Attractant and Disruptant Semiochemicals for *Dendroctonus jeffreyi* (Coleoptera: Curculionidae: Scolytinae)

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ABSTRACT Jeffrey pine, *Pinus jeffreyi* Greville and Balfour, is a dominant yellow pine and important overstory component of forests growing on diverse sites from southwestern Oregon to Baja California to western Nevada. The Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins (Coleoptera: Curculionidae: Scolytinae), is monophagous on Jeffrey pine and its primary insect pest. Despite the importance of *P. jeffreyi*, difficult terrain, environmental concerns, and lack of roads can constrain pest management activities. Semiochemicals are often easier to apply and more environmentally acceptable than other options, but they are lacking in this system. Attractants have been identified, but field bioassays have been limited because of infrequent or short duration outbreaks and a lack of beetles during nonoutbreak periods. Disruptant semiochemicals have not been assessed for *D. jeffreyi* during outbreak conditions; however, commercially available semiochemicals have been implicated as disruptants for this bark beetle. The objective of this study was to identify the most effective commercially available attractant and disruptant semiochemicals for *D. jeffreyi*. Our highest observed catch occurred with the blend of 5% 1-heptanol and 95% n-heptane. When this was used to challenge potential disruptant semiochemicals, the combination of S-(-)-verbenone and the green leaf volatile blend (*cis*-3-Hexenol and 1-Hexanol) reduced trap catch by ≈80%. However, frontalin was most effective, reducing the number of *D. jeffreyi* caught by >96%. Within each year of the study, the percentage female of *D. jeffreyi* caught with our attractant decreased from start to end of the experimental period. On average, our first collection in a year (mid-June to early July) was 59% female, whereas our last (mid-August) was 34%. Frontalin was equally or more effective against females (the pioneering sex) than males, providing optimism that semiochemical disruption may be possible for protecting Jeffrey pines from *D. jeffreyi*.

KEY WORDS *Pinus jeffreyi*, tree protection, frontalin, pheromone, green leaf volatiles

Jeffrey pine, *Pinus jeffreyi* Greville and Balfour, is an important overstory component of forests in California and throughout its natural range, which extends from southwestern Oregon to northern Baja California and east to western Nevada (Jenkinson 1990). It competes well on cold, harsh sites (Jenkinson 1990) and large, high-value specimens enhance some of the most popular recreational areas in northern California. The Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins 1909 (Coleoptera: Curculionidae: Scolytinae), is monophagous on Jeffrey pine and its primary insect pest (Smith et al. 2009). Populations of *D. jeffreyi* exhibit extreme "boom-or-bust" cycles, causing high levels of host mortality during extended droughts (Smith et al. 2009), but being limited in numbers at other times, as indicated by catches in attractant-baited traps or lack of host mortality (Renwick and Pitman 1979, Paine et al. 1999). During the late 2000s, increased host mortality caused by *D. jeffreyi* in the Lake Tahoe region provided an abundant population of beetles for practical measurement of semiochemical effects.

Numerous semiochemicals have been applied in forested ecosystems to mediate the host selection process of insects (Borden 1993). Insect host selection has been described as a catenary process with five steps: host-habitat finding, host finding, host recognition, host acceptance, and host suitability (Kogan 1994). It culminates in reproduction, after acceptance or rejection of a resource by each insect (Kennedy 1965, Miller and Strickler 1984). Semiochemicals may mediate the process; for example, attractants may enhance or focus host finding and disruptants may prevent its completion. Disruption may occur at any step, and via any one or more sensory modalities (gustation, hearing, olfaction, vision); this is an implicit goal of pest management. Other terms have been used to describe this primarily olfactory phenomenon with bark beetles (antiattractant, antiaggregant, inhibitor); we use disruptant because it remains descriptive across sensory modalities, uses a host selection framework, and consistently refers to individuals. Semio-

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chemicals deployed as disruptants for bark beetles usually target host finding (or trap finding, a surrogate). Commercial products with activity against multiple species of *Dendroctonus* are available, but they have not been measured with *D. jeffreyi.*

