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RESEARCH

Influence of Release Rate and Location of Release Devices of Pheromone Component *endo*-Brevicomin on Attraction of the Southern Pine Beetle

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Abstract

endo-Brevicomin, a pheromone component for tree-killing bark beetle *Dendroctonus frontalis* Zimmermann, the southern pine beetle, has a "peaked," biphasic dose-response, being synergistic with attractants (pheromone component frontalin and host odors) at low release rates and attraction-reducing at high rates. Displacing an *endo*-brevicomin release device up to tens of meters from an attractant-releasing trap can increase synergistic effects. We investigated the interaction of *endo*-brevicomin device release rate and displacement. When one of a pair of 6 m distant, attractant-baited traps received an *endo*-brevicomin device varying in release rate across four orders of magnitude, catches in the *endo*-brevicomin amended and unamended traps peaked at the same, intermediate release of *endo*-brevicomin. However, catches were higher in the trap lacking *endo*-brevicomin at all but the lowest release rates, at which catches did not differ. When *endo*-brevicomin releasers were placed varying distances from an attractant-baited trap, tested release rates (0.45, 3.4, and 24 mg/d) enhanced catches at 4, 8, or 16 m distance, but, at 0 m, catch enhancement occurred only at the lowest rate and the highest rate produced catch reduction or no change. Our results indicate that *endo*-brevicomin releasers simultaneously produce long-range attraction-enhancing and short-range attraction-reducing effects for *D. frontalis*. These effects may promote switching of attack focus to adjacent hosts and propel growth of infestations. Our findings also indicate that maximum augmentation of trap catches should occur with the *endo*-brevicomin device displaced. Displacement short distances may preserve *endo*-brevicomin's long-range attractive effects while lessening short-range inhibitory effects.

Keywords Synergism · Biphasic · Dose-response · Trap · Displacement · Attraction

Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) include some of the most potent disturbance agents of forests worldwide, and many species utilize semiochemicals to mediate key components of their life history (Byers 1989a; Gitau et al. 2013; Raffa et al. 2015). "Aggressive" bark beetle species in the genera *Dendroctonus* and *Ips* are capable of colonizing and killing healthy, vigorous trees through rapid aggregation involving hundreds to thousands of individuals (Fargo et al. 1978; Kärvemo and Schroeder 2010; Lindgren and Raffa 2013). Resin depletion from these semiochemical-driven mass attacks weakens host defenses sufficiently to allow gallery establishment and oviposition (Berryman et al. 1989; Franceschi et al. 2005; Raffa and Berrymann 1983). A mass attack results in rapid tree death both from the damage of tunneling in the phloem and introduction of weakly pathogenic fungi (Paine et al. 1997; Raffa et al. 2005). Pheromone components released by beetles newly arriving on a host tree attract conspecifics that join in the mass attack and then release their own attractive pheromone components (Borden 1982; Schlyter and Anderbrant 1989; Sullivan 2016). Some of these compounds decline in attractiveness and may become repellant at sufficiently high concentrations (Borden et al. 1987; Byers 1983a; Rudinsky

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and Ryker 1980). Such high concentrations are ostensibly associated with high densities of beetle attacks; hence, this response presumably prevents over-colonization of a host tree and moderates intraspecific competition (Byers 1989b; Miller et al. 1990, 2005; Paine et al. 1999). Repellant effects may help shift the focus of mass attack to less colonized portions of the same host or onto adjacent hosts, a phenomenon termed "switching" (Gara and Coster 1968; Byers 1983a; Powell et al. 1998; Schlyter et al. 1987; Sullivan and Brownie 2022). Bark beetle pheromone components with a biphasic dose-response have been termed "multifunctional" because their attractive and attraction-reducing properties can serve different functional roles (Borden 1997; Rudinsky 1973; Symonds and Elgar 2004).

The southern pine beetle, *Dendroctonus frontalis* Zimmermann, is a major mortality agent and economic pest of pines (*Pinus*) that is native to the southern and eastern USA southward to Central America (Clarke and Nowak 2010; Hain et al. 2011). The major attractive pheromone components mediating its mass attacks appear to be frontalin (released by attack-initiating females) and *endo*-brevicomin (released by males attracted to, and pairing with, these females) (Pureswaran and Sullivan 2012; Renwick and Vité 1969; Sullivan et al. 2007). Frontalin is attractive alone to both sexes of the beetle but is synergized strongly by *endo*-brevicomin as well as host odors, particularly the volatile components of pine resin (Billings 1985; Munro et al. 2020; Staeben et al. 2015; Sullivan 2016; Sullivan et al. 2022).

endo-Brevicomin, which does not attract *D. frontalis* to traps without frontalin, has complex effects on *D. frontalis* behavior (Salom et al. 1992; Sullivan and Brownie 2021; Sullivan et al. 2007, 2011; Vité and Renwick 1971; Vité et al. 1985). The effects of *endo*-brevicomin on catches are biphasic, with a peaked dose-response curve (Sullivan 2016; Sullivan and Brownie 2021). However, synergistic effects of *endo*-brevicomin on trap catches have been found to occur with the *endo*-brevicomin release device displaced up to 32 m from the trap (Sullivan and Mori 2009). To our knowledge, such area-wide synergistic effects have not been documented for a pheromone component of any other bark beetle species (Andersson et al. 2011). One apparent by-product of this area-wide synergism and biphasic dose-response is that background *endo*-brevicomin in the environment can alter the effects of adding *endo*-brevicomin devices to attractant-baited traps (Sullivan and Brownie 2021). These background levels can cause a reversal from catch enhancement to catch reduction depending on the concentration of this background and the rate of *endo*-brevicomin release from the attractant-baited trap (Sullivan and Brownie 2021). This "background effect" likely explains the opposite effects of *endo*-brevicomin devices on trap catches inside (catch reduction) or distant from (catch enhancement) active *D. frontalis* infestations, as well as the apparent loss of biphasic effects (loss of attraction enhancement at low release rates) inside infestations (Sullivan et al. 2011).

