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Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps

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Abstract

Olfactory deterrents have been proposed as tree protectants against attack by bark beetles, but their development has been hindered by a lack of knowledge of host selection behavior. Among the primary tree-killing (aggressive) *Dendroctonus*, vision appears to be an integral part of the host selection process. We evaluated the importance of vision in host finding by *D. brevicomis* LeConte, and our ability to affect it by modifying the visual stimulus provided by attractant-baited multiple-funnel traps. White-painted traps caught -42% fewer *D. brevicomis* than black traps in California, USA ($P < 0.05$). Visual treatments were less effective ($P < 0.0001$) than olfactory disruptants (verbenone with ipsdienol), which reduced catch by about 78%. When combined, olfactory and visual disruptants resulted in -89% fewer *D. brevicomis* being caught, but this combination was not more effective than olfactory disruptants alone ($P > 0.05$). Our results demonstrate that the visual component of *D. brevicomis* host finding behavior can be manipulated, but that *D. brevicomis* may be more affected by olfactory than visual disruptants. In contrast, visual disruption is more pronounced in the southern pine beetle, *Dendroctonus frontalis* Zimmermann, suggesting that non-insecticidal tree protection strategies for these related species should differ.

Introduction

The western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae), is a native, tree-killing bark beetle in western North American pine forests (Miller & Keen, 1960). Ponderosa pine, *Pinus ponderosa* Laws., and Coulter pine, *Pinus coulteri* D. Don., are preferred hosts (Miller & Keen, 1960). Although *D. brevicomis* is a natural and integral species in forests dominated by ponderosa pine, it is intermittently responsible for widespread mortality. During the 1988 to 1995 drought in California, *D. brevicomis* was estimated to kill more than 3 million cubic meters of ponderosa pine timber (Shea, 1995; USDA, 1996). Of particular concern during outbreaks is the protection of high-value pines that occur in recreation areas, watersheds, and wildland-urban interfaces. Despite an apparent willingness of landowners to pay for effective tree protectants, there are limited prophylactic treatments available. Conventional insecticides, while effective (Hall et al., 1982; Shea et al., 1984; Haverty et al., 1985, 1998), may be prohibited in the future, necessitating alternative solutions.

Semiochemicals provide a promising tool for manipulating the behavior of *D. brevicomis*. Mass attack by *D. brevicomis* follows the release of (+)-exo-brevicomin and (-)-frontalin (Silverstein et al., 1968; Bedard et al., 1969; Kinzer et al., 1969; Wood et al., 1976), which are synergized by the host compound myrcene (Bedard et al., 1969). Recruitment is believed to be terminated by the relative level of antiaggregation pheromones, primarily (−)-verbenone and ipsdienol (Borden, 1997). In addition, the host compound 4-allylanisole is reported to have mild antiaggregation activity when released at high rates (Hayes & Strom, 1994; Hobson, 1995). Although verbenone and ipsdienol reduced trap catch by > 75% (Paine & Hanlon, 1991; Bertram & Paine, 1994b), they have proven to be inconsistent in protecting individual trees (Bedard et al., 1980; Bertram & Paine, 1994b; Shea, unpublished).

For the southern pine beetle, *Dendroctonus frontalis* Zimmermann, visual disruptants alone or with olfactory disruptants can significantly reduce aggregation behavior (Strom et al., 1999). *Thanasimus dubius* (F.) (Coleoptera: Cleridae), a common predator of *D. frontalis* in the southeastern region of the United States, are also strongly affected by visual stimuli (Strom et al. 1999). These results suggest that *D. brevicomis,* a close relative of *D. frontalis* (Wood, 1982), and its major predator, *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae), may respond in a similar manner, and that a combination of olfactory and visual disruptants may be useful for improving the effectiveness of non-insecticidal tree protection tactics.

In this study our objectives were: (1) to determine whether visual disruption is possible with *D. brevicomis,* as assessed by white multiple-funnel traps compared to black, and (2) to evaluate the magnitude of visual disruption in combination with, and relative to, olfactory disruption. Overall our goal is to ascertain the potential utility of these factors for tree protection.

