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VISUAL AND SEMIOCHEMICAL DISRUPTION OF HOST FINDING IN THE SOUTHERN PINE BEETLE

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Abstract. The importance of visual silhouettes for host finding by the southern pine beetle (SPB), *Dendroctonus frontalis* (Coleoptera: Scolytidae), and the potential for disruption of this process using visual deterrents were evaluated with multiple-funnel traps, painted white or black, and with clear, white, or black Plexiglas sticky panels. All traps and panels were baited with the SPB attractant frontalure. The effect of combined semiochemical and visual disruption was evaluated in funnel traps by including the antiaggregation pheromone verbenone, or the repellent/inhibitory host compound 4-allylanisole, in addition to the attractant. Visual treatments had a highly significant effect on catch of SPB and the predatory clerid beetle *Thanasimus dubius*. In attractant-baited traps, white paint alone reduced the average number of SPB caught by 72% in Florida and 68% in Louisiana. The repellent 4-allylanisole reduced catch of SPB by 56% in Florida and 45% in Louisiana. Verbenone was eluted at 25% of the targeted rate and did not affect total catch in either place. White panels trapped 79% fewer SPB than black, and 55% fewer than clear, with both differences significant. Clear panels also caught significantly fewer (−54%) SPB than black panels. Capture of *T. dubius* was reduced significantly by clear (−61%) or white (−56%) panels compared to black but did not differ significantly between clear and white panels. The percentage of female SPB captured was not significantly changed by visual treatments but was, as expected, reduced by verbenone. Neither visual nor semiochemical treatments influenced the sex ratio of *T. dubius.* The potential for using visual disruptants for protection of trees was assessed in front of a single SPB infestation by painting trees either white or black to 4.5 m. White trees showed fewer landings by SPB and a reduced density of successful and total SPB attacks within, but not above, the painted area. These results show that both SPB and *T. dubius* can be significantly affected by altering visual silhouettes, and that visual and semiochemical treatments, especially used in combination, may increase effectiveness of bark beetle disruption strategies.

Key words: Cleridae; Dendroctonus frontalis; *host selection;* Thanasimus dubius; *vision; visual behavior.*

INTRODUCTION

Host selection by insects consists of a series of five steps: host-habitat finding, host finding, host recognition, host acceptance, and host suitability (Kogan 1994). These steps lead to acceptance or rejection of a resource (Kennedy 1965, Miller and Strickler 1984). Under appropriate conditions, individuals progressively narrow their search, responding to environmental stimuli with programmed behaviors, until they locate a suitable host. If conditions are not appropriate the process is disrupted, thus ‘‘stranding’’ the insect at a previous step (Kogan 1994). Because insects sense environmental variables through multiple sensory modalities, each potentially linked to behavioral events associated with host selection, there are multiple opportunities to disrupt insect host selection by targeting a variety of sensory cues. Interplay between or among modalities during host selection is common, thereby increasing behavioral plasticity (Harris and Miller 1982, Prokopy and Owens 1983, Miller and Strickler 1984), further suggesting that disruption may be enhanced by targeting more than one sensory cue.

The southern pine beetle, *Dendroctonus frontalis* Zimmermann, is an aggressive, tree-killing bark beetle that primarily attacks standing trees (Gara et al. 1965; see Moser et al. 1987 for exceptions). Its host range includes pine species common to the southern United States, with loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* L.) the most frequently infested (Price et al. 1992). Host selection by this beetle involves a variety of sensory cues, likely including olfaction, vision, mechanoreception, and gustation (Gara et al. 1965, Kinzer et al. 1969, Elkinton and Wood 1980, White 1981, Raffa and Berryman 1982, Payne 1986). Successful reproduction of SPB depends upon mass attack of conspecifics overwhelming host defenses and causing tree death (Raffa and Berryman 1987). This is accomplished through pheromonally me-

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diated aggregation and necessarily leads to multiple models for host selection, i.e., the majority of beetles find hosts by secondary (pheromonal) signals, while first-attacking, pioneer beetles (Borden 1974) use other means that are not fully understood at present.

Olfactory cues are considered to be the most important stimuli for attracting and inhibiting bark beetles (Wood 1982). This belief, combined with the need to understand and modify bark beetle behavior and develop efficient trapping methods, has concentrated behavioral research of scolytids on semiochemicals (Wood 1982, Payne and Billings 1989, Salom et al. 1992, Hayes et al. 1994). Semiochemicals have important effects on behavior, have been widely used to monitor populations, and have been effectively used at times to control bark beetle infestations (Borden 1993, 1997). Because of variability of responses to semiochemicals among individual beetles (Berisford et al. 1990), management tactics based on semiochemicals can vary in effectiveness (Rudinsky et al. 1974, Borden et al. 1986, Borden 1993, 1997, Shea 1994). In addition, attempts to improve effectiveness of inhibitory semiochemicals against SPB through increasing elution rates or applying multiple elutants have not significantly changed results (Hayes et al. 1994). This suggests that a better understanding of the bark beetle host selection process could be used to improve the effectiveness of management tactics that include behavioral deterrents.

Visual orientation of bark beetles to hosts has long been considered an important component of their host selection process (Gara et al. 1965, Shepherd 1966, Lanier 1983, Payne and Coulson 1985, Borden et al. 1986, Payne 1986, Turchin and Odendaal 1996). Many species of scolytids, including SPB, land on dark, vertical objects, and this feature often is incorporated into traps to increase their effectiveness (Lindgren 1983). Management of the SPB routinely includes cutting trees in front of infestations, in part to remove nearby vertical silhouettes. Gara et al. (1965) proposed three models of SPB host selection, one of which suggests that when an area has aggregation pheromone present (i.e., in an actively expanding infestation) vision is the most important orientation behavior.

