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The Role of Wind and Semiochemicals in Mediating Switching Behavior in the Southern Pine Beetle (Coleoptera: Curculionidae: Scolytinae)

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Abstract

Aggressive bark beetles colonize and kill healthy conifers through pheromone-mediated mass aggregation. In several species, the focal point of aggregation moves progressively from mass-attacked ‘focus trees’ to adjacent, unattacked ‘recipient trees’, resulting in infestation growth. This process, termed ‘switching’, is hypothesized to be mediated in whole or in part by antiaggregation pheromones released by beetles as colonization intensifies on a focus tree. We tested this hypothesis with the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae), by using a windvane apparatus that maintained an unbaited, black, cylindrical trap (surrogate for a recipient tree) continuously 4 m downwind from an identical trap baited with synthetic aggregation attractant (surrogate for a focus tree). In two of three replicated trials, addition of pheromone components with antiaggregation activity, *endo*-brevicomin or verbenone, to the upwind trap caused a significant but small (<15%) increase in the proportion of beetles caught in the downwind trap. In one of two trials with *endo*-brevicomin, this shift was associated with a significant reduction in catches in the downwind trap and an overall reduction in catches of beetles by the trap pair. This suggests that an inhibitor-induced increase in landings on the recipient relative to the focus tree may be countered by the radial effects of the inhibitor, which at sufficiently high release may reduce responses to both the focus and recipient tree. We discuss spatial factors that might govern the role of antiaggregation pheromones in stimulating infestation growth as well as additional factors that likely govern switching behavior.

Key words: antiaggregation, pheromone, bark beetle, host selection, anemotaxis

Aggressive, tree-killing species of bark beetle in the genus *Dendroctonus* (Coleoptera: Curculionidae: Scolytinae) include some of the most significant disturbance agents and economic pests of conifer forests worldwide. They can colonize healthy, vigorous trees by attacking rapidly and in sufficient numbers to overwhelm a host’s constitutive resin defenses (Raffa and Berrymann 1983, Raffa et al. 1993, Weed et al. 2015). Such ‘mass attacks’ are mediated by aggregation pheromones that focus colonization on individual trees (Berryman et al. 1989, Raffa 2001). As mass attack on a tree intensifies, arriving beetles begin to land on and attack adjacent, unattacked trees, and the focus of mass attack ‘switches’ to these latter trees (Gara 1967, Renwick and Vité 1970, Schlyter and Anderbrant 1989). This continuous shift in mass attacks from ‘focus’ trees to adjacent ‘recipient’ trees can cause rapid accumulations of dead trees and infestation growth (Gara and Coster 1968, Bentz et al. 1996, Powell et al. 1998). In the genus *Dendroctonus*, switching is likely mediated at least in part by the capacity of aggregation attractant to increase densities of beetles in the immediate area and stimulate attacks on adjacent, uninfested trees (Vité 1970, Furniss et al. 1972, Klutsch et al. 2017, Sullivan et al. 2021). Additionally, a rapid reduction in beetle production of aggregation pheromone occurs following the establishment in the host (Vité and Crozier 1968, Coster and Vité 1972, Coster et al. 1977, Byers et al. 1984, Pureswaran and Sullivan 2012).

In many species, pheromone components that reduce response to the aggregation attractant (termed ‘antiaggregation pheromones’) are released by beetles as colonization proceeds and may play a role in terminating mass attack and regulating attack densities on the bole (Renwick and Vité 1970, Byers 1989, Borden 1997, Pureswaran et al. 2000). Furthermore, antiaggregation pheromones mediate switching by inhibiting beetle response to focus trees (Borden 1989). Beetles attracted to a focus tree by aggregation attractant may be repelled at close approach, thus inducing landings on adjacent trees (Geiszler et al. 1980, Borden et al. 1987, Schlyter et al. 1987b). Models of succession of attacked trees within *Dendroctonus* infestations have incorporated antiaggregation pheromones as a driver of switching (Powell et al. 1998). However, there have been no tests with the compounds themselves to determine their capacity to influence switching-associated behaviors.

The southern pine beetle, *Dendroctonus frontalis* Zimmermann is an aggressive killer of pines throughout much of the eastern United States and from Arizona south to Nicaragua (Clarke and Nowak 2010, Hain et al. 2011). Localized infestations are initiated primarily in the spring in one or a few compromised trees and then may expand outward to immediately adjacent trees throughout the summer (Gara and Coster 1968, Schowalter et al. 1981, Ayres et al. 2011). Due to the short generation time of this species and long duration of warm temperatures suitable for flight and development in much of the beetles' range (Birt 2011), infestations can grow rapidly and damage may eventually encompass dozens or hundreds of hectares (Clarke and Billings 2003). Direct control of this pest has focused on suppression of the growth of infestations (Swain and Remion 1983, Billings 2011). Since infestation growth is driven by the beetles' switching behavior (Gara 1967, Renwick and Vité 1970, Feldman et al. 1980), an understanding of the mechanisms causing switching may allow better informed and more efficacious implementation of control measures.

Mass aggregation in *D. frontalis* is induced by the attractant frontalin produced by attacking females (the attack-initiating sex), synergistic *endo*-brevicomin from arriving males, and volatile compounds in host pine resin (e.g., *alpha*- and *beta*-pinene) (Renwick and Vité 1969, Sullivan et al. 2007, Munro et al. 2020). It has been hypothesized that attacks and landings are induced on adjacent trees when they become engulfed by the aggregation pheromone plume from mass-attacked trees (Gara et al. 1965, Gara and Coster 1968, Schowalter et al. 1981). This is inferred from observations that artificial and natural releasers of aggregation attractant can stimulate mass attack on nearby pines and, at high release rates, on downwind trees located as far as tens of meters away (Gara et al. 1965, Vité 1970).

Response to aggregation attractant can be reduced by numerous compounds produced by *D. frontalis* (Sullivan 2011). However, male-produced antiaggregation pheromone components verbenone and *endo*-brevicomin (which are inhibitory when released in high quantities) have received the most basic research and application development (Vité and Renwick 1971, Payne et al. 1977, Payne and Richerson 1979, Watterson et al. 1982, Salom et al. 1992, Clarke et al. 1999, Sullivan et al. 2007). Both pheromone components have been proposed to play a role in terminating mass attack and inducing switching when attack densities and the cumulative release of these compounds attain magnitudes sufficient to inhibit response to aggregation attractant from the focus tree (Renwick and Vité 1970, Payne and Coulson 1985, Salom et al. 1992).

