Measuring the Effective Sampling Area of a Pheromone Trap for Monitoring Population Density of Southern Pine Beetle (Coleoptera: Scolytidae)

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ABSTRACT Multifunnel traps baited with frontalin and turpentine have been used to investigate dispersal of southern pine beetles, *Dendroctonus frontalis* Zimmermann, and are routinely used in the southern United States to monitor population trends of this serious forest pest. However, there is no quantitative data on the effective sampling area of these traps that would allow us to convert numbers of beetles caught in a trap to their absolute population density (numbers per hectare). We conducted field studies to determine the effective sampling area of the multifunnel trap. Using field releases of marked beetles, we estimated how the probability of capture declines with distance between the trap and the release point. The estimated relationship between the capture probability and distance is then translated into the effective sampling area. The effective sampling area for the multifunnel trap was estimated as ≈0.1 ha. Our results also indicate that the capture efficiency of a trap declines with increased density of host trees around the trap. We discuss our findings in the context of previous studies that measured attraction to pheromone traps in other species of bark beetles and in the gypsy moth.

KEY WORDS bark beetles, gypsy moth, pheromone-baited traps, attraction, dispersal, population monitoring

THE PHEROMONE-BAITED TRAP has become one of the most widely used methods for sampling insect populations. Because aggregation pheromones induce directed movement of insects toward the trap, pheromone-baited traps can gather insects from a wide area, and thus can be used to sample sparse insect populations (Wall 1989). An additional advantage is that pheromones are typically very specific in attracting the target species (and possibly close relatives, as well as certain natural enemies who use the prey pheromone as kairomone), thus obviating the need to sort through massive amounts of insect material collected in nonspecific traps. Natural and synthetic pheromones are known for hundreds of insect species, especially those of economic importance (Klassen et al. 1982, Jutsum and Gordon 1989, Ridgway et al. 1990). One of these insects is the southern pine beetle, *Dendroctonus frontalis* Zimmermann, the most serious insect pest of pine forests in the southern United States (Price et al. 1992). Early attempts to use aerially distributed frontalin for disruption of southern pine beetle aggregations were not successful (Vité et al. 1976). Currently, synthetic pheromone is used primarily for monitoring purposes. Traps baited with frontalin and turpentine have been deployed from east Texas to Maryland since 1986 to monitor trends of southern pine beetle populations (Billings 1988). Pheromone traps also have been used in studies of southern pine beetle dispersal (Turchin and Thoeny 1993), and to test the efficacy of mass-attack inhibitors (Vité and Renwick 1971, Payne et al. 1978, Hayes et al. 1994).

One drawback of using pheromone traps in population surveys and dispersal studies, however, is that these traps provide an estimate of relative rather than absolute population density (Wall 1989). To be able to translate the number of insects captured in a pheromone trap into an estimate of absolute population density (the number of insects per unit of area), we need to know the trap's effective sampling area (sometimes referred to as the absolute efficiency). Until now, no information has been available on the effective sampling area of southern pine beetle pheromone traps. In fact, we believe that results presented in this paper constitute the 1st attempt to estimate the absolute efficiency of the pheromone trap for any bark beetle (but see Discussion for related approaches).

The effective sampling area of the southern pine beetle pheromone trap, with which we are concerned here, is the translation coefficient (α) between the population density of bark beetles emerging from brood trees (B) and the numbers

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of beetles captured in a single pheromone trap (T). Thus, $T = \alpha B$. Because the units of T are beetles, and units of B are beetles per square meter, α is measured in square meters, or units of area. That is why we refer to α as the effective sampling area of a trap; it is the area by which we need to divide the trap catch to obtain an estimate of population density, $\hat{B} = T/\alpha$. We emphasize that effective sampling area does not correspond to any actual area (within which insect density is measured), but rather is a density conversion coefficient.