Vision has been largely ignored in studies of host orientation and in the development of new management tactics, which are usually semiochemically based. Our objectives were to determine whether the orientation of SPB to simulated hosts (i.e., traps) can be disrupted by altering the appearance of visual silhouettes, and, if so, to determine its importance relative to, and in conjunction with, semiochemical deterrents for tree protection.

MATERIALS AND METHODS

Semiochemical effects of paint

According to the manufacturer, the only difference between the two spray paints that we used is pigmentation (S. DiSalzatore, Krylon Division of the Sherwin-Williams Company, 30 January 1996, *personal communication*), not volatile solvents or carriers. Laboratory bioassays were used to examine potential repellent effects of each paint on walking SPB (Hayes et al. 1994). Sticky panels made from Plexiglas that was clear or colored (without paint) were used to compare total catch when visual silhouettes were altered without paint. Potential alteration of elution rates (i.e., the rate of evaporation of the semiochemical from the lure), due to different temperatures of white- and black-painted traps, was assessed by placing two traps, one white and one black, in two light environments: full sun and full shade. Light levels were measured using a ceptometer (Decagon, Pullman, Washington) read in four cardinal directions at two times (0930, 4 September 1996; 1230, 6 September 1996). Elution rates of frontalure were measured gravimetrically on 26 August and 17 September 1996. Six elution devices (Table 1) were placed on each trap.

Funnel trap studies

To determine the disruptive potential of visual treatments alone and in combination with semiochemicals, six treatments were tested simultaneously (Table 1) using 16-unit multiple funnel traps (Phero Tech, Incorporated, Delta, British Columbia, Canada). Traps were painted either white or black (three traps of each) with glossy spray paint (Krylon Division, Sherwin-Williams Company, Solon, Ohio). Black paint (applied over the black plastic) was used to control for potential semiochemical effects of the paint, as well as any potential differences in escape rates due to any physical alterations of the trapping surface. Each of the six traps contained the SPB attractant frontalure (Table 1). Additionally, to test the effectiveness of visual treatments combined with semiochemicals, one trap of each color also contained the antiaggregation pheromone verbenone or the host-produced repellent compound 4-allylanisole.

Treated traps were randomly placed along the most active front of SPB infestations, at least 10 m apart and from unattacked trees. Traps were collected daily for six consecutive days and systematically rotated after each collection so that each treatment appeared in each location once (Hayes et al. 1994). Total catches of SPB and a major predator, *Thanasimus dubius* (F.) (Coleoptera: Cleridae), were counted from daily collections. Each 6-d set of collections was considered one replicate. In Florida, five sites were used to produce six replicates in June 1995. In July 1995, two sites in Louisiana were used for four additional replicates.

Sticky panel studies

To eliminate any possibility of paint volatiles affecting SPB behavior, and to include a ‘‘no silhouette’’ treatment (i.e., clear to the human eye), an experiment was conducted using sticky panels (61 × 41 × 0.32

TABLE 1. Description of semiochemical and visual treatments used in SPB and *T. dubius* trapping studies in Florida and Louisiana.

A) Semiochemical treatments

Semiochemical	Elution device	Rate	Reported function
Frontalure[†]	transfer pipette	80 mg/d[‡]	aggregation pheromone
	transfer pipette	46–58 mg/d[§]	
	transfer pipette	48–56 mg/d[‖]	
Verbenone	sponge inside bag	35 mg/d[¶]	multifunctional/inhibit aggregation
4-allylanisole	vial with wick	160 mg/d[#]	inhibit aggregation/repellent

B) Visual treatments

Trap	Type	Color	Surface
Funnel traps	16 funnel	black or white	paint[††]
Sticky panels	61 × 45 cm	black, white, clear	Plexiglas[‡‡]

Note: Antiaggregation semiochemicals, verbenone and 4-allylanisole, were eluted individually from traps with frontalure.

[†] Frontalure is an SPB attractant consisting of a 2:1 ratio of alpha-pinene, a host-produced synergist, and frontalin, an aggregation pheromone.

[‡] Hayes et al. 1994.

[§] Lower value is elution rate of frontalure on black traps in low light ($\overline{X} = 11.5$ mmol·m^{-2}·s^{-1}); higher value is elution rate on black traps in full sun (1913.8 mmol·m^{-2}·s^{-1}).

[‖] Elution rates as above but on white traps. Note that elution rates between black and white traps did not differ within a light environment (low light: $t = 0.62$, df = 10, $P = 0.55$; full sun: $t = 1.20$, df = 10, $P = 0.26$).

[¶] M. Dalusky and C. W. Bersiford, *unpublished data.* Note that the elution rate of verbenone is ~25% that used for inhibition in many field studies.

[#] Hayes et al. 1994.

[††] Gloss black (number 81601) or gloss white (number 81501) spray paint (Krylon Division of the Sherwin-Williams Company, Solon, Ohio).

[‡‡] AtoHaas Plexiglas MC, AtoHaas, Philadelphia, Pennsylvania.

cm thick) constructed from clear, black, or white Plexiglas (Table 1), covered with clear polyethylene film (0.1016 mm thick) and coated with Stikem Special (Michel and Pelton Company, Emeryville, California).

A single pipette of frontalure (Table 1) was attached to each panel. Panels were placed in a six-position array, as described above, with each treatment being represented two times. After each collection period, traps were rotated sequentially until each trap had appeared in each location twice (12 collection periods; 12 replications).