Materials and methods

Two experiments were conducted, each laid out as a linear transect of 16-unit multiple-funnel traps (Lindgren, 1983) (Phero Tech, Inc., Delta, BC, Canada), painted white (gloss white, product number 81501) or black (gloss black, product number 8 1601; Krylon Division, Sherwin-Williams, Inc., Solon, OH), and placed >0.16 km apart.

Experiment 1 was conducted from 26 May to 3 July 1998 in a mixed pine forest at Darling Ridge, CA (mean elevation -915 m). Trap placement followed criteria established by Shea et al. (1984), except that traps were hung from poles rather than non-host trees to reduce the possibility of visual interference from non-host stems. Four treatments were as follows; unbaited black traps (N = 5), attractant-baited black traps (N = 10), unbaited white traps (N = 5), and attractant-baited white traps (N = 10). Elution rates are unaffected by trap color (Strom et al., 1999), so semiochemicals were released from standard, commercially-available devices (Table 1). Because we believed *a priori* that unbaited traps would catch very few *D. brevicomis,* only 5 replicates of unbaited traps were employed.

Table 1. Release devices and rates for semiochemicals (all racemic) used in two experiments to assess the effectiveness of visual disruptants, alone and in combination with olfactory disruptants, on *D. brevicomis*

Semiochemicals*	Release devices	Elution rates (mg/24 h)
Attractant		
Exo-brevicomin	400 μl polyethylene vial	1.7
Frontalin	400 μl polyethylene vial	2.6
Myrcene	15 ml polyethylene bottle	100.0
Disruptant		
Verbenone	bubble cap	8-12.0
Ipsdienol	bubble cap	0.11

*All semiochemicals and devices from Phero Tech, Inc., Delta, BC Canada. Elution rates calculated by Phero Tech at 23 °C except 25 °C for ipsdienol.

Experiment 2 was conducted from 24 August to 2 1 September 1998 in a mixed conifer forest near Grizzly Flat, CA (mean elevation -1400 m). Protocols were similar, and four treatments were: attractant-baited black traps, attractant-baited black traps with antiaggregant semiochemicals (Table 1), attractant-baited white traps, and attractant-baited white traps with antiaggregant semiochemicals (N = 10 for each treatment). This design allowed us to assess the effectiveness of each disruptant type (olfactory and visual), in relation to each other and in combination. All *D. brevicomis* and *T. chlorodia* were collected weekly and counted. In Experiment 2, we determined the sex-ratio of *D. brevicomis* caught by identifying the sex of 50 individuals (or < *50* if fewer *D. brevicomis* were caught) from each trap at each collection period by the presence or absence of a prothoracic mycangium on females (Tate & Bedard, 1967).

Statistical analyses. In Experiment 1, mean daily captures of *D brevicomis* in each trap, determined from sums over the experimental period, were transformed by their natural log to best meet the assumptions of parametric statistics. The Univariate Procedure (SAS, 1988) was used to evaluate transformed data and residuals. Because only *2 D. brevicomis* and *3 T. chlorodia* were caught in unbaited traps in this experiment, only data from baited traps were analyzed. For Experiment 2, visual and semiochemical effects on catches and sex-ratio of *D. brevicomis* were eval-

Table 2. Analysis of variance (ANOVA) results from two experiments that evaluated the effects of visual (Experiment 1) or olfactory and visual (Experiment 2) disruptants on host finding by *D. brevicomis* in California

Source	DF	MS	F	P
Experiment 1				
Visual disruptant	1	2.11	9.78	0.0058
Error	18	0.216		
Experiment 2				
Visual disruptant	1	3.10	4.97	0.0321
Olfactory disruptant	1	22.02	35.31	<0.0001
Visual × olfactory	1	0.002	0.00	0.9588
Error	36	0.624		

uated by analysis of variance (ANOVA) followed by the LSD means separation test (SAS, 1988) if ANOVA yielded a significant F-value ($P < 0.05$). Because transformed data for *T. chlorodia* did not meet the necessary assumptions for parametric analysis, nonparametric analyses were used instead (χ^2 approximations of the Kruskal-Wallis test to compare catches of black and white traps in Experiment 1, and the Friedman test for comparison of catches in Experiment 2) (Hollander & Wolfe, 1973).