To understand our conceptual approach to estimating effective sampling area, imagine that density of emerging beetles, B, is constant in space. Movement paths of individual beetles will be very complex, because they will be responding to the constantly shifting, filamentous pheromone plume emanating from the trap. To estimate effective sampling area, however, all we need to know is the average proportion of captured insects that started at the distance r from the trap. Let this proportion be $P(r)$. The number of beetles emerging in an annulus centered on the pheromone trap of unit width and radius r is the product of beetle density and the area of the annulus, $B \times 2\pi r$. The number of beetles from this annulus that will be captured in the trap is $P(r) \times B \times 2\pi r$. Finally, the total number of beetles captured in the trap will be the sum of captured beetles originating from all possible annuli (with radius varying from 0 to infinity):

$$T = \int_0^\infty 2\pi r P(r) B \, dr.$$

Thus, if we know $P(r)$, effective sampling area can be estimated by

$$\alpha = \frac{T}{B} = 2\pi \int_0^\infty r P(r) \, dr. \qquad (1)$$

Note that we are not assuming all beetles r meters away from trap are equally likely to be recaptured by it. In other words, equation 1 does *not* assume that effective sampling area is circular. Clearly, there will be directional effects; beetles downwind will be more likely to be attracted to the trap than beetles starting upwind. Additionally, wind speed and direction are variable, and the "pheromone plume" will be broken up by such objects as trees. Thus, a typical effective sampling area will be of elongated, irregular, and constantly shifting shape. The function $P(r)$ averages over all these directional effects because it is the proportion of all beetles evenly distributed in the annulus of radius r that will be trapped. The process of trapping itself averages over time, since we cannot distinguish between beetles caught early during the trapping interval (for example, when wind was blowing from the North) from beetles caught later (when wind shifted and was from the East). Finally, our derivation is not affected if beetles are distributed patchily, provided that the trap is placed randomly with respect to any clumps (see the discussion by Elkinton and Cardé 1980).

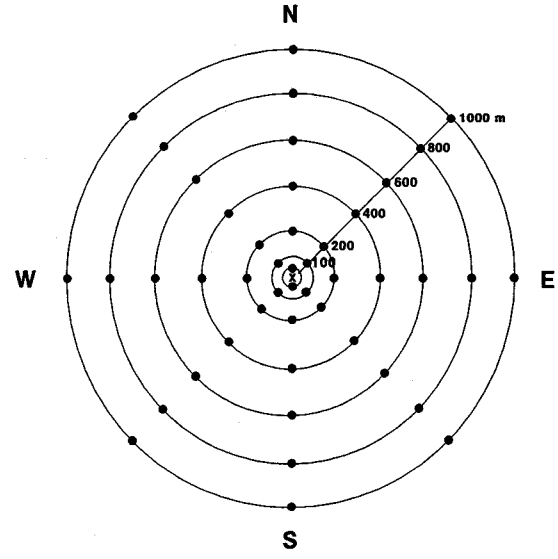

Fig. 1. Single-release–multiple-trap design. Cross indicates central release point; circles indicate positions of pheromone traps.

Our empirical approach, therefore, was to estimate $P(r)$ in field studies, then use equation 1 to calculate our estimate of the effective sampling area. We also realized that the attraction area of a trap may be affected by many other variables. We thought that one of the most important could be the stand composition within which a trap is placed; therefore, we selected experimental areas that represented a wide spectrum of stand conditions.

Materials and Methods

Pheromone traps. All experiments used 16-unit funnel traps (Lindgren 1983). This trap is based on the premise that a prominent vertical silhouette is important for orientation of bark beetles to mass-attacked trees (Gara et al. 1965, Lindgren 1983). Traps were suspended from string stretched between 2 hardwood (nonhost) trees, hung on small hardwoods, or supported by specially constructed metal tripods. The top of each trap was between 3 and 4 m above the ground. Each trap was baited with a 0.5-ml vial of frontalin (99.8% chemically pure 1,5-dimethyl-6,7-dioxabicyclo 3,2,1 octane) and a 120-ml bottle (fitted with a cotton wick) of natural steam-distilled southern pine turpentine. Attracted beetles fall into a receiving cup, where they die as a result of exposure to vaporizing pesticide.