Effect of tree painting on landing and colonization

The effect of painting potential host trees on infestation by SPB and *Ips* spp. was evaluated in a 14-yr-old loblolly pine plantation located at Idlewild Research Station, Clinton, Louisiana. In front of an active SPB infestation, 15 trees were selected and randomly assigned three visual treatments (unpainted, black, or white), giving five replications of each treatment. Trees were painted to ~4.5 m using latex house paint (Wal-Mart, Incorporated, Bentonville, Arkansas) in July 1995. Sticky traps (9 × 30 × 1.25 cm thick) were attached to each painted tree at 2.5 m on 11 July 1995. They consisted of wood, painted black or white to match each tree, covered with 0.1016 mm thick ‘‘visqueen’’ (Poly America, Grand Prairie, Texas) that was coated with Stickem Special and misted lightly with permethrin (2% concentration in water). Sticky traps were collected approximately every other day until trees were felled.

When the active front of the SPB infestation had moved past the group of treated trees, trees were evaluated and, if mass attacked, felled and sampled for attacks at roughly 2-m intervals. Attacks were identified as SPB (successful or unsuccessful) or nuptial chambers of *Ips* spp. Three species of *Ips* were present (*I. avulsus, I. calligraphus, I. grandicollis*), but no effort was made to attribute damage to individual species.

Reflectance spectra

Reflectance spectra of visual treatments were generated by comparison to a white standard using a Labsphere RSA-HP-84 integrating sphere (Labsphere, North Sutton, New Hampshire) attached to a Hewlett-Packard HP 8452A Diode Array spectrophotometer.

Statistical analyses

The numbers of SPB or *T. dubius* caught during each collection period were transformed by ($\log_{10}[Y + 1]$) to normalize data and reduce heteroscedasticity of variances. Funnel trap experiments were analyzed by mixed-model ANOVA using a randomized block experimental design with a 2 × 3 factorial treatment structure and site as the (random effect) blocking factor (PROC GLM; SAS Institute 1994). Data from Florida and Louisiana were analyzed separately. For sticky panel experiments, data were analyzed using a two-way mixed-model ANOVA with date of collection representing replicates and including the effects of visual treatment, as well as appropriate interaction terms, in the model (PROC GLM; SAS Institute 1994). Collection date and its interaction terms were considered random variables. Means were compared using the Least

Significant Difference procedure (LSD; SAS Institute 1994) only if the overall model and the individual main effect were significant. Where interaction terms were not significant ($P > 0.10$) across analyses, they were removed from ANOVA models. The effect of treatments on the percentage of females captured in funnel traps was determined with the SAS system for categorical data analysis (PROC CATMOD; SAS Institute 1994). Individual contrasts were used to compare means where appropriate.

To determine the effect of trap color and environmental light on elution rates, mean elution rates of frontalure on black and white traps were compared using t tests for each date in each light environment.

The average sum of SPB and clerids captured on sticky traps placed on painted trees were analyzed by t test. Sums were used for analysis because the total number of captures is the most relevant due to the strong temporal component of mass attacks among trees in the study. The mean number of SPB attacks, total and successful, was analyzed by one-way ANOVA. Attack data from each tree were pooled to produce two means: one from below 4.5 m (4.5 m was the top of the painted area on painted trees) and one from above 4.5 m, with separate analyses conducted for each of the two locations. The mean number of *Ips* nuptial chambers below 4.5 m was not subjected to statistical analysis because of the frequency of zeros in the data set. One white tree was not attacked by either SPB or *Ips,* and was excluded from the analysis.

RESULTS

Semiochemical effects of paint

Neither paint had any repellent effect on walking SPB in the laboratory (white: 22 SPB tested, 11 female and 11 male, 0 repelled; black: 21 SPB tested, 10 female and 11 male, 0 repelled). Additionally, our results obtained with Plexiglas panels were similar to those obtained with painted funnel traps (Figs. 1 and 2), further suggesting that semiochemical effects of black and white paint, if any exist, were similar. Comparison of frontalure-only treatments shows that white Plexiglas panels caught 79% fewer SPB than black, while white-painted funnel traps caught 72% fewer SPB in Florida and 68% fewer in Louisiana than their black counterparts.

There was no significant difference observed between frontalure eluted from black ($\bar{X} = 46$ mg/d, low light; 58 mg/d, full sun) or white ($\bar{X} = 48$ mg/d, low light; 56 mg/d, full sun) funnel traps within each light treatment ($t = 0.6187$, df = 10, $P = 0.5499$, low light; $t = 1.2035$, df = 10, $P = 0.2565$, full sun).

Funnel trap studies

SPB.—In Florida, white multiple funnel traps caught 72% fewer SPB's than black traps when both traps were baited with attractant alone (Fig. 1A). Semiochemical treatment also significantly influenced trap catch of SPB (Table 2). The repellent 4-allylanisole reduced catch of SPB by 56 and 97% when placed on black and white traps, respectively, when compared to the black treatment with attractant only (Fig. 1A). Due to such factors as infestation size and pine basal area, site was a significant explanatory variable (Table 2). The interaction terms visual × semiochemical treatments and site × visual × semiochemical treatments were not statistically significant for the Florida data.

In Louisiana, catches of SPB averaged less than half those in Florida (Fig. 1B), with site again being significant and visual treatment being the most significant factor. White traps with attractant only caught 68% fewer SPB than the semiochemically equivalent black treatment. The repellent 4-allylanisole reduced trap catch by 45% alone and by 83% in combination with white paint. There was no significant interaction between semiochemical and visual treatments in either Florida or Louisiana.