Similar to other *Dendroctonus*, *D. jeffreyi* uses semiochemicals to promote mass attack of its host, a necessity for overwhelming host tree defenses, colonization, and beetle reproduction. Potential attractant semiochemicals for *D. jeffreyi* have been identified, but field bioassays have been limited by infrequent or short duration outbreaks and a paucity of beetles during nonoutbreak years. Based on concentrations present in hindgut tissues, Pitman et al. (1969) list brevicomin as a major component in male *D. jeffreyi* and *trans*-verbenol as a major component in females. They list minor components as *trans*-verbenol in males and *cis*-verbenol and brevicomin in females. Paine et al. (1999) more recently identified the brevicomin in male *D. jeffreyi* as (+)-*exo*-brevicomin, but they did not detect it in females. Verbenone is produced by male *D. jeffreyi* (Pitman et al. 1969) and is also present in host volatiles (Shepherd et al. 2008). Attacking female beetles (the pioneering sex in *Dendroctonus*) have the pheromones 1-heptanol and 2-heptanol as major components (Renwick and Pitman 1979). These pheromones are oxidized products of n-heptane, which accounts for ≈95% of the volatile component of host oleoresin (Smith 2000). Renwick and Pitman (1979) found that 1-heptanol, in combination with n-heptane, was attractive to *D. jeffreyi*, whereas 2-heptanol was not. However, this observation was based on only 128 beetles trapped during their 6-wk study. Paine et al. (1999) confirmed the attraction of 1-heptanol and n-heptane to *D. jeffreyi* at apparently low beetle populations, and also found that female catch was enhanced by the addition of racemic *exo*-brevicomin.

With the possible exception of frontalin (Paine et al. 1999), disruptant semiochemicals have not been specifically identified for *D. jeffreyi.* Frontalin is common in *Dendroctonus*, is produced by male *D. jeffreyi* (Paine et al. 1999, Hall et al. 2002), and was found to reduce trap catch of females (but not males) when attractant-baited traps caught relatively low numbers (2.8 beetles per day; Paine et al. 1999). Verbenone disrupts multiple *Dendroctonus* species, including *D. valens* LeConte (Gillette et al. 2001) and *D. ponderosae* Hopkins (Ryker and Yandell 1983), a species closely related to *D. jeffreyi* (Hopkins 1909). The so-called nonhost or green leaf volatiles (GLV herein; see Zhang and Schlyter 2004 for review) have broad-spectrum activity with scolytids, often synergizing the effects of verbenone or allowing reduced dosages to be deployed (e.g., Wilson et al. 1996, Borden et al. 1998, Zhang and Schlyter 2004). Verbenone holds a United States Environmental Protection Agency registration for use against some species of bark beetles and GLV blends are available from commercial vendors for research purposes.

Consistent efficacy is a major concern with deploying disruptant semiochemicals against bark beetles, but the localities in which Jeffrey pines occur make them an attractive option for protecting high-value resources threatened by *D. jeffreyi.* Spraying of tree boles with synthetic insecticides is generally effective against *Dendroctonus* bark beetles in western North America (Haverty et al. 1998, Fettig et al. 2006) and carbaryl, in particular, has shown toxic activity to *D. jeffreyi* in log assays (Smith 1982). In addition, circumstantial evidence suggests that bole sprays are effective for protecting host trees against *D. jeffreyi* (Smith et al. 2009), but difficulties remain for areas in which this is not a viable treatment option. Prevention of *D. jeffreyi* impacts through thinning can be effective at the stand level (Egan et al. 2011); however, a more targeted, specific tree method is sought for high-value trees when acutely threatened. In addition, significant limitations exist to the application of either bole sprays or thinning treatments to *P. jeffreyi* (e.g., terrain, environmental concerns), making the identification of an effective disruptant semiochemical a pest management priority for this system.

The objective of this study was to assess semiochemicals for manipulating *D. jeffreyi* in areas with significant, current beetle-caused mortality of Jeffrey pine. These environmental conditions were available during the late 2000s with increased activity of *D. jeffreyi* in the Lake Tahoe region. We performed four sequential funnel trap bioassay experiments to identify the best attractant for *D. jeffreyi* and then used it to measure commercially available disruptants, including S-(-)-verbenone, GLV (a blend of *cis*-3-Hexenol and 1-Hexanol), and frontalin. Nontarget effects on insect behavior are of interest when semiochemicals are deployed, so common insect predators and other *Dendroctonus* species also were tallied from trap collections.