Single Release, Multiple Traps. The first study (May–July 1990) examined the probability of recapturing a beetle originating from ≤ 1 km away from the pheromone trap. This study used single-point releases of marked beetles and recapture

with a grid of multiple pheromone traps (Fig. 1). Single-release–multiple-trap design is most efficient for studying long-distance probabilities of recapturing beetles, because each trap at 1,000 m from the release point is expected to recapture a small number of beetles; therefore, the data is subject to large stochastic fluctuations. By averaging numbers over 8 traps (Fig. 1), we reduce the effects of stochastic variation. However, the problem with this design is that it is not well suited for examining short-distance recapture probability; if traps are placed too close to each other, their attractive areas will overlap and the probability of recaptures will be underestimated (Elkinton and Cardé 1980). In addition, traps nearest the release point will tend to deplete the numbers of dispersing beetles, biasing downward the recapture probability at longer distances (Turchin and Thoeny 1993). To avoid these potential problems, no traps were placed closer than 50 m from the release point, and we used only 2 traps at 50 m and 4 traps at 100 m (Fig. 1). This spacing was sufficient to reduce the interference effects, because the recapture probability of a beetle originating 50 m from a trap was only ≈1–2%.

Sources of emerging beetles were secured by locating southern pine beetle infestations, cutting infested pines (brood stages were pupae and callow adults) into bolts (1.2–1.8 m), and transporting bolts to the release points. Bolts were sprayed with a fluorescent pigment (Day-Glo, Cleveland, Ohio). As beetles emerged from dusted bolts, they marked themselves with fluorescent dust. Fluorescent dust appears to have minor or no effects on southern pine beetle survival and dispersal (Cook and Hain 1992). In short, this self-marking procedure appears to be noninvasive and minimally disturbs the natural course of southern pine beetle emergence.

Traps in the recapture array were censused 3 times a week. Captured beetles were collected, brought to the laboratory, and examined under an ultraviolet lamp for fluorescent dust. A recaptured individual was considered marked only if its membranous wings had multiple micronized dust particles (this procedure minimized the probability of misclassifying an unmarked individual because the only cases of dust contamination in the collection cup involved unmarked insects picking up dust on their thorax or legs). A more detailed description of the methods (that is, spatial locations of grids and the estimation of the number of beetles released) can be found in Turchin and Thoeny (1993). We used all replicate releases for which an estimate of the number of released beetles was available (see Table 1 in Turchin and Thoeny 1993), but we excluded the fall replicates because the dispersal pattern during the fall is quite distinct (for example, the median dispersal distance in the fall is twice that of summer). In all, we used 6 replicates—temporal replicates 3 and 4 at spatial grid 1, replicate 2 at grid 2, and replicates 1, 2, and 3 at grid 4 (see Turchin and Thoeny 1993).

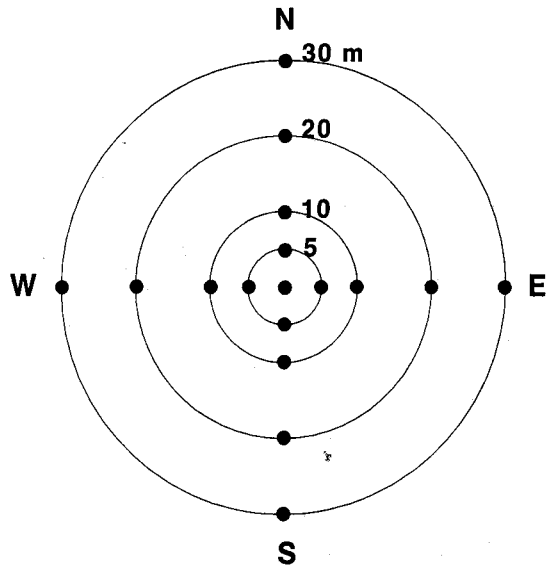

Fig. 2. Multiple-release–single-trap design. Filled circles indicate positions of dusted bolts with southern pine beetle brood.

