Evaluation of traps used to monitor southern pine beetle aerial populations and sex ratios

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Abstract
1 Various kinds of traps have been employed to monitor and forecast population trends of the southern pine beetle (*Dendroctonus frontalis* Zimmermann; Coleoptera: Scolytidae), but their accuracy in assessing pine-beetle abundance and sex ratio in the field has not been evaluated directly.

2 In this study, we used fluorescent powder to mark pine beetles emerging from six isolated infestations. We then compared estimates of total abundances and proportions of males emerging from within each infestation to the estimates from three types of traps: passive sticky traps (2, 5, 10 and 20 m away from the source of beetles), multi-funnel traps baited with pine beetle attractants (100 m away) and pine trees baited with attractants (also 100 m away).

3 We found that the proportion of males captured in traps was significantly affected by the type of trap used.

4 Within an infestation, equal proportions of males and females were marked (0.53 ± 0.02 males; mean ± SE), but the proportions captured in trap trees and passive traps were more female biased (0.42 ± 0.03 and 0.46 ± 0.01 males, respectively). On the other hand, funnel traps provided an estimate of the proportion of males that was nearly identical to the proportion from within infestations (0.51 ± 0.03).

5 Numbers of marked beetles captured in traps were uncorrelated with the numbers of marked beetles emerging from the focal infestations. This suggests that traps positioned around an infestation may not be effective at estimating relative abundances of beetles within the infestation.

Keywords Bark beetles, *Dendroctonus frontalis*, dispersal, insect traps, mark–release–recapture, population monitoring.

Introduction

Forest pest managers employ pheromone or semiochemical baited traps, light traps, passive or non-attractive traps (drift fences, pitfall, malaise and sticky traps) and trap plants to estimate pest population size and sex ratio (Southwood, 1979; Muirhead-Thomson, 1991). Information from these traps can be used in assessing current activity levels, predicting growth rates, forecasting future population trends, and for determining whether, or when, to implement control measures (Hain, 1980; Dent, 1991). Despite their widespread use, we rarely have direct evidence for whether these traps provide unbiased estimates of the true density and sex ratio of a forest pest population (but see Weslien & Lindelöw, 1989; Safranyik & Linton, 1993; Thorpe et al., 1993; Carter et al., 1994). This is particularly problematic for traps baited with semiochemicals because they are often differentially attractive to males or females and so can greatly bias sex-ratio estimates (Bombosch, 1988; Vité & Baader, 1990). Laboratory studies, in which the true sex ratio is experimentally defined, have often been employed to test whether a bias in captures exists, but the comparable test in the field has not been undertaken. Differences in trap estimates of sex ratio between the laboratory and field can arise because of sex-related differences in long-range olfactory responses,

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dispersal ability or survivorship. To test for sex-ratio bias in trap captures in the field, one would need to compare the sex ratio of the insect in the surrounding environment (the true sex ratio) with the sex ratio of insects captured in traps. One way to obtain the former sex ratio would be to set it experimentally, by releasing marked insects of known sex ratio into the environment.

The southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is a serious pest of pine forests in the south-eastern United States and Central America, and traps deployed in the field are used for both research purposes and to forecast population trends (e.g. Vité, 1970; Coster *et al.*, 1977; Billings, 1988; Turchin *et al.*, 1991; Cronin *et al.*, 1999). The most widely used trap device is the multi-funnel Lindgren trap (Lindgren, 1983; Billings, 1988), which is baited with a combination of the southern pine beetle aggregation pheromone, frontalin, and the host plant-produced compound α-pinene or loblolly pine turpentine (e.g. Kinzer *et al.*, 1969; Payne *et al.*, 1978; Coster & Johnson, 1979; Billings, 1985). In addition to baited traps, researchers have employed passive sticky traps (Turchin & Simmons, 1997) and trap trees (Coster *et al.*, 1977; Wagner *et al.*, 1979; Reeve *et al.*, 1998; Cronin *et al.*, 1999) to monitor pine beetle populations. To date, there is much known about how the abundance and sex ratio of captured insects varies with time of day, stage of attack, trap height, concentrations and ratios of semiochemicals (Renwick & Vité, 1969; Coster *et al.*, 1977; Payne *et al.*, 1978), but the number and sex ratio of captured beetles have never been compared with an independent estimate of the true abundance and sex ratio of beetles present in the surrounding environment. We provide such a test by comparing estimates of the total number and sex ratio of marked pine beetles emerging from within six well isolated and naturally occurring infestations with estimates from traps centred around each infestation. Traps used include passive, baited tree and funnel traps that were positioned up to 100 m away from the site of beetle emergence.

