Area-Wide Efficacy of a Localized Forest Pest Management Practice

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ABSTRACT Few experimental studies have examined the movement of forest pest populations, particularly in response to management tactics that disrupt the growth of pest infestations. We quantified the interinfestation patterns of dispersal of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), by monitoring the fates of fluorescently marked beetles after emergence from small natural infestations. Dispersal patterns from 3 untreated infestations were compared with those from 6 infestations treated with the widely used disruption suppression tactic, cut-and-leave (infested trees are felled and left in the forest). Among untreated infestations, 10 ± 4% (±1 SE) of the marked beetles were successful in colonizing experimentally created infestations located 100–500 m away. The highest proportion of marked beetles was recaptured at the nearest experimental infestations (at 100 m) and recaptures declined precipitously with distance from the source. Dispersal by beetles emerging from disrupted infestations showed a similar pattern to untreated infestations with respect to distance, but a much greater fraction of the beetles were recaptured at each distance. Overall, colonization success for treated infestations was 37 ± 6%, almost a 4-fold increase over untreated infestations. This suggests that by altering the dispersal patterns of beetles, the cut-and-leave suppression tactic may favor increased densities of flying beetles, and possibly more infested timber, in the surrounding region. Effective control of mobile pests may be enhanced by expanding our spatial scope and seeking to maximize the area-wide, not just the local, efficacy of management tactics.

KEY WORDS *Dendroctonus frontalis*, bark beetles, dispersal, mark-recapture experiment, pest management strategies, spatial dynamics

IT WAS RECOGNIZED at least 20 yr ago (e.g., Kennedy and Way 1979) that obtaining quantitative information on insect pest movement is crucial for developing effective management strategies. Despite this realization, the examples of studies providing a comprehensive picture of movement in widely dispersing pest species are disappointingly few (but see Anderbrandt 1985; Weseloh 1985, 1987; Salom and McLean 1989, 1991; Turchin and Thoeny 1993). What is even more striking is the paucity of studies that have examined the consequences of human intervention on pest movement patterns. In fact, we know of no studies that have experimentally evaluated the effects of management strategies on the dispersal of insect pests in forest systems.

In the absence of any evidence to the contrary, pest managers have generally assumed that if a pest supression tactic works locally, then it must be an effective tactic globally. A particularly striking example comes from the suppression practice of 1 of the most damaging forest insect pests, the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). One of the widely practiced approaches, "cut and leave," relies on the physical disruption of infestation growth through the felling of infested trees and leaving them to decay on the forest floor. There is considerable evidence that cut-and-leave is capable of disrupting and stopping the growth of southern pine beetle infestations (Ollieu 1969, Payne and Billings 1989, Payne et al. 1991), but the fate of beetles dispersing from the suppressed infestation is unknown. In perhaps the most optimistic assessment of insect pest powers of dispersal, a recent Environmental Impact Statement (USDA 1987) suggested that "beetles that are forced by the effects of control to fly farther than the next trees are likely to die." Clearly, this statement needs to be empirically evaluated if we hope to improve the regional management of the southern pine beetle.

The southern pine beetle exhibits population cycles, with outbreaks occurring at 7- to 8-yr intervals (Turchin et al. 1991). Weakened, stressed, or genetically susceptible pines (*Pinus* spp.) are typically attacked by the southern pine beetle, except during epidemic years when all pines are potentially vulnerable (Thatcher et al. 1980, Cates and Alexander 1982, Cook and Hain 1988, Price et al. 1992). The 1st beetles to arrive at a new host excavate tunnels into the phloem and cambial layers, eliciting sap secretions from the entrance holes that contain oleoresins (pre-

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Table 1. Characteristics of untreated and cut-and-left infestations

Infestation	National Forest	Date treated	Infestation size	Proportionate growth	No. marked
Untreated					
TH-I	Kisatche, LA	24 June 1994	13	1.46	91,112
DS-I	Sabine, TX	3 Aug. 1994	27	0.59	143,826
TB-I	Homochitto, MS	30 May 1995	22	1.23	48,945
Mean (1 SE)			20.7 (4.1)	1.09 (0.63)	94,628 (27,446)
Cut-and-leave					
MS-III	Homochitto, MS	11 Aug. 1993	48	0.29	—[a]
TH-II	Kisatche, LA	22 July 1994	27	0.68	16,121
PAT	Sabine, TX	19 Aug. 1994	39	0.15	33,741
DS-II	Sabine, TX	30 Aug. 1994	23	0.0	55,370
CS	Homochitto, MS	20 June 1995	48	0.18	27,391
TB-II	Homochitto, MS	28 June 1995	48	0.0	75,133
Mean (SE)			38.3 (4.7)	0.22 (0.10)	41,551 (10,552)

Infestation size is the number of infested trees at the start of the experiment, and proportionate growth is the ratio of new attacks to original infestation size.