Inclusion of *endo*-brevicomin in trapping lures for *D. frontalis* increases catches as much as 40-fold (Sullivan et al. 2007), and the semiochemical has been added to lure combinations used in traps for forecasting *D. frontalis* outbreaks and detecting populations moving northward in response to a warming climate (Dodds et al. 2018; Munro et al. 2021; Sullivan et al. 2021). The current, recommended operational lure consists of devices of frontalin and a host odor blend (α- and β-pinene in a 2:1 ratio) attached directly to a multiple funnel trap and an *endo*-brevicomin device attached to a hardwood tree or shrub branch located 4–6 m from the trap (Sullivan et al. 2021). This deployment of the *endo*-brevicomin device was recommended based on experimental observations of catch enhancement often occurring with such displacement but never a catch reduction (Sullivan and Mori 2009; Sullivan and Brownie 2021; Sullivan et al. 2016; authors' unpublished data). Furthermore, by displacing the device, bycatches of insects attracted to *endo*-brevicomin, whose presence in samples may complicate *D. frontalis* counts, are reduced (Shepherd and Sullivan 2017).

However, it is possible that the increase in catches resulting from displacement of the *endo*-brevicomin device could be duplicated by reducing the release rate of the device on the trap. Thus, the same catch enhancement might be achieved while consuming less semiochemical. Equivalence in results of movement of the device and adjustment of its release rate (for the purposes of this paper, the "dose/distance equivalence hypothesis") might be expected since both should change the concentration of *endo*-brevicomin associated with the location of the trap and downwind of it. With dose/distance equivalence, displacement of a biphasic attraction modifier from an attractant-baited trap should have the outcome displayed in Fig. 1. Notably, (1) maximum catches achievable by adjusting the release rate should be the same with the device either on or displaced from the trap, and (2) at low release rates, displacing the release device from the trap should reduce synergistic effects.

We investigated variability in *D. frontalis* trap catches due to the interaction of *endo*-brevicomin release rate and displacement of the release device. The first experiment was a test of the dose/distance equivalence hypothesis performed with pairs of adjacent, attractant-baited traps where only one (the "collocated trap") received an *endo*-brevicomin device of a variable release rate. Experiments 2 and 3 further examined the dose/distance relationship, but with single traps where both the *endo*-brevicomin device release rate and displacement distance from the attractant-baited trap were adjusted simultaneously. We intended to determine whether the above predictions of dose/distance equivalence were observed for *endo*-brevicomin and thus whether different

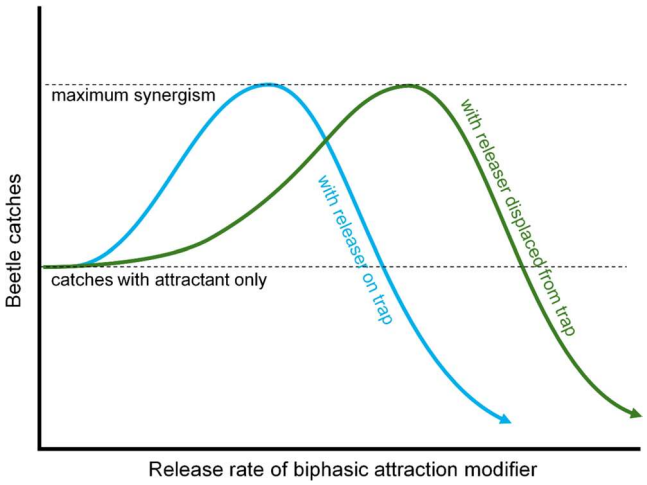

Fig. 1 Representation of the "dose/distance equivalence hypothesis" for a biphasic attraction modifier where variation in position of the release point and variation in release rate of the modifier have identical consequences for catches in an attractant-baited trap. Equivalence in results of movement of the device or adjustment of its release rate might be expected since both should change the concentration of attraction modifier associated with the location of the trap and downwind of it

expectations apply to this compound's behavior and perhaps to that of other biphasic semiochemicals.

Methods and Materials

Trapping trials were executed using 12-unit multiple-funnel traps (funnels: 19 cm upper opening diameter, 5.5 cm lower opening diameter, height 11 cm, extending into next lower funnel 3 cm; Synergy Semiochemicals, Delta, British Columbia, Canada). Traps were established adjacent to minor roads in mature stands of mixed pine/hardwoods in the Homochitto National Forest in southwestern Mississippi, USA (within 3 km of N31.43° W91.19°). During the experiments, the Homochitto National Forest was in non-outbreak status (92, 0, and 3 *D. frontalis* infestations in 2007, 2008, and 2014, respectively, within a 776 km^2 area; data courtesy USDA Forest Service). The stands were hilly, and traps were not positioned uniformly with respect to topography. Traps or trap pairs were >200 m apart, >10 m from the nearest pine, and hung 1–1.5 m (trap bottom) above the ground on metal poles. Catch collection cups contained several centimeters of propylene glycol and water to retain and preserve captured insects. Catches were collected at intervals of 3–14 d; relatively longer intervals were required during periods when beetle abundances were low. *Dendroctonus frontalis* were counted, and sex was determined by the frontal tubercles of males and the pronotal callus of females (Wood 1982). Traps were uniformly baited with attractive pheromone component frontalin and a source of host odors (as a synergist to frontalin; differed among tests as described below). Lure release rates were measured gravimetrically (or in the case of capillary devices, change in the height of the meniscus in the capillary) while devices were suspended in a fume hood. Frontalin was released from a pair of capped, low density polyethylene microcentrifuge tubes (400 µl capacity) filled with 200–300 µl racemic frontalin [>98% purity; Chem Samples Company (Columbus, Ohio, USA, now ChemSampCo, Trenton, New Jersey, USA) or BASF (Ludwigshafen, Germany)] at a rate over 24 days of 7.3±0.4 SD mg/d at mean 24° C. Racemic *endo*-brevicomin (≥95% purity; <3% *exo*-brevicomin; Synergy Semiochemicals) passively evaporated from either glass capillaries, glass vials (open or with hole through cap), or autosampler vial inserts (Table 1).