The roles of *endo*-brevicomin and verbenone as mediators of switching in *D. frontalis* have not been directly studied. Artificial releasers of *endo*-brevicomin (but not verbenone) applied to individual mass-attacked trees were found capable of reducing landings and attacks (Richerson and Payne 1979), but it was not investigated whether this application was associated with an increase in attacks on adjacent trees. We hypothesized that, if these inhibitors mediate switching, then they should shift beetle orientation from an aggregation attractant-releasing, focus tree surrogate (a baited trap with an elongate, cylindrical shape and similar diameter and shade as a host pine) to an adjacent, unbaited, recipient tree surrogate. Furthermore, we hypothesized that a major predator of *D. frontalis*, *Thanasimus dubius* Fabricius (Coleoptera, Cleridae), that utilizes the pheromones of its prey to locate them, might show a parallel switching behavior to maximize contact with its prey. Our tests were performed with the surrogate focus and recipient trees suspended from a large windvane apparatus that maintained the recipient surrogate constantly downwind from the focus surrogate. *Dendroctonus frontalis* and other bark beetles respond to attractive semiochemicals through anemotaxis (upwind flight) (Mcmullen and Atkins 1962; Byers 1983, 1988, 1996; Schlyter et al. 1987a), a behavior that should result in relatively greater interaction of attracted beetles with downwind rather than other trees. This suggests that switching should be favored in the downwind direction, and the windvane arrangement was intended to test our hypotheses with surrogate and focus trees in their natural orientation. We also report results of an experiment that used the windvane-suspended surrogates to investigate the hypothesis that switching should occur predominantly downwind.

Materials and Methods

Pairs of 12-unit multiple funnel traps (Lindgren 1983) were suspended 4 m apart from windvanes erected within openings of mixed pine/hardwood stands on the Homochitto National Forest in Mississippi, USA (31.43°N, 91.19°W). This distance between the traps is a typical average tree spacing in an overstocked (>120 ft^2/acre; 90 m^2/ha), and thus susceptible, pine stand (Nowak et al. 2015). Each windvane consisted of a horizontally-arranged cross constructed from 2.5 m lengths of bamboo pole extending from a polyvinyl chloride (PVC) cross tee fitting (Fig. 1). The cross was suspended 2.5 m above the ground and stabilized by nylon cords attached to both the PVC cross tee and the ends of the bamboo poles; the opposite ends of the cords were fastened to a low-friction swivel eye positioned ~1.5 m directly above the PVC cross tee. The opposite side of the swivel was attached to the midpoint of a rope suspended between two large hardwood trees located >12 m apart. A vertically-oriented, triangular tailfin (sides 1.2, 1.2, and 1.7 m) was attached to the end of one of the bamboo poles to keep one axis of the cross aligned with the wind. The tailfin consisted of clear, heavy-gauge plastic sheeting stretched between the arms of a 'V' constructed of small-diameter PVC pipe. Each trap of the pair was suspended (with the trap bottoms 1–1.5 m above ground level) from the ends of either the windwise or crosswind-oriented arms of the cross depending on the experiment and treatment. The attachment point for the 'downwind' trap was 0.7 m upwind of the attachment point of the tailfin. We did not measure the minimum windspeed capable of rotating the windvane; however, the lightest sensible movement of the air appeared sufficient to rotate the apparatus into alignment with the wind. Windvane/trap assemblies were positioned >100 m apart to minimize potential interference among lures. In all trapping experiments, trap cups were filled with dilute propylene glycol to preserve captured insects, and catches were collected at 6 - 18 d intervals. Captured *D. frontalis* were sorted by sex, and these and captured *T. dubius* were tabulated.

Unless noted otherwise, statistical analyses were performed separately on *D. frontalis* (sexes separately and summed) and *T. dubius* for every experiment. The experimental designs for all experiments had certain common features. At most, six windvanes (factor 'windvane')

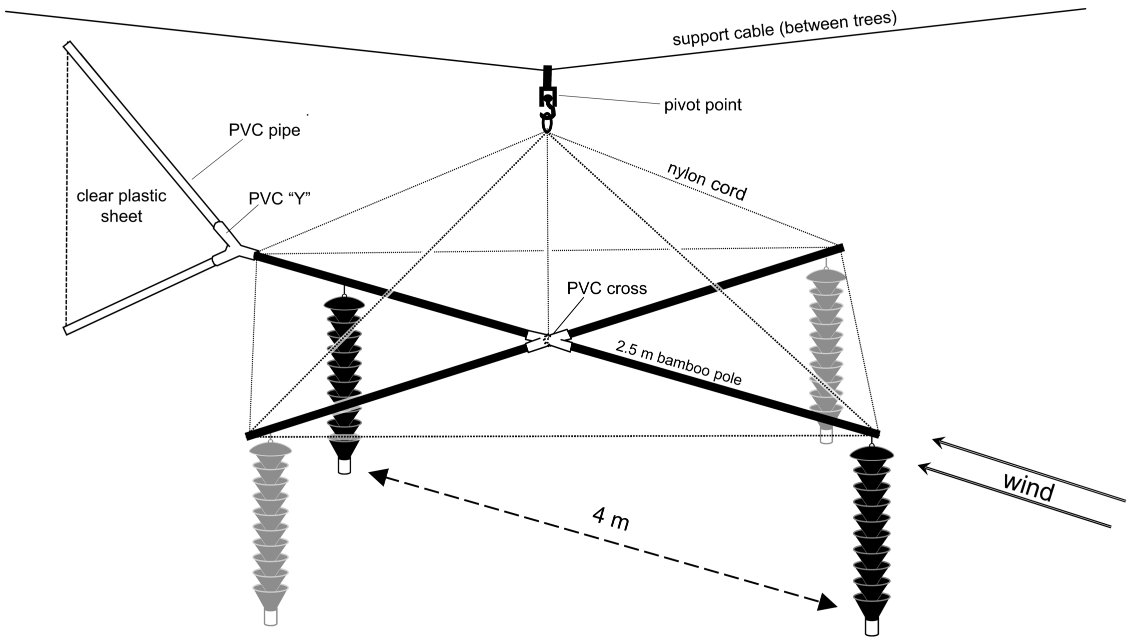

Fig. 1. Windvane apparatus used for maintaining pairs of traps either crosswind (grey) or aligned with the wind (black).

were available at any one time. Experiments had three treatments, and the windvanes were grouped into two blocks (factor 'block') consisting of three adjacent windvanes. There were three or six collection dates (factor 'date') with reassignment of treatments to windvanes within blocks after each collection. Reassignment was according to randomization without replacement (with six dates, a complete rotation of treatments occurred twice), so that, within each block, windvanes and collection dates were analogous, respectively, to the rows and columns of a Latin square (or with six dates, a Latin rectangle). There was a 'split-plot' aspect to the design, where a pair of traps on a windvane together represented a whole plot, and individual traps on the windvane corresponded to sub-plots which received different levels of a sub-plot factor, either trap position relative to wind direction or presence or absence of lures. The analysis of variance (ANOVA) model, therefore, differed according to whether or not the dependent variable was a single value per windvane and collection date (total catch per windvane or proportion of catch in the unbaited trap of the pair), or catch for individual traps. To examine whether the response to whole plot or sub-plot factors differed by sex for *D. frontalis,* catch within each trap was tabulated separately for males and females and sex was considered a sub-sub-plot factor in a split–split plot ANOVA. All ANOVAs were carried out using SAS Proc Mixed with the Kenward-Roger method (Kenward and Roger 1997) for calculating denominator degrees of freedom (SAS 9.4, SAS Institute, Cary, NC).