[a] Samples for determining number marked were lost.

dominantly composed of α-pinene). These oleoresins coupled with the release of southern pine beetle pheromone, frontalin, causes beetles in the vicinity to congregate at the site of attack (Kinzer et al. 1969, Renwick and Vité 1969, Payne et al. 1978). As the attack reaches capacity, congregating beetles attack adjacent pines, thereby expanding the area of infestation. Reemerging individuals and their offspring contribute to the continued growth of the infestation, but an unknown percentage disperse farther away to a similarly unknown fate (Hain 1989, Turchin and Thoeny 1993).

Present suppression strategies for the southern pine beetle focus on controlling individual infestation expansion to reduce forest resource losses, not on area-wide management of southern pine beetle populations (USDA 1987). When salvage is not feasible on federal or state lands, the cut-and-leave method is frequently employed (Billings 1980, Swain and Remion 1981, USDA 1987). Cut-and-leave was developed with the idea that suppression of an infestation would be achieved by increasing brood mortality and disrupting normal beetle movement by forcing beetles to fly farther in search of hosts (Ollieu 1969, Billings 1980, USDA 1987). Although it has been shown that this tactic can be effective in achieving local suppression of infestation growth (Ollieu 1969, Payne and Billings 1989, Payne et al. 1991), the underlying cause for this success is unknown. Hodges and Thatcher (1976), Palmer and Coster (1978), and Moser et al. (1987) demonstrated that brood mortality rates (caused by increased exposure of felled trees to direct sunlight, rain, and ground-dwelling predators) in felled trees were no higher than those for standing trees. Furthermore, the assumption that cut-and-leave will force surviving beetles to disperse, and that these dispersers will have reduced success in locating a new host beyond the focal infestation, remains largely untested (but see Moore et al. 1979).

Another important unresolved issue is whether cut-and-leave is effective at broader spatial scales (Kelley et al. 1986, Carter et al. 1991, Turchin and Thoeny 1993). Beetles emigrating from felled trees may exacerbate pest problems in the surrounding forest, either by increasing the proliferation (the establishment of new infestations) of infestations or contributing to the expansion of existing infestations. Billings and Pase (1979), and more recently Fitzgerald et al. (1994), addressed the former issue by comparing the probability of proliferation around salvaged versus cut-and-left infestations. By analyzing records of infestation treatments in Texas, the studies concluded that cut-and-leave either had no effect (Fitzgerald et al. 1994) or decreased (Billings and Pase 1979) proliferation. The latter issue, whether pine beetles emerging from cut-and-left infestations contribute to the expansion of existing infestations in the surrounding area, has not been addressed.

The purpose of this study was to address whether a suppression tactic applied locally (on a scale of meters or tens of meters) affects pest population distributions at the area-wide scale (hundreds of meters and kilometers). Specifically, we tested whether beetles emerging from cut-and left, relative to untreated, infestations differed in the pattern of interinfestation movement (dispersal to experimentally created infestations up to 500 m away), and in the relative contributions of dispersing beetles to the growth of adjacent infestations. Our results suggest that suppressing bark beetle infestations by the cut-and-leave tactic results in increasing the flow of dispersers from the suppressed infestation that can contribute to the growth of adjacent infestations. The significance of this finding is broader than the implications for the control of bark beetles, because it provides possibly a 1st real-world example of why the spatial dimension should be considered in the design of efficacious pest management programs.

Materials and Methods

Infestation Selection and Treatment. *Site Selection.* Our experimental study spanned 3 yr (1993–1995) and 3 National Forests in the southeastern United States (Table 1). Only infestations meeting the following criteria were included in the study. (1) Infestations had to be small, between 13 and 48 trees (primarily loblolly pine, *Pinus taeda* L.), killed by southern pine beetle. This is within the size range for which cut-and-leave is an accepted suppression tactic (Billings 1980). (2) Average tree size of infested pines had to be 25–50 cm diameter at breast height (dbh). (3) Infestations also had to show evidence of active growth. We monitored infestations anywhere from 1 wk to 2 mo, and if any new trees came under attack during that period we deemed the infestations active. (4) In a 1-km radius surrounding the infestation, we required that a minimum of ≈75% of the area was forested and codominated by host pines (loblolly and shortleaf [*P. echinata* Mill.]). (5) Finally, to minimize the occurrence of any nonexperimental sources of attraction we required that no other southern pine beetle infestations be present within the 1-km radius. The research was generally carried out in the summer; which is a period when beetle dispersal is at its lowest (Turchin and Thoeny 1993) and cut-and-leave is a recommended practice (USDA 1987).

