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Responses by *Dendroctonus frontalis* and *Dendroctonus mesoamericanus* (Coleoptera: Curculionidae) to Semiochemical Lures in Chiapas, Mexico: Possible Roles of Pheromones During Joint Host Attacks

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Abstract

In southern Mexico and Central America, the southern pine beetle *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae) commonly colonizes host trees simultaneously with *Dendroctonus mesoamericanus* Armendáriz-Toledano and Sullivan, a recently described sibling species. We hypothesized that cross-species pheromone responses by host-seeking beetles might mediate joint mass attack, bole partitioning, and reproductive isolation between the species. Previous studies had indicated that *D. frontalis* females produce frontalin and that female *D. mesoamericanus* produce frontalin, *endo*-brevicomin, and ipsdienol (males of both species produce *endo*-brevicomin and possibly ipsdienol). In field trapping trials in the Mexican state of Chiapas, *D. frontalis* was attracted to the lure combination of turpentine and racemic frontalin; racemic *endo*-brevicomin enhanced this response. In a single test, *D. mesoamericanus* was attracted in low numbers to the combination of turpentine, racemic frontalin, and racemic *endo*-brevicomin after the addition of racemic ipsdienol; in contrast, racemic ipsdienol reduced responses of *D. frontalis.* Inhibition of *D. frontalis* was generated in both sexes by (+)- and racemic ipsdienol, but by (−)-ipsdienol only in females. Logs infested with *D. mesoamericanus* females (the pioneer sex in *Dendroctonus*) attracted both species in greater numbers than either *D. frontalis* female-infested or uninfested logs. Our data imply that *D. frontalis* may be more attracted to pioneer attacks of *D. mesoamericanus* females, and that this could be owing to the presence of *endo*-brevicomin in the latter. Possible intra- and inter-specific functions of semiochemicals investigated in our experiments are discussed.

Key words: coexistence, bark beetle, reproductive isolation, syntopic species, pheromone

Semiochemicals play critical roles during colonization of new hosts by aggressive bark beetles (Coleoptera: Curculionidae: Scolytinae). These semiochemicals may include pheromones produced by con- and heterospecific beetles as well as volatiles from the host tree (Borden 1974, Wood 1982). Aggregation pheromones concentrate conspecific attacks on individual trees and thereby mediate mass attacks that overwhelm host defenses (Raffa 2001, Six and Bracewell 2015); anti-aggregation pheromones reduce attraction of conspecifics and regulate attack densities (Byers 1989). These pheromones may also function secondarily as kairomones or synomones and mediate interactions among multiple species attacking the same or adjacent hosts (Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980, Schlyter and Anderbrant 1993, Ayres et al. 2001). Beetles may "eavesdrop" on aggregation pheromones of other species to locate their host resources, or through cross-attraction engage in joint mass attacks that mutually increase the probability of colonization success (Svihra et al. 1980, Wagner et al. 1985, Økland et al. 2009). Species-specific differences in pheromone composition, release timing, and spatial distribution of attacks along the host bole can reduce the potentially deleterious effects of intermixing of species such as interspecific competition and hybridization (Byers and Zhang 2011).

The bark beetle *Dendroctonus frontalis* Zimmermann is an important mortality agent for *Pinus* spp. in the eastern and southwestern United States, Mexico, and Central America (Wood 1982, Billings et al. 2004). Across its wide distribution, *D. frontalis* is commonly found coexisting on the same hosts with other closely related species of bark beetles (Zúñiga et al. 1995, Moser et al. 2005, Davis and Hofstetter 2009). Within a zone extending from the state of

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Michoacán, Mexico to northern Nicaragua, *D. frontalis* commonly coexists on the same hosts with *Dendroctonus mesoamericanus* Armendáriz-Toledano and Sullivan, a recently described sibling species (Sullivan et al. 2012; Armendáriz-Toledano et al. 2014, 2015). Like *D. frontalis*, *D. mesoamericanus* appears to be an aggressive, tree-killing bark beetle species capable of causing landscape-scale mortality of pines (Midtgaard and Thunes 2002, Armendáriz-Toledano et al. 2015).

Previous investigations indicated that both species utilize pheromones and that there are differences and overlap in pheromone composition, which likely affect the species' interactions in nature. In reciprocal cross-attraction studies in an olfactometer, walking males of both species were more strongly attracted by odors arising from entrances of conspecific than heterospecific females (Niño-Domínguez et al. 2015). Volatiles collections and extracts of adult beetles indicated that females (the pioneer sex in the genus *Dendroctonus*) of both species produce the common *Dendroctonus* pheromone component frontalin, whereas female *D. mesoamericanus* additionally produce ipsdienol and *endo*-brevicomin (Sullivan et al. 2012). *endo*-Brevicomin is produced by males of both species and ipsdienol by at least some *D. frontalis* males (Sullivan et al. 2012). In olfactometer studies, ipsdienol and *endo*-brevicomin strongly enhanced attraction of walking *D. mesoamericanus* males while inhibiting responses of *D. frontalis* males to frontalin and *alpha*-pinene, hence these two compounds likely mediate discrimination of female entrances by mate-seeking males and enhance reproductive isolation of the species (Niño-Domínguez et al. 2015).