For analyses in which the dependent variable was the proportion of catches by one trap of the pair (catch in this trap divided by sum of catches by both traps), the data received an arcsine square root transformation if necessary to address distributional assumptions of the ANOVAs. If the denominator of such a ratio was zero (summed catches by both traps were zero), the data entry was treated as a missing value. For analysis of counts for individual traps or traps summed, data received a square-root, cube-root, or log transformation as appropriate. For all experiments, suitability of the transformation was determined through examination of residuals plots. All-pairwise contrasts among treatments received a Tukey adjustment ($\alpha = 0.05$), unless noted otherwise.

Experiment 1. The Role of Wind in Determining the Direction of Switching

This experiment investigated the degree to which wind direction might alter the frequency of beetle encounters with trees adjacent to a focus tree and thereby influence the selection of a recipient tree. The treatments had the surrogate for the focus tree (trap releasing aggregation attractant) as either (1) the upwind trap, (2) the downwind trap, or (3) one of the crosswind traps of each windvane. The opposite trap (surrogate for the potential recipient tree) lacked semiochemical releasers. The aggregation attractant consisted of the female-produced pheromone component frontalin, the male-produced pheromone component *endo*-brevicomin, and turpentine as a source of host odors. All were released from separate devices. Frontalin (racemic, >98% purity, Chem Samples Co., Columbus, Ohio, USA) was released from four capped 400 µl-capacity polyethylene microcentrifuge tubes (total rate of 14 mg/d at ~24°C); turpentine (steam-distilled from *Pinus taeda* L.; Hercules Inc., Brunswick, GA) from a 250 ml-capacity, Boston-round type, brown glass bottle with three 3/8 diam. cotton dental wicks protruding 3 cm from the mouth (~10 g/d at ~24°C); and *endo*-brevicomin [99% (+)-enantiomer; 95% purity, synthesized as described in Sullivan et al. (2007)] from a glass capillary (1.17 mm i.d. × 20 mm) secured open end up inside an inverted 4 ml capacity glass vial (0.23 mg/d at 23°C; device construction detailed in Sullivan and Mori 2009). The experiment ran from 8 November to 4 December 2007. The frontalin and *endo*-brevicomin devices were attached to the fourth funnel from the trap bottom; the turpentine device was immediately below the rim of the trap's cover to protect the wicks from rain.

We tested for treatment effects on (1) proportion of catches in the unbaited trap and (2) catches by the windvane (both traps summed). Mixed-model ANOVAs were performed on both dependent variables with fixed factor treatment and random factors windvane and date. To test for a significant divergence from the null hypothesis of a 1:1 ratio of catches by the two traps of the crosswind treatment, a 95 % confidence interval was obtained for the mean proportion to determine whether the interval contained a null value of 0.5. To test for an interaction between *D. frontalis* sex and treatment, the fixed effects for the split-split plot ANOVA were whole plot factor 'trap position' (upwind, downwind or crosswind), sub plot factor 'baited' (yes or no) and sub sub plot factor beetle sex, plus all interactions. Random factors were block, date, and windvane in block, with whole plot error and sub plot errors being, respectively, the interaction between trap position, date and windvane nested in block and that between baited, trap position, date, and windvane nested within block.

Experiments 2 and 3. Potential for *endo*-Brevicomin to Promote Downwind Switching

Traps were arranged with the surrogate focus tree (baited trap) upwind from the surrogate recipient tree (unbaited trap). The upwind trap invariably received frontalin and turpentine (as described in experiment 1). In experiment 2, treatments were: (1) no addition of *endo*-brevicomin, (2) a low release of *endo*-brevicomin from the upwind trap (device as in experiment 1), and (3) a high release of *endo*-brevicomin from the upwind trap. This latter device released 2.7 mg/d at ~24°C and consisted of two 100 µl-capacity gas chromatograph autosampler inserts (3 mm i.d.) secured mouth-upward inside an inverted 7 ml-capacity glass vial. They were filled with *endo*-brevicomin from the same source as experiment 1. Experiment 2 ran from 27 September to 8 November 2007.

Experiment 3 was identical to experiment 2 except that a 'background' of *endo*-brevicomin was created for all windvanes by the deployment of three release devices (a polyethylene 'blister'-type device; 0.5–0.8 mg/d at ~24°C, racemic, >95% purity, Chemtica International, Santo Domingo, Costa Rica) attached to the tops of 1.5 m-tall plastic poles located 20 m from the windvane and arranged in an equilateral triangle with vertices oriented at 0°, 120°, and 240° relative to north (Sullivan and Brownie 2021). We included this background because *D. frontalis* catches in treatment 1 of experiment 2 had been too low in the absence of *endo*-brevicomin to permit meaningful statistical contrasts with treatments 2 and 3. The addition of *endo*-brevicomin background produced sufficient catches in treatment 1 through the area-wide synergistic effects of this pheromone component (Sullivan and Mori 2009, Sullivan and Brownie 2021). Such levels of *endo*-brevicomin background would likely be present inside of a growing SPB infestation (Sullivan and Brownie 2021). Experiment 3 ran from 10 January to 26 March 2008.

The experimental design for both experiments 2 and 3 was similar to experiment 1, except that three additional collections were carried out allowing a second rotation of treatments among windvanes within blocks. To detect treatment effects on percent catches of beetles in the downwind trap, we performed a mixed-model ANOVA with fixed factor treatment and random effects block, date, windvane within block, and the interaction of block and treatment. To test for differences among treatments in mean catches per windvane, as well as catches in the downwind trap alone, for both experiments we performed a split-plot ANOVA with whole plot factor treatment and sub plot factor trap position (upwind or downwind); random factors were date and windvane, and whole plot error was the interaction among date, treatment, and windvane. To test specifically for differences between treatments with respect to catch in the downwind trap, we used an LSmeans statement with option Slice = trap position. For both ANOVAs, pairwise comparisons among treatment means received a Bonferroni correction for three contrasts. To test for treatment interactions with sex, we performed a modified split-split plot ANOVA on catch partitioned by sex for each individual trap, with whole plot, sub plot, and sub sub plot factors treatment, trap position, and sex, respectively. The random effects were block, date, windvane nested in block, the interaction between treatment and block, the interaction among treatment, date, and windvane nested within block, and the interaction among trap position, treatment, date, and windvane nested within block.