Multiple Releases, Single Trap. The second study (June 1991) addressed the short-range (<50 m) probabilities of recapture. Because we could not use the single-release–multiple-trap design for reasons stated above, we instead used a multiple-release–single-trap design. The trap was placed in the center, and 16 dusted bolts were placed around the trap in 4 cardinal directions and at distances of 5, 10, 20, and 30 m (Fig. 2). All bolts at the same distance from the trap were dusted with the same fluorescent color. We could use only 4 different distances because we had only 4 dust colors that could be readily distinguished from each other under ultraviolet light. Bolts were treated in exactly the same way as in the 1990 study, apart from being cut shorter (60–90 cm; shorter bolts were more stable when stood upright around the trap). The study areas were located in the same area that was used during the 1990 studies (Catahoula Wildlife Management Reserve, Kisatchie National Forest, LA). At the center of each study area, we measured the basal area of pines using a 10-factor prism and counting only trees with diameters at least 10 cm and heights of 1.4 m (Husch 1982). The number of beetles emerging from each bolt was estimated in the following way. After cutting bolts from beetle-infested pines, we counted and recorded all emergence holes on each bolt. Bolts were then moved to experimental areas and placed around traps. A subsample of 16 bolts, which were treated in exactly the same way as the experimental bolts (that is, dusted with fluorescent mark), was placed in emergence cans (1 bolt per can) for calibration purposes. Beetles emerging from each can

Table 1. Summary of multiple-release–single-trap study

Replicate[a]	Pine BA, m^2/ha	No. beetles released	% Recaptured from: 5 m	10 m	20 m	30 m	Avg
7	0	466	27.2	6.7	2.6	1.7	9.6
6	2	7,241	6.9	5.9	2.2	2.1	4.3
1	8	9,205	10.4	8.1	3.9	8.1	7.6
5	8	9,434	3.0	11.3	5.1	5.0	6.1
4	12	6,642	7.4	6.3	4.0	5.9	5.9
3	18	7,539	1.5	0.8	2.1	1.2	1.4
1	22	7,570	1.8	0.8	1.7	1.7	1.5

[a] Replicates are arranged in order of increasing pine basal area (BA).

were collected and counted 3 times a week. At the end of the study, field bolts were moved to the laboratory, where the emergence holes were counted again. The emergence holes on calibration bolts also were counted. A regression was performed relating the number of beetles emerging in each calibrating can to new emergence holes appearing on the bolt in the can (last count minus 1st count). This calibrating relationship was used to infer the number of beetles emerging from each field bolt, based on the number of new emergence holes appearing on the bolt during the course of the experiment.

The study was replicated 7 times. When looking for each experimental area, we attempted to locate a range of stand conditions that would cover the normal range observed within the Kisatchie National Forest. Thus, sites 2 and 3 were characterized by high host (loblolly, *Pinus taeda* L., and shortleaf, *P. echinata* L., pines) density as measured by their basal area (Table 1). Sites 1 and 6 were dominated by hardwoods and had low pine density, whereas sites 4 and 5 were roughly equal mixtures of pines and hardwoods. Site 7 was in a plantation of longleaf pine (*P. palustris* Mill., a species highly resistant to southern pine beetle; average diameter of trunks at breast height ≈10 cm). All bolts were placed in the study areas on 16 June and removed on 28 June. Pheromone traps were emptied every day, and beetles were taken to the laboratory, where they were examined under an ultraviolet lamp for the presence of mark.

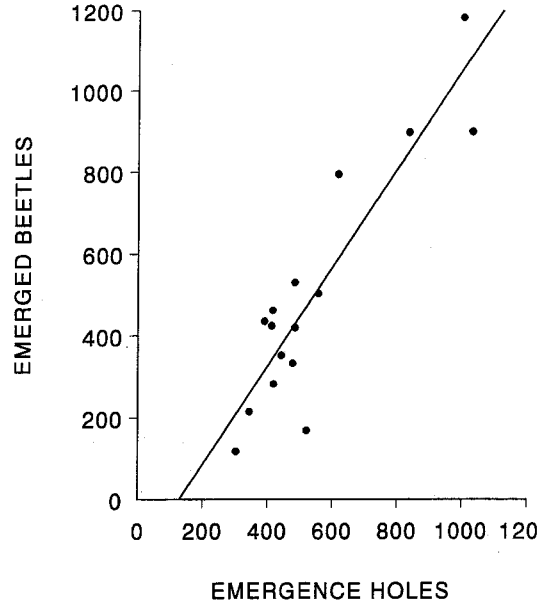

Fig. 3. Relationship between number of beetles emerging from a bolt and number of new emergence holes.