Although olfactometer studies have characterized a sex pheromone for *D. mesoamericanus*, it is not clear whether these same compounds also function in attracting both sexes to host trees under attack (i.e., serve as an aggregation pheromone). Trap lures consisting of frontalin, *endo*-brevicomin, and host odors (i.e., distilled pine resin) attract *D. mesoamericanus* in significant but very low numbers even in areas with conspicuous populations (Sullivan et al. 2012, authors' observations). Ipsdienol, which significantly enhanced attraction of *D. mesoamericanus* males in some olfactometer trials, has not been included in experimental trapping lures (Niño-Domínguez et al. 2015). In contrast to *D. mesoamericanus*, flying *D. frontalis* of both sexes are attracted in large numbers to traps baited with the combination of frontalin, *endo*-brevicomin, and host odors (distilled pine resin or purified *alpha*-pinene), which appears to function as their aggregation attractant (Moreno et al. 2008, Sullivan et al. 2011). As flying beetles of both species respond positively to at least two pheromone components produced by the other species (i.e., frontalin and *endo*-brevicomin), these data imply that semiochemicals should influence interspecific interactions during joint host colonization. In particular, these data suggest that some cross-attraction likely occurs. However, it is unlikely that these synthetic lures are fully representative of the odors produced by naturally occurring attacks, and trials with natural (and thus presumably complete) sources of semiochemicals are needed.

The objective of this study was to determine whether odors previously identified in laboratory olfactometer assays as affecting inter- and intra-specific responses of *D. frontalis* and *D. mesoamericanus* produce similar effects on flying insects. In the aforementioned olfactometer tests, both the natural odor blend produced by female attacks of either species (air from female gallery entrances) and two compounds that qualitatively distinguished these odors (*endo*-brevicomin and ipsdienol) elicited strong discrimination by male beetles of both species (Sullivan et al. 2012, Niño-Domínguez et al. 2015). We therefore hypothesized that flying beetles should likewise demonstrate a strong preference for logs infested with female conspecifics, and that the components of the attractive olfactometer blends (including some or all of frontalin, *endo*-brevicomin, ipsdienol, and host odors) might be combined to produce attractive and species-specific trapping lures. Information on cross-attraction and cross-inhibition of odor blends should elucidate the role of specific semiochemicals in attack synchronization, host partitioning, and reproductive isolation between these two species during co-colonization of hosts.

Materials and Methods

Trapping experiments were conducted in a mixed pine-oak forest (with the predominant pine species being *Pinus oocarpa* Shiede and *Pinus maximinoi* H.E. Moore) within Lagunas de Montebello National Park, La Trinitaria, Chiapas, Mexico (16° 07′1.93″ N, 91° 44′ 8.57″ W). The area was experiencing a low-level outbreak of *D. frontalis* and *D. mesoamericanus* in which individual infested trees and flying beetles were present year-round and localized infestations occurred during the fall months.

Trapping Experiments With Synthetic Semiochemicals

Twelve-unit multiple funnel traps (Synergy Semiochemicals, Burnaby, BC, Canada) were suspended from metal poles with the trap bottoms positioned at least 50 cm above of ground. Trap cups contained either a piece of fumigant insecticide strip (VAPORTAPE, Hercon Environmental, Pennsylvania, USA) or a 10:1 solution of water and liquid soap to retain and kill captured insects. Unless noted otherwise, traps were placed >100 m from the nearest *Dendroctonus* spp. infested tree, and >20 m from other pines. Lines of traps composing statistical blocks were >500 m apart, whereas traps within these blocks were 100–200 m apart. Except for the turpentine releasers (which were suspended inside the top funnel), lures were attached midway between top and bottom of each trap. Insects collected from trap cups were preserved in 70% alcohol, and catches of *D. frontalis* and *D. mesoamericanus* were distinguished by the presence of diagnostic striations on the preepisternal area of the prothorax and a reduced mycangium on females of the latter species; beetles were sexed by the prominence of the frontal tubercles in males (Armendáriz-Toledano et al. 2015). The origin, enantiomeric composition, release rate, and purity of lure contents and devices are given in Table 1. When treatment positions were re-randomized, only the lures were moved.

Experiment 1

We compared beetle responses to six different lure combinations of racemic pheromone components and host odors (in the form of turpentine): 1) turpentine + frontalin, 2) turpentine + ipsdienol, 3) turpentine + *endo*-brevicomin, 4) turpentine + frontalin + ipsdienol, 5) turpentine + frontalin + *endo*-brevicomin, and 6) turpentine + frontalin + *endo*-brevicomin + ipsdienol. Three randomized complete blocks (with each block consisting of a line of six traps with one of the six treatments assigned randomly to each) were deployed. Accumulated catches were collected after 11 and 15 d at which time treatment positions were re-randomized without replacement within blocks. A final catch collection was made at 51 d (i.e., lure positions were re-randomized twice). The experiment was executed 7 April to 28 May 2013.

Experiment 2

The six lure treatments of Experiment 1 were re-tested with an additional three: 7) turpentine alone, 8) turpentine + *endo*-brevicomin + ipsdienol, and 9) frontalin + *endo*-brevicomin + ipsdienol. These treatments were included to ascertain the separate

Table 1. Specifications of lures for field trapping experiments

Semiochemical	Abbreviation	Experiment	Source[a]	Purity[b]	Chirality	Release device	Release rate (mg/d)[c]	Temp (°C)[d]
Pheromone component								
Frontalin	F	1, 2	Synergy	>95%	Racemic	Microcentrifuge tube	2.5	23
		3A, 3B	Synergy	>98%	Racemic	Microcentrifuge tube	6	22–24
endo-Brevicomin	E	1, 2	Synergy	>95%	Racemic	Bubble-cap	0.4–0.8	22–24
		3A, 3B	Synergy	93%	Racemic	Flexlure	0.5	25
Ipsdienol	I	1, 2	Synergy	93%	Racemic	Bubble-cap	0.7	25
		3A, 3B	Contech	97%	Racemic	Bubble-cap	1.6	25
		3A, 3B	Contech	>96%	(+3/−97)	Bubble-cap	1.6	25
		3A, 3B	Contech	>96%	(+97/−3)	Bubble-cap	1.6	25
Host volatiles								
Turpentine[e]	T	1, 2, 3A, 3B	Pinosa	–	–	Wick bottle[f]	4 g/d	25

[a] Synergy Semiochemicals Corp., Burnaby, BC; Contech Enterprises (now Scotts), Victoria, BC; Pinosa Inc., Morelia, México.