Experimental Treatments. We tested the effects of 2 experimental treatments on the interinfestation dispersal of the southern pine beetle. The 1st was an experimental control in which naturally expanding infestations were left as untreated infestations. The 2nd treatment involved the application of the disruptive suppression tactic, cut-and-leave (treated). For this treatment, all infested pines (containing attacking adults or developing brood) plus a 15-m buffer strip of uninfested pines were felled toward the center of the infestation and left where they lay (Billings 1980, Swain and Remion 1981).

It was our original intention to assign the treatments completely at random to the infestations meeting the criteria outlined above. However, to increase the number of usable infestations, 3 untreated infestations were subsequently treated with cut-and-leave (TH-I, DS-I, and TB-I). In all cases, at the completion of the untreated replicate, the existing infestations still met the 5 criteria listed above. Two important sources of bias that may have arisen from this methodological constraint are that infestation size or beetle activity may have increased between treatment applications. The following evidence suggests that neither potential bias significantly affected our conclusions. First, neither infestation size nor the growth rate of infestations changed in a consistent way between the time infestations were designated as an untreated, and later as a treated, infestation (Table 1), and importantly, both variables were included in the analysis of variance (ANOVA) model to account for any site-related differences in dispersal. Second, we could detect no difference in the proportion of marked beetles landing on trap trees ($F = 0.05$; df = 1, 14; $P = 0.823$) between the 3 redesignated treated infestations and the 3 treated-only infestations. Third, because southern pine beetle dispersal varies with the time of year (Thatcher and Pickard 1964, Turchin and Thoeny 1993) and untreated infestations were generally monitored earlier in the summer than cut-and-left infestations (Table 1), we included time of replicate initiation in the analysis of interinfestation movement. Finally, to ensure that there was no carryover effect between treatment applications, the 4–6 trap trees that came under attack during the untreated phase were removed to eliminate any semiochemicals attractive to southern pine beetle. This also served to maintain trap trees at a constant number and state of attack among sites and treatments.

Marking Pine Beetles. *Untreated Infestations.* Six to 8 pines that were infested with late larval or pupal southern pine beetles were selected from within each infestation. We thoroughly coated the bark of the tree trunk with fluorescent pigment (Day-Glo Color, Cleveland, OH) from a height of 1–7 m above the tree base. The coated area encompassed most of the infested region of each tree. Directly above the fluorescent-coated area we fastened a clear-plastic (0.5 mm thick) tarp around the trunk with duct tape and tied the outer tarp edges to the surrounding vegetation. This umbrella-like structure, with a radius of 1.5 m, protected the fluorescent pigment from the rain.

At the midpoint of each tree we attached a trap to estimate emerging beetle density and proportion of beetles detectably marked. The emergence trap had a plywood frame with a hole (10 by 80 cm) cut in the center. A foam rubber gasket was attached to one side, and a fine-meshed polyethylene screen with a collecting jar at the bottom was attached to the opposite side of the frame. The trap was bolted to the tree and the gasket formed a seal that prevented emerging beetles from escaping. Emerging beetles would fall into the collecting jar where they were quickly killed by a small piece of No-Pest Strip (Bio-Strip, Reno, NV; [AI] 2-2-dichlorovinyl dimethyl phosphate).

Based on our emergence trap data, the dusting technique was 100% effective in marking emerging beetles. Pine beetles emerging from the coated trees marked themselves by crawling through the fluorescent powder. Most significantly, the wings became coated with dust in the process of expanding them before the initiation of flight (Turchin and Thoeny 1993). Dust on the wings is protected by the elytra and appears to be relatively permanent (Rhodes et al. 1998). This method of marking beetles appears to have no appreciable effect on flight initiation by southern pine beetle (Cook and Hain 1992) or gallery production (Rhodes et al. 1998), but does reduce the longevity of adult beetles by 20% in the laboratory (Cook and Hain 1992). Because most beetles are recaptured shortly after emergence (Cook and Hain 1992, Turchin and Thoeny 1993), this method of marking may result in a slight underestimation of dispersal rates, but should not affect the comparison among treatments.