Experiment 4. Potential for Verbenone to Promote Downwind Switching

This experiment was largely identical to experiment 3 except the high and low releasers of *endo*-brevicomin were replaced by releasers of verbenone. The treatments were (1) none, (2) low, or (3) high verbenone release from the upwind trap. The enantiomeric ratio of verbenone was 33%(+):67%(−), which is the ratio present in newly-emerged *D. frontalis* males (Grosman et al. 1997) and recommended for *D. frontalis* management (Clarke et al. 1999). The low-rate device (~6 mg/d at ~23°C) was a 2 × 5 cm packet made from 4 mil clear polyethylene tubing with heat-sealed ends; 1 ml verbenone was absorbed on two layers of washed, dye-free burlap inside the packet. A 'roof' made from white polyethylene provided shade to the device when deployed. The high-rate device (60 mg/d at ~23°C) was a white polyethylene pouch containing an absorbent pad with 7.5 g verbenone (Chemtica). Experiment 4 ran from 25 April to 25 June 2008.

Statistical analyses were identical to those for experiments 2 and 3.

Results

Experiment 1. The Role of Wind in Determining the Direction of Switching

Proportion of total capture in the unbaited trap for *D. frontalis* (separately for each sex and for sexes summed) and *T. dubius* differed strongly depending on the position of the baited relative to the unbaited trap ($P < 0.001$ in all cases, Table 1). Very few *D. frontalis* were trapped in the unbaited trap unless it was downwind from the baited trap, in which case catches in both traps were similar (Fig. 2). The ratio of catches between the two traps when crosswind differed significantly from 1:1. Summed catches for the windvanes did not differ significantly among the three possible trap/lure arrangements except for male *D. frontalis* ($F_{2,8} = 5.45$, $P = 0.032$) for which significantly greater catches occurred when the lure was present on the upwind trap rather than on one of the crosswind traps (Table 2). A significant interaction between sex of *D. frontalis* and factor baited (i.e., the baited or unbaited trap of the pair) was detected

Table 1. Proportion of trap catch (mean ± SE) in the unbaited trap [i.e., unbaited/(baited + unbaited)] of each windvane in experiment 1

Lure placement	All *D. frontalis*	Female *D. frontalis*	Male *D. frontalis*	*T. dubius*
Crosswind	0.05 ± 0.03a	0.04 ± 0.02a	0.07 ± 0.07a	0.15 ± 0.04a
Downwind	0.02 ± 0.01a	0.04 ± 0.02a	0.01 ± 0.01a	0.09 ± 0.02a
Upwind	0.56 ± 0.06b	0.68 ± 0.05b	0.49 ± 0.07b	0.51 ± 0.04b
	$F_{2,10} = 74.5$[a] $P < 0.001$	$F_{2,7.76} = 74.0$ $P < 0.001$	$F_{2,10} = 60.3$ $P < 0.001$	$F_{2,13} = 25.3$ $P < 0.001$

[a] ANOVA results within sex/species. Data were transformed for statistical analyses; however, displayed means and SEs are for the untransformed data. Means associated with the same letter did not differ significantly (Tukey test, α = 0.05.

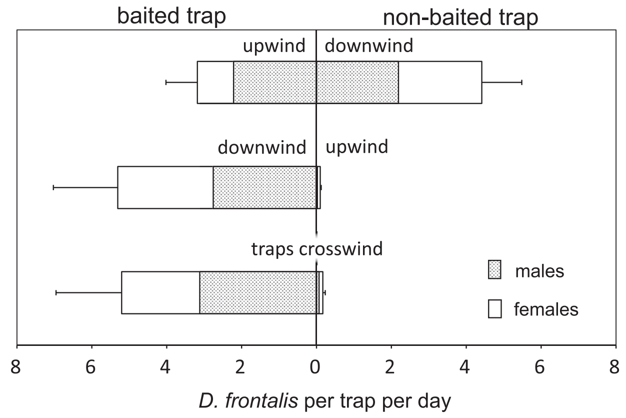

Fig. 2. Experiment 1. Catches of *D. frontalis* in pairs of multiple funnel traps suspended 4 m apart from a windvane to maintain them continuously in either a windwise or crosswind orientation. One trap was baited with frontalin, *endo*-brevicomin and turpentine, whereas the opposite trap was not baited. Statistics for means contrasts are in Tables 1 and 2.

Table 2. Trap catches summed (beetles per trap per day; mean ± SE) for both traps of each windvane in experiment 1

Lure placement	All *D. frontalis*	Female *D. frontalis*	Male *D. frontalis*	*T. dubius*
Crosswind	5.37 ± 1.78	2.19 ± 0.72	3.19 ± 1.07a	9.75 ± 4.18
Downwind	5.41 ± 1.73	2.63 ± 0.84	2.78 ± 0.90ab	6.83 ± 1.59
Upwind	7.60 ± 1.75	3.19 ± 0.91	4.40 ± 0.96b	8.08 ± 2.98
	$F_{2,8} = 4.10$[a]	$F_{2,8} = 3.32$	$F_{2,8} = 5.45$	$F_{2,8} = 0.17$
	$P = 0.060$	$P = 0.089$	$P = 0.032$	$P = 0.848$

[a] ANOVA results within sex/species. Data were transformed for statistical analyses; however, displayed means and SEs are for the untransformed data. Means associated with the same letter did not differ significantly (Tukey test, $\alpha = 0.05$). Lettering 6is absent if $P > 0.05$ in ANOVA.

($F_{1,30} = 12.0$, $P = 0.002$); however, there was no significant interaction between sex and treatment ($F_{2,30} = 3.03$, $P = 0.063$), nor was there a three-way interaction among sex, treatment, and factor baited ($F_{2,30} = 0.47$, $P = 0.63$).

Experiment 2. Potential for *endo*-Brevicomin to Promote Downwind Switching: *endo*-Brevicomin Background Absent

There was no significant treatment effect on the proportion of catches of females, males, or total *D. frontalis* ($F_{2,23.2} = 3.15$, $P = 0.062$; $F_{2,1.87} = 0.77$, $P = 0.57$; $F_{2,2.73} = 1.26$, $P = 0.41$, respectively) or *T. dubius* ($F_{2,3} = 0.01$, $P = 0.99$) in the downwind trap of the windvanes (Fig. 3, Table 3). However, there was a highly significant treatment effect with respect to catches of both sexes and total *D. frontalis* with both traps averaged ($F_{2,23} \geq 24.7$, $P < 0.001$) and for catches in the downwind traps alone ($F_{2,33} \geq 27.1$, $P < 0.001$) (Table 4). In pairwise contrasts among treatments, windvanes with an *endo*-brevicomin device on the upwind trap caught significantly more (20–26 fold) *D. frontalis* than windvanes that lacked an *endo*-brevicomin device, but catches did not differ significantly between windvanes with either a low or high release *endo*-brevicomin device. These pairwise contrast results for *D. frontalis* were the same for sexes summed, sexes individually, and for catches in the downwind trap alone (Table 4). There was a significant interaction between treatment and sex of *D. frontalis* on catch per windvane ($F_{2,66} = 6.39$, $P = 0.003$), between sex and trap position (i.e., whether traps were upwind or downwind; $F_{1,66} = 10.1$, $P = 0.002$), and a three-way interaction among sex, treatment, and trap position ($F_{2,66} = 3.52$, $P = 0.035$). There was no treatment effect on catches of *T. dubius* either for traps averaged ($F_{2,23} = 1.35$, $P = 0.28$) or for the downwind trap alone ($F_{2,33} = 0.85$, $P = 0.43$).