Results

Correlation Between Emergence Holes and Emerging Beetles. Regression showed that the number of beetles emerging from each calibration bolt was closely related to the number of new emergence holes (Fig. 3). The relationship between the number of emerging beetles and the number of new emergence holes was characterized by an estimated intercept of −157 and a slope of 1.2 (SEM = 0.16) (r = 0.9, P = 0.001, n = 15). We conclude that counts of emergence holes provide a reasonably accurate estimate of the number of emerging beetles.

Probability of Capture as Function of Distance. Average proportions of marked and released beetles recaptured during each of 7 multiple-release–single-trap experiments and 6 single-release–multiple-trap experiments are shown in Tables 1 and 2. Average recapture proportion was about 0.1 in the close vicinity of a trap and declined to <0.0001 at a distance of 1,000 m (Fig. 4).

Table 2. Summary of single-release–multiple-trap study

Replicate	No. beetles released	Avg % recaptured at: 50 m	100 m	200 m	400 m	600 m	800 m	1 km
1–3	29,460	0.107	0.057	0.047	0.046	0.051	0.007	0.006
1–4	4,735	0.359	0.005	0.026	0.024	0.040	0.011	0.011
2–2	10,211	4.813	0.130	0.088	0.004	0.002	0.006	0.001
4–1	89,861	1.318	0.147	0.097	0.022	0.004	0.002	0.001
4–2	2,869	2.039	0.166	0.057	0.030	0.109	0.013	0.026
4–3	9,143	0.771	0.071	0.127	0.011	0.021	0.007	0.004

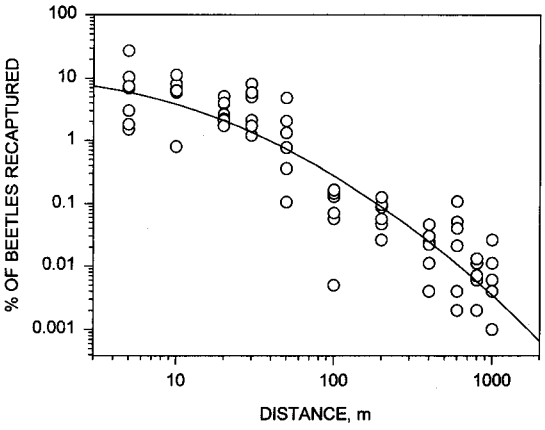

Fig. 4. Percentage of recaptured beetles, $P(r)$, as a function of distance, r. Data from both short-range ($r \leq 30$ m) and long-range experiments ($r \geq 50$ m) combined. Solid line depicts the fitted relationship $\log_{10}P(r) = -1.04 - 0.38\ (\log_{10}r)^2$.

The quantitative nature of the relationship between the proportion recaptured $P(r)$ and distance was analyzed with response surface methodology (Box and Draper 1987). There was a positive relationship between the variance and the mean of the dependent variable, $P(r)$. Following Turchin and Thoeny (1993), we log-transformed the dependent variable, which effectively homogenized the variance (Fig. 4). To determine which transformation of the independent variable (r) was best, we performed separate regressions using no transformation, square-root, logarithmic, and inverse. The best results, as judged by the coefficient of determination R^2, were obtained with the logarithmic transformation. Thus, the $P(r)$ curve was fitted using log-transform on both variables ($Y = \log P$ and $X = \log r$). Linear regression of Y on X was highly significant ($F = 351$; df = 1, 68; $P < 0.0001$; $R^2 = 0.83$). There was also significant nonlinearity (adding the quadratic term to the equation significantly improved the fit, $F = 4.68$; df = 1, 67; $P < 0.05$). However, adding a term involving X to a regression of Y on X^2 did not significantly improve the fit ($F = 0.84$; df = 1, 67; NS). Thus, the most parsimonious model is $Y = -1.04 - 0.38$ (SEM = 0.03) X^2 (Fig. 4). This 2-parameter model explained 85% of the variance in the data ($P \ll 0.0001$, $n = 70$). Our estimate of the relationship between the proportion recaptured and the distance from trap to the release point, then, is

$$P(r) = 10^{-1.04-0.38(\log r)^2} \qquad (2)$$

(all logarithms are to the base 10). We emphasize that this relationship is not theoretically motivated but is simply a result of an empirical curve-fitting approach (see Box and Draper 1987). Our primary goal is to fit the noisy data with a smooth curve, which we then can substitute into equation 1.