Materials and Methods

Experiments were conducted in California, near Lake Tahoe on the Lake Tahoe Basin Management Unit and the Humboldt-Toiyabe National Forest (both USDA Forest Service) at Luther Pass (elevation ≈2,358 m). Forests in the area were dominated by mixed conifer and second-growth Jeffrey pine stands, consisting of large trees (>50 cm diameter breast height) growing singly or in small clusters. From 2006 to 2008, droughty conditions in the area (monthly Palmer Drought Index ranged from −0.28 in May of 2006 to −3.48 in February of 2009; http://www1.ncdc.noaa.gov/pub/data/cirs/drd964x.pdsi.txt) coincided with increased tree mortality caused by *D. jeffreyi* from 2006 to 2009 (4.2 trees per hectare, Aerial Detection Monitoring Program, USDA Forest Service, Region 5, Forest Health Protection, Vallejo, CA; http://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046696) and provided suitable conditions for measuring semiochemicals for their potential in managing *D. jeffreyi.*

A series of four experiments was conducted from 2007 to 2009 to measure attractant and disruptant effects of semiochemicals for *D. jeffreyi;* each exper-

Table 1. Estimated average release rates of semiochemicals from devices used in this study

Device	Chemical	Test Location[b]	Dates	Test Duration	Temperature[a]	Mass Loss/d
250-ml bottle (Lure A)[c]	95:5 heptane: heptanol	Luther Pass, CA	19 July-16 Aug. 2007	29 d	18.7[d]	≈1 g
Synergy 16-ml bottle[e]	Heptane	Pineville, LA	17 April–4 May 2007	≈2 wk	20.2	≈550 mg
APT[f]	95:5 heptane: heptanol	Pineville, LA	31 Aug.–7 Sept. 2007	≈1 wk	26.2	1.01 g[g]
Synergy high heptanol	Heptanol	Pineville, LA	31 Aug.–25 Oct. 2007	≈2 mo	23.7	≈60 mg
Synergy low heptanol	Heptanol	Pineville, LA	31 Aug.–25 Oct. 2007	≈2 mo	23.7	<10 mg
Synergy *exo*-brevicomin[h]	*exo*-brevicomin	Synergy laboratory	—-	—-	20	125 μg
Synergy pouch[i]	Verbenone	Missoula, MT	5 June–21 Sept. 2007	80 d	20.1	66 mg[g]
Synergy pouch[j]	GLV	Missoula, MT	5 June–21 Sept. 2007	80 d	20.1	97 mg[g]
Synergy microcentrifuge tubes[k]	Frontalin	Pineville, LA	6 April–7 June 2007	62 d	17.6	6.8 mg[g]

Data were obtained during their use in these experiments, from other field-generated assessments, or from device suppliers.

[a] Average in degrees Celsius.

[b] Pineville, LA and Missoula, MT data taken from http://www.fs.fed.us/foresthealth/technology/elutionrate/lure.htm.

[c] Nalgene HDPE bottle, Thermo Fisher Scientific, Rochester, NY.

[d] From weatherunderground.com for listed dates; Tahoe Vista, CA, elevation 1,935 m. Accessed 13 Nov. 2007.

[e] Synergy Semiochemicals, Corp., Burnaby, BC, Canada.

[f] APTIV, Inc., Portland, OR.

[g] Full sun rate (http://www.fs.fed.us/foresthealth/technology/elutionrate/lure.htm).

[h] MPB flex lure, rate supplied by Synergy Semiochemicals, Inc.

[i] S-(-)-verbenone pouch with 7.5-g load.

[j] GLV pouch with 10 g of the green leaf volatile blend *cis*-3-Hexenol and 1-Hexanol (Synergy Semiochemical, Corp., personal communication).

[k] SPB lure, 600-mg load as two tubes with 300 mg each of racemic frontalin.

iment built on results garnered previously in the series. All experiments used 12-unit multiple-funnel traps (Lindgren 1983), located individually and at least 0.16 km apart to assure independence (Shea et al. 1984); each trap was considered an independent experimental unit. Traps were deployed in a transect extending ≈5 km along California State Route 89, with the timing of initial setup each year based on twice-monthly observations of *D. jeffreyi* phenology in nearby trees. Treatments were assigned to trap locations using a completely randomized design and left in-place for the duration of the experiment (4–7 wk). A piece of No Pest Strip ≈2.5 cm square (Dichlorvos 18.6%, Hot Shot, St. Louis, MO) was inserted into each collecting cup to kill captured insects. Trap contents were collected approximately weekly, transported to our laboratory, and frozen until evaluation. The sex of each intact *D. jeffreyi* was determined by observing the dorsal, posterior margin of the penultimate abdominal tergite, which in males is used for stridulating and is angular and more heavily sclerotized (Lyon 1958). In addition to *D. jeffreyi*, we counted *Temnochila chlorodia* Mannerheim and associated *Dendroctonus*, most notably the red turpentine beetle, *Dendroctonus valens* LeConte. Clerids, including *Enoclerus lecontei* Wolcott and *E. sphegeus* F., were sparse in our samples and were counted collectively as Cleridae.