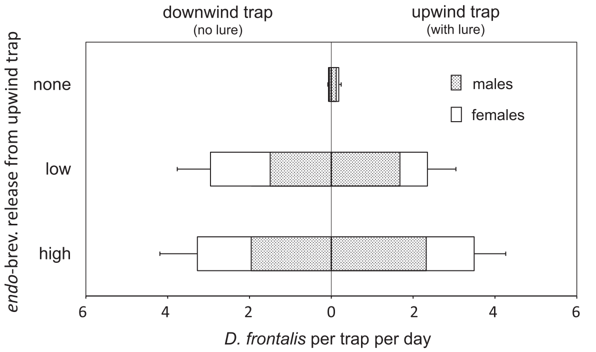

Fig. 3. Experiment 2. Catches of *D. frontalis* in pairs of multiple funnel traps suspended 4 m apart from a windvane to maintain them continuously in a windwise orientation. The upwind trap was invariably baited with frontalin and turpentine, and it additionally had an *endo*-brevicomin device with either a low or high release rate (approximately 0.2 and 3 mg/d respectively) or had no additional release device. Statistics for means contrasts are in Tables 3 and 4.

Experiment 3. Potential for *endo*-Brevicomin to Promote Downwind Switching: *endo*-Brevicomin Background Present

Analysis of the proportion of catches in the downwind trap revealed a strong outlier (studentized residual greater in absolute magnitude than 4.5) that was associated with a single collection from a windvane that was found with significant damage when catches were retrieved. This outlier was removed from all analyses in experiment 3. There was a strong treatment effect on the proportion of catches in the downwind trap for females, males, and total *D. frontalis* ($F_{2,27.1} = 11.9$, $P < 0.001$; $F_{2,22.7} = 7.93$, $P = 0.002$; $F_{2,27} = 30.1$, $P < 0.001$, respectively) but not *T. dubius* ($F_{2,3} = 0.23$, $P = 0.81$) (Fig. 4, Table 3). Catches of both sexes and total *D. frontalis* were shifted significantly (by a mean value of 8–13%) to the downwind trap when either a low or high release *endo*-brevicomin device was at the upwind trap, but the degree of this effect did not differ significantly between low and high release devices (Table 3).

There was a highly significant treatment effect on *D. frontalis* catches averaged for both traps ($F_{2,22} \geq 22.9$, $P < 0.001$) and in downwind traps alone ($F_{2,32} \geq 15.1$, $P < 0.001$) for females, males, and sexes summed (Table 4). For *D. frontalis* sexes either singly or summed, catches per windvane and catches in the downwind trap were significantly lower than the other two treatments when the high-rate *endo*-brevicomin device was at the upwind trap, and there was no difference between the low-rate and no device treatments. Catches in windvanes with high release *endo*-brevicomin in the upwind trap were roughly one-third of catches in windvanes with no *endo*-brevicomin. There was no interaction between treatment and sex of *D. frontalis* trapped by each windvane ($F_{2,64} = 3.01$, $P = 0.056$), a marginal interaction among sex, treatment, and trap position on the windvane ($F_{2,64} = 3.22$, $P = 0.046$), and a strong interaction between sex and trap position ($F_{1,64} = 67.6$, $P < 0.001$). There was no treatment effect on catches of *T. dubius* either for traps averaged ($F_{2,22} = 0.60$, $P = 0.56$) or for the downwind trap alone ($F_{2,32} = 0.18$, $P = 0.83$).

Table 3. Proportion trap catch (mean ± SE) in the downwind trap [downwind/(downwind + upwind)] of each windvane in experiments 2–4

Experiment	Additional lure on upwind trap	All *D. frontalis*	Female *D. frontalis*	Male *D. frontalis*	*T. dubius*
2 (no *endo*-brev. background)	None	0.28 ± 0.09	0.25 ± 0.17	0.26 ± 0.14	0.47 ± 0.02
	Low rate *endo*-brev.	0.55 ± 0.02	0.67 ± 0.07	0.40 ± 0.06	0.47 ± 0.02
	High rate *endo*-brev.	0.50 ± 0.04	0.56 ± 0.08	0.46 ± 0.04	0.48 ± 0.05
		$F_{2, 2.73} = 1.26$[a] $P = 0.41$	$F_{2, 23.2} = 3.15$ $P = 0.062$	$F_{2, 1.87} = 0.77$ $P = 0.57$	$F_{2, 3} = 0.01$ $P = 0.99$
3 (*endo*-brev. background present)	None	0.46 ± 0.02a	0.55 ± 0.03a	0.39 ± 0.03a	0.49 ± 0.02
	Low rate *endo*-brev.	0.57 ± 0.02b	0.68 ± 0.03b	0.51 ± 0.02b	0.49 ± 0.07
	High rate *endo*-brev.	0.57 ± 0.02b	0.63 ± 0.04b	0.52 ± 0.03b	0.53 ± 0.05
		$F_{2, 27} = 30.1$ $P < 0.001$	$F_{2, 27.1} = 11.9$ $P < 0.001$	$F_{2, 22.7} = 7.93$ $P = 0.002$	$F_{2, 3} = 0.23$ $P = 0.81$
4 (*endo*-brev. background present)	None	0.38 ± 0.02a	0.41 ± 0.03	0.36 ± 0.02a	0.47 ± 0.04
	Low rate verbenone	0.44 ± 0.04ab	0.46 ± 0.05	0.41 ± 0.03a	0.52 ± 0.04
	High rate verbenone	0.50 ± 0.03b	0.52 ± 0.06	0.49 ± 0.03b	0.47 ± 0.05
		$F_{2, 23} = 8.33$ $P = 0.002$	$F_{2, 28} = 2.15$ $P = 0.14$	$F_{2, 23} = 9.21$ $P = 0.001$	$F_{2, 22} = 0.43$ $P = 0.65$

Upwind trap always baited with frontalin and turpentine; downwind trap had no lure. *endo*-Brevicomin is abbreviated '*endo*-brev.'

[a] ANOVA results for the indicated experiment and sex/species. Data were transformed where appropriate for statistical analyses; however, displayed means and SEs are for the untransformed data. Means associated with the same letter did not differ significantly (Tukey test, $\alpha = 0.05$). Lettering is absent if $P > 0.05$ in ANOVA.