[b] As provided by manufacturer.

[c] As provided by manufacturer or measured gravimetrically by the authors.

[d] Temperature at which release rate measurements were made.

[e] Turpentine was steam-distilled commercially from *Pinus oocarpa* Schiede ex Schltdl.

[f] Wick bait consisted of a filled 150-ml amber glass bottle with a cotton lamp wick extending 2 cm above the cap.

importance of frontalin and turpentine in producing the observed attraction by *D. mesoamericanus* in Experiment 1 to the four-component blend, and allow comparisons of pheromone-containing lure combinations with those of host odors alone. Three randomized complete blocks (with each block consisting of a line of nine traps with one of the nine treatments assigned randomly to each) were established with >100 m between blocks and >100 m between traps within blocks. Catches were collected daily at which time lure positions were re-randomized without replacement within each block. Nine randomizations/collections were made during the experiment such that every lure treatment was at every trap position for a single day/collection. This procedure resulted in three 9 × 9 Latin squares with traps within each block as columns and collection dates as rows. The experiment was conducted 13–21 November 2013.

Experiment 3

This two-part test was performed to determine the possible effects of the enantiomeric composition of *endo*-brevicomin and ipsdienol on responses to the tested lures. In Experiments 1 and 2, lures of these two compounds were racemic, whereas the enantiomeric compositions produced by female *D. mesoamericanus* are >99% (+) and >95% (+), respectively (Niño-Domínguez et al. 2015). As antipodes of *endo*-brevicomin and ipsdienol, respectively, have been demonstrated to sometimes have antagonistic effects with *Dendroctonus* or *Ips* bark beetles (Vité et al. 1985, Seybold 1993), we wished to see if such antagonism might have affected the outcome of Experiments 1 and 2. Frontalin enantiomers have not been shown to be antagonistic in *Dendroctonus,* including *D. frontalis* (Wood et al. 1976, Payne et al. 1982, Lindgren 1992). In Experiment 3A, the tested lure combinations included turpentine, racemic frontalin, racemic *endo*-brevicomin plus (1) no additional compound, (2) racemic ipsdienol, (3) (+)-ipsdienol, or (4) (−)-ipsdienol. Three randomized complete blocks of four traps each were established, and the experiment was executed as a multiple Latin-square design similar to Experiment 2. Insect collections and lure re-randomizations were performed daily on 1–5 November 2013. In Experiment 3B, the tested lure combinations included turpentine, frontalin, plus (1) racemic *endo*-brevicomin + racemic ipsdienol, (2) (+)-*endo*-brevicomin + racemic ipsdienol, and (3) racemic *endo*-brevicomin + (+)-ipsdienol. Three randomized complete blocks of three traps each were established, and the experiment was executed as a multiple Latin-square design similar to Experiment 2. Insects were collected and treatment positions re-randomized daily for 3 d. The experiment was completed 19–21 of November 2014. (+)-*endo*-Brevicomin was released from a glass capillary (1 mm i.d.) that had the bottom end heat-sealed and was filled to 1 cm below the capillary opening. The capillary was secured open-end-up inside of an open, inverted 4-ml-capacity glass vial (Sullivan and Mori 2009) that was taped to a trap spoke. This device had a release of 0.23 mg/d (at 23±2°C) and the contents were >99% enantiomerically and >95% chemically pure (Sullivan et al. 2007).

Trapping Experiments Using Natural Semiochemical Sources (Experiment 4)

We tested beetle responses to logs (30-cm-long; 12–15 cm diameter) of healthy *P. oocarpa* that were artificially infested with 30 females of either species or left uninfested (three treatments). Females had emerged during the previous 3 d from naturally infested logs collected at the park. Beetles were collected daily as they emerged within cloth bag enclosures, and collected beetles were held in refrigeration on moistened paper wipers before use. To force attacks, beetles were confined by screen disks within evenly distributed pits drilled into the bark (Niño-Domínguez et al. 2015); uninfested control logs received pits but no beetles. After 12–15 h, the screen disks were removed, and the bolts were enclosed in zippered, fine nylon-mesh screen bags to prevent unintended beetle attacks when in the field.

In the field, logs were suspended from pipe standards between two 12-unit multiple funnel traps. Additionally, two black plastic cards (11 by 14 cm) coated with insecticide-impregnated adhesive were also attached on opposite sides of each screen bag at 90° from the funnel traps. Both sticky cards and funnel traps were used to help ensure sufficient captures. Three randomized complete blocks of three log-traps each were established, and the experiment was executed as a multiple Latin-square design similar to Experiment 2. Blocks (and traps within blocks) were arranged as segments of a ring surrounding a small *Dendroctonus* infestation; traps were located between 20–150 m from the nearest infested tree. This intentional placement of traps relatively closer to infested trees was done to help ensure sufficient catches of beetles for statistical analysis. Traps were spaced 25–35 m apart within blocks and >25 m between blocks. Trapped insects were collected (and sticky cards replaced with new) and log treatments were re-randomized daily for 3 d. Captures by the cards and funnel traps were summed for analyses. Within 12 h of the completion of trapping, the infested logs were dissected to determine the numbers of females still present in each treatment.

Statistical Analysis

All insect catches consisted of non-normally distributed data, with many treatments having zero catches. For all analyses of data sets that included zero-catching treatments, we used an $X + 1$ transformation, then a generalized linear model (GLM) analysis. For Experiments 1 and 2, we applied a GLM analysis with blocks and treatment as factors, and for Experiments 3A, 3B, and 4, a GLM analysis with rows, columns, and treatment as factors. Effects of treatment, sex, the interaction between sex and treatment, and the effect of treatment within sex were tested for significance. A Poisson or negative binomial distribution was applied to all data according to best obtained fit. For Experiments 1, 3A, and 4, we used a negative binomial distribution, and for Experiments 2 and 3B, a Poisson distribution. Both analyses used a logarithmic function with $\alpha = 0.05$; these were followed by treatment pairwise contrasts within sex or treatment when sex response was mixed. A Mann–Whitney test was used for pairwise contrasts for sex within each treatment as well as comparisons when one treatment of the contrast caught no insects.