Semiochemical treatment significantly affected sex ratio in both Florida ($\chi^2_2 = 308.05$, $P = 0.0000$) and Louisiana ($\chi^2_2 = 100.61$, $P = 0.0000$), while visual treatment did not ($\chi^2_1 = 0.06$, $P = 0.8117$, Florida; $\chi^2_1 = 0.15$, $P = 0.6970$, Louisiana). Verbenone had the greatest effect on capture of females in both places, catching 65.6% females in Florida (compared with frontalure alone, 39.3% females, $\chi^2_1 = 231.53$, $P = 0.0000$; or frontalure with 4-allylanisole, 25.9%, females, $\chi^2_1 = 154.99$, $P = 0.0000$) and 64.5% in Louisiana (compared with frontalure alone, 37.2% females, $\chi^2_1 = 80.52$, $P = 0.0000$; or frontalure with 4-allylanisole 33.2% females, $\chi^2_1 = 65.44$, $P = 0.0000$). The interaction between semiochemical and visual treatments was not significant in Florida ($\chi^2_2 = 4.36$, $P = 0.1128$) but was significant in Louisiana ($\chi^2_2 = 13.47$, $P = 0.0012$). This effect was made significant by a higher percentage of females captured in black verbenone traps compared to white verbenone traps (67% female vs. 55% female) and a lower percentage of females in black 4-allylanisole traps compared to white (31% female vs. 40% female). Because the magnitude of this effect was small compared to the main effect of the semiochemical, comparisons were made between semiochemical treatments, as previously described.

Thanasimus dubius.—Although more than twice as many *T. dubius* were caught in Louisiana than in Florida (1679 vs. 793), reductions in catches caused by the white silhouettes were similar, 85% in Florida and 88% in Louisiana. Site was again a significant variable (Table 2). In both states, total clerid capture was unaffected by semiochemical treatment, as was sex ratio ($\chi^2_2 = 2.09$, $P = 0.3523$). In Florida, the percentage of female clerids captured varied from a low of 40.9% in white verbenone traps to a high of 52.5% in white frontalure traps, while in Louisiana the percentage of females varied from 45.9% in black traps baited with frontalure and 4-allylanisole to 59.7% in white traps baited with

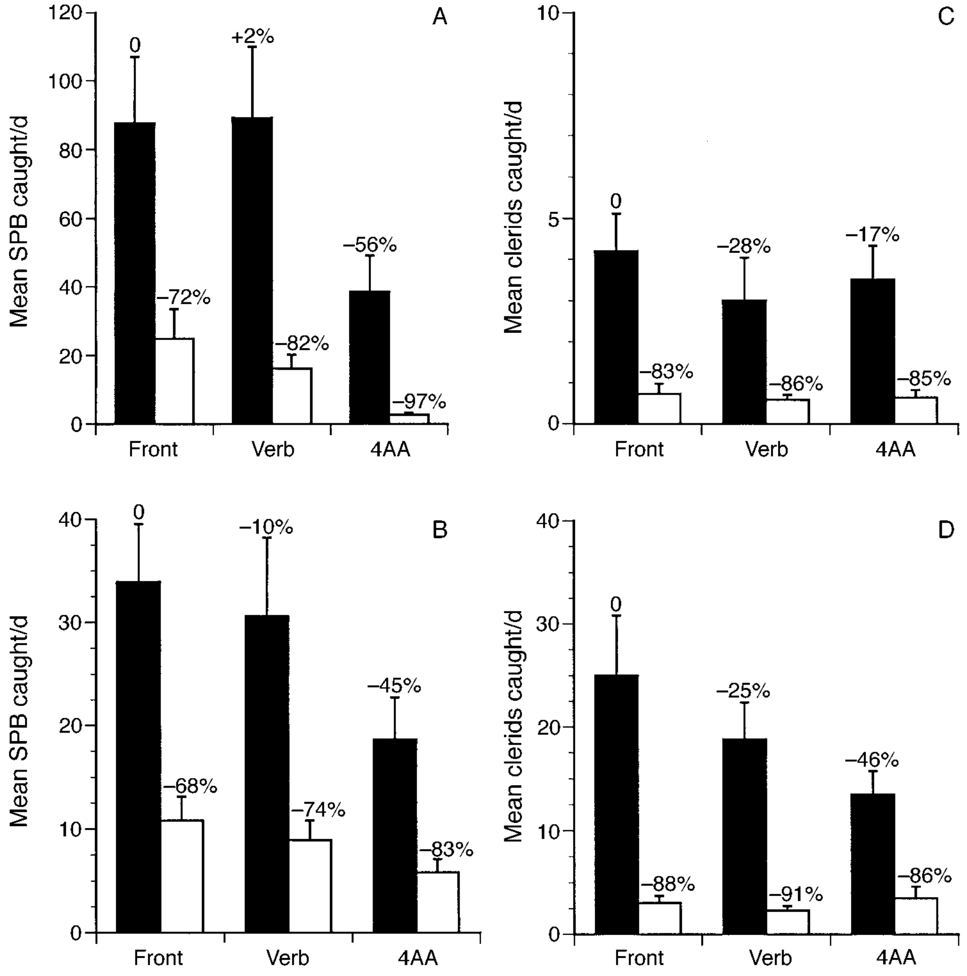

FIG. 1. Mean (+1 SEM) catch per collection date of southern pine beetle (A, B) and *Thanasimus dubius* (clerids) (C, D) in funnel traps at sites in Florida (A, C) and Louisiana (B, D). Traps had semiochemical (Front = frontalure alone; Verb = verbenone + frontalure; 4-AA = 4-allylanisole + frontalure) and visual (black bars denote black traps; white bars, white traps) treatments. All traps included the attractant frontalure. Note that values of the vertical (y) axes differ among panels.

frontalure and verbenone. However, visual treatment had a small effect on sex ratio of clerids caught ($\chi^2_1 = 4.59$, $P = 0.0322$). White traps caught more female clerids (54.9%) than did black traps (47.8%), but white traps caught only 224 clerids, while black traps captured 1455 clerids. The interaction between semiochemical and visual treatments was not significant ($\chi^2_2 = 0.59$, $P = 0.7428$).