Results

In Experiment one 15,696 *D. brevicomis* were caught in attractant-baited black traps and 8,354 in white traps. The mean daily capture of ***D. brevicomis*** in white traps was significantly reduced by 43.8% from that in black traps (Table 2, Figure 1). There was no similar reduction in the capture of ***T. chlorodia*** ($\chi^2_1 = 0.47$, $P = 0.527$) (Figure 1).

In Experiment two black traps captured 16,429 ***D. brevicomis*** and white traps 9,260. Both visual and semiochemical disruptants caused a significant reduction in catches of ***D. brevicomis*** (Table 2), but the latter effect was much more pronounced (Figure 1). White traps with antiaggregants caught 88.3% fewer ***D. brevicomis*** than attractant-baited black traps. Black traps accounted for 75.4% of the 1,573 *T. chlorodia* captured. Both visual ($\chi^2_1 = 5.81$, $P = 0.016$) and semiochemical treatments ($\chi^2_1 = 14.39$, $P < 0.0001$) caused significant disruption, and ***T. chlorodia*** responded in a proportionally similar manner to their ***D. brevicomis*** prey (Figure 1). Female ***D. brevicomis*** ranged from 52.6% to 60.2% of catches among treatments in Experiment 2. In no case did any treatment cause a significant alteration in sex ratio ($F_{2,37} = 1.09$, $P = 0.347$).

Discussion

Our results demonstrate that host finding by ***D. brevicomis*** can be disrupted by modifying the visual silhouette offered by multiple-funnel traps, which are designed to provide visual stimuli similar to a host. The reduction in response to attractant-baited traps was similar in magnitude to that observed using verbenone alone (Paine & Hanlon, 1991; Bertram & Paine, 1994b), but less than to the combination of verbenone and ipsdienol (Table 2, Figure 1) (Paine & Hanlon, 1991; Bertram & Paine, 1994a, b). The lack of a significant increase in response to the combination of visual and olfactory disruptants over that caused by the olfactory disruptant alone indicates that ***D. brevicomis*** are more responsive to olfactory disruptants than visual, and less responsive to visual disruptants than ***D. frontalis*** (Strom et al., 1999). Similar to their prey, ***T. chlorodia,*** the most common predator of ***D. brevicomis*** in this study, were less affected by visual treatments than olfactory (Figure 1), a pattern different from *T. dubius*, their predatory counterparts in the southeastern United States.

Verbenone and ipsdienol in combination have a highly significant effect in traps, but have not consistently protected trees from attack by ***D. brevicomis*** (Bertram & Paine, 1994a; Shea, unpublished). As noted by Bertram & Paine (1994b) and observed in Figure 1, verbenone and ipsdienol reduce, but do not eliminate, catches of ***D. brevicomis*** from attractive traps. This suggests that undeterred individuals could accumulate to successfully attack a tree despite the presence of disruptant semiochemicals.

Although ***D. brevicomis*** and ***D. frontalis*** are closely related (Wood, 1982), they exhibit differences in behavior that may explain the observed disparity in response to visual disruptants. Host selection by both species involves a few pioneering individuals that must locate hosts without the benefit of aggregation pheromones, as well as a more abundant group of conspecifics that is aided in host finding by aggregation pheromones produced by previously arriving individuals (Borden, 1974; Raffa et al., 1993). How-