Results

In Experiment 1, *D. frontalis* catches were influenced by treatment ($D = 398.3$, $gl = 678$, $\chi^2_{0.050,\ 5} = 44.6$, $P < 0.001$), sex ($D = 189.5$, $gl = 682$, $\chi^2_{0.050,\ 1} = 5.3$, $P = 0.022$), and a treatment by sex interaction ($D = 420.5$, $gl = 672$, $\chi^2_{0.050,\ 11} = 539.9$, $P < 0.001$). Responses by each sex of *D. frontalis* to traps were significantly affected by lure treatment (for males: $D = 224.7$, $gl = 336$, $\chi^2_{0.050,\ 5} = 72.8$, $P < 0.001$; for females: $D = 193.9$, $gl = 336$, $\chi^2_{0.050,\ 5} = 38.1$, $P < 0.001$). For both sexes, the most attractive lure was the turpentine/frontalin/*endo*-brevicomin combination (Fig. 1). Elimination of either frontalin or *endo*-brevicomin significantly reduced catches of this three-component lure. Addition of ipsdienol to either the turpentine/frontalin or the turpentine/frontalin/*endo*-brevicomin combinations significantly reduced attraction. Males and females were caught in significantly different numbers by lure treatments turpentine/frontalin ($Z = -3.73$, $P < 0.001$), turpentine/frontalin/ipsdienol ($Z = -2.26$, $P = 0.024$), and turpentine/frontalin/*endo*-brevicomin/ipsdienol ($Z = -3.32$, $P = 0.001$); for all of these contrasts, more males than females were trapped. For *D. mesoamericanus* (which were caught in very low numbers; total catch = 16), there was a significant effect just to treatment ($D = 439.8$, $gl = 678$, $\chi^2_{0.050,\ 5} = 34.2$, $P < 0.001$). With sexes combined, there was a significant treatment effect for lure blend ($D = 194.8$; $gl = 336$; $\chi^2_{0.050,\ 5} = 27.5$; $P < 0.001$). *Dendroctonus mesoamericanus* was attracted to the complete mix of turpentine/frontalin/*endo*-brevicomin/ipsdienol in greater numbers than any other tested combination of components (Fig. 2). Elimination of *endo*-brevicomin and/or ipsdienol from this four-component blend significantly reduced beetle attraction. The two lure combinations lacking frontalin caught no *D. mesoamericanus*. Despite the low *P*-values of tests, we recommend caution in interpreting results owing to the very small treatment-associated differences in catches and overall very low beetle catches in this experiment.

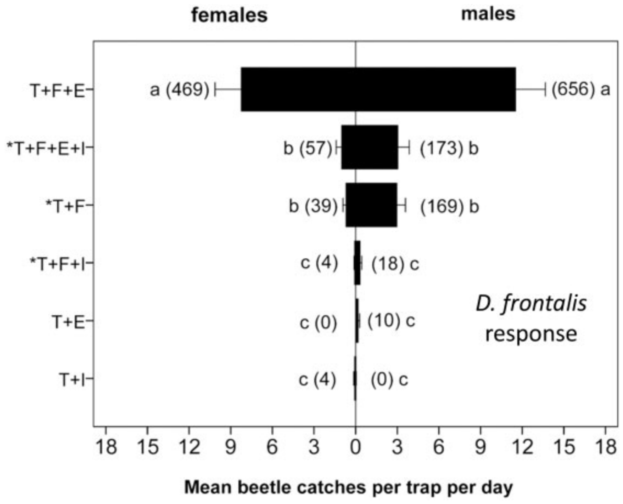

Fig. 1. Mean numbers of *D. frontalis* caught in funnel traps during April-May 2013 in Parque Nacional Lagunas de Montebello, Chiapas, Mexico (Experiment 1). Lures were combinations of frontalin (F), ipsdienol (I), *endo*-brevicomin (E), and turpentine (T). Within sex, treatments associated with the same lowercase letter did not differ significantly. Treatment effects were analyzed with GLM using a negative binomial distribution and a logarithmic function; a Wald test was used for pairwise comparisons between treatment means within each sex ($\alpha = 0.05$). An asterisk associated with a particular lure combination indicates a significant difference in response between the sexes (Mann–Whitney test, $\alpha = 0.050$). Numbers in parentheses indicate raw catches.

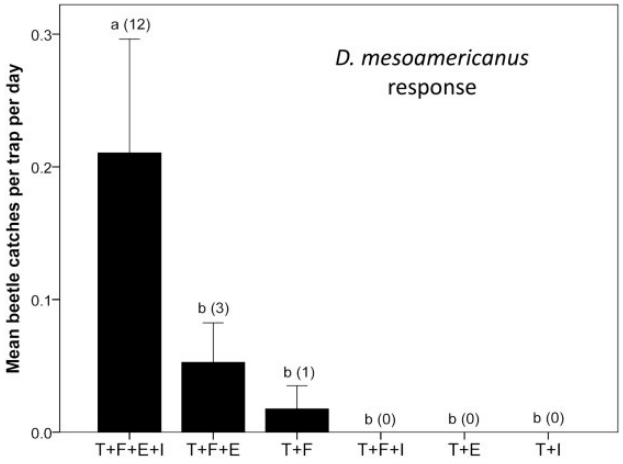

Fig. 2. Mean numbers of *D. mesoamericanus* caught in funnel traps during April–May 2013 in Parque Nacional Lagunas de Montebello, Chiapas, Mexico (Experiment 1). Lures were combinations of frontalin (F), ipsdienol (I), *endo*-brevicomin (E), and turpentine (T). Statistical analysis is same as in figure 1. As there was no sex by treatment interaction, sexes were combined. Treatments associated with the same lowercase letter did not differ significantly. Numbers in parentheses indicate raw catches.