Experiment 4. Potential for Verbenone to Promote Downwind Switching

There was a strong treatment effect on the proportion of catches in the downwind trap of the pair with respect to numbers of *D. frontalis* for males and sexes summed ($F_{2, 23} = 9.21$, $P = 0.001$; $F_{2, 23} = 8.33$, $P = 0.002$; respectively) but not for females ($F_{2, 28} = 2.15$, $P = 0.14$) or *T. dubius* ($F_{2, 22} = 0.43$, $P = 0.65$) (Fig. 5, Table 3). For sexes summed and males, only the high release verbenone device caused a significant shift (a mean 8–13%) in beetle catches to the downwind trap compared to the absence of verbenone. There was not a significant treatment effect for catches of *D. frontalis* females, males, or sexes summed for averaged catches of both traps ($F_{2, 2} \leq 1.21$, $P \geq 0.45$), or catches by the downwind trap ($F_{2, 33} \leq 0.62$, $P \geq 0.55$) (Table 4). There was an interaction between sex and trap position ($F_{2, 66} = 7.39$, $P = 0.008$), but no interaction between sex and treatment ($F_{2, 66} = 2.86$, $P = 0.064$) or among sex, treatment, and trap position ($F_{2, 66} = 0.98$, $P = 0.38$). There was no treatment effect on catches of *T. dubius* either averaged for the two traps ($F_{2, 2} = 0.44$, $P = 0.70$) or for the downwind trap alone ($F_{2, 33} = 0.61$, $P = 0.55$).

Discussion

Results of experiment 1 are consistent with strong anemotaxis by flying *D. frontalis* responding to their aggregation attractant. Unbaited traps positioned 4 m downwind of a source of aggregation attractant caught 10-fold more *D. frontalis* than unbaited traps positioned 4 m laterally or upwind, a finding consistent with the beetles approaching the attractant primarily from downwind. Anemotaxis is likely universal in flying bark beetles orienting toward an odor source (Schlyter et al. 1987a; Byers 1988, 1996). Furthermore, attractant-releasing and downwind traps caught similar numbers of beetles, indicating that a high proportion of beetles may not proceed directly to a source of aggregation attractant but instead interact with downwind, tree-like objects within the pheromone plume. This interpretation is consistent with observations that *D. frontalis* often land on downwind trees before reaching a semiochemical source (Coster and Gara 1968, Vité 1970).

High levels of ambient aggregation attractant (such as would have occurred directly downwind of the baited traps in this study), cause *D. frontalis* to alight on nearby objects with dark vertical silhouettes (Gara et al. 1965, Vité et al. 1976, Payne 1986). Visual cues are important to host selection in *D. frontalis* (Strom et al. 1999, Strom and Goyer 2001), and they may become the dominant cues when beetles encounter a location with high levels of aggregation attractant in the environment (Payne 1986). However, it is likely that, rather than displaying a directed response, a portion of beetles caught in the unbaited downwind traps merely collided with the traps incidentally while orienting to the attractant. Regardless, it is clear that beetles were far more concentrated downwind of the attractant than in other directions, a factor that alone should increase the likelihood of a successful mass attack in the downwind direction (Coster and Johnson 1979). Furthermore, evidence suggests that the SPB aggregation attractant induces beetles to enter the bark in addition to concentrating them in an area or mediating their orientation (Gara et al. 1965, Coster and Gara 1968, Vité 1970), hence beetles should receive greater stimulation to begin mining into trees in the downwind direction.

Nonetheless, proximity appears to be the predominant factor determining the sequence of trees attacked within a *D. frontalis* infestation (Gara and Coster 1968, Johnson and Coster 1978, Schowalter et al. 1981). Normal variability in wind direction (which the windvanes removed as a factor in our tests) no doubt reduces the potential for wind to determine the next recipient tree. However, the general tendency for *D. frontalis* infestations to grow downwind confirms that wind plays a significant role in directing the progressive movement of the attack focus within infestations (Coster et al. 1978).

Three models have been proposed for the mechanism underlying redirecting of bark beetle attacks from focus to recipient trees (generalized from Geiszler et al. 1980): (A) The 'passive' model in which the primary cause is loss of attractiveness of the focus tree due to depletion of resin defenses and the simultaneous decline in production of aggregation pheromone. (B) The 'threshold' model, in which aggregation pheromone released from the focus tree stimulates aggregation and attacks on recipient trees when the pheromone plume engulfs the latter. The 'second-hand' attractant and the stimulation of attractant-releasing attacks on the recipient tree would cause its attractiveness to increase above the level of the focus tree as the latter became saturated with established, non pheromone-producing beetle

Table 4. Trap catches (beetles per trap per day; mean ± SE) in experiments 2–4 for both traps of each windvane or the downwind trap alone

Experiment	Additional lure on upwind trap	Averaged catches of both traps of each windvane				Catches in the downwind trap of each windvane			
		All *D. frontalis*	Female *D. frontalis*	Male *D. frontalis*	*T. dubius*	All *D. frontalis*	Female *D. frontalis*	Male *D. frontalis*	*T. dubius*
2 (no *endo*-brev. background)	None	0.13 ± 0.04a	0.04 ± 0.02a	0.08 ± 0.04a	2.91 ± 0.33	0.07 ± 0.03a	0.02 ± 0.02a	0.05 ± 0.03a	2.71 ± 0.41
	Low rate *endo*-brev.	2.65 ± 0.47b	1.07 ± 0.32b	1.59 ± 0.40b	3.42 ± 0.55	2.95 ± 0.70b	1.46 ± 0.36b	1.50 ± 0.38b	3.30 ± 0.80
	High rate *endo*-brev.	3.38 ± 0.60b	1.25 ± 0.35b	2.14 ± 0.52b	3.44 ± 0.43	3.28 ± 0.88b	1.32 ± 0.41b	1.96 ± 0.48b	3.11 ± 0.43
		$F_{2,23} = 43.9$[a] $P < 0.001$	$F_{2,23} = 24.7$ $P < 0.001$	$F_{2,23} = 30.2$ $P < 0.001$	$F_{2,23} = 1.35$ $P = 0.28$	$F_{2,33} = 46.9$ $P < 0.001$	$F_{2,33} = 27.8$ $P < 0.001$	$F_{2,33} = 27.1$ $P < 0.001$	$F_{2,33} = 0.85$ $P = 0.43$
3 (*endo*-brev. background present)	None	38.2 ± 6.9a	15.9 ± 3.1a	22.3 ± 4.3a	5.64 ± 0.95	35.6 ± 6.5a	17.8 ± 3.4a	17.8 ± 3.1a	5.65 ± 1.06
	Low rate *endo*-brev.	32.0 ± 6.1a	12.7 ± 2.7a	19.3 ± 3.7a	5.86 ± 1.09	37.3 ± 7.4a	17.0 ± 3.2a	20.3 ± 4.3a	5.84 ± 1.20
	High rate *endo*-brev.	12.7 ± 2.3b	5.4 ± 1.2b	7.4 ± 1.3b	5.17 ± 1.02	15.1 ± 2.6b	7.03 ± 1.37b	8.04 ± 1.4b	5.23 ± 1.13
		$F_{2,22} = 34.7$ $P < 0.001$	$F_{2,22} = 22.9$ $P < 0.001$	$F_{2,22} = 46.5$ $P < 0.001$	$F_{2,22} = 0.60$ $P = 0.56$	$F_{2,32} = 21.0$ $P < 0.001$	$F_{2,32} = 15.1$ $P < 0.001$	$F_{2,32} = 23.2$ $P < 0.001$	$F_{2,32} = 0.18$ $P = 0.83$
4 (*endo*-brev. background present)	None	17.0 ± 8.26	7.66 ± 3.58	9.36 ± 4.74	1.50 ± 0.40	14.2 ± 6.9	7.16 ± 3.45	7.01 ± 3.42	1.52 ± 0.40
	Low rate verbenone	11.9 ± 5.86	5.90 ± 2.87	6.01 ± 3.00	1.74 ± 0.71	10.9 ± 5.6	5.50 ± 2.68	5.35 ± 2.95	2.06 ± 0.92
	High rate verbenone	6.99 ± 2.43	3.64 ± 1.27	3.35 ± 1.18	1.31 ± 0.35	6.97 ± 2.53	3.76 ± 1.38	3.20 ± 1.16	1.31 ± 0.35
		$F_{2,2} = 1.21$ $P = 0.45$	$F_{2,2} = 1.13$ $P = 0.47$	$F_{2,2} = 1.21$ $P = 0.45$	$F_{2,2} = 0.44$ $P = 0.70$	$F_{2,33} = 0.56$ $P = 0.58$	$F_{2,33} = 0.62$ $P = 0.55$	$F_{2,33} = 0.53$ $P = 0.60$	$F_{2,33} = 0.61$ $P = 0.55$