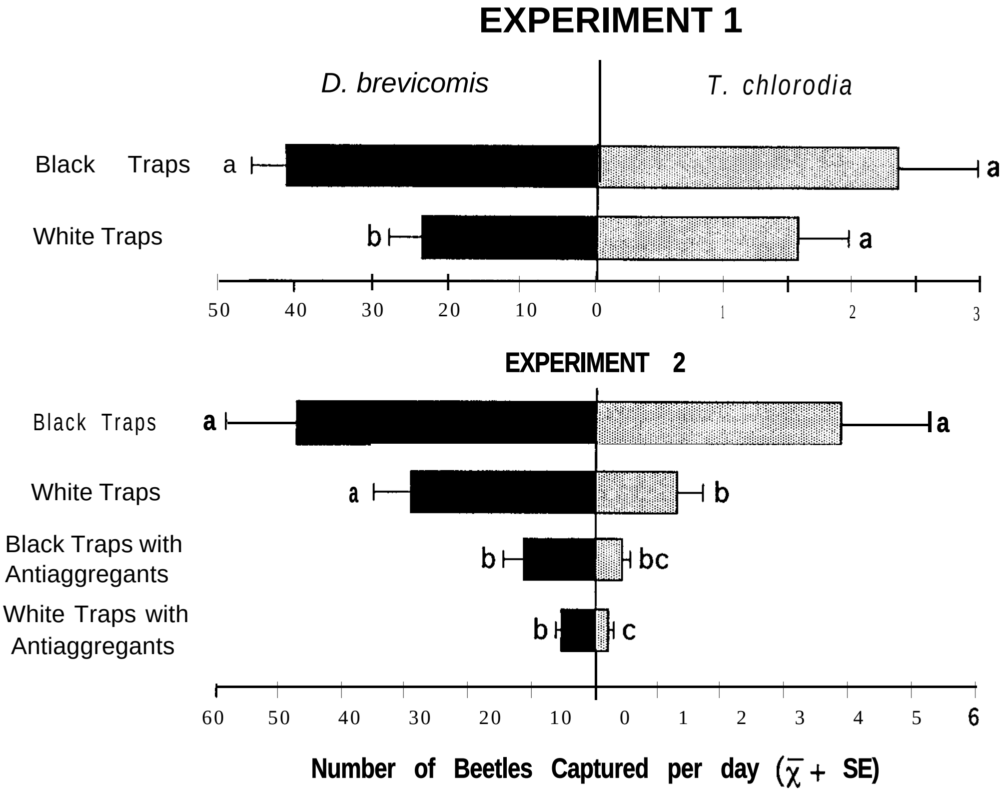

Figure **I. Comparative catches of** *D. brevicomis* **and** *T. chlorodia*, **respectively, in response to attractant-baited multiple funnel traps with a visual disruptant (Experiment I), or visual and olfactory disruptants, alone and together (Experiment 2). Bars within an experiment and species and with the same letter are not significantly different (P < 0.05) as determined by separate analyses (ANOVA for** *D. brevicomis* **in Experiment I: LSD test for** *D. brevicomis* **in Experiment 2: Kruskal–Wallis test for** *T. chlorodia* **in Experiment I; Friedman test for** *T. chlorodia* **in Experiment 2).**

ever, Gara et al. (1965) hypothesized that *D. frontalis* may rely heavily on visual cues in host finding, particularly during infestation expansion, where new attacks are concentrated primarily on adjacent trees and proceed through areas where semiochemicals, both potentially disruptive and attractive, are present from numerous trees and in high concentrations. In this situation, short-range host finding by vision may be more adaptive than long-range olfactory guidance. In contrast, *D. brevicomis* typically ‘group kill’ pines, with semiochemical-mediated attacks by a single generation being concentrated on a focal tree with attackers ‘spilling over’ onto adjacent trees (Miller & Keen, 1960). This difference suggests that *D. brevicomis* may not rely upon vision as heavily as *D. frontalis* when aggregation semiochemicals are present. Thus, resource managers might rely more on combinations of visual and semiochemical disruptants for the protection of individual pines from attack by *D. frontalis* than they would for *D. brevicomis*.

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