as likely to be landed upon by *D. brevicomis* as healthy control trees (Moeck et al., 1981).

A beetle that lands on a tree and attempts to find a place on the bark to bore is termed a pioneer if there are few others present. Pioneers are presumed to encounter significant host resistance and resin when attacking compared to later arrivals (joiners) when the tree has succumbed (Raffa and Berryman, 1979; Wood, 1982; Byers, 1995). Only males, in the case of *Ips*, or females, in the case of *Dendroctonus*, initiate the entrance tunnel and can be pioneers, but the joining sex in the early stages of colonization must incur some increased risks of resinosis. One hypothesis is that, since pioneers must attack the tree and survive to produce pheromone before the rest of the population can exploit the resource, pioneers must be the largest and most vigorous beetles of the population. In
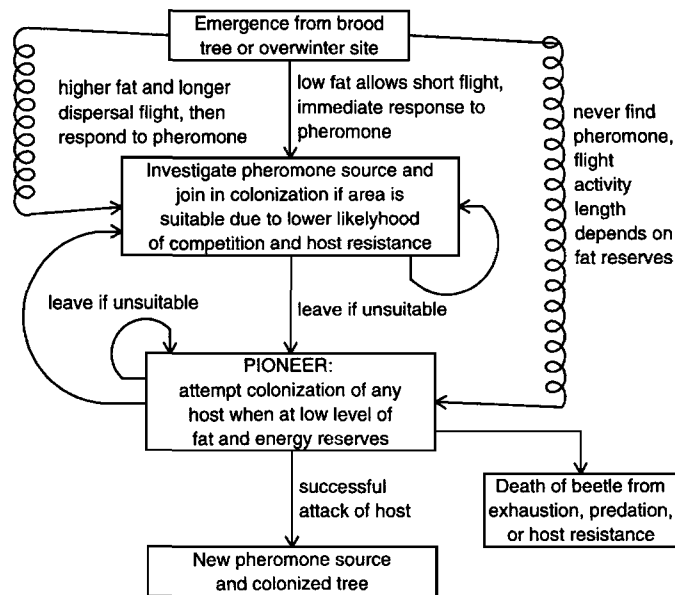
FIG. 6. Conceptual model of dispersal and host-seeking ecology of "aggressive" bark beetles that use aggregation pheromones. Factors such as the beetle's amount of fat reserves, encountering of pheromone, and level of competition and host suitability determine whether a beetle joins resident beetles in colonizing a tree or is the first pioneer to attack.

Figure 6, a scheme is presented for dispersal flight under various conditions and circumstances. An individual would undertake a pioneer strategy, in my view, only if no pheromone were encountered during the dispersal, or after leaving unsuitable colonization areas, so that finally fat reserves became low (cf. Figure 5.6 in Byers, 1995). In this desperate state, the beetle would attempt to bore into any tree and, if lucky, would find a tree of low resistance (Figure 6). Thus, smaller beetles, those that suffered severe larval competition, or those that have used up their fat reserves in flight, regardless of size, are hypothesized to be the pioneers.

There are still many questions regarding the behavior of bark beetles during the dispersal and host selection period. For example, for how long do beetles fly in nature, how random are the paths, and how often do they land? There is a large body of literature on observations but few experiments from which conclusions can be drawn. The question as to what the flight paths of beetles might look like was investigated in the simulations that varied combinations of the EAR and AMT stepwise. The data for *I. typographus* [unflown in Duelli et al. (1997) and

Zolubas and Byers (1995)] were best fit if the beetles had a straight flight path after release. This is in accordance with the theory that newly emerged beetles would have fat reserves and tend initially to ignore pheromone and hosts. The data for flown *I. typographus* (Duelli et al., 1997), however, could not be fit by any combination of EAR–AMT. The method also focused on a combination of EAR–AMT for *T. lineatum*, where a quite small EAR of 0.2 m was needed with a winding AMT path of 36° to predict the recapture rates by Salom and McLean (1989) on the three trap rings of 5, 25, and 100 m radii. Although the flight time of beetles is unknown, this may not affect the recapture rates significantly because most beetles disperse outward and do not return (a 10-min flight gave similar results to the hour-long flight). One trap ring allows too many possible EAR–AMT pairs to be of any use in predicting flight paths, although some degree of circuitous path is indicated. In any case, simulations reveal that catch per trap ring in relation to radial distance can be influenced significantly by the beetle's AMT, which has not been measured directly in the field.

The equation and simulation models useful for analyzing other systems of trap rings can be obtained as a compiled program for IBM-compatible personal computers by downloading the software (RINGTRAP.ZIP) from the internet (http://www.vsv.slu.se/johnb/software.htm).

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