Table 1 Release rates and construction of *endo*-brevicomin release devices

Experi-ment #	Device[1]	Device volume (ml)	Opening diameter (mm)	Height (mm)	Approx. quantity filled (g)	Number devices deployed	Elution rate in lab[2] (mg/d±s.d.)
1	Capillary	0.0010	0.20	32	0.0004	1	0.0050±0.0001
1	Capillary	0.0030	0.35	32	0.001	1	0.0153±0.0003
1	Capillary	0.010	0.63	32	0.004	1	0.056±0.001
1	Capillary	0.035	1.2	32	0.014	1	0.158±0.006
1, 2, 3	Capillary	0.035	1.2	32	0.014	3	0.45±0.01
1	Vial insert	0.2	3.7	30	0.05	1	1.52±0.04
2	Open vial	1.2	6.0	40	0.30	1	3.4±0.1
1	Vial with hole in cap	15	7	70	0.36	1	7.8±0.4
2, 3	Open vial	8	13	38	1.5	1	24±1
1	Open vial	20	17	56	1.4	1	38±4

All devices were glass enclosures open on one end or with hole in cap; compound passively evaporated through this opening. Capillaries were flame-sealed at the bottom end and secured vertically. Openings of all devices were protected from rain under inverted vials, beakers, or plastic cups.

Release rates were measured while devices were inside a fume hood (avg. 25° C) for 12 or 32 d (for vials or capillaries, respectively; measured once). Rate for capillaries was determined by measuring change in meniscus height and converting volume to mass by multiplication with the density of *endo*-brevicomin (0.99 g/ml, measured in lab); otherwise, release was determined gravimetrically.

The capillaries and vials were protected from rain inside inverted glass vials, beakers, or plastic beverage cups. Frontalin and *endo*-brevicomin devices (when not displaced) were attached at the fourth funnel from the bottom of the trap, whereas the host odor device was secured near the top of the trap. During experiments, pines adjacent to traps were regularly checked for the presence of pitch tubes and other evidence of *D. frontalis* attack. If attacked trees were not being mass-attacked, traps were moved a further 10–20 m away which typically caused attacks to cease; if being mass-attacked, traps were moved at least 80 m away from the infested trees and the experiment continued.

Experiment 1

Dose-response to endo-*brevicomin released from one of a pair of adjacent traps* Two groups of nine pairs of traps separated by 6 m were established where one trap of each pair received a device releasing one of eight different rates of *endo*-brevicomin spread across four orders of magnitude or no *endo*-brevicomin (nine treatments). The trap with *endo*-brevicomin was located in a random direction (0°, 40°, 80°, 120°, 160°, 200°, 240°, 280°, or 320° from North) from the trap without. All traps were baited with α-pinene and frontalin. Host odor α-pinene [77% (-)-enantiomer; chemical purity > 85%; release rate over 37 d of 2.4 ± 0.1 SD g/d at mean 26° C] was released through sealed, opaque plastic bags (Synergy Semiochemicals). Within each group, all nine treatments were assigned to pairs at random. At each catch collection, treatments were reassigned randomly without replacement to pairs within groups, and catches were collected and re-randomizations performed until every treatment had been at every pair once. This resulted in a multiple Latin squares design with two squares (= groups) with pairs as columns and collections as rows. The experiment was conducted from 9 April to 19 May 2014.

Experiments 2 & 3

Interaction of endo-*brevicomin release rate and device distance from single traps.* For both experiments, traps were arranged into two groups of seven traps each receiving one of seven treatments, and the experimental design was multiple Latin squares as in experiment 1. Traps were baited identically with frontalin and host odor source turpentine. Turpentine was steam distilled from *P. taeda* L. (Hercules Inc., Brunswick, Georgia, USA) and released from a 250 ml brown glass bottle filled with turpentine and with a cotton dental wick (1 cm diam.) immersed in the turpentine and protruding 2–3 cm through the bottle cap [release rate ~ 7 g/d at mean 23° C over several days]. *endo*-Brevicomin release devices were either placed on the trap directly or secured to a plastic gardening stake at 1.5 m above the ground and displaced from the trap at a distance determined by the treatment. The direction of the stake relative to the trap was randomized within each trap group (0°, 51°, 103°, 154°, 206°, 257°, or 309° from North). In experiment 2, six of the treatments consisted of all possible combinations of three *endo*-brevicomin release rates ["low" (0.45 mg/d), "medium" (3.4 mg/d), and "high" (24 mg/d); Table 1] with two distances of the *endo*-brevicomin device from the trap [either attached directly to the trap ("0 m distance") or 8 m away]. In experiment 3, six of the treatments consisted of all possible combinations of two release rates ["low" (0.45 mg/d) and "high" (24 mg/d); Table 1] with three distances of the *endo*-brevicomin device from the trap (0, 4, and 16 m). For both experiments there was also an *endo*-brevicomin-lacking control treatment. The *endo*-brevicomin release rates were selected to span the range of rates having either synergistic or inhibitory effects with *D. frontalis* when released directly from an attractant-baited trap. Experiments 2 and 3 were conducted 7 November 2007 to 17 January 2008, and 20 February to 13 May 2008, respectively.