Cut-and-Left Infestations. Following application of the cut and leave treatment, 4–6 felled trees with brood in the late larval to pupal stage were cut into 1.0- to 1.5-m lengths (bolts). The bolts were transported to the center of the infestation (where the trees originally stood), coated with fluorescent powder, and stacked together on their ends. A piece of tarpaulin (3.65 by 3.05 m) was stretched above the bolts to protect them from the rain. It was our assumption that although protective tarps may have provided some beneficial shading for the brood in the dusted bolts (similar to the umbrella-like structures placed on trees in untreated infestations), any advantage gained from tarping may be lost to the more rapid dessication of host material experienced in bolts. Emergence traps were attached to 6 randomly chosen bolts for estimation of emerging beetle density. On average, we used fewer trees in the treated than in the untreated infestations to minimize the disruption to the integrity of the felled infestation. Because we dealt in proportions of marked beetles dispersing, this discrepancy between treatments should have had little impact on our results.

Estimating Number of Marked Southern Pine Beetle. Mayyasi et al. (1976) demonstrated that the distribution of pine beetles emerging along the length of an infested pine trunk is well represented by a hump-shaped curve of the form, $y = ax(1\text{-}x)e^{bx}$, where y is the density of beetles at relative height x (height/total trunk height), and a and b measure the amplitude and shape of the curve, respectively. Although b is likely to remain constant, the absolute value of a is expected to vary in space and time because of differences in plant resistance, abundance of predators, variation in the weather, and so on. We used our emergence trap data (taken at approximately midbole) to recalibrate this parameter and then to predict the total number of marked beetles emerging from each dusted tree. First, the actual density (Y_a) of marked beetles (per 100 cm^2) at the trap midpoint was estimated from the total number of beetles captured in the emergence traps. Estimates of a and b (37.44 and 0.4158, respectively) from Mayyasi et al. (1976, table III) were used to determine the expected density (Y_e) at the same location. For each tree (t), the ratio of Y_a to Y_e provided a conversion factor (k_t) that rescaled the density-distribution curve (altered the amplitude) to reflect the environmental differences among trees, localities, and years. Using this conversion factor, we calculated from the equation above, the sum total of marked beetles emerging from each tree (n_t) and the total emerging from each untreated infestation ($N = \Sigma n_i$).

The accuracy of this methodological approach was verified using an independent group of 43 infested pines (unpublished data). For each pine, bark samples were obtained at 1-m intervals along the bole and the number of beetles emerging from each sample determined from a count of emergence holes. The total number of southern pine beetles emerging from a tree was then estimated by fitting emergences from all bark samples to the nonlinear model of Mayyasi et al. (1976). From the bark sample taken at midbole, we also used the method outlined above to estimate the density of emerging southern pine beetles. A correlation analysis indicated a strong positive association between the 2 estimates of emergence ($R = 0.88$, $P < 0.001$) with the slope not significantly different than 1. This indicates that our method did not consistently under- or overestimate beetle emergence density per tree.

Estimating the total number of marked beetles in the cut-and-leave treatment was much simpler. Because emergence traps were placed on a random subset of bolts, we assumed that variations in southern pine beetle density were also randomly distributed among bolts. As such, the total number of marked southern pine beetle at each site (N) = (number of southern pine beetles from emergence traps) × (bark area of all bolts combined) / (total area of emergence traps) (Table 1).

Recapturing Pine Beetles. *Interinfestation Dispersal.* We define interinfestation dispersal as the movement away from an infestation to a different infestation. Although in practice, movement 3–30 m beyond the infestation boundaries (the buffer strip for salvage or cut-and-leave; USDA 1987) has been implicitly accepted as meeting our definition (Billings 1980, Swain and Remion 1981), we use 100 m as an arbitrary, but minimum, distance qualifying as movement away from the focal infestation. Because the availability of standing host pines has been greatly reduced within the treated infestations, we predict that southern pine beetles will disperse more readily and have higher interinfestation colonization rates from cut-and-left than untreated infestations.