Integrating equation 1 using $P(r)$ from equation 2, we obtain an estimate of the effective sampling area of $\hat{\alpha} = 1{,}090$ m^2. Thus, effective sampling area is estimated as $\approx$0.1 ha (0.25 acre).

Effects of Stand Conditions. Stand conditions had a striking effect on the attractive power of the trap (Table 1). The recapture probability in each replicate short-range attraction study, averaged over all 4 distances (the right-most column in Table 1) varied by almost an order of magnitude between the longleaf plantation and stands dominated by hardwoods on one hand and the densest loblolly and shortleaf pine stands on the other (Table 1). This effect was statistically significant, as indicated by a linear regression of average recapture probability on the host pine basal area ($F = 9.2$; df = 1, 5; $P < 0.03$).

Discussion

Initially, the most surprising result of this study was the low proportions of released beetles that we were able to recapture with the multifunnel traps. Even when released right next to the trap, less than 1 in 10 beetles, on average, was recovered in our study (Fig. 4). One possible explanation for such low recapture rates is that beetles are not primed to respond to pheromone immediately after emergence, but first need to go through a period of dispersal (Atkins 1959). However, laboratory studies indicate that the magnitude of this effect is rather modest (for example, the proportions of preflight and postflight males responding to pheromone was 0.62 and 0.79, respectively [Andryszak et al. 1982]). Results of such laboratory bioassays using walking beetles should be interpreted cautiously, yet they suggest that the effect of dispersal flight is only a partial explanation of the observed low recapture rates. In addition, this explanation does not account for the observed relationship between stand composition and the recapture probability (Table 1).

An alternative (or, possibly, a complementary) explanation is based on the observation that, in the vicinity of pheromone sources, southern pine beetles use visual cues to locate and land on the closest vertical object (Gara et al. 1965). A pheromone trap provides a weaker visual cue than nearby trees, thus most beetles are "fooled" into landing on trees rather than on the trap. According to this explanation, a pheromone trap surrounded by many competing vertical silhouettes will capture a small proportion of beetles. Indeed, the lowest recapture rate was observed in the 2 replicates where the density of mature pines was the highest (replicates 2 and 3; Table 1). By contrast, the highest observed recapture rate, 27%, occurred within replicate 7, where young longleaf pines (with diameters of $\approx$10 cm) provided much weaker visual cues to beetles than the pheromone trap.

The observation that only a small proportion of beetles flying in the vicinity of a trap will be cap-

tured does not invalidate in any way our estimate of the conversion coefficient between the population density of emerging beetles and the trap catch (the effective sampling area). Despite a low efficiency of capturing attracted beetles, the estimated effective sampling area of the multifunnel trap is a respectable 0.1 ha.

A previous study (Turchin and Thoeny 1993) indicated that the median dispersal distance of beetles in summer is ≈0.45 km. Thus, many beetles captured in an average pheromone trap will come from hundreds of meters away. In effect, a pheromone trap averages fluctuations of beetle density over space and time. Using the estimated effective sampling area, forest managers can infer directly the densities of southern pine beetle brood that emerged within a given area. Suppose that we have employed a number of traps to survey a particular area. We need to collect the trap catches for a period of time at least as long as the generation time of the southern pine beetle (that is, 1 mo during late spring and early summer). During this time, 1 complete generation of beetles will emerge. Adding trap catches over the month, dividing them by the number of traps to obtain average catch per trap, and further dividing them by the effective sampling area, we obtain an estimate of the average number of southern pine beetle brood per hectare during the month of the survey. We stress, however, that the specific estimate of effective sampling area = 0.1 ha obtained in our study should be used with caution. We have already discussed how stand composition affects the effective sampling area. The effective sampling area is also likely to change with season. For example, in late summer, southern pine beetle dispersal is greatly curtailed. The effect of shorter dispersal distance is to decrease the effective sampling area (because fewer beetles originating far from a trap will reach its vicinity). Additionally, the distribution of beetles in summer is highly clumped, because most beetles are attacking host trees on the periphery of the infestation where they emerged. Thus, traps situated outside active infestations will underestimate true beetle numbers in summer. During spring, few active infestations are typically present. The distribution of beetles is, therefore, less clumped, and trap catches will reflect beetle densities more faithfully. Thus, Billings (1988) showed that early-season (March–May) trap catches provide useful information for forecasting southern pine beetle activity later in the year. Another complication is that the traps used by forest managers (see Billings 1988) differ from those we have used (they consist of 12 rather than 16 funnels). For all these reasons, our estimate of effective sampling area should be considered at best an approximation of the actual coefficient that translates southwide survey catches into beetle densities. Ideally, the experiments reported here would be repeated using the procedures identical to the ones used in the southwide survey, and the estimate of effective sampling area = 0.1 ha would be further refined.