Statistical Analysis

For all tests $\alpha = 0.05$. The dependent variable (hereafter, "trap catch") was the numbers of *D. frontalis* caught in each individual trap divided by the number of days that the assigned treatment had been in place. Effects of treatment on trap catch were analyzed with mixed-model *ANOVA*s by using PROC MIXED in SAS 9.4 (Cary, North Carolina, USA). Data were transformed to address distributional assumptions of normality and homoscedasticity with either a square root or cube root transformation chosen based on examination of residuals plots. For the analyses, class variables included each Latin square (square) and the collection date (date). For each experiment, an *ANOVA* was initially performed with the sex of the beetles (sex) as a fixed effect to detect for possible interactions with treatment variables. For experiments 1 and 2, a second *ANOVA* was performed with sexes summed. Experiment 1 had additional class variables: location of the trap pair (pair), the trap of the pair to which the *endo*-brevicomin device was assigned (brevicomin), and release rate of *endo*-brevicomin (dose). For experiment 1, the first ANOVA [$\sqrt{(x+0.1)}$ transformation] had fixed effects dose, brevicomin, and sex (and all interactions), date, date*dose, date*brevicomin, date*dose*brevicomin, and date*sex; random effects were pair(square), date*square, date*dose*pair(square), and date*dose*brevicomin*pair(square). The second *ANOVA* [$\sqrt[3]{(x+0.1)}$ transformation] had fixed effects dose, brevicomin, date and all interactions; random factors were pair(square) and date*dose*pair(square). Catches by traps within each pair were compared with

an analysis of simple effects (a SLICE statement of the dose*brevicomin interaction) and a Holm-Bonferroni correction for nine contrasts. For traps either with or without *endo*-brevicomin, all pairwise comparisons were made among doses with *t-test*s followed by a Holm-Bonferroni correction for 36 contrasts. The relationship of *endo*-brevicomin release rate to the ratio between catches in the two traps of each pair was fit to a two-parameter power function. Experiments 2 and 3 had two additional class variables: one of the seven pairings of a particular release rate and distance of the *endo*-brevicomin device from the trap (dose-distance) and the trap position (trap). In experiment 2, the first *ANOVA* ($\sqrt[3]{x}$ transformation) had fixed effects dose-distance, date, sex, sex*date, and sex*dose-distance; random effects were square, trap(square), dose-distance*square, and dose-distance*date*trap(square). The second *ANOVA* ($\sqrt[3]{x}$ transformation) had fixed effect dose-distance, and random effects square, trap(square), dose-distance*square, date, and date*dose-distance. All pairwise comparisons among levels of dose-distance were performed with a *Tukey* test. In experiment 3, the *ANOVA* [$\sqrt[3]{(x+0.1)}$ transformation] had the same fixed and random effects as the first *ANOVA* of experiment 2. The effect of dose-distance within sex was determined with an analysis of simple effects (a SLICE statement of the interaction of dose-distance*sex). All pairwise comparisons among levels of dose-distance were performed with *t-test*s followed by a Holm-Bonferroni correction for 21 contrasts.

Results

In experiment 1, traps caught a mean 60% males, and an interaction was detected between sex and dose ($F=4.63$, $df=8$, 298, $P<0.001$), but not an interaction between sex and brevicomin ($F=1.45$, $df=1$, 298, $P=0.23$), nor was there a 3-way interaction between sex, dose, and brevicomin ($F=1.26$, $df=8$, 298, $P=0.26$). Differences in the dose-response pattern for males and females were subtle and not readily interpretable (Online Resource 1); notably, the ranking of dose levels with respect to mean catches by trap pairs were identical for both sexes. The proportions of males trapped ordered by increasing release rate from zero were 0.80, 0.79, 0.78, 0.57, 0.60, 0.60, 0.57, 0.64, 0.61 (trap with *endo*-brevicomin) and 0.56, 0.69, 0.64, 0.51, 0.60, 0.59, 0.59, 0.62, 0.66 (trap without *endo*-brevicomin). Response by total *D. frontalis* was significantly influenced by *endo*-brevicomin release rate (factor dose; $F=48.6$, $df=8$, 64, $P<0.001$), by whether the trap was assigned the *endo*-brevicomin device or not (factor brevicomin; $F=53.9$, $df=1$, 81, $P<0.001$), and by an interaction between these two factors ($F=5.35$, $df=8$, 81, $P<0.001$). Both the trap of the pair assigned the *endo*-brevicomin device and the trap lacking *endo*-brevicomin showed a peaked response to release rate of *endo*-brevicomin, with catches being greater than the check (no *endo*-brevicomin) at the third (0.056 mg/d) and all higher release rates of *endo*-brevicomin (Fig. 2).

Catches differed significantly between the two traps of the pair at the fifth (0.45 mg/d) and all higher dose levels. The ratio of catches between the two traps was related to release rate of *endo*-brevicomin by a log-log regression ($y=1.77x^{0.115}$, $R^2=0.928$), and the proportion of beetles trapped by the *endo*-brevicomin-lacking trap increased steadily above the tested *endo*-brevicomin release rate of 0.0153 mg/d (Fig. 3).