Sticky panel studies

The effects of Plexiglas sticky traps on SPB (Fig. 2) were similar to those found with funnel traps baited with attractant alone (Fig. 1A, B). Date of collection was significant ($F_{11,22} = 34.0714$, $P < 0.0001$, MSE = 0.1343); this is not surprising since the dynamics of SPB infestations vary dramatically over short periods of time. The effect of visual treatment was highly significant ($F_{2,22} = 59.4348$, $P < 0.0001$), with white panels ($\bar{X} \pm 1$ SE = 68 ± 13.7 SPB) catching 79% fewer than black (320 ± 60.5 SPB; $P < 0.0001$) and 55% fewer than clear (149 ± 37.5 SPB; $P < 0.0014$). Clear panels caught significantly (−54%) fewer SPB than black panels ($P < 0.0001$). The interaction between date and visual treatment was not significant ($F_{22,36} = 1.5105$, $P = 0.1328$).

T. dubius also were significantly affected by panel color ($F_{2,11} = 19.7158$, $P < 0.0001$, MSE = 0.2175). Catch on clear and white panels did not differ ($P = 0.3364$). Both clear and white caught fewer *T. dubius* than black ($P < 0.0001$); clear reduced catch by 61% and white by 56%. The catch of clear panels did not differ significantly from that of white, suggesting that clerids respond differently than SPB in this regard. Date ($F_{11,22} = 4.7643$, $P < 0.0009$) had a significant effect on total catch, and the interaction between date and visual treatment also had a small, but significant, effect on the total number of *T. dubius* caught ($F_{22,36} = 2.3734$, $P < 0.0103$).

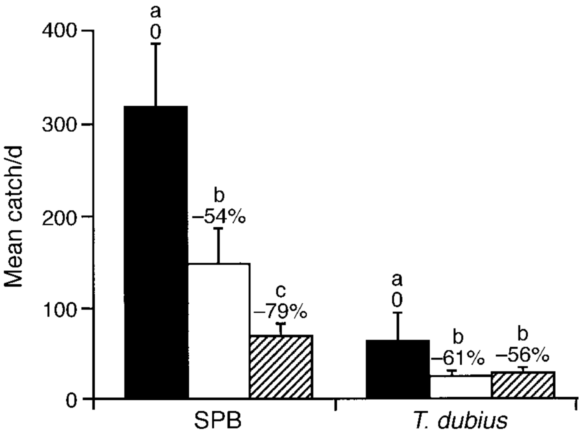

FIG. 2. Mean (+1 SEM) catch per collection date of southern pine beetle (SPB) and *Thanasimus dubius* (clerids) on sticky panels baited with frontalure in Louisiana. Treatments consisted of clear (white bars), black (black bars), or white (hatched bars) Plexiglas panels. Different letters indicate significant differences between treatments (least significant difference test; $P < 0.05$).

Effect of tree painting on landing and colonization

All of the unpainted and black-painted trees were attacked by SPB. Four of five white trees were attacked by SPB; however, the pattern of colonization differed from the other two treatments (Fig. 3). Sticky traps showed that more SPB landed on black trees (74.4 ± 17.6 SPB) than white (16.4 ± 2.9 SPB; $t = 3.25$, $P = 0.0117$, df = 8). Although very few clerids were captured, they followed the same pattern with total landings on black trees (3.8 ± 0.02 clerids) being greater than white (0.8 ± 0.37 clerids; $t = 3.20$, $P = 0.0127$, df = 8).

Below 4.5 m, paint had a significant effect on the density of SPB attacks ($F_{2,11} = 28.76$, $P < 0.0001$, MSE = 8.37). Attack density was highest on unpainted trees (16.9 ± 2.05 attacks/500 cm^2), followed by black (10.2 ± 0.32 attacks/500 cm^2) and white (2.2 ± 0.72 attacks/500 cm^2). For SPB, all three treatment means were significantly different (unpainted vs. black, $P < 0.0036$; vs. white, $P < 0.0001$; black vs. white, $P < 0.0017$; least significant difference test, SAS Institute 1994). The density of *Ips* nuptial chambers below 4.5 m was not subjected to statistical analysis due to the prevalence of zeros; however, the pattern of attack by *Ips* in white vs. unpainted or black trees appears to differ (Fig. 3B). Below 4.5 m the density of *Ips* attacks is higher in white trees, suggesting that an interaction between visual treatment and resource utilization by SPB and *Ips* is possible.

Reflectance spectra

Reflectance spectra of visual treatments are presented in Fig. 4. With the exception of noise in the 300-350 nm ultraviolet range, reflectance of the three white surfaces employed is, as expected, markedly higher than the three black surfaces. Clear and black Plexiglas reflect to a similar degree, yet catch of SPB and *T. dubius* differed between them, suggesting that reflectance is only one of several visual properties utilized by these species for host finding. We have included an average reflectance spectrum from loblolly pine bark for comparison (Fig. 4), although we did not measure landing rates on unpainted trees.