Southern pine beetle life history

The southern pine beetle is distributed throughout the south-eastern United States and into Central America (Payne, 1980). Beetles initiate attack on stressed or susceptible pines (*Pinus* spp.) by excavating tunnels into the phloem and cambial layers of their host (Thatcher *et al.*, 1980; Cook & Hain, 1988). The combination of sap that exudes from the entrance holes (containing oleoresins) and the release of southern pine beetle pheromone causes beetles in the vicinity to congregate at the site of attack (Kinzer *et al.*, 1969; Renwick & Vité, 1969; Payne *et al.*, 1978). As the attack reaches host capacity, congregating beetles shift attack to adjacent pines, thereby expanding the area of infestation. Infestations may continue to expand either until host material is exhausted, a suppression tactic is implemented, or cold temperatures preclude beetle emergence and flight. One commonly used tactic is cut-and-leave, in which infestation growth is disrupted through the felling of both pine-beetle infested trees and adjacent uninfested 'buffer' trees (Billings, 1980; Swain & Remion, 1981). Despite intensive pest management efforts, the southern pine beetle continues to inflict significant timber losses, amounting to over $300 million during

the most recent outbreak in the southern part of the United States (Anon, 1996).

Materials and methods

Marking beetles in infestations

In the summer of 1994, during the period from 24 June to 30 August, we selected six small pine-beetle infestations from several national forests in the south-eastern United States. These infestations were chosen because they were small in size (13–48 infested trees), composed primarily of loblolly pine, *Pinus taeda* L. (a preferred host; Thatcher *et al.*, 1980), and infested trees were 25–50 cm in diameter at breast height (d.b.h.). In addition to these features, we determined through aerial and ground surveys that there were no other multiple tree pine-beetle infestations within a 5-km radius of the focal infestations. Previous work (Turchin & Thoeny, 1993; Cronin *et al.*, 1999) has shown that the number of emigrant pine beetles drops off rapidly with distance from site of origin; thus, our focal infestations would be the primary source of pine beetles in that particular area.

Three of the six infestations were left untreated. In each of these infestations, we selected six to eight pines that were infested with beetles in late-larval or pupal stages and coated the bark with fluorescent pigment (Day-Glo Color Corporation, Cleveland, OH) from a height of 1–7 m above the tree base. Directly above the fluorescent-coated area, we erected an umbrella-like tarp made of clear plastic (radius 1.5 m) to protect the fluorescent pigment from the rain. The tarp was attached to the tree with duct tape and extended outward by tying string between the tarp edges and surrounding vegetation.

In the remaining three infestations, we applied the disruptive suppression tactic, cut-and-leave. Following the protocol outlined by Billings (1980) and Swain & Remion (1981), all infested pines plus a 15 m buffer strip of uninfested pines were felled toward the centre of the infestation. Four to six of the felled trees that contained developing pine beetles were selected and cut into 1.0–1.5 m lengths (bolts). The bolts were transported to the centre of the infestation, coated with fluorescent powder and covered with a 3.65×3.0 m piece of tarpaulin to protect the powder from the rain. The effect of cut-and-leave on the abundance and sex ratio of recaptured beetles was of secondary concern to us relative to the effect of different traps. We performed this treatment as part of a separate study designed to examine the effect of suppression tactics on pine-beetle movement (Cronin *et al.*, 1999).

Based on the studies of Turchin & Thoeny (1993) and Cronin *et al.* (1999), the above dusting technique is 100% effective in marking emerging beetles. Upon emergence, pine beetles crawl through the fluorescent powder and accumulate it on their body and wings (Turchin & Thoeny, 1993). Powder on the wings is protected by the elytra and is relatively permanent (Rhodes *et al.*, 1998). This method of marking beetles appears to have no appreciable effect on flight initiation or gallery production by the southern pine beetle (Cook & Hain, 1992; Rhodes *et al.*, 1998), but does reduce the longevity of adult beetles by 20% in the laboratory (Cook & Hain, 1992). However, most beetles are

captured shortly after emergence; thus, estimates of sex ratio are unlikely to be affected by this method of marking.

Emergence density and sex ratio

The beetles emerging from dusted trees or bolts in each infestation served as our release (source) population. For the untreated infestations, we determined the abundance and sex ratio of pine beetles by fastening an emergence trap at mid bole (4.5 m above ground) to each of the pines coated with fluorescent powder. We constructed each trap from a 30×100 cm piece of plywood with a 10×80 cm hole cut in the centre. A foam gasket was glued around the outer edge of one side of the hole, and fine-meshed screening was stapled to the other side. A collecting jar was attached at the bottom of the screen. When bolted to the tree, the gasket formed a seal that prevented emerging beetles from escaping. As beetles emerged, they fell into the collecting jar and were killed by a small piece of No-Pest Strip (Bio-Strip, Inc., Reno, Nevada; active ingredient, 2–2-dichlorovinyl dimethyl phosphate).

We used the following procedure to extrapolate from the number of marked pine beetles captured in emergence traps to the total number emerging from each fluorescent-dusted tree. We based the distribution of beetles along the pine trunk on the equation

$$y_x = ax(1-x)e^{bx}$$

where y is the density of beetles at relative height x, and a and b measure the amplitude and shape of the curve, respectively (Mayyasi *et al.*, 1976). From a large number of pines, Mayyasi *et al.* (1976) estimated a and b to be 37.44 and 0.42, respectively, and obtained a very good fit to the curve. Although we used these parameter estimates to determine the density of beetles at each height (y_x), we used our emergence trap data to recalibrate the amplitude and then to predict the total number of marked beetles emerging from each dusted tree (see Cronin *et al.*, 1999). First, the actual density (Y_a) of marked beetles (per 100 cm²) at the trap midpoint was estimated from the total number of beetles captured in the emergence traps. We then calculated the expected density (Y_e) at the same location using Mayyasi *et al.* (1976) estimates of a and b. For each tree (t), the ratio of Y_a to Y_e provided a conversion factor (k_t) that re-scaled the density–distribution curve (altered the amplitude, a) to reflect the environmental differences among trees and localities. Using this conversion factor, we calculated from the equation above the sum total of marked beetles emerging from each fluorescent-coated tree (n_t) and the total emerging from each untreated infestation ($N = \Sigma n_t$). Based on an independent analysis of infested trees (Cronin *et al.*, 1999), n_t provides an unbiased and reliable estimate of the number of emerging pine-beetle adults per tree.