In Experiment 2, traps caught a mean 67% males (range among treatments 64–74%), and there was a marginally significant interaction between sex and the *endo*-brevicomin dose-distance combination ($F=2.45$, $df=6$, 85, $P=0.031$); however, rankings of dose-distance combinations by catch numbers were the same for both sexes (Online Resource 2) so analyses were performed with sexes summed. Response by summed sexes of *D. frontalis* was significantly influenced by main effect dose-distance ($F=14.3$, $df=6$, 18.7, $P<0.001$). All three release rates of *endo*-brevicomin (0.45, 3.4, and 24 mg/d) significantly enhanced catches above the level of the check (no *endo*-brevicomin) when devices were positioned 8 m away, but only at the low rate were catches significantly increased when devices were placed on the trap (Fig. 4).

When the *endo*-brevicomin device was on the trap, catches declined significantly between the low and high release rates, whereas catches did not differ significantly among the three release rates when the device was located eight meters away. At both the medium and high release rates, catches were significantly greater with the *endo*-brevicomin device located 8 m away rather than on the trap. The effect of displacement was more apparent at higher release rates; the difference in catches between 0 and 8 m separation at 0.45, 3.4, and 24 mg/d was 1.5, 9.0, and 36-fold, respectively.

In experiment 3, traps caught a mean 64% males (range among treatments 60–72%), and there was a significant interaction between sex and the *endo*-brevicomin dose-distance combination ($F=3.74$, $df=6$, 70, $P=0.003$). The effect dose-distance was significant both for females ($F=22.5$, $df=6$, 70, $P<0.001$) and males ($F=29.6$, $df=6$, 70, $P<0.001$). For both sexes, the high release rate of *endo*-brevicomin produced significantly lower catches than the check when the device was attached directly to the trap; otherwise, the presence of *endo*-brevicomin caused significantly higher catches (Fig. 5).

Increasing the distance of the high-release *endo*-brevicomin device from the trap (0 m to 4 m or 16 m) significantly increased catches for both sexes, whereas displacement

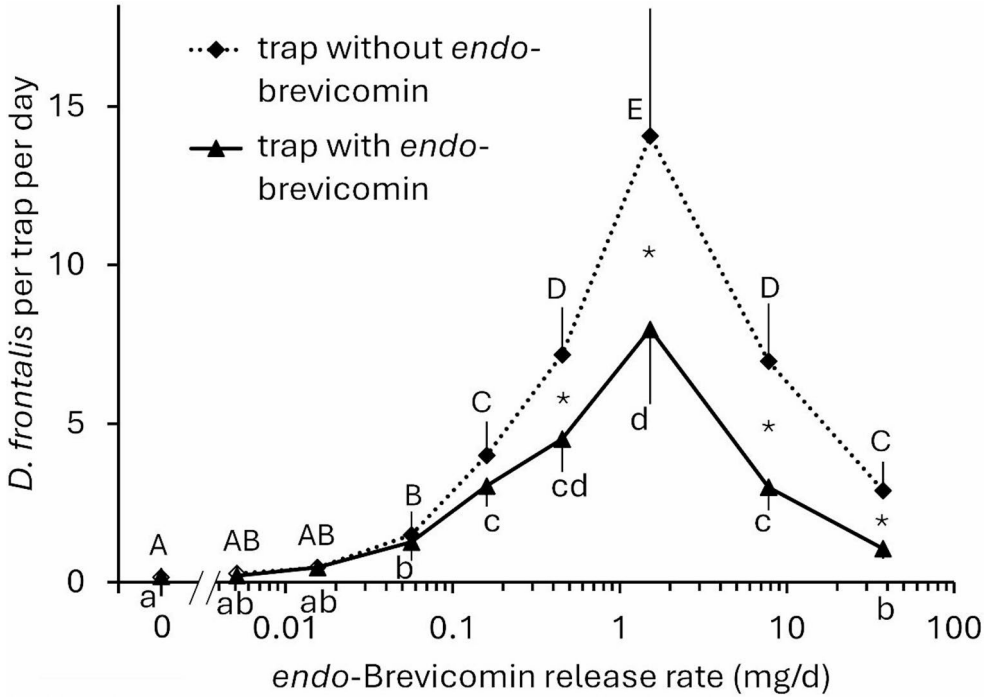

Fig. 2 Experiment 1: Response of *D. frontalis* to widely spaced funnel trap pairs (6 m separation within pairs), with both traps releasing identical rates of frontalin and α-pinene, but with one trap of the pair releasing one of eight different rates of *endo*-brevicomin (or none). Error bars display standard error of the mean of raw catch data; however, statistical tests were performed with cube root transformed data to meet parametric assumptions. Asterisks indicate that the two traps of the pair differed significantly from one another in catches [analysis of simple effects (SLICE statement in SAS) of the trap*dose interaction; $\alpha = 0.05$ with Holm-Bonferroni correction for nine contrasts]. Mean catches associated with the same upper-case (traps without *endo*-brevicomin device) or lower-case (traps with *endo*-brevicomin device) letter did not differ significantly (*t-test*, $\alpha = 0.05$ with a Holm-Bonferroni correction for 36 contrasts)