DISCUSSION

The results demonstrate that host selection by the southern pine beetle can be disrupted by both visual and semiochemical deterrents, and when combined their action shows promise for reducing attacks to levels that may effectively protect trees. The total number

TABLE 2. ANOVA tables for trapping studies with funnel traps (Florida and Louisiana; semiochemical treatments were frontalure [FL] only, FL + verbenone, FL + 4-allylanisole; visual treatments were white paint, black paint).

Factor	df	MS	*F*	*P*
Florida				
Southern pine beetle				
Site	4	71.9	53.11	0.0001
Visual treatment	1	97.4	71.89	0.0001
Semiochemical treatment	2	17.0	12.55	0.0002
Site × Vis. × Sem.†	22	1.4	1.36	0.1417
Residual	186	1.0		
Total	215			
T. dubius				
Site	4	2.42	5.91	0.0022
Visual treatment	1	22.09	53.88	0.0001
Semiochemical treatment	2	0.64	1.57	0.2110
Site × Vis. × Sem.†	22	0.41	0.76	0.7576
Residual	186	0.71		
Total	215			
Louisiana				
Southern pine beetle				
Site	1	9.99	7.33	0.0303
Visual treatment	1	35.69	26.19	0.0014
Semiochemical treatment	2	8.08	5.93	0.0311
Site × Vis. × Sem.†	7	1.86	2.47	0.0806
Residual	132	0.86		
Total	143			
T. dubius				
Site	1	5.64	12.28	0.0099
Visual treatment	1	67.97	148.03	0.0001
Semiochemical treatment	2	0.61	1.34	0.3226
Site × Vis. × Sem.†	7	0.46	0.67	0.6941
Residual	132	0.83		
Total	143			

Notes: T. dubius is *Thanasimus dubius* LeConte, a clerid predator of the southern pine beetle. The interaction term visual treatment × semiochemical treatment was not significant ($P > 0.10$) in each case and was deleted from the ANOVA model.

† The 3-way interaction term (site × visual × semiochemical treatment) was used as the denominator for *F* tests on main effects.

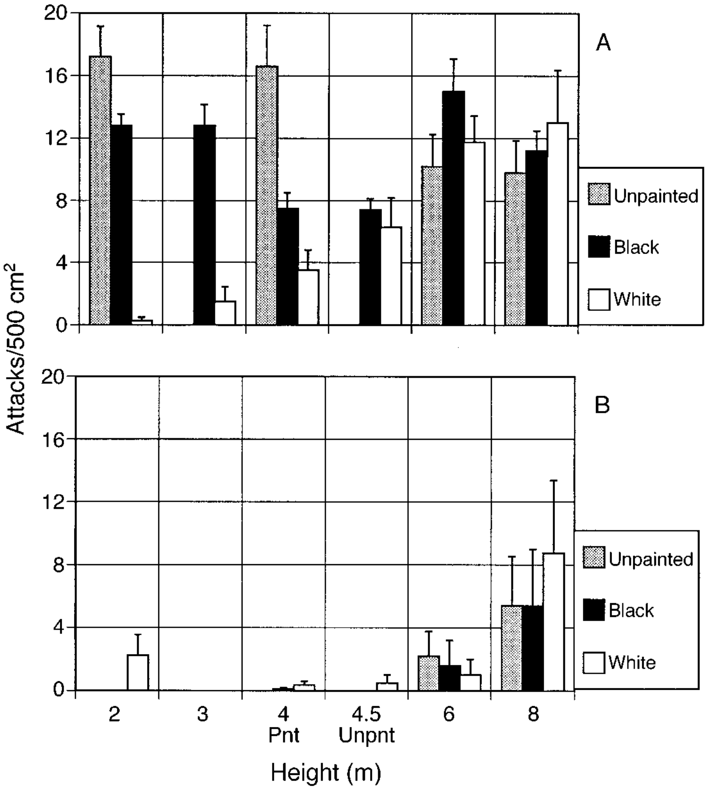

FIG. 3. Attack density (number/500 cm^2) of (A) southern pine beetle (SPB) or (B) *Ips* species on loblolly pine stems, painted white or black to 4.5 m, or unpainted (4 Pnt = in paint; 4.5 Unpnt = above paint). Data are from five replicate trees taken from a single SPB infestation, Louisiana 1995. Note that there are no data for unpainted trees at 3 m or 4 m.

of beetles necessary for host tree mortality is unknown, but it is clear that high densities of beetles must attack rapidly for healthy trees to be killed. For example, Raffa and Berryman (1983) determined that 40 successful attacks per square meter are necessary for lodgepole pine, *Pinus contorta,* to succumb to attack by *Dendroctonus ponderosae* Hopkins. With SPB, Hodges et al. (1979) suggest that 100 attacks/m^2 were necessary to overcome the defenses of an ''average'' loblolly or shortleaf pine. Neither of these studies gives data on the minimum area over which these densities must occur for tree death. In trying to determine the total number of SPB needed for mortality, Cook and Hain (1987) observed that ~2000 SPB caged onto a tree bole were insufficient to overcome the defenses of most loblolly and shortleaf pines in their study. Although tree death depends on rate of beetle recruitment, tree size, and defensive capabilities, it is not necessary for protective treatments to eliminate landings, because host defenses can thwart a significant number of attacking individuals (Thatcher et al. 1980, Cook and Hain 1987). The ~90% reduction that we observed when visual and semiochemical deterrents were combined may be enough for tree protection, but studies specifically addressing this potential application need to be carried out. In addition, as our tree attack data show (Fig. 3A, B), the effects on nontarget species must be evaluated as well (Hayes and Strom 1994).