Immediately after the treatment of infestations, we established an array of "trap trees" centered on the infestation and extending in 4 cardinal directions. The purpose of the trap trees was to mimic an incipient beetle infestation (a single tree infestation) for dispersing southern pine beetles to colonize. The advantage to this approach is that the number and size of infestations as well as the distance from the focal infestation can be controlled, thus minimizing variation in recapture number. Three trap trees were established in each direction at a distance of 100, 200, and 500 m from the center of the infestation. Only shortleaf or loblolly pine with a dbh of 25–50 cm was used. On each trap tree we placed 3 pairs of sticky traps to monitor southern pine beetle arrivals. The traps consisted of a 500-cm^2 plywood panel with a piece of clear plastic stapled to the surface. Tanglefoot (Grand Rapids, MI) was liberally applied to the plastic surface and was sprayed with the insecticide permethrin to ensure that the beetles died before crawling off the sticky traps. The trap pairs were placed on opposite sides of the tree at a height of 2, 5, and 8 m.

Just before the emergence of marked beetles, the trap trees were baited with southern pine beetle aggregation pheromone, frontalin (0.5-ml vial of 99.8% chemically pure 1,5-dimethyl-6,7-dioxabicyclo 3,2,1-octane), and steam-distilled turpentine (120 ml bottle). This concentration of chemicals has an effective sampling area of $\approx$0.1 ha (Turchin and Odendaal 1996), but as pine beetles congregate to the trap tree, the natural concentration of attractive volatiles and the sampling area increases dramatically. Our studies (unpublished data; see also Reeve et al. 1998) suggest that the temporal sequence and spatial distribution of attacks on artificially baited trees follow closely the pattern observed for natural incipient infestations.

One to 2 times per week sticky traps from trap trees were examined and all southern pine beetles were collected. At the same time, we also collected southern pine beetles from emergence traps. Later, we used a dissecting microscope (10×) with a UV light source to inspect beetles for the presence of fluorescent dust. For each sample, the number of marked beetles was recorded. In addition, the area surrounding the experimental infestation and trap trees was canvassed for the presence of fresh attacks. In the event that trap trees became filled with attacking beetles (the point at which captures drop off following a steady increase), traps and baits were removed and transferred to the nearest suitable pine. This ensured that each trap location had host material in a suitable stage of attack. Traps were never moved more than once per location. Censuses were continued until the trees in the center of the infestation that were coated with fluorescent powder ceased to emerge beetles, usually 2–3 wk and 4–6 census dates.

Estimating Trap Tree Attacks. To estimate the number of marked pine beetles attacking each trap tree we added together all the marked southern pine beetles caught on the 6 sticky traps and divided that by the total area of the traps (0.3 m^2). This density estimate was then multiplied by the area of the tree under attack to yield an estimate of the total number of marked pine beetles attacking the tree (A). Tree area was calculated as the product of the dbh and the length of the attacked bole. For comparisons among experimental infestations, we converted recaptures into L_d, the proportion of the total number of marked beetles in the site that landed on a trap tree at distance d. Here, $L_d = A/N$ (where N = total number of marked beetles in that infestation) and represents the contribution of beetles from the source to a target infestation.

Colonization of Trap Trees. To verify that dispersing beetles could successfully attack host trees, we obtained bark samples from trap trees at 2-wk intervals until all marked beetles had emerged from the focal infestations. In total, 2–3 samples were obtained from each site. Pairs of 1-dm^2 samples were taken at opposite sides of the trunk and at 1-m intervals along the length of the attacked bole. Adult southern pine beetles were excised from the bark galleries and were examined for the presence of fluorescent dust. Based on a study by Rhodes et al. (1998), the fluorescent powder can be retained for >96 h during gallery production and oviposition in the inner bark. Marked beetles in galleries would indicate the ability to successfully colonize the host tree. We also compared the proportion of marked beetles on sticky traps with the proportion found in bark samples. Similar proportions would indicate that marked beetles were as capable of forming galleries once the host has been encountered (landed upon) as the naturally occurring, unmarked southern pine beetles. For this analysis, we used only the 100-m trap trees because they comprised the majority of trees successfully attacked. We made no attempt to compare directly the density of marked beetles in the bark to that on the traps because the time frame for taking bark samples was such that early attacking adults could reemerge from the tree before samples were collected. This would have led to an underestimate of the density of marked beetles found in the galleries.

Statistical Analysis. *Interinfestation Dispersal.* We used a completely randomized factorial analysis of covariance (ANCOVA) to determine the effect of 2 fixed factors, treatment (treated or untreated) and distance (100, 200, 500 m), on the proportion of marked southern pine beetles landing on trap trees (L_d). We also included infestation size, infestation growth rate, and time at which each replicate was initiated (relative to the earliest replicate: TB-I; Table 1) as covariates in the model. Before analysis, the proportions from the 4 directions for each distance were averaged and L_d was log-transformed to achieve normality and homogenize variances. Type III sums of squares were used to adjust for different numbers of replicates between treatments (Wilkinson 1990).