In Experiment 2, there were significant effects for treatment ($D = 48.0$, $gl = 461$; $\chi^2_{0.050,\ 8} = 76.1$, $P < 0.001$), sex ($D = 116.0$, $gl = 468$; $\chi^2_{0.050,\ 1} = 8.1$, $P = 0.004$), and a treatment by sex interaction ($D = 39.1$, $gl = 452$; $\chi^2_{0.050,\ 17} = 85.0$, $P < 0.001$) for *D. frontalis*. Both female ($D = 20.3$, $gl = 38$, $\chi^2_{0.050,\ 8} = 33.3$, $P < 0.001$) and male ($D = 107.5$, $gl = 218$, $\chi^2_{0.050,\ 8} = 112.7$, $P < 0.001$) *D. frontalis* differed significantly in response to different lure blends, and, as in Experiment 1, the blend turpentine/frontalin/*endo*-brevicomin was more attractive to either sex of *D. frontalis* than the other

Table 2. Mean (±SE) catches of *D. frontalis* and *D. mesoamericanus* (per trap/day) in funnel traps baited with combinations of synthetic semiochemicals during November 2013 at Parque Nacional Lagunas de Montebello, Chiapas, Mexico (Experiment 2)

Lure[a]	*D. frontalis*		*D. mesoamericanus*	
	Females	Males	Females	Males
T	0.00 ± 0.00 (0)c	0.00 ± 0.00 (0)c	0.00 ± 0.00 (0)	0.00 ± 0.00 (0)
T + F	0.04 ± 0.04 (1)c*	0.52 ± 0.19 (14)bc	0.04 ± 0.04 (1)	0.00 ± 0.00 (0)
T + I	0.00 ± 0.00 (0)c	0.00 ± 0.00 (0)c	0.04 ± 0.04 (1)	0.04 ± 0.04 (1)
T + E	0.04 ± 0.04 (1)c	0.07 ± 0.05 (2)c	0.00 ± 0.00 (0)	0.04 ± 0.04 (1)
T + F + I	0.00 ± 0.00 (0)c	0.07 ± 0.05 (2)c	0.04 ± 0.04 (1)	0.04 ± 0.04 (1)
T + F + E	1.70 ± 0.50 (46)a*	5.00 ± 0.90 (136)a	0.04 ± 0.04 (1)	0.07 ± 0.05 (2)
T + E + I	0.04 ± 0.04 (1)c	0.04 ± 0.04 (1)c	0.00 ± 0.00 (0)	0.00 ± 0.00 (0)
T + F + E + I	0.30 ± 0.10 (8)b	0.89 ± 0.38 (24)b	0.00 ± 0.00 (0)	0.04 ± 0.04 (1)
F + E + I	0.00 ± 0.00 (0)c	0.22 ± 0.10 (6)bc	0.00 ± 0.00 (0)	0.00 ± 0.00 (0)

Numbers in parentheses indicate raw insect catches. Within sex and species, treatments associated with the same lowercase letter did not differ significantly (GLM with a Poisson distribution and logarithmic function followed by a Wald test for pairwise comparisons between treatments within sex; $\alpha = 0.05$), and an asterisk indicates significant differences in catches between the two sexes (Mann–Whitney test, $\alpha = 0.05$). No significant treatment effects were detected for *D. mesoamericanus*.

[a] T, turpentine; F, frontalin; I, ipsdienol; E, *endo*-brevicomin.

combinations (Table 2). Elimination of either frontalin or *endo*-brevicomin, or the addition of ipsdienol, significantly reduced attraction of either sex to this three-component mixture. Turpentine by itself was unattractive to *D. frontalis*, whereas elimination of this host kairomone from the four-component lure (turpentine/frontalin/*endo*-brevicomin/ipsdienol) significantly reduced catches of females. Significant differences in male and female catches were detected for the turpentine/frontalin/*endo*-brevicomin ($Z = 2.536$, $P = 0.011$) and turpentine/frontalin treatments ($Z = -2.575$, $P = 0.010$) to which significantly more males than females responded. For *D. mesoamericanus,* there was no significant treatment, sex, or treatment/sex interaction effect (Table 2). However, catches of *D. mesoamericanus* were extremely low (two or fewer beetles were trapped by any lure treatment).

In Experiment 3A, there was a significant effect for treatment ($D = 23.6$, $gl = 86$, $\chi^2_{0.050,\,3} = 12.6$, $P = 0.005$), sex ($D = 30.8$, $gl = 88$, $\chi^2_{0.050,\,1} = 5.4$, $P = 0.020$), and a treatment by sex interaction ($D = 18.3$, $gl = 82$, $\chi^2_{0.050,\,7} = 17.9$, $P = 0.012$) where both sexes of *D. frontalis* (for females: $D = 20.3$, $gl = 38$, $\chi^2_{0.050,\,3} = 16.749$, $P = 0.001$; for males: $D = 11.4$, $gl = 38$, $\chi^2_{0.050,\,3} = 23.982$, $P < 0.001$) showed significant preferences for treatment blends. Both racemic and (+)-ipsdienol reduced the attraction of both sexes of *D. frontalis* to the blend of turpentine, frontalin, and *endo*-brevicomin, whereas (−)-ipsdienol had no effect on male catches but reduced catches of females (Table 3). The Mann–Whitney *U* test did not detect differences between male and female catches within any treatment. For *D. mesoamericanus* catches, there were no significant effects for treatment or sex, but there was a significant treatment by sex interaction ($D = 64.9$, $gl = 82$; $\chi^2_{0.050,\,7} = 14.2$, $P = 0.042$), and male catches demonstrated a significant treatment effect ($D = 35.6$, $gl = 38$; $\chi^2_{0.050,\,3} = 10.310$, $P = 0.016$). For males, the blend of turpentine, frontalin, *endo*-brevicomin, and ipsdienol was more attractive when the ipsdienol was the (−)-enantiomer (trapping five insects) rather than the (+)-enantiomer or the racemate (which caught no beetles).