Published experiments investigating scolytid responses to visual cues have reported mixed results; however, most studies were designed specifically to improve trapping efficiency and have limited their interpretations to effects on attraction (Lindgren et al. 1983, Dubbel et al. 1985, Fatzinger 1985). *Trypodendron lineatum* (Olivier) responding to attractants were unaffected by clear traps or those of a different hue (i.e., dominant wavelength) (Lindgren et al. 1983, Dubbel et al. 1985), but white traps, where included, caught the fewest individuals (Dubbel et al. 1985). Catch of *Ips typographus* L. depended upon trap location and spacing, with interactions between sensory modalities (olfaction and vision) and environments (wooded and open) being observed (Niemeyer 1985). *Ips montanus* (Eichhoff) and *Dendroctonus ponderosae* preferred dark colors over light ones, and fewer *D. terebrans* (Olivier) were caught in traps painted glossy white than flat black (Fatzinger 1985). Although the appearance of clear traps is based on human perception, and may therefore be misleading (see Fig. 4), the lack of a no-silhouette treatment from these previously cited experiments makes it difficult to determine whether differences were due to attraction or repellency of the different treatments.

The relationship between scolytid responses to colors and their visual physiology is unclear, and, to our knowledge, it is unknown whether true color vision (i.e., the ability to distinguish colors according to their wavelength composition at any intensity [Browne and

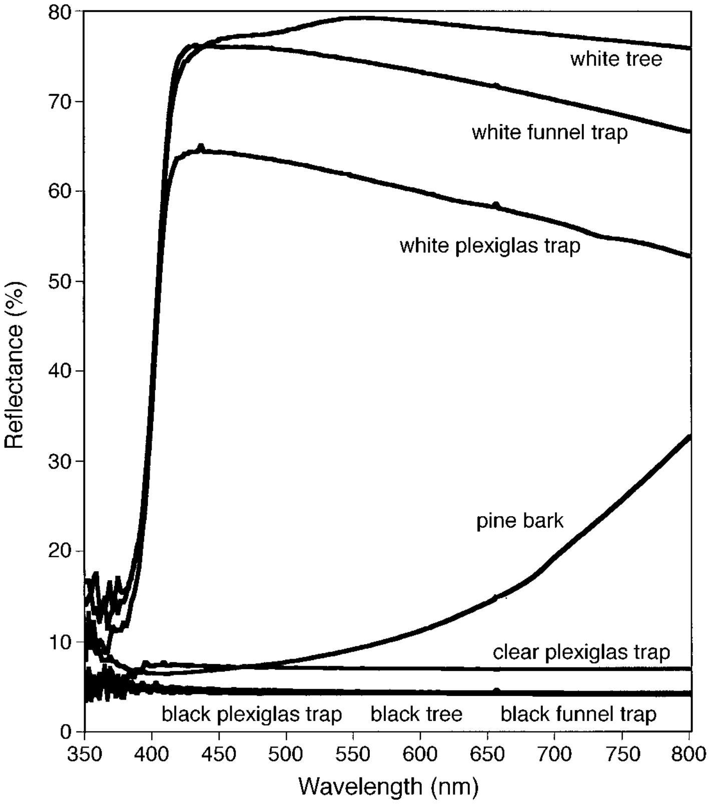

FIG. 4. Reflectance spectra for treatments utilized in host-finding disruption studies. (Loblolly pine spectrum is the mean of bark from 11 trees.)

Bennett 1981]) exists in this family. In the laboratory, Groberman and Borden (1981, 1982) found good correlation between electroretinogram (ERG) responses and walking behavior for *Ips paraconfusus* Lanier, *Dendroctonus pseudotsugae* Hopkins, and *T. lineatum.* They found two sensitivity maxima in the visual range (400–700 nm), one at ~450 nm (blue) and one at ~520 nm (green) for both *I. paraconfusus* and *D. pseudotsugae* (Groberman and Borden 1982). In walking assays, *T. lineatum* and *D. pseudotsugae* were similarly attracted to these wavelengths (Groberman and Borden 1981); however, their studies excluded ultraviolet light (300–400 nm), a range in which there is often another peak of response. Clearly more research is necessary before the relationship between light environments and field behavior of bark beetles is understood and treatments can be successfully applied.

Loblolly pine bark (Fig. 4) may produce a highly visible signal under a forest canopy. Although it varies considerably to the human eye, Hailman (1979) reports loblolly pine bark to be dark orange (see Fig. 4), a hue which produces a highly visible signal in the yellow–green light of woodland shade (Endler 1993). The visibility of these relatively long wavelengths for bark beetles is undetermined; however, hues reflecting long wavelengths often effectively capture forest-dwelling insects such as *Aedes* mosquitoes (Browne and Bennett 1981, Muir et al. 1992) and various scolytids (Schonherr 1977, Moser and Browne 1978, Lindgren et al. 1983). Whether this is because these hues are more or less visible is unknown. Data from our study indicate that white traps are apparent to SPB, but avoided, while black traps are attractive. The latter appears also to be true for *T. dubius,* as suggested by Wyatt et al. (1993). Although attack density was intermediate on black-painted trees, we did not attempt to evaluate the relative difference in attraction between black and unpainted trees. Clearly an increased understanding of the ecological mechanisms of visual attraction and repellency are important for the use of visual disruption in management.