Upwind trap always baited with frontalin and turpentine; downwind trap had no lure. *endo*-Brevicomin is abbreviated '*endo*-brev.'

[a] ANOVA results for the indicated experiment and sex/species. Data were given an appropriate transformation for statistical analyses; however, displayed means and SEs are for the untransformed data. Means associated with the same letter did not differ significantly (Tukey test, $\alpha = 0.05$). Lettering is absent if $P > 0.05$ in ANOVA.

pairs (Pureswaran and Sullivan 2012). (C) The 'repelling model' in which beetles attracted to aggregation attractant on the focus tree are diverted onto recipient trees by close-range repellant effects of antiaggregation pheromones. These hypotheses are not mutually exclusive, and possibly all three mechanisms contribute to switching behavior in *D. frontalis*.

Our results provide support for both hypotheses B and C. The high proportion of catches in unbaited traps downwind of baited traps illustrates the capacity of aggregation attractant to concentrate *D. frontalis* at locations at least as distant as commonplace spacing among trees within susceptible pine stands. This is consistent with hypothesis B and agrees with a wealth of observations that aggregation attractant alone can stimulate mass attack on adjacent trees by aggressive bark beetles including *D. frontalis* (e.g., Gara et al. 1965; Vité 1970; Hansen et al. 2006; Hayes et al. 2008, 2009; Ross 2021). However, the single tested release rate of attractant from our upwind traps resembled that of multiple mass-attacked trees (Sullivan and Clarke 2021), and thus our tests may exaggerate the implied role that attractants have under typical conditions in inducing mass attack of distant trees. [High rates were chosen to ensure sufficient catches for meaningful statistical inferences.] Higher release of attractants can cause bark beetles to land at points further from the source (Vité 1970, Tilden et al. 1983).

Additionally, our data provide some support for hypothesis C. In experiments 3 and 4, both *endo*-brevicomin and verbenone released from the focus tree surrogate caused a significant shifting in response of total *D. frontalis* to the recipient tree surrogate (Figs. 3 and 4; Table 3). This shift was small (mean 11–13% of total catches; Table 3), and substantially less than the shift due to positioning the recipient surrogate downwind of the focus surrogate (42–64% depending on sex; Table 1). This suggests greater importance for model B than C in driving switching in *D. frontalis*; however, this comparison does not account for semiochemical release rates that may not have been representative of those in nature.

In experiment 2, *endo*-brevicomin on the upwind trap did not produce a detectable shift in catches to the unbaited, downwind trap; however, we do not believe this is inconsistent with the *endo*-brevicomin-caused shift observed in experiment 3. Catches in the control treatment (no *endo*-brevicomin on the upwind trap) of experiment 2 were too low for meaningful contrasts among treatments in catch proportions by trap pairs. Additionally, *endo*-brevicomin added to the upwind trap caused a very large increase in catches in both traps, a response seemingly inconsistent with a switching influence. *endo*-Brevicomin has a biphasic dose-response, and it is a strong attractant synergist for *D. frontalis* at low concentrations but an attraction inhibitor at high concentrations (Sullivan and Mori 2009, Sullivan 2016). Release of *endo*-brevicomin from the upwind traps in experiment 2 was apparently insufficient to produce inhibition but sufficient to enhance attraction. *endo*-Brevicomin background produced by artificial devices or infested trees appears to alter the dose-response of *D. frontalis* responding to *endo*-brevicomin released with attractants, reducing the release rate of *endo*-brevicomin necessary to cause a decrease in response (Sullivan et al. 2011, Sullivan and Brownie 2021). We believe that this effect explains why *D. frontalis* attraction was reduced by the high-rate *endo*-brevicomin device at the upwind trap in experiment 3 (with artificial *endo*-brevicomin background present) but not 2. Since the artificial *endo*-brevicomin background in this study likely reflected that present in an active *D. frontalis* infestation (Sullivan and Brownie 2021), the result of experiment 3 is likely more representative of events in nature than that of experiment 2.

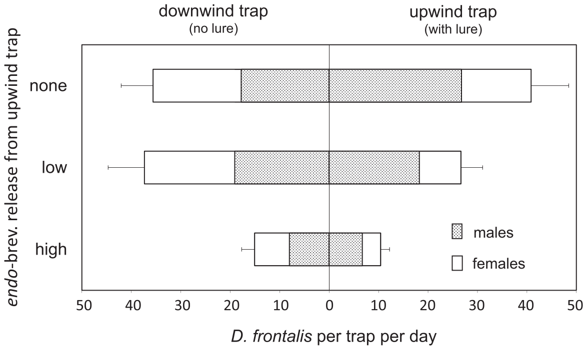

Fig. 4. Experiment 3. Catches of *D. frontalis* in pairs of multiple funnel traps suspended 4 m apart from a windvane to maintain them continuously in a windwise orientation. The upwind trap was invariably baited with frontalin and turpentine, and it additionally had an *endo*-brevicomin device with either a low or high release rate (approximately 0.2 and 3 mg/d, respectively) or had no additional release device. A background of *endo*-brevicomin in the environment was provided by three releasers of *endo*-brevicomin arranged 20 m away from the windvane and in an equilateral triangle. Statistics for means contrasts are in Tables 3 and 4.