In Experiment 3b, there was a significant effect of sex for *D. frontalis* captures ($D = 39.6$, $gl = 48$; $\chi^2_{0.050,\,1} = 4.6$, $P = 0.037$; with more males being trapped), but no effect of lure treatment, nor a treatment by sex interaction. For *D. mesoamericanus,* there was no effect owing to treatment, sex, or a treatment by sex interaction. However, catches were extremely low for both sexes (only—one to two insects per treatment; Table 3).

In Experiment 4, both species discriminated among log treatments used as trap lures. For *D. frontalis* (Fig. 3), there was a significant effect for log treatment ($D = 13.1$; $gl = 47$; $\chi^2_{0.050,\,2} = 6.49$, $P = 0.039$) but no sex effect or sex by treatment interaction. With sexes summed, there was likewise a significant effect for log treatment ($D = 10.5$; $gl = 20$; $\chi^2_{0.050,\,2} = 9.34$, $P = 0.009$), with higher numbers of *D. frontalis* trapped at logs infested with *D. mesoamericanus* females than at either *D. frontalis* female-infested logs or uninfested logs ($\chi^2_{0.050,\,2} = 14.2$, $P = 0.001$), and these latter two treatments did not differ significantly in their catches. *Dendroctonus mesoamericanus* catches (Fig. 4) were affected by treatment ($D = 44.8$, $gl = 47$, $\chi^2_{0.050,\,2} = 40.2$, $P < 0.001$), sex ($D = 37.6$, $gl = 48$, $\chi^2_{0.050,\,1} = 8.65$, $P = 0.003$), and a treatment by sex interaction ($D = 2.34$, $gl = 44$, $\chi^2_{0.050,\,5} = 70.3$, $P < 0.001$). Females were trapped in very low numbers and there was no significant effect for log treatment ($D = 15.6$, $gl = 20$, $\chi^2_{0.050,\,2} = 1.84$, $P = 0.398$). However, males strongly discriminated among log treatments ($D = 22.9$, $gl = 20$, $\chi^2_{0.050,\,2} = 25.9$, $P < 0.001$), with higher catches at conspecific female-infested logs than at either *D. frontalis* female-infested or uninfested logs (neither of which caught *D. mesoamericanus*). Significantly more male than female *D. mesoamericanus* were trapped at logs infested with conspecific females ($Z = -2.800$, $P = 0.011$). Within 12 h of completion of the experiment, 23–27 females were still present within nuptial chambers of the bait logs for either species.

Discussion

Our study detected differences in the response of flying *D. frontalis* and *D. mesoamericanus* to synthetic or natural pheromone sources, and these results are consistent with the hypothesis that the two species have differing colonization strategies when they are co-infesting trees. *Dendroctonus mesoamericanus* was previously shown to be attracted to the lure combination of (±)-frontalin, (±)-*endo*-brevicomin, and turpentine (Moreno 2008), and our data suggest that (±)-ipsdienol may further enhance this combination as a trap lure for this species. This effect was detected in only one test (Experiment 1), which had very low catches. The effect was not observed in Experiments 2 and 3a, which included this same treatment contrast but trapped even fewer insects. Similar attractive responses were observed in two of three laboratory assays in which attraction of walking male *D. mesoamericanus* was enhanced when

Table 3. Mean (±SE) catches of *D. frontalis* and *D. mesoamericanus* (per trap/day) in funnel traps baited with combinations of synthetic semiochemicals during November 2013 in Parque Nacional Lagunas de Montebello, Chiapas, Mexico (Experiment 3)

Lure	*D. frontalis*		*D. mesoamericanus*	
	Female	Male	Female	Male
Experiment 3A				
T + F + E[a]	1.5 ± 0.6 (18)a	3.5 ± 1.0 (42)a	0.2 ± 0.1 (2)	0.2 ± 0.1 (2)ab
T + F + E + I (±)	0.0 ± 0.0 (0)c	0.7 ± 0.3 (8)b	0.2 ± 0.2 (2)	0.0 ± 0.0 (0)b
T + F + E + I (+)	0.2 ± 0.1 (2)bc	0.4 ± 1.5 (5)b	0.0 ± 0.0 (0)	0.0 ± 0.0 (0)b
T + F + E + I (−)	0.8 ± 0.4 (9)b	3.3 ± 1.5 (40)a	0.0 ± 0.0 (0)	0.4 ± 0.2 (5)a
Experiment 3B				
T + F + E (±) + I (±)	0.1 ± 0.1 (1)	0.2 ± 0.2 (2)	0.1 ± 0.1 (1)	0.2 ± 0.2 (2)
T + F + E (+) + I (±)	0.2 ± 0.2 (2)	0.4 ± 0.4 (4)	0.0 ± 0.0 (0)	0.2 ± 0.2 (2)
T + F + E (±) + I (+)	0.1 ± 0.1 (1)	0.8 ± 0.8 (7)	0.2 ± 0.2 (2)	0.0 ± 0.0 (0)

Numbers in parentheses indicate raw insect catches. Within sexes and species, treatments associated with the same letter did not differ significantly [GLM with a negative binomial or Poisson distribution (in Experiments 3A and 3B, respectively) with a logarithmic function followed by a Wald test for comparisons between treatments within sex; α = 0.05]. No significant treatment effects were detected for either species in Experiment 3B.