It was much simpler to estimate the total number of marked beetles in the cut-and-left infestations. In these sites, emergence traps were placed on a random subset of bolts; thus, we assumed that variations in pine-beetle density were also randomly distributed among bolts. As such, the total number of marked pine beetles at each site, N, was (number of pine beetles from emergence traps) × (bark area of all bolts combined)/(total area of emergence traps).

For both untreated and cut-and-left infestations, the sex ratio (proportion of males in the sample) was estimated directly from the captures of beetles in the emergence traps.

Trapping pine beetles

The source of beetles used to evaluate the efficiency of our traps was the marked beetles in each infestation. If the sex ratio of marked beetles caught in a dispersal trap was similar to the sex ratio of beetles emerging from the fluorescent-dusted trees or bolts, it would indicate that these traps provided an unbiased estimate of the true sex ratio in the surrounding area. Also, the strength of a correlation between the total number of marked beetles per site and the number of marked beetles recaptured within a particular dispersal trap would indicate the effectiveness of each trap as a predictor of pine-beetle abundance within the area. Below, we describe the traps used in this study.

Passive sticky traps. Passive sticky traps were constructed from a 1 m wide by 1.5 m tall wooden frame with saran screen stapled across one side. Tanglefoot (Tangle Trap Corp., Grand Rapids, MI) was applied liberally to both sides of the screen. The traps were orientated toward the dusted trees or bolts and were positioned at four distances (2, 5, 10 and 20 m) in three directions at 120° angles from each other. The close proximity of these traps to the source of beetles was necessary to ensure an adequate recapture rate. For untreated infestations, the sticky traps were centred around only one dusted tree (coated with a different fluorescent pigment to distinguish it from the other coated trees).

The height of the sticky traps varied between the treated and untreated infestations in order to adjust for the difference in height of the developing brood. For untreated infestations, trap height (height of upper edge) was set at 5 m, which corresponded approximately to the trunk height of maximal beetle density (Mayyasi *et al.*, 1976). By contrast, trap height for treated infestations was set at 2 m because bolts were lower to the ground (similar to the position of felled trees). In a separate study, we detected no difference in pine beetle recaptures or sex ratio between 2 m and 5 m traps that were positioned at the same distance from pine beetle brood within both cut-and-left and untreated infestations (J. T. Cronin, P. Turchin and J. L. Hayes, unpublished).

Tree traps. These traps, which were intended to mimic incipient pine beetle infestations (Coster *et al.*, 1977; Reeve *et al.*, 1998; Cronin *et al.*, 1999), were established in four cardinal directions at a distance of 100 m from the centre of the infestation. Only loblolly or shortleaf pines (*P. echinata*) with a d.b.h. of 25–50 cm were used. On each baited tree we placed three pairs of small sticky traps to monitor pine beetle arrivals. Each trap consisted of a 50×10 cm piece of plywood with a clear plastic sheet of equal size stapled to the surface. Tanglefoot was applied liberally to the plastic surface and was sprayed with the insecticide permethrin® to ensure that the beetles died before crawling off the traps. The trap pairs were placed on opposite sides of the tree at a height of 2, 5 and 8 m. Just prior to the emergence of marked beetles, the trap trees were baited with the 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 equipped with a cotton wick to aid in the volatilization of the compound; Billings, 1988). 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 uninfested pine. This ensured that each trap location had host material in a suitable stage of attack.

Funnel traps. The funnel trap (Phero Tech, Delta, B.C., Canada) consisted of a 1.5 m long vertical array of 16-unit funnels that was designed to mimic the silhouette of a pine and provide the beetles with a familiar object to orientate toward (Lindgren, 1983; Billings, 1988; 12-unit funnels are also used). Traps were baited with frontalin and turpentine and were hung from non-host trees (oak or hickory), with the bottoms 1.5 m from the ground. Attracted beetles dropped through the funnels and into a cup that contained a piece of No-pest strip to kill them. We deployed funnel traps at a radius of 100 m from the source of marked pine beetles and equidistant between the tree traps; thus, the nearest distance between any of the eight traps deployed at 100 m from the source of pine beetles was 71 m. Because these traps have an effective sampling area of only about 0.1 ha (Turchin & Odendaal, 1996), we expected little interference among them.