Kogan (1994) proposes that olfaction and vision are likely the most important senses for host finding, an idea supported by our data with SPB. Bark beetles, like SPB, that rely on aggregation to kill trees for successful reproduction, necessarily have more than one method of host selection. Pioneering individuals (Borden 1974) attack first, without benefit of aggregation pheromone, while all others have the opportunity to respond to pheromones. Gara et al. (1965) proposed that both olfaction and vision are important for host-finding by SPB, with their relative importance depending upon local conditions. For example, they suggest that vision is the most important sensory modality when an area has aggregation pheromone present; beetles land on vertical silhouettes without regard to whether or not they are hosts. Although not explicitly tested by Gara et al. (1965) or others for SPB, available data suggest that host recognition by bark beetles is gustatory, not taking place until the adult bores through the outer bark to the phloem (Elkinton and Wood 1980, Raffa and Berryman 1982).

Life history characteristics may relate visual and olfactory cues to host-finding strategies of bark beetles (Raffa et al. 1993). Prokopy and Owens (1978) hypothesize that generalist vs. specialist insects, categories usually applied in the context of chemical ecology, might also be useful for describing visual behavior. They suggest that visual orientation is dependent upon the formation of search images based on plant morphological characters that afford visual distinction of hosts. The result that SPB were greatly affected by our visual treatments (both white and clear) and that this species is, at most, oligophagous, suggests that SPB may be considered a visual specialist (sensu Prokopy and Owens 1978). However, we propose that this designation depends on host form (vertical vs. horizontal silhouettes) rather than species. In the presence of attractants, SPB lands readily upon any dark, vertical silhouette, including nonhosts (Gara et al. 1965). *Dendroctonus ponderosae*, also considered an aggressive species (Raffa et al. 1993), lands randomly on vertical objects (Hynum and Berryman 1980) and does not distinguish between susceptible and resistant hosts until gustation (Raffa and Berryman 1982). Closely related, less aggressive species (e.g., *Ips pini* (Say) and *Ips perroti* Swaine) that readily attack nonvertical host material, but have similarly limited host species ranges, do not seem to be as affected by our visual treatments (B. D. Ayres, *unpublished data*). Byers (1993) used baited ‘‘puddle’’ traps, apparently without any silhouette, to effectively capture *I. typographus*, suggesting that this species is not affected by visual silhouettes when aggregation pheromone is present. Whether these patterns of attack and trap results are related to these *Ips* spp. being visual generalists, due to their propensity to attack multiple host forms, or alternatively, that *Ips* species simply use vision less than *Dendroctonus* species, remains to be seen but needs testing. Lindgren et al. (1983) report that the ambrosia beetles *T. lineatum* and *Gnathotrichus sulcatus* (LeConte) also considered unaggressive scolytids, are similarly unaffected by trap color, although materials used were relatively nonreflective, and white was not included in the treatments.

We hypothesize that the importance of visual silhouettes for scolytid host finding is related to their level of aggression and host utilization patterns. Less aggressive species often are able to use olfaction to locate hosts, i.e., have demonstrated primary attraction (Raffa et al. 1993), and may infest branches or horizontal hosts, sometimes preferring these over vertical forms (Gara et al. 1965). These species may be considered visual generalists, leading them to be less affected by visual treatments (Prokopy and Owens 1978). Aggressive species, on the other hand, do not tend to orient by way of primary attractants (Moeck et al. 1981, Raffa et al. 1993), and land predominantly on vertical objects, suggesting that they are visual specialists. In tying together visual ecology and insect management, Prokopy and Owens (1978) suggest that visual specialists, the aggressive bark beetles in our hypothesis, can be more easily manipulated using visual deterrents.

White color (paint) significantly reduced landings and attacks of SPB on trees in our study, suggesting that the use of a nonattractive colored surface (e.g., white) has potential for tree protection. SPB attacks were concentrated on the stem area primarily above the white paint (Fig. 3), leading us to believe that painting higher (perhaps up to and into the live crown) or using a semiochemical deterrent in addition to the paint, as was effective with funnel traps, would increase the effectiveness of this treatment for protection of individual trees. Black paint appeared to have an intermediate effect on attack density (Fig. 3); however, we cannot separate these effects between pre- and post-landing.

Visual treatments may increase management alternatives for control of SPB infestations. Buffer areas of uninfested trees are routinely felled at the advancing edge of SPB infestations to enhance the effectiveness of cut-and-remove or cut-and-leave control strategies (Thatcher et al. 1980). Cutting a buffer eliminates vertical silhouettes in close proximity to aggregation pheromone and provides distance between potential hosts and emerging beetles; however, it also necessitates that the number of uninfested trees that are cut is greatly increased. Vertical silhouette modification could be substituted for felling in areas with high-value trees, while still providing protection from lethal attacks.

Our data for the southern pine beetle demonstrate that multiple deterrents (e.g., semiochemical and visual) can increase the effectiveness of management tactics based on behavioral manipulation of this bark beetle, and perhaps others. For visual silhouette modification to be operationally feasible, methods other than paint will probably have to be developed. In addition, semiochemicals currently used for SPB management are eluted at very high rates compared to other species, perhaps suggesting that more effective compounds or mixtures are yet to be identified. Research and development of semiochemicals is ongoing, and more efficacious products, that are easier to apply, may be available in the future. However, disruption strategies that target multiple behavioral modalities may be more effective for management of those species that use vision as an important component in their host selection process.

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