[a] T, turpentine; F, frontalin; I, ipsdienol; E, *endo*-brevicomin.

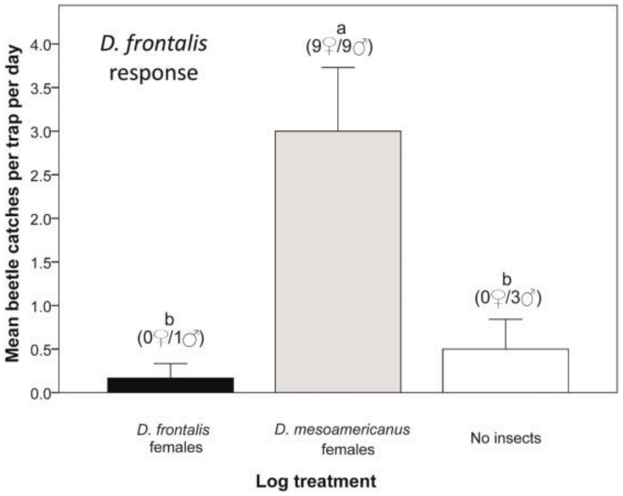

Fig. 3. Numbers of *D. frontalis* caught in traps baited with either female-infested or uninfested logs during December 2013 in Parque Nacional Lagunas de Montebello, Chiapas, Mexico (Experiment 4). Bait logs were each infested with 30 females of either species; uninfested control logs had 30 mechanical drill holes but no insects. Numbers in parentheses indicate raw catches. There was no significant treatment by sex interaction, therefore sexes were combined for analyses (GLM with a Poisson distribution and logarithmic function followed by a Wald test for pairwise comparisons between treatments within sex; α = 0.05). Treatments labeled with the same lowercase letter did not differ significantly within sex.

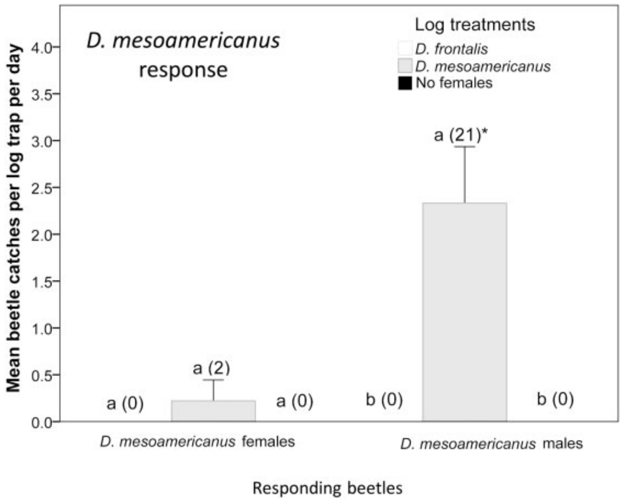

Fig. 4. Numbers of *D. mesoamericanus* caught in traps baited with either female-infested or uninfested logs during December 2013 in Parque Nacional Lagunas de Montebello, Chiapas, Mexico (Experiment 4). Details as in Figure 3. An asterisk indicates a significant difference between sexes in their response to the indicated treatment (Mann–Whitney test, α = 0.050).

(±)-ipsdienol was added to this same three-component blend of frontalin, *endo*-brevicomin, and host odors (i.e., racemic *alpha*-pinene; Niño-Domínguez et al. 2015).

For *D. frontalis,* the results of Experiments 1 and 2 resemble those of previous studies that demonstrated synergism among frontalin, *endo*-brevicomin, and host odors as trap lures for both sexes of *D. frontalis* in the southeastern United States (Vité et al. 1985, Sullivan et al. 2007) and in Chiapas, Mexico (Moreno et al. 2008). Additionally, both racemic and (+)-ipsdienol substantially reduced responses of one or both sexes of *D. frontalis* to attractive blends (i.e., turpentine and frontalin, either with or without *endo*-brevicomin; Experiments 1, 2, and 3a), whereas the (−)-enantiomer reduced responses of females but not males (Experiment 3a). Ipsdienol has been found in paired male *D. frontalis* in Chiapas (Sullivan et al. 2012) and Arizona (B.T.S. unpublished data), but it has not been reported from populations in the eastern United States (Sullivan et al. 2011). Our study represents the first evidence that ipsdienol is an attraction inhibitor for *D. frontalis* and, as it can be produced by *D. frontalis*, that it could possibly function as an antiaggregation pheromone component for this species. Ipsdienol has previously been identified in just two additional species of *Dendroctonus* (*D. brevicomis* LeConte and *D. ponderosae* Hopkins) and, as with *D. frontalis*, only in males (Byers 1982, Hunt et al. 1986). For both species, ipsdienol inhibits response to attractant baited traps, and it may likewise be an antiaggregation pheromone for them (Byers 1982, Hunt and Borden 1988). *Dendroctonus mesoamericanus* thus appears to be unique in that ipsdienol is produced predominantly by females (Sullivan et al. 2012) and may enhance rather than reduce attraction of conspecifics. The inhibition of attraction by ipsdienol may additionally mediate *D. frontalis* avoidance of pines being attacked by potentially competing species of *Ips* that produce ipsdienol (Hofstetter et al. 2012). For example, the range of *Ips* *calligraphus* (Germar) includes Montebello Park (Wood 1982; authors' observations), and populations of this species in the southeastern United States are reported to produce 21% (+)-ipsdienol (Birgersson et al. 2012).