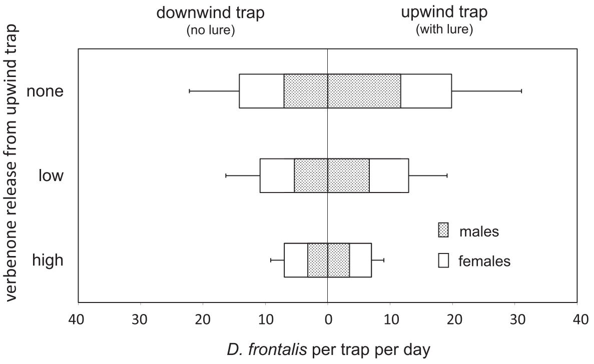

Fig. 5. Experiment 4. Catches of *D. frontalis* in pairs of multiple funnel traps suspended 4 m apart from a windvane to maintain them continuously in a windwise orientation. The upwind trap was invariably baited with frontalin and turpentine, and it additionally had a verbenone device with either a low or high release rate (approximately 6 and 60 mg/d, respectively) or had no additional release device. A background of *endo*-brevicomin in the environment was provided by three releasers of *endo*-brevicomin arranged 20 m away from the windvane and in an equilateral triangle. Statistics for means contrasts are in Tables 3 and 4.

The sex ratio was shifted more towards females in the downwind relative to the upwind trap. *Dendroctonus frontalis* females have been shown to land further from sources of aggregation pheromone than males (Hughes 1976), and it may be typical in bark beetles for the sex that initiates attacks to land further from the source of aggregation pheromone (Byers 1989). This is likely an adaptation for the gallery-initiating sex to avoid competition for the phloem resource. The sexes also differed in the degree of shift to the downwind trap caused by an inhibitor in the upwind trap (there was a significant statistical interaction among the presence of inhibitor, sex, and trap position in experiments 2–4), although the difference was strong only for verbenone. Males but not females exhibited a significant shift in catches downwind in response to verbenone, which agrees with studies indicating that females are less inhibited by verbenone than are males (summarized in Sullivan and Clarke 2021). If verbenone does not significantly influence the switching response of the attack-initiating sex, then its influence on the movement of the attack focus within infestations may be limited.

Although results of experiments 3 and 4 indicate that inhibitory semiochemicals could shift beetle responses from a focus to a recipient tree, this shift evidently could be accompanied by an overall reduction in responses to both trees, and, most significantly, to the recipient tree. In experiment 3 (Fig. 4), the high rate of *endo*-brevicomin resulted in an 11% shift in catches to the downwind trap but was accompanied by an approximately 58% reduction in catches by this trap (both these effects were statistically significant). In experiment 4, the data were suggestive of a similar pattern for verbenone (Fig. 5), although we did not detect a significant reduction in catches in the downwind trap. These results suggest that inhibitors could promote shifting of attacks from a focus to a recipient tree, but, simultaneously, reduce attacks and the odds of successful colonization of the recipient tree. Antagonists of bark beetle attractants can reduce beetle responses to sources of attractant in the immediately surrounding area and not only at the point of release (Andersson et al. 2011, Ross and Sullivan 2021). Thus, the capacity for a bark beetle attraction inhibitor to promote switching while not interfering with successful mass attack and infestation growth should be in part determined by the spatial dynamics of the inhibitor's activity. Anti-attractant pheromones that reduce beetle responses within a large radius around trees may play a lesser role in mediating switching than anti-attractants that influence responses only close to the point of release. Radial effects of attraction-inhibiting semiochemicals have received significant attention in bark beetles (Nijholt et al. 1981, Zhang and Schlyter 2003, Andersson et al. 2011, Byers et al. 2018, Ross and Sullivan 2021); however, we are not aware of studies relating active radius of inhibitors to their influence on infestation dynamics.

Adults of the predator *T. dubius* are attracted to the *D. frontalis* aggregation attractant (Vité and Williamson 1970), land on trees being mass attacked, and feed on arriving *D. frontalis* (Dixon and Payne 1979). *Thanasimus dubius* exhibited a somewhat greater tendency to be trapped crosswind and upwind of baited traps than did its prey. Additionally, unlike *D. frontalis*, *T. dubius* showed no tendency to shift to downwind traps in response to *D. frontalis* attraction inhibitors at upwind, baited traps. This is consistent with previous evidence of differing orientation responses to *D. frontalis* pheromones by *D. frontalis* and its major predator (Salom et al. 1992, Hayes et al. 1994, Sullivan et al. 2016), and our data suggest that *T. dubius* does not adjust its host seeking behavior to match that of its prey when the latter is responding to semiochemical switching cues. Thus *D. frontalis* might be less subject to predation when switching to a new host, and switching behavior may provide *D. frontalis* some refuge from predation. Differing responses by bark beetles and their predators to semiochemicals have been previously suggested as providing bark beetles some degree of predation avoidance (Aukema and Raffa 2000, Raffa et al. 2007).

Dendroctonus frontalis responses to semiochemicals can be influenced by a range of factors such as wind speed, temperature, time of year, and population density that presumably could have impacted our experimental outcomes and their generality (Sullivan 2011, 2016). Limitations in the number of windvanes available and time constraints for completing the project determined our choice of the dates for the experiments (fall through early summer). Our only prerequisite was the presence of sufficient flying beetles for statistically meaningful contrasts of trap catches. However, infestation establishment and growth occur in spring through early fall, hence the experiments did not generally overlap with the time of year when switching behaviors are most likely to occur or be consequential to pest management. Furthermore, *Dendroctonus frontalis* varies to some degree in its attractive responses to semiochemicals during the year (Sullivan et al. 2016).

Our experiments examined only the circumstance where the recipient tree had not yet received attacks and therefore was not yet releasing aggregation attractant. Evidence indicates that *endo*-brevicomin could also promote *D. frontalis* switching after attacks have begun on the recipient tree. Increasing the release rate of *endo*-brevicomin from one of a pair or trio of similarly baited (frontalin/host odor), adjacent traps will cause an increasing proportion of the catches to occur in the *endo*-brevicomin-lacking traps (Sullivan and Mori 2009, authors' unpublished data). At the highest release of *endo*-brevicomin tested in these studies, the *endo*-brevicomin-amended and *endo*-brevicomin-free traps approached 1:2 in their ratio of catches (roughly a 17% shift in responses to the latter traps). Hence *endo*-brevicomin could both increase the likelihood of attack initiation on a recipient tree and then continue to promote shift in attack focus once these attacks have begun.

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Author Contributions

CB performed statistical analyses, and BTS executed all other aspects of the work aided by the aforementioned technical assistance.

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