We note that a more sophisticated ANOVA model that incorporated the replication within each infestation (4 replicate directions) was also tested using SYSTAT (Wilkinson 1990). This model included the following main effects: distance, treatment, site nested within treatment (random effect), and direction nested within site within treatment (fixed); plus the 3 covariates and all associated interaction terms. A comparison between the 2 models revealed no qualitative difference in significance levels for sources of variation that were shared between models, nor were any of the additional model terms (e.g., direction within a site) of significance. We therefore opted to report results from the simpler of the 2 models.

Colonization of Trap Trees. For the 100-m trap trees from each site, we obtained paired estimates of the fraction of southern pine beetles on traps and in bark samples that were marked with fluorescent powder (averaged for the 4 replicate trees). We therefore tested for differences between these 2 fractions using a paired *t*-test. The distribution of mean proportions was skewed to the right, but approached normality following a log transformation of the data.

Results

Experimental Infestations. The 9 infestations used in this study ranged from 13 to 48 currently infested trees; treated infestations were significantly larger than untreated infestations (t = 2.49, P = 0.04; Table 1); hence we used size as a covariate in subsequent analyses (see *Materials and Methods* for details). As anticipated, during the experimental period, untreated infestations continued to expand in size, increasing by an average of 20.7 ± 3.3 trees. Four of the 6 cut-and-left infestations also continued to expand in size after treatment, increasing by 6.6 ± 3.3 trees. Although untreated infestations grew (measured as the ratio of newly attacked trees to initial infestation size) by an average of >109% relative to 22% for treated infestations (Table 1), we did not detect a statistically significant effect of treatment (F = 3.30; df = 1, 6; P = 0.325) or the covariate infestation size (F = 0.14; df = 1, 6; P = 0.726) on infestation growth (log transformed). However, this result may have

Table 2. ANOVA results for the effect of trap distance, treatment (untreated versus cut-and-leave), and 3 covariates (infestation size, infestation growth rate, and time of replicate initiation) on the proportion of marked pine beetles landing on trap trees (L_d)

Source	df	MS	F	P
Distance	2	39.803	24.641	<0.001
Treatment	1	8.070	4.997	0.041
Distance*Treatment	2	3.006	1.861	0.190
Infestation size	1	1.576	0.976	0.339
Infestation growth rate	1	0.599	0.371	0.552
Time of initiation	1	0.007	0.004	0.949
Error	15	1.615		

L_d was log-transformed prior to analysis.

been a consequence of the limited statistical power associated with this test ($1 - \beta = 0.28$; see Cohen 1988).

Interinfestation Dispersal. The most significant pattern observed from marked beetles was that recaptures declined precipitously with distance. This pattern was the same for the untreated and treated infestations. Based on an ANCOVA, distance explained 73% of the overall variance in L_d (Table 2; Fig. 1). All possible pairwise comparisons among the 3 trap distances indicated significant differences between means (Tukey honestly significant difference (HSD), $P < 0.01$). More importantly, we found that the proportion landing on trap trees in the treated infestations was significantly greater than in the untreated infestations (Table 2; Fig. 1; note that the y-axis is on a logarithmic scale). The overall difference between untreated and treated infestations is best shown by summing proportions landing per trap into the total proportion landing on all traps per site (= sum of all 12 trap tree L_ds). The total proportion landing on trap trees was in the untreated sites 0.097 ± 0.036, and in treated sites, 0.366 ± 0.061 ($t = 3.053$, $P = 0.022$). Infestation size, infestation growth rate, distance * treatment, and time of replicate initiation had no significant effect on proportion landing (Table 2).

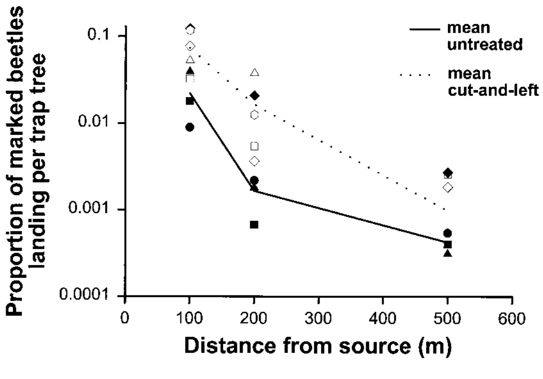

Fig. 1. Proportion of marked pine beetles that landed on trap trees (L_d) relative to the distance from their source (infestation). Closed symbols (TH-I, circle; DS-I, square; TB-I, triangle) and solid lines represent individual untreated infestations and their mean, respectively; open symbols (TH-II, circle; DS-II, square; PAT, diamond; TB-II, triangle; CS, hexagon) and dotted lines reflect the same for cut-and-left infestations.