Censusing traps

Emergence and dispersal traps (passive, funnel and tree traps) were checked once a week and all pine beetles were collected. Censuses were repeated until we ceased to capture beetles in the emergence traps (usually 3–4 weeks). In the laboratory, each insect was carefully inspected for fluorescent powder using a dissecting microscope (10×) with an ultraviolet light source. For the purposes of this study, we combined samples from the same trap type and distance, but located in different directions, and then recorded the number of marked beetles captured and their sex ratio (proportion of the marked beetles that were males).

Statistical analysis

We first tested whether pine beetle numbers or sex ratio at the site of emergence (based on emergence traps) and from dispersal traps (passive, tree and funnel) varied with respect to suppression treatment and census week. A two-way factorial ANOVA was performed in which infestation treatment (untreated or cut-and-leave) and census week (1–3; those sites with four censuses usually netted very few recaptured beetles and so were combined with census week 3) were the main effects and either pine beetle number (natural-log transformed) or proportion of males was the dependent variable. Separate tests were performed for the site of emergence and each type of trap. All analyses were performed in SYSTAT (Wilkinson, 1990).

In a second series of tests, we examined whether the proportion of males varied among traps. In one test, we used a one-way ANOVA to evaluate whether trap distance (2, 5, 10 and 20 m) had any effect on the proportion of males recaptured on the passive sticky traps. We then tested whether the proportion of marked males varied among the different trap types (emergence, passive, tree and funnel) using a one-way ANOVA. Pairwise comparisons were made using Tukey's HSD test (Sokal & Rohlf, 1995).

Finally, we assessed whether captures of beetles at the three different traps could be useful as a predictor of pine beetle abundances in the surrounding area. To make this evaluation, we examined the correlation between the number of marked pine beetles emerging from each of the six infestations (*N*) and the number of marked beetles recaptured at each of the traps. Numbers were log-transformed to achieve normality and the analysis was performed in SYSTAT (Wilkinson, 1990) using Pearson's product-moment correlation (Sokal & Rohlf, 1995).

Results

Census period or the interaction between census period and suppression treatment had no effect on the abundance of marked pine beetles or the proportion of males captured in each type of trap (Table 1). In addition, suppression treatment affected

Table 1 ANOVA results for the effect of census week (1, 2 or 3) and infestation treatment (untreated or cut-and-left) on the number of beetles and proportion males from each trap source. Numbers presented are the *F*-statistic and associated *P*-value (in parentheses)

Source of SPB	Number of SPB		Proportion of males	
	Census week	Treatment	Census Week	Treatment
Site of emergence	1.01 (0.40)	1.52 (0.24)	0.34 (0.72)	0.05 (0.82)
Passive traps				
2 m	0.61 (0.56)	0.33 (0.58)	1.69 (0.23)	1.84 (0.20)
5 m	0.04 (0.96)	3.67 (0.08)	1.47 (0.27)	2.25 (0.16)
10 m	0.24 (0.79)	4.96 (0.05)	2.93 (0.10)	0.06 (0.81)
20 m	0.16 (0.86)	6.23 (0.03)	1.42 (0.29)	0.09 (0.77)
Tree traps	1.13 (0.36)	0.15 (0.70)	1.12 (0.36)	8.10 (0.02)
Funnel traps	0.14 (0.87)	0.30 (0.59)	1.74 (0.22)	1.12 (0.31)

The level of α (type I error rate) was adjusted to account for potential comparison-wise error that was introduced by conducting multiple ANOVA's on the same data set. Using the Dunn–Šidák correction, the adjusted error rate was α′ = 1 − (1 − α)^{1/k}; where *k* = the number of comparisons (Sokal & Rohlf, 1995). Here α′ = 0.007, for *k* = 7. Because the census week–treatment interaction was insignificant in all cases (*P* > 0.05), it was excluded from the table.

abundances and proportion of males in only a few of these trap comparisons (two of seven abundances, and one of seven proportions; $P < 0.05$). However, when the type I error rate, α, was adjusted using the Dunn–Šidák correction (Sokal & Rohlf, 1995) to account for possible comparison-wise error, none of the *P*-values were small enough to conclude that abundances or proportions differed among treatments. For all subsequent analyses, we pooled census dates and treatments.

Sex ratios

Based on estimates from emergence traps, the mean proportion of males in the fluorescent-coated trees or bolts was 0.53 (Fig. 1). This was indistinguishable from a 1 : 1 sex ratio (95% CI's for the proportion of males overlap 50%; Fig. 1). Among passive sticky traps, we could find no effect of distance ($F_{3,20} = 0.44$, $P = 0.73$) on proportion of males. However, the proportion of males did vary
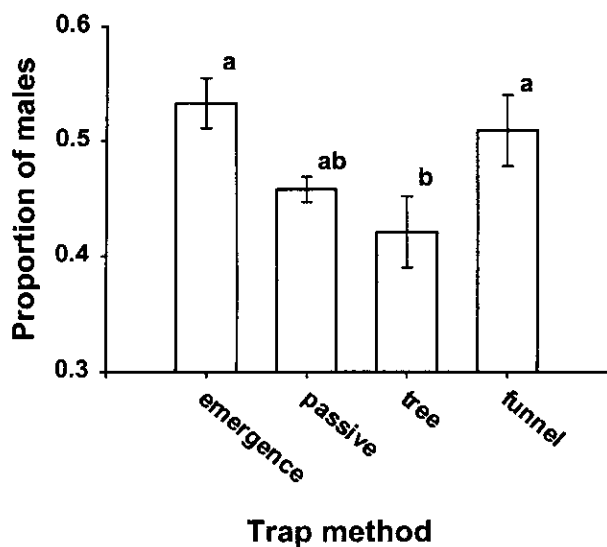