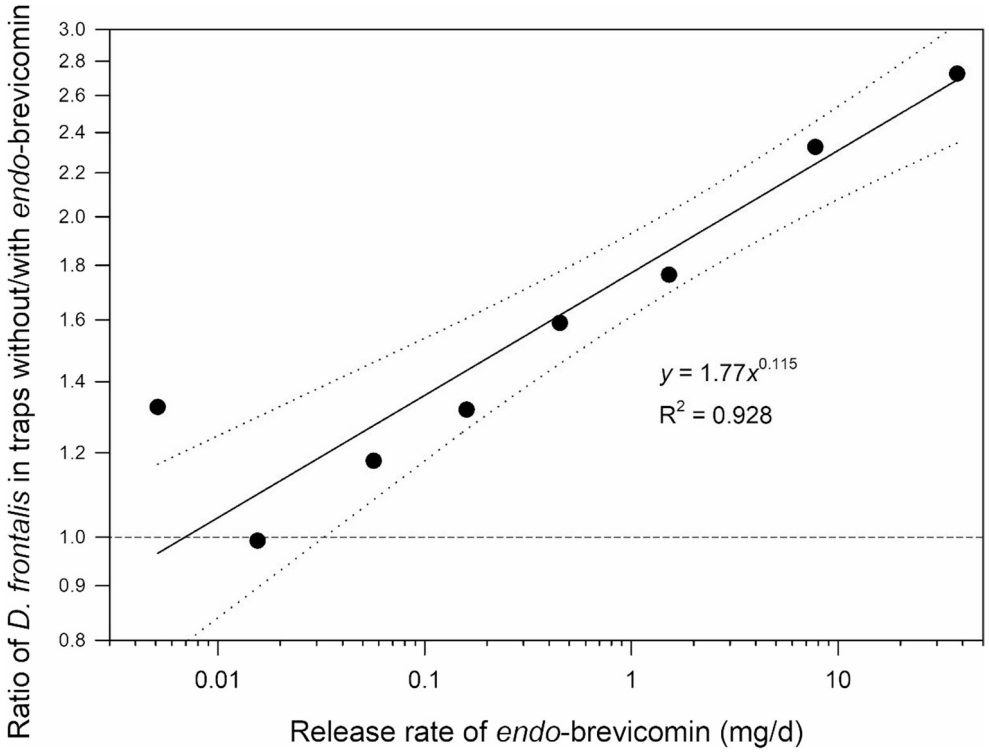

Fig. 3 Experiment 1: Beetle trap preference (=proportion caught in the trap of the pair lacking *endo*-brevicomin) regressed against *endo*-brevicomin release rate. Both the X and Y axes are log-scaled, and dotted lines represent the 95% confidence interval

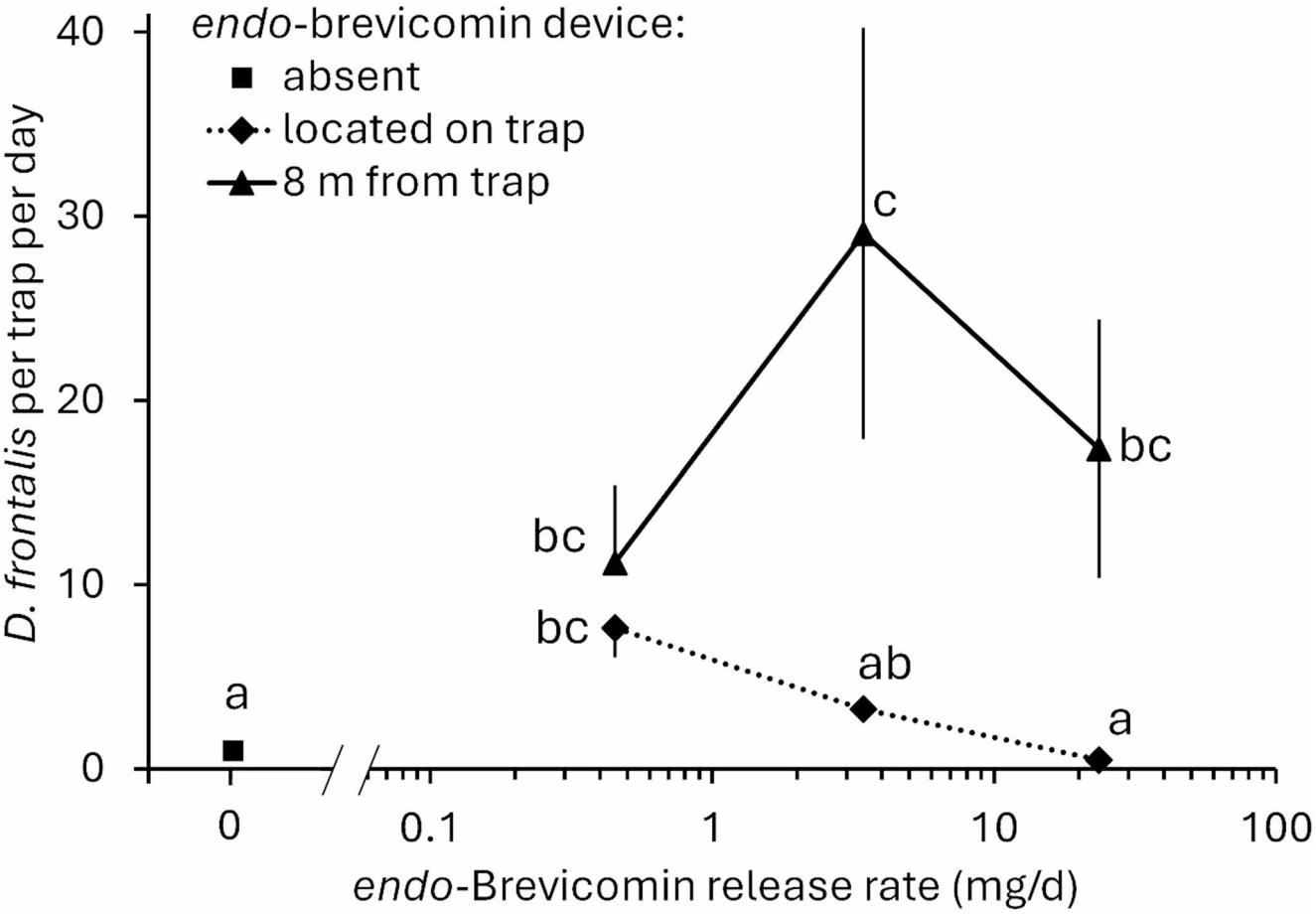

Fig. 4 Experiment 2: Response of *D. frontalis* to widely spaced, single funnel traps baited with an invariable release rate of frontalin and turpentine plus a variable release rate of *endo*-brevicomin from a device located either on or 8 m from the trap. Error bars display standard error of the mean of raw catch data; however, cube-root transformed data were used for statistical tests for meeting parametric assumptions. Treatment means associated with the same letter did not differ significantly (*Tukey* test, $\alpha = 0.05$)

caused no significant change in catches for the low rate device. With 4 m distance of the *endo*-brevicomin device from the trap, more females were trapped with the low than the high release rate of *endo*-brevicomin.