Colonization of Trap Trees. Bark samples, taken from trap trees during and immediately after the termination of the experimental replicate, revealed marked pine beetles in the process of gallery formation. These results clearly indicate that marked pine beetles have contributed to the successful attack of these trees. Based on the 100 m tree traps from all experimental sites combined, 9.1 ± 1.4% of the pine beetles caught on sticky traps were marked with fluorescent powder, whereas 6.6 ± 1.5% of the beetles recovered from bark samples were marked (this difference was not significant; $t = 1.62$, df = 8, $P = 0.15$). In addition, there was no difference between the treated and untreated infestations in the ratio of the fraction landing to the fraction colonizing the tree ($t = 0.80$, df = 7, $P = 0.45$).

Discussion

There are many forest and agricultural pests for which managers employ, or are considering, suppression tactics that affect pest movement. Some tactics, including interplanting nonhost plants, mixed plantings of resistant cultivars, thinning of hosts, or clearcutting, alter the host habitat and consequently may indirectly affect pest movement. Other tactics, such as the use of attractive or deterrent semiochemicals or pheromones, are expressly designed to disrupt pest movement. This study demonstrates that these tactics can affect pest movement at large spatial scales (linear dimension of 1 km). Fundamental changes in pest movement patterns can have significant consequences for the pest's temporal and spatial population dynamics (for recent reviews see Tilman and Kareiva 1997, Turchin 1998) or area-wide management (Kennedy and Way 1979, Stinner et al. 1983). In situations where the suppression tactic succeeds locally by dispersing pests away from an area of outbreak (i.e., dispersal rates are increased), the tactic may in course militate against the area-wide or regional control of the pest. Under this senario, effective control of mobile pests may be better accomplished by expanding our spatial scope and seeking to maximize the area-wide, not local, efficacy of management tactics.

Mark-recapture experiments clearly indicate that southern pine beetles can be very successful after dispersal from their natal infestation. Ten percent of the beetles emerging from natural, untreated infestations were successful in locating and colonizing experimental infestations 100–500 m away from their origin. We consider this a minimum estimate of the pine beetle's colonization rate because nonrecaptured beetles could have attacked trees beyond our 500-m study area. Interestingly, the rate of successful dispersal increased 4-fold (37%) after the disruption suppression tactic, cut-and-leave.

The rates of interinfestation dispersal reported here are conditionally dependent on the spatial arrangement and size of the target infestations (in this study, 1-tree infestations). If trap trees had been more tightly clustered around the source infestation, the number of baited trees per location (infestation size) increased, or the number of experimental infestations increased, we would expect the proportion of beetles recaptured in the area surrounding a focal infestation to increase. With regard to the proximity of infestations to the source, this is predicted by the data (Fig. 1). If the assumption that each infestation does not interfere with a beetle's likelihood of encountering any other infestation is met, then it would be possible to use the relationship between distance and L_d to estimate the proportion of dispersers locating each infestation. Summing the results for all infestations within the region could then give the overall expected rate of dispersal success to existing infestations. Although the reliability of this is untested, it would offer a qualitative guide to the potential success of the dispersers under natural conditions.

We can offer 1 possible explanation for the higher colonization rates by beetles emerging from treated, than from untreated, infestations. The latter infestations generally had more active growth during the period of beetle emergence (3 times as many new trees came under attack during the experiment; see also Table 1). The presence of a greater number of trees emanating attractive volatiles (frontalin and α-pinene; see Kinzer et al. 1969, Renwick and Vité 1969, Payne et al. 1978) on the periphery of the infestation may have favored the retention of a greater proportion of beetles emerging from the untreated infestations. Although we did not attempt to recapture marked beetles on trees under attack in the expanding head of an infestation, it is logical to assume that a portion of those marked beetles participated in the congregation and mass attack of those trees. As such, trees under attack in a growing infestation probably represent a sink for dispersing pine beetles, removing them from the pool of insects available for inter-infestation dispersal. This idea certainly embodies our general understanding of how infestations expand through time in the absence of suppression measures (Thatcher et al. 1980). Beetles in cut-and-left infestations generally have fewer attractive pines in the area where they emerge (unless a breakout occurs); thus, a larger percentage of them is expected to drift off into the forest. This may explain why a much higher percentage of beetles succeeded in interinfestation dispersal. If this hypothesis is true, we would predict that the total proportion of marked beetles recaptured on experimental trap trees would decrease as the number of trees under attack, or the proportionate growth (Table 1), in the focal infestation increased. While the trend was in the right direction, we could not detect a negative relationship between the 2 ($R^2 = 0.29$, $P = 0.137$). Additional experiments are needed to directly test this hypothesis and to ascertain the relative contribution of beetles to the growth of their natal infestation and to new infestations in the surrounding area.