As ipsdienol appears to have opposite effects on flying individuals of either species, this semiochemical could promote spatial separation of attacks and landings by the two species and thereby play some role in mediating partitioning of the host resource between them. Also, as ipsdienol is produced by female *D. mesoamericanus* but not by female *D. frontalis*, it could mediate avoidance by flying males of portions of the bole with solitary females of the other species. Laboratory olfactometer assays indicated that ipsdienol (in addition to *endo*-brevicomin) likely plays a parallel role for males after landing on the host in allowing them to discriminate gallery entrances of con- and heterospecific females (Niño-Domínguez et al. 2015). Thus, the interspecific difference in response to ipsdienol by both flying and walking males could presumably enhance reproductive isolation (Niño-Domínguez et al. 2015). Our results also imply that the presence or absence of ipsdienol in trapping lures would provide some capacity to target either *D. mesoamericanus* or *D. frontalis,* respectively.

The aggregation pheromone of *D. frontalis* includes both frontalin and (+)-*endo*-brevicomin, with the latter being contributed by males (Vité et al. 1985, Sullivan et al. 2007). Consequently, attacks by *D. frontalis* pairs can be substantially more attractive to conspecifics than attacks by solitary females (Sullivan et al. 2007, but see Svihra 1982). One possible mechanism for the preference of flying *D. frontalis* for odors of female *D. mesoamericanus* attacks in logs is that female *D. mesoamericanus* produce these two components of the aggregation pheromone for *D. frontalis* (i.e., female-produced frontalin and male-produced (+)-*endo*-brevicomin; Sullivan et al. 2012, Niño-Domínguez et al. 2015), whereas female *D. frontalis* produce only frontalin. However, in trapping Experiments 1 and 2, ipsdienol released at approximately an equal rate as *endo*-brevicomin nullified the synergistic effect of the latter on catches of *D. frontalis*. As female *D. mesoamericanus* release ipsdienol and *endo*-brevicomin at similar rates (Niño-Domínguez et al. 2015), these data would suggest that production of *endo*-brevicomin by *D. mesoamericanus* is not a sufficient explanation for the greater attraction of *D. frontalis*. One should note that it is possible that *D. frontalis'* greater attraction to *D. mesoamericanus*-infested logs might not have occurred if the logs had been infested with both sexes rather than females alone, and future experiments should investigate this.

The preference by flying *D. frontalis* males for odors of female *D. mesoamericanus* over female conspecifics is the reverse of what was observed in a walking olfactometer study in which odors of conspecific female attacks were strongly preferred by males of each respective species (Niño-Domínguez et al. 2015). Again, this contrast was possibly owing to the production of *endo*-brevicomin by *D. mesoamericanus* females. *endo*-Brevicomin can disrupt attractive responses by walking male *D. frontalis* over a range of doses (Rudinsky et al. 1974, Niño-Domínguez et al. 2015), despite its capacity to be a potent attractive synergist for flying *D. frontalis* (Sullivan et al. 2011). The preference of male *D. frontalis* while walking but not in flight for odors of unpaired conspecific females suggests that semiochemical-mediated location of potential mates by male *D. frontalis* occurs predominantly following landing on the host. Before landing, a positive response to *endo*-brevicomin likely functions in bringing male *D. frontalis* to a host tree undergoing mass attack by either one or both species and thus to a location where mates and food are present.

Flying male *D. mesoamericanus* showed no cross-attraction to traps baited with *D. frontalis* female-infested logs, and, likewise, *D. mesoamericanus* were not attracted to traps baited with synthetic odor blends associated with *D. frontalis* females (i.e., frontalin with host odors alone; Sullivan et al. 2012; present study, but with caution advised owing to low catches in the relevant experiments). This preference shown by flying *D. mesoamericanus* resembled the strong preference of walking male *D. mesoamericanus* for odors of conspecific female entrances in olfactometer studies (Niño-Domínguez et al. 2015). In these olfactometer studies, *D. mesoamericanus* males displayed minimal attraction to odors of *D. frontalis* females, and evidence indicated that this was owing to the absence of ipdienol and *endo*-brevicomin in association with entrances of *D. frontalis* females. The apparently enhanced attraction of *D. mesoamericanus* by ipsdienol and *endo*-brevicomin lures in Experiment 1 is consistent with the hypothesis that these two compounds mediated discrimination of female-infested logs by flying *D. mesoamericanus*.

In the genus *Dendroctonus*, the female is responsible for selecting new hosts, and she initiates a mass attack through release of all or part of the aggregation pheromone. The results of the trap-log study imply that both *D. frontalis* and *D. mesoamericanus* should be more attracted to such "pioneer" attacks by *D. mesoamericanus* females than those of *D. frontalis* females. This would suggest that pioneer attacks by female *D. mesoamericanus* might possess a significantly greater likelihood of success in initiating mass attacks by one or both species and accelerate colonization. In trees that are jointly colonized, however, it is not yet known if one species predominantly initiates the mass-attack.

Our study utilized racemic frontalin and *endo*-brevicomin in all tests except in Experiment 3b (which attempted to compare beetle response to (+)-*endo*-brevicomin and the racemate); however, catches were too low to be informative. This test was done to determine whether the use of the racemate rather than solely the (+)-enantiomer (as produced by females of both species) might be one possible reason for low attraction of *D. mesoamericanus* to synthetic lures. Although the enantiomeric ratios of both frontalin and *endo*-brevicomin produced by *D. frontalis* depart strongly from racemic ($\geq$85% (−) frontalin and >99% (+)-*endo*-brevicomin; Payne et al. 1982, Sullivan et al. 2007, Niño-Domínguez et al. 2015), published data suggest that behavioral responses of this species differ little if at all when either the racemic mixture or the insect-produced enantiomeric ratio are used in trap lures (Payne et al. 1982, Vité et al. 1985, Sullivan and Mori 2009, Sullivan et al. 2011). The effect of the use of racemic lure components with *D. mesoamericanus* remains unknown as is the reason, more generally, why the experiments here as well as others performed with synthetic lure blends have to date trapped so few *D. mesoamericanus*.

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