Discussion

Experiment 3 (Fig. 5, those treatments where *endo*-brevicomin devices were not displaced from the trap) demonstrated that *endo*-brevicomin is a dose-dependent, biphasic attraction modifier (enhancing attraction at low release rates, inhibiting attraction at high rates) for *D. frontalis*. Evidence of such biphasic effects was reported previously (Sullivan 2016; Sullivan and Brownie 2021). Furthermore, in experiment 3 (Fig. 5), a high release rate device of *endo*-brevicomin caused a significant reduction in catches when attached to an attractant-baited trap but catch enhancement when displaced from the trap 4 and 16 m. This result illustrates a biphasic displacement response for *endo*-brevicomin that corresponds to its biphasic dose-response; that is, inhibitory effects were reversed to attraction-enhancing effects by either reducing the release rate or displacing the release point of *endo*-brevicomin from the attractant. This observation agrees with the dose/distance equivalence hypothesis illustrated in Fig. 1.

However, results of experiment 1 (in which one trap of a pair of 6 m separated, attractant-baited traps received an *endo*-brevicomin device of varying release rate) conflicted with predictions of the dose/distance equivalence hypothesis. In experiment 1 (Fig. 2), (1) maximum catches achieved by adjusting the release rate of the *endo*-brevicomin device were significantly higher for the trap lacking *endo*-brevicomin (i.e., displaced from the device; 14.1 beetles/trap/d) than the collocated trap (8.0 beetles/trap/d) of the pair, and (2) catches were never higher for the trap of the pair with the collocated *endo*-brevicomin device. Between an *endo*-brevicomin release rate of 0.056 mg/d (the threshold of behavioral effects) and 1.52 mg/d (peak catches), preference for the displaced trap of the pair increased concurrently with