Figure 1 The mean proportion ($+$ 95% C.I.) of males recaptured in relation to different trap methods. Data from untreated and cut-and-left infestations were combined because no difference in sex ratio was detected between the two treatments. Means with different letters are significantly different (Tukey's HSD, $P < 0.05$).

significantly among the four different trap types (emergence, all passive traps combined, trees and funnels) ($F_{3,21} = 4.13$, $P = 0.02$; Fig. 1). In particular, tree traps were more heavily biased in favour of females (0.42) than the emergence traps. Passive traps were also slightly more biased in favour of females (0.46) than emergence traps, but the difference was not significant (Fig. 1). Funnel traps provided an estimate of the proportion of males that was most similar to the proportion emerging from infested trees (0.51).

Relative abundance

In forested areas where the only apparent pine beetle activity for at least 5 km in any direction was our target infestation, we could find no correlation between the total number of beetles marked within the focal infestation and the numbers of marked beetles captured in traps surrounding that infestation (pooled among census periods; Table 2, Fig. 2). This was true even for passive traps that were only 2–20 m from the source of emerging pine beetles. In addition, there was no correlation in captures of marked pine beetles between any of the traps, except for the 5 m and 10 m passive traps (Table 2). We note, however, that the captures of marked pine beetles were strongly correlated with the captures of unmarked pine beetles within each trap type ($R > 0.78$, $P < 0.05$; except for 2 m passive traps, where $R = 0.57$ and $P = 0.24$). Because marked and unmarked beetles probably emanated from the same isolated infestation, these strong correlations suggest that the marked beetles were dispersing in a manner similar to the remainder of the source population.

It is unlikely that this lack of a positive correlation between pine beetle abundance in the source population and traps could be attributed to low statistical power of our test. Even though sample sizes (six infestations) and power ($1 - \beta < 0.20$; Cohen, 1988) were low, correlational trends were generally in the opposite direction (see Fig. 2). Furthermore, it is unlikely that the correlation was obscured by the influx of pine beetles into traps from areas other than our source infestation: there was no evidence of beetle activity within a 5 km radius surrounding each focal infestation. Because pine beetle dispersal success (the likelihood of beetles locating a new infestation or baited trap) declines

Table 2 The correlation of recaptured southern pine beetles between the various types of traps. Pearson's product moment correlations, *R*, and the level of significance, *P*, are reported above and below the diagonal, respectively

	Total marked	Passive traps				Tree traps	Funnel traps
		2-m	5-m	10-m	20-m		
Total marked	–	−0.345	−0.502	−0.419	0.122	0.440	−0.220
2-m passive	0.503	–	−0.883	0.899	0.757	−0.784	0.059
5-m passive	0.311	0.341	–	0.975	0.942	−0.574	−0.011
10-m passive	0.408	0.270	0.019	–	0.891	−0.683	−0.017
20-m passive	0.818	0.831	0.100	0.306	–	−0.358	0.215
Tree traps	0.390	0.755	0.996	0.952	0.487	–	−0.059
Funnel traps	0.682	0.977	0.990	0.984	0.683	0.912	–

Numbers of recaptured beetles were log-transformed prior to analysis. Total marked is based on the number of beetles captured in emergence traps.

precipitously with distance (Turchin & Thoeny, 1993; Cronin *et al.*, 1999), at most, only a tiny fraction ($<<1\%$)

of beetles beyond 5 km would probably have found their way into our traps.

Discussion

Passive, tree and funnel traps have had a long history of use in research and monitoring pine beetle populations in the south-eastern United States (Vité, 1970; Coster *et al.*, 1977; Wagner *et al.*, 1979; Billings, 1980, 1988; Turchin & Simmons, 1997; Reeve *et al.*, 1998; Cronin *et al.*, 1999). To our knowledge, this is the first study to directly assess trap efficiencies for the southern pine beetle in the field. Although there are no intraspecific comparisons, studies with the congeneric mountain pine beetle (*D. ponderosae* Hopkins) did show a positive, albeit low, correlation between tree-trap captures and emerging beetle density (Safranyik & Linton, 1993).

Sex ratios

Equal numbers of male and female pine beetles emerged from within each of the six infestations. This is in accord with the 1 : 1 sex ratio reported by Osgood & Clark (1963) and Coulson *et al.* (1976) for beetles emerging from naturally infested pines. Our results suggest that funnel traps provide the most accurate estimate of the true sex ratio for the area in which the traps are deployed. Other studies using funnel traps have found similar proportions of males in their samples (Coster *et al.*, 1977; Payne *et al.*, 1978). As a monitoring tool, tree traps significantly overestimated the proportion of female pine beetles in the surrounding area. A likely explanation for this bias toward females is that trees undergo more complex chemical changes as the attack sequence progresses. Later during the attack sequence of a tree, as gallery production approaches a maximum, the concentrations of pine beetle-produced pheromones verbenone, exo-brevicomin and endo-brevicomin begin to rise (Renwick & Vité, 1969; Payne *et al.*, 1978, 1992). High concentrations of each of these compounds have a greater repellent effect on male than on female pine beetles (Renwick & Vité, 1969; Payne *et al.*, 1978, 1992). Another possibility is that because females tend to disperse farther and fly for longer periods of time than males (Kinn *et al.*, 1994; Kinn & Parresol, 2000), fewer males may have reached these traps. This latter hypothesis seems less likely considering our results from the funnel traps that were also positioned at 100 m from the source of beetles.