Implications for Southern Pine Beetle Management. Our results have important implications for the management of the southern pine beetle, particularly with regard to the development of area-wide management of southern pine beetle populations. We provide much needed quantitative data on the proportion of beetles that can potentially colonize existing infestations in the surrounding area. Because this proportion was so high, averaging at least 37% for the disrupted infestations, we conclude that cut-and-leave has the potential to exacerbate pine beetle problems by contributing beetles to the growth of existing neighboring infestations. Although the cut-and-leave tactic is quite effective at suppressing the local activity of an infestation (Ollieu 1969, Payne and Billings 1989, Redmond and Nettleton 1990, Payne et al. 1991), it may not be effective when considered at broader spatial scales, such as national forests (see Carter et al. 1991).

Billings and Pase (1979) drew the opposite conclusion concerning the area-wide impact of cut-and-leave. These 2 conclusions are not at odds with one another because the studies address different (but related) issues. Billings and Pase (1979) addressed the issue of proliferation (the establishment of new infestations in the vicinity of the focal infestation), whereas our study focused on the contribution of beetles to the expansion of existing infestations. It is the combination of these 2 factors that determine the area-wide impact of the emigrants from an infestation. In the absence of nearby infestations, we expect the area-wide efficacy to be great, in comparison to untreated infestations, because cut-and-leave decreases proliferation (Billings and Pase 1979). However, in the presence of nearby infestations, the area-wide efficacy of cut-and-leave may be lower because emerging beetles may colonize and contribute to the growth of those infestations.

Cut-and-leave is recommended for use during the summer months on small and inaccessible infestations (USDA 1987). However, during periods of outbreak, salvage constraints tend to cause an increase in 1) the frequency of occurrence of cut-and-leave (M. Ayres, unpublished data) and 2) the time from detection to the application of suppression tactics (J.T.C., unpublished data). During epidemic years, the mean distance between infestations is likely to decrease, shortening the dispersal distance necessary for pine beetles to travel. Because dispersal success is dramatically increased when distance to a target infestation is decreased (Fig. 1), we would expect a larger fraction of beetles emerging from a treated infestation to contribute to the growth of other existing infestations. Consequently, the area-wide efficiency of cut-and-leave may be lower during times of outbreak.

The obvious solution to improved area-wide southern pine beetle management would be to more quickly treat with suppression other infestations in the vicinity of a cut-and-left infestation. Given that this option might not be feasible in times of outbreak, one possible solution would be to employ variations of the cut-and-leave that increase mortality of pine beetles in felled trees. Application of insecticidal sprays such as Dursban or cutting the tops off of felled trees (i.e., cut-and-top) have been shown to increase beetle mortality (Fitzpatrick et al. 1979, Billings 1980, Hertel et al.

1980) and should therefore reduce the number of beetles emigrating from those infestatoins. Nothing is known about the potential impact of these additional steps on the natural enemies of the southern pine beetle, however, but this should be pursued before these techniques are instituted for the broad-scale control of the southern pine beetle.

As in numerous agricultural pest management programs, there are other suppression tactics for the southern pine beetle that are designed only to disrupt beetle movement, not kill the beetles. These tactics include the use of repellant pheromones such as verbenone (Payne and Billings 1989, Payne et al. 1992, Miller et al. 1995; Salom et al. 1995), endo-brevicomin (Salom et al. 1992), 4-allylanisole (Hayes and Strom 1994), and various combinations of each. One of those compounds, verbenone, is being vigorously tested for its efficacy in the suppression of infestation growth. However, these tests currently do not address the efficacy at spatial scales beyond that of the focal infestation. We hope that this study will encourage others to examine the area-wide efficacy of new management practices.

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