Other Approaches to Measuring Attraction Area. Several aspects of our approach are conceptually similar to the previous work by Swedish ecologists on the effective attraction radius of bark beetle pheromone traps (Byers et al. 1989, Schlyter 1992). There is, however, an important difference between our approaches. Our effective sampling area is defined as the translation coefficient between trap catch and the density of *emerging beetles* (numbers per unit of area), whereas the equivalent quantity estimated by Byers et al. (1989) and Schlyter (1992) translates between the trap catches and the density of *flying beetles* (numbers per unit of volume). The approach of Byers et al. (1989) is to compare the catches of flying insects passively intercepted by cylindrical sticky screens to the same kinds of screens made attractive with bark beetle pheromone and deployed similarly in the same general area. If C_p is the catch in the passive trap, C_a is the catch in the active (pheromone-baited) trap, A_p is the area sampled by the passive trap, and A_a the effective sampling area of the active trap (the quantity of interest), then A_a can be calculated by

$$A_a = \frac{C_a A_p}{C_p}. \tag{3}$$

The effective sampling radius R_a (which Byers et al. [1989] call effective attraction radius; but see Schlyter 1992) is then $\sqrt{A_a/\pi}$ (assuming circular attraction area). It is readily seen that effective sampling area as defined as this article (α) and A_a are not equivalent. For example, 2 bark beetle species could be characterized by the same emergence density, but because 1 species lives longer, its aerial density will be higher. Another complication is that the density of emerging beetles is measured per unit of area, but the aerial density of beetles is measured per unit of volume, and typically will vary with height above ground. The 2 definitions of effective sampling area–volume could be reconciled if we knew how to translate between the numbers of beetles emerging per unit of area and the aerial density of beetles. Because the 2 quantities measure 2 very different things, their estimates are quite different. Most estimates of R_a for various bark beetles are on the order of 1 m (Schlyter et al. 1992, Table 3), implying that A_a is 3 orders of magnitude less than α.

Our approach is more closely related to the one taken by Elkinton, Cardé, and coworkers in their studies of the efficiency of gypsy moth traps, and our results parallel theirs in several instances. For example, the efficiency of the multifunnel trap in recapturing attracted beetles is on a par with the efficiency of the standard pheromone trap used to monitor gypsy moth abundance; gypsy moth "milk carton" traps capture only 9.6% of those males that approach within 2 m of them (Elkinton and Childs

1983). Nevertheless, the effective sampling area of milk carton traps is quite impressive. Elkinton and Cardé (1980) estimated that a rectangular grid of gypsy moth traps placed at 800-m intervals will capture 4% of gypsy moth males released at spatially uniform density (their approach is conceptually similar to ours, but it estimates effective sampling area directly rather than via an intermediate step of estimating $P(r)$). Thus, the effective sampling area of each trap is $\alpha = 0.04 \times 800 \times 800 = 25{,}600$ m^2, or 2.56 ha. The traps used in that study were Pherocon 1C, which are approximately twice as attractive as the milk carton trap (Elkinton and Childs 1983), so the attractive area of the milk carton trap is ≈1.2 ha, or an order of magnitude stronger than the multifunnel trap. This quantitative difference is probably explained by more refined behavioral mechanisms used by male moths to orient toward the source of sex pheromone, compared with the aggregation pheromone system of bark beetles. This comparison shows that the concept of effective sampling area can be used for quantitative interspecific comparisons of the absolute efficiency of pheromone-baited traps.

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