Relative abundance

Our data raise questions about the use of trap devices in providing an accurate estimate of the relative abundance of southern pine beetles at the infestation level. In the end, we can only speculate as to the cause for the surprising lack of a positive correlation between pine beetle abundance in the source population and traps. Our study focused on the correlation at a scale of a 100 m radius surrounding a pine beetle source population (an infestation), and replicates spanned several overlapping generations. The lack of a correlation between the abundance of beetles emerging from an infestation and trap captures in the area immediately surrounding that infestation does not preclude the usefulness of these traps as tools for
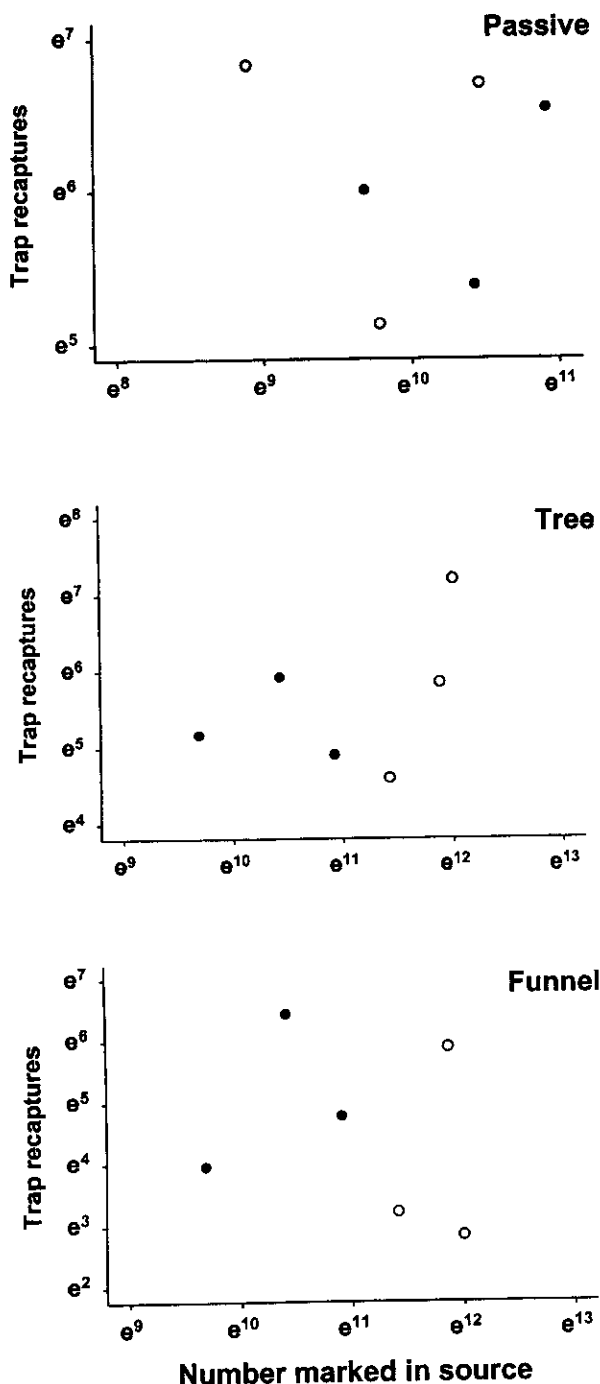

Figure 2 The relationship between the number of beetles marked with fluorescent powder in the focal infestation and the number of marked beetles recaptured in each of three types of traps: passive traps at 2 m, tree traps at 100 m and funnel traps at 100 m from the infestation. Data are reported on a logarithmic scale (base *e*). ○ and ● represent untreated and cut-and-left infestations, respectively. The 5-, 10- and 20-m passive traps were excluded because the pattern of recaptures mirrored that of the 2-m passive traps.

estimating population sizes and fluctuations at broader spatial scales. For example, Lindgren funnel traps (Lindgren, 1983) have been a standard census tool for successfully forecasting southern pine beetle population trends for more than 12 years (Billings, 1988). The use of baited funnel traps in the early spring at much wider spatial scales, as few as three traps per county or ranger district (> 1000 km^2), has proven to be relatively effective at forecasting population trends across the south-eastern United States (Billings, 1988; Anon, 1998). In this trapping scheme, traps are collected for a relatively short period of time in the spring (4–6 weeks) and purposefully located away from infestations. Captures from funnel traps that were positioned at 3.2 km intervals within and around an area of outbreak in Gainesville, Florida during 1994–95 failed to provide any correlation with the regional abundances of the southern pine beetle (J. Meeker, personal communication). More tests at different temporal and spatial scales, seasons and levels of beetle activity are needed to validate the general use of these traps as monitoring tools for the southern pine beetle.