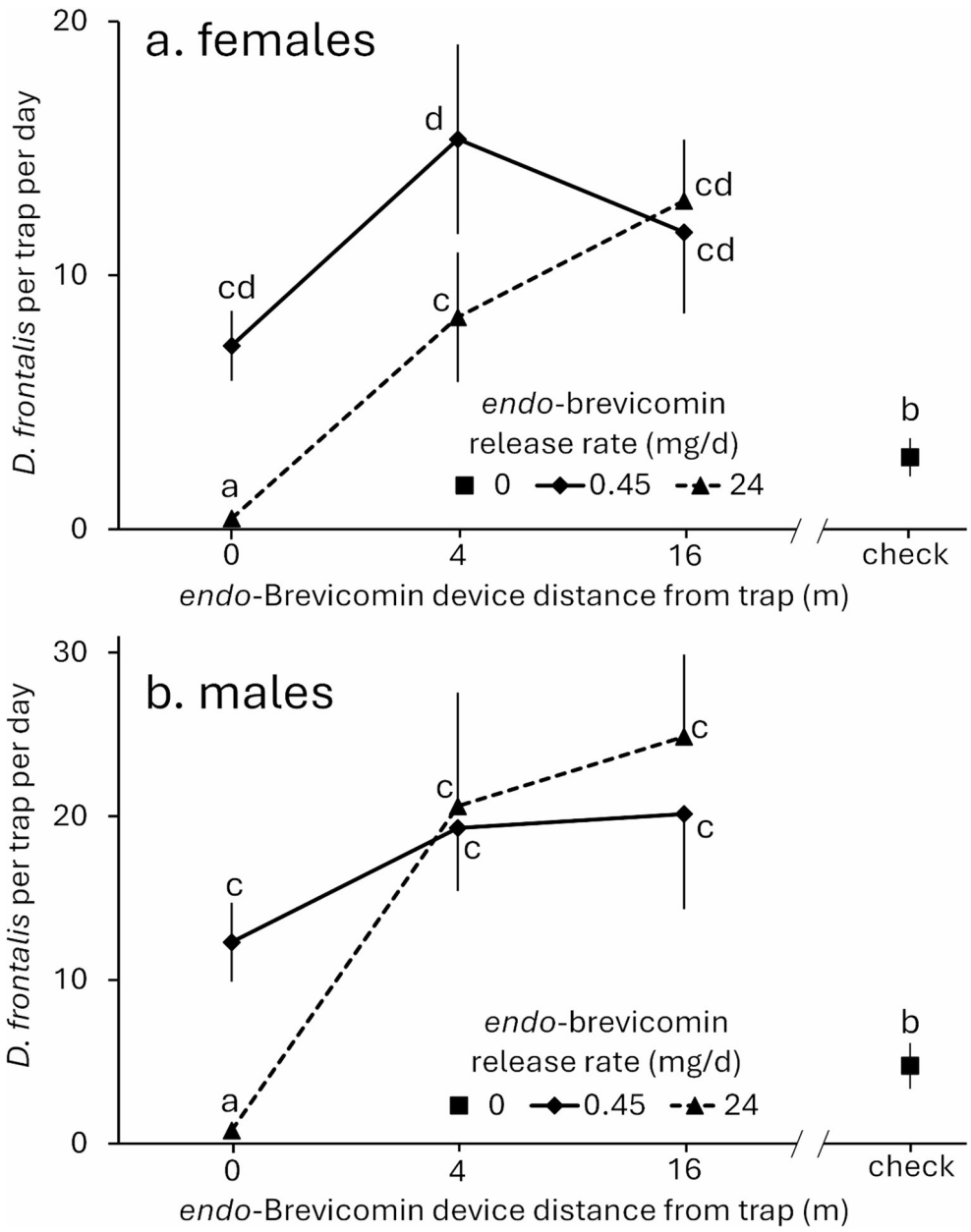

Fig. 5 Experiment 3: Response by female (**a**) and male (**b**) *D. frontalis* to widely spaced, single funnel traps baited with an invariable release rate of frontalin and turpentine plus a variable release rate of *endo*-brevicomin from a device located either on or 4 or 16 m from the trap. Error bars display standard error of the mean of raw catch data; however, cube root transformed data were used for statistical tests for meeting parametric assumptions. Treatment means associated with the same letter did not differ significantly (*t-test*, $\alpha = 0.05$ with Holm-Bonferroni correction for 21 contrasts)

catches by both traps. This suggests that long-range attraction-enhancing effects of *endo*-brevicomin occurred invariably with short-range attraction-inhibiting effects. Evidence of long-range attractive effects coupled with short-range repellant effects has been reported previously for *endo*-brevicomin with *D. frontalis* (Sullivan and Brownie 2022).

In contrast, the responses observed in experiments 2 and 3 (Figs. 4 and 5) did not violate the aforementioned expectations of the dose/distance equivalence hypothesis as (1) greatest catches obtained with the *endo*-brevicomin device displaced from the trap did not differ significantly from greatest catches with the device collocated, and (2) we cannot exclude the possibility that *endo*-brevicomin devices with lower release rates than those tested might have produced higher catches when collocated with, rather than displaced from, the traps. However, the results of experiments 2 and 3 show that a source of *endo*-brevicomin can create a broad zone of attractant synergism (at least 16 m in radius), and this may surround a much smaller zone (in this study, less than 4 m radius) of attraction inhibition when the release rate is sufficiently elevated. In another experiment, the radius of synergistic effects was shown to be as much as 32 m (Sullivan and Mori 2009).

The results of the experiments imply that, as beetle attacks and *endo*-brevicomin release increase on a mass-attacked tree, both long-range attraction-enhancing effects (affecting the mass attacked and surrounding trees) and short-range attraction-reducing effects (affecting primarily the

mass-attacked tree) would increase simultaneously, with the result that net attractive effects of *endo*-brevicomin would be higher for surrounding trees than the mass-attacked tree. Relatively greater attractiveness of the surrounding trees should promote switching of the focus of mass attack to these trees. Semiochemicals have been proposed to play a role in mediating switching in other bark beetle systems (Borden 1997; Geiszler et al. 1980; Schlyter et al. 1987). The rapid growth of bark beetle infestations is attributed to switching behavior (Bentz et al. 1996; Gara and Coster 1968; Powell et al. 1998), and our study adds to other evidence indicating the likely importance of *endo*-brevicomin in expansion of *D. frontalis* infestations (Sullivan and Mori 2009; Sullivan and Brownie 2022). Other semiochemicals likely contribute to switching in *D. frontalis* as well, including the attraction-inhibiting pheromone verbenone and the aggregation pheromone component frontalin (Sullivan 2016; Sullivan and Brownie 2022). The long-range attractive response to *endo*-brevicomin should have selective benefits for the beetles, as the semiochemical should be an indicator of successful establishment by beetle pairs on hosts and thus signal the presence of susceptible breeding substrate. Simultaneously, high levels perceived when approaching an individual host would indicate low availability of unoccupied phloem to gallery-initiating females and reduced mate availability to males (Byers 1983b; Sullivan and Brownie 2022).

It should be noted that all experiments used a similar composition and release rate of frontalin/host odor attractant (albeit a composition and rate resembling that of the recommended operational lure for *D. frontalis*), and an undetected interaction between the composition and release rate of the attractive lure components and the release rate and displacement distance of *endo*-brevicomin devices may have influenced the effects observed. Time of year has been shown to influence displacement-caused attraction enhancement by *endo*-brevicomin (it is more pronounced in winter and spring) (Sullivan et al. 2022), and thus variables other than release rate of *endo*-brevicomin devices can influence the outcome of displacement. Also, it is likely that the highest tested release rates of *endo*-brevicomin in our experiments exceeded those ever associated with a single location in nature, as it has been estimated that one tree mass-attacked by *D. frontalis* releases only 0.12–0.52 mg *endo*-brevicomin per day (Sullivan and Mori 2009).

Experiment 1 indicated that the augmenting effects of *endo*-brevicomin on *D. frontalis* trap catches are greater when the device is positioned a small distance (6 m) from the trap. We propose that displacement of *endo*-brevicomin devices small distances may reduce this semiochemical's short-range inhibitory effects while preserving its long-range attractive effects. As suggested by experiments 2 and 3 (Figs. 4 and 5), maximization of *endo*-brevicomin's synergism of attractants for *D. frontalis* may require adjustment of both release rate and the distance of device displacement. However, our results indicate that detection of *D. frontalis* in practice may be optimized by displacement of the *endo*-brevicomin device from the trap baited with frontalin and host odors (as is the current recommendation). Enhancement in potency of attractive lures through separation of components may be possible with other bark beetles (Sullivan 2023).

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Declarations

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