For many forest pest species, trap captures provide the foundation for assessing relative population densities and time-series trends, as well as to indicate whether control measures should be implemented (Hain, 1980; Dent, 1991). Despite the significant role played by traps, the critical assumption that trap captures are related to actual pest activity levels in the field is often untested. Until trap captures are compared with actual pest abundances at a broad range of spatial and temporal scales, we will not be able to translate captures into estimates of pest density.

Acknowledgements

References

Anon (1996) *Forest Insect and Disease Conditions in the United States, 1995.* USDA Forest Service, Washington D.C.

Anon (1998) *SPB Update, June 1998.* USDA Forest Service, Southern Research Station, Pineville, Louisiana, U.S.A.

Billings, R.F. (1980) Direct control. *The Southern Pine Beetle* (ed. by R. C. Thatcher, J. L. Searcy, J. E. Coster and G. D. Hertel), pp. 179–192. USDA Technical Bull. 1631. Department of Agriculture, Washington DC.

Billings, R.F. (1985) Southern pine bark beetles and associated insects: effects of rapidly-released host volatiles in response to aggregation pheromones. *Zeitscrift für Angewandte Entomology*, 99, 483–491.

Billings, R.F. (1988) Forecasting southern pine beetle infestation trends with pheromone traps. *Integrated Control of Scolytid Bark Beetles* (ed. by T. L. Payne and H. Saarenmaa), pp. 295–306. Virginia Polytechnic Institute and State University, Blacksburg, VA.

Bombosch, S. (1988) Some considerations on the use of bark beetle pheromones. *Integrated Control of Scolytid Bark Beetles* (ed. by T.

L. Payne & H. Saarenmaa), pp. 263–265. *UFRO Working Party and XVII International Congress of Entomology Symposium, Vancouver, B.C., Canada.* Vancouver Polytechnic Institute/State University of Blacksburg, Virginia.

Carter, M.R., Ravlin, F.W. & McManus, M.L. (1994) Estimating gypsy moth (Lepidoptera: Lymantriidae) egg mass density using male moths captured in pheromone-baited milk-carton traps. *Environmental Entomology*, 23, 556–561.

Cohen, J. (1988) *Statistical Power Analysis for the Behavioral Sciences.* 2nd edn. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Cook, S.P. & Hain, F.P. (1988) Resistance mechanisms for loblolly and shortleaf pines to southern pine beetle attack. *Mechanisms of Woody Plant Defenses against Insects. Search for Patterns* (ed. by W. J. Matson, J. Levieux and C. Bernard-Dagans), pp. 295–304. Springer-Verlag, New York.

Cook, S.P. & Hain, F.P. (1992) The influence of self-marking with fluorescent powders on adult bark beetles (Coleoptera: Scolytidae). *Journal of Entomological Science*, 27, 269–279.

Coster, J.E. & Johnson, P.C. (1979) Characterizing flight aggregation of southern pine beetle. *Environmental Entomology*, 8, 381–387.

Coster, J.E., Payne, T.L. & Hart, E.R. & Edson, L.J. (1977) Aggregation of the southern pine beetle in response to attractive host trees. *Environmental Entomology*, 6, 725–731.

Coulson, R.N., Mayyasi, A.M. & Folt, J.L., Hain, F.P. & Martin, W.C. (1976) Resource utilization by the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Canadian Entomologist*, 108, 353–362.

Cronin, J.T., Turchin, P., Hayes, J.L. & Steiner, C.A. (1999) Area-wide efficacy of a localized forest pest management practice. *Environmental Entomology*, 28, 496–504.

Dent, D. (1991) *Insect Pest Management.* Oxford University Press, Oxford.

Hain, F.P. (1980) Sampling and predicting population trends. *The Southern Pine Beetle* (ed. by R. C. Thatcher, J. L. Searcy, J. E. Coster and G. D. Hertel), pp. 107–135. USDA Technical Bulletin 1631. US Department of Agriculture, Washington, D.C.

Kinn, D.N. & Parresol, B.R. (2000) Seasonal changes in southern pine beetle flight potential and energy reserves. *Environmental Entomology*, in press.

Kinn, D.N., Perry, T.J., Guinn, F.H., Strom, B.L. & Woodring, J. (1994) Energy reserves of individual southern pine beetles (Coleoptera: Scolytidae) as determined by a modified phosphovanillin spectrophotometric method. *Journal of Entomological Science*, 29, 152–163.

Kinzer, G.W., Fentiman, A.F., Jr, Page, T.L., Foltz, R.L., Vité, J.P. & Pitman, G.B. (1969) Bark beetle attractants, identification, synthesis and field bioassay of a compound isolated from *Dendroctonus frontalis. Nature*, 221, 447–448.

Lindgren, B.S. (1983) A multiple funnel trap for scolytid beetles (Coleoptera). *Canadian Entomologist*, 115, 299–302.

Mayyasi, A.M., Coulson, R.N., Foltz, J.L. & Hain, F.P. & Martin, W.C. (1976) Functional description of within-tree larval and progeny-adult populations of *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Canadian Entomologist*, 108, 363–372.

Muirhead-Thomson, R.C. (1991) *Trap Responses of Flying Insects.* Academic Press, San Diego, CA.

Osgood, E.A. & Clark, E.W. (1963) Methods of sexing and sex ratios of the southern pine beetle *Dendroctonus frontalis* Zimm. *Canadian Entomologist*, 95, 1106–1109.

Payne, T.L. (1980) Life history and habits. *The Southern Pine Beetle* (ed. by R. C. Thatcher, J. L. Searcy, J. E. Coster and G. D. Hertel), pp. 7–28. USDA Forest Service Technical Bulletin 1631. US Department of Agriculture, Washington DC.

Payne, T.L., Billings, R.F., Berisford, C.W., Salom, S.M., Grosman, D.M., Dalusky, M.J. & Upton, W.W. (1992) Disruption of *Dendroctonus frontalis* (Col., Scolytidae) infestations with an inhibitor pheromone. *Journal of Applied Entomology*, **114**, 341–347.

Payne, T.L., Coster, J.E. & Richerson, J.V., Edson, L.J. & Hart, E.R. (1978) Field response of the southern pine beetle to behavioral chemicals. *Environmental Entomology*, **7**, 578–582.

Reeve, J.D., Rhodes, D.A. & Turchin, P. (1998) Scramble competition in southern pine beetle (Coleoptera: Scolytidae). *Ecological Entomology*, **23**, 433–443.

Renwick, J.A.A. & Vité, J.P. (1969) Bark beetle attractants. mechanism of colonization by *Dendroctonus frontalis*. *Nature*, **224**, 1222–1223.

Rhodes, D.J., Hayes, J.L. & Steiner, C.A. (1998) Retention of external and internal markers in southern pine beetles (Coleoptera: Scolytidae) during gallery construction. *Journal of Entomological Science*, **33**, 221–232.

Safranyik, L. & Linton, D.A. (1993) Relationships between catches in flight and emergence traps of the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Col. Scolytidae). *Journal of the Entomological Society of British Columbia*, **90**, 53–61.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. 3rd edn. W. H. Freeman, New York.

Southwood, T.R.E. (1979) *Ecological Methods with Particular Reference to the Study of Insect Populations*. 2nd edn. Methuen, London.

Swain, K.M. & Remion, M.C. (1981) *Direct Control of the Southern Pine Beetle*. USDA Forestry Series, Agricultural Handbook Combined Forest Pest Research and Development Program. Agricultural Handbook No. 575. US Department of Agriculture, Pineville, Louisiana.

Thatcher, R.C., Searcy, J.L., Coster, J.E. & Hertel, G.D. (1980) *The Southern Pine Beetle*. USDA, Forestry Series Technical Bulletin 1631. US Department of Agriculture, Washington DC.

Thorpe, K.W., Ridgway, R.L. & Leonhardt, B.A. (1993) Relationship between gypsy moth (Lepidoptera: Lymantriidae) pheromone trap catch and population density: comparison of traps baited with 1 and 500 micrograms (+) – disparlure lures. *Journal of Economic Entomology*, **86**, 86–92.

Turchin, P., Lorio, P.L., Jr, Taylor, A.D. & Billings, R.F. (1991) Why do populations of southern pine beetles (Coleoptera: Scolytidae) fluctuate. *Environmental Entomology*, **20**, 401–409.

Turchin, P. & Odendaal, F.J. (1996) Measuring the effective sampling area of a pheromone trap for monitoring population density of southern pine beetle (Coleoptera: Scolytidae). *Environmental Entomology*, **25**, 582–588.

Turchin, P. & Simmons, G. (1997) Movement of animals in congregations: an Eulerian analysis of bark beetle swarming. *Animal Aggregations: Three-Dimensional Measurement and Modeling* (ed. by J. K. Parrish, W. M. Hamner and C. T. Prewitt), pp. 113–125. Cambridge University Press, Cambridge.

Turchin, P. & Thoeny, W.T. (1993) Quantifying dispersal of southern pine beetles with mark–recapture experiments and a diffusion model. *Ecological Applications*, **3**, 187–198.

Vité, J.P. (1970) Pest management systems using synthetic pheromones. Symposium on population attractants. *Contributions of the Boyce Thompson Institute*, **24**, 343–350.

Vité, J.P. & Baader, E. (1990) Present and future use of semiochemicals in pest management of bark beetles. *Journal of Chemical Ecology*, **16**, 3031–3041.

Wagner, T.L., Gagne, J.A., Doraiswamy, P.C., Coulson, R.N. & Brown, K.W. (1979) Development time and mortality of *Dendroctonus frontalis* in relation to changes in tree moisture and xylem water potential. *Environmental Entomology*, **8**, 1129–1138.

Weslien, J. & Lindelöw, C. (1989) Trapping a local population of spruce bark beetles *Ips typographus* (L.): population size and origin of trapped beetles. *Holarctic Ecology*, **12**, 511–514.

Wilkinson, L. (1990) *SYSTAT. The System for Statistics*. Systat, Evanston, Illinois.