Release of semiochemicals from passive elution devices was estimated from mass or volume lost. We measured all semiochemical release devices, excepting *exo*-brevicomin, which lost too little mass to measure accurately; its release rate was provided by Synergy Semiochemicals, Corp., Burnaby, BC, Canada (Table 1). Release of the attractant blend in experiment 2 was determined by volume lost from bottles during the experiment. Other devices were measured in a separate field setting either in Missoula, MT or Pineville, LA (Table 1).

Experiment 1 was conducted from 15 June to 18 July 2007 and measured five semiochemical attractant treatments: blended heptane and heptanol (95:5 vol:vol) (APT; APTIV, Inc., Portland, OR); high release heptanol with heptane bottle (HRHH); high release heptanol, heptane bottle, and *exo*-brevicomin (HRHHE); low release heptanol and heptane bottle (LRHH); and low release heptanol, heptane bottle, and *exo*-brevicomin (LRHHE) (all from Synergy Semiochemicals, Corp.; Table 1). The blended APT lure required weekly replacement and heptane bottles (16 ml; Synergy Semiochemicals, Corp.) were refilled as needed with n-heptane (99%+, Acros Organics, Geel, Belgium). Twenty-five traps were deployed, providing five replicates per treatment. The experimental design also allowed for comparisons between treatments with high versus low heptanol and presence or absence of *exo*-brevicomin.

Experiment 2 was conducted later in 2007 (19 July to 16 August) and measured the disruptant effect of S-(-)-verbenone (BeetleBlock 7.5 g, Synergy Semiochemicals, Corp.) + GLV (a 10-g blend of *cis*-3-Hexenol and 1-Hexanol, Synergy Semiochemicals, Corp.) on *D. jeffreyi*. Both components disrupt host finding of a number of scolytid species, including *D. ponderosae*, although typically the GLV blend is more effective as an additive to verbenone than alone (Borden et al. 1998). Because there is no information on semiochemical disruption of *D. jeffreyi* (beyond the possibility of frontalin), we used components of the best available generic disruptant combination for pine-infesting *Dendroctonus*. The attractant lure in this experiment (Lure A) was an improved version of the APT lure from experiment 1, and was the same for all traps. It consisted of a 250-ml brown bottle (Nalgene HDPE bottle, Thermo Fisher, Inc., Rochester, NY), loaded with 100 ml of blended (95:5 vol:vol) n-heptane (99%+, Acros Organics): heptanol (99%, Alfa-

Aesar, Ward Hill, MA). A single hole (0.36 cm) was drilled into the cap for semiochemical emission. This provided a release rate similar to that of the APT lure in experiment 1 (Table 1), but one that did not require weekly replacement during the experiment. Twenty-four traps were deployed, providing 12 replicates per treatment.

The final two experiments were conducted in 2008 (experiment 3) and 2009 (experiment 4), and included racemic frontalin (Synergy Semiochemicals, Corp.), a common *Dendroctonus* pheromone and one that was indicated previously as a disruptant for *D. jeffreyi* (Paine et al. 1999). In 2008, we deployed traps from 24 June to 5 August. Semiochemical treatments were: Lure A, Lure B (75:25 n-heptane: l-heptanol blend), Lure A + verbenone (two pouches), Lure A + verbenone + GLV (one pouch each), and Lure A + frontalin (600-mg southern pine beetle load [2 microcentrifuge tubes at 300 mg each]). Each treatment was replicated five times for a total of 25 traps.

Experiment 4 was conducted from 29 June to 17 August 2009. This experiment focused on the effects of frontalin and comparing the best disruptants from previous treatments. Lure A was included in every trap and was the lone treatment in six traps. Three additional treatments included one or more disruptant semiochemicals: 300-mg frontalin (one microcentrifuge tube), 600-mg frontalin, or 600 mg frontalin with verbenone + GLV (one pouch each). Each of the four treatments was replicated six times for a total of 24 traps.

Experiments were designed primarily for analysis of total catch (i.e., trap sums) by treatment (one-way analysis of variance [ANOVA]). However, because we collected traps approximately weekly and identified the sex of each intact beetle, we began the data analysis for each experiment with a repeated measures (split-plot) ANOVA, using sex as the subplot factor, to estimate the importance of interactions between sex and treatments. When this interaction was not significant (NS, $P > 0.05$; all cases except for experiment 1), we proceeded to use one-way ANOVA to determine treatment effects on total catch (trap sums) or percentage female. For experiment 1, we subjected the counts of *D. jeffreyi* to one-way ANOVA separately for each sex. Response variables were transformed as necessary by their square root, natural logarithm, or arcsine (whichever was considered best from examination of distributions and residual plots) before ANOVA, whenever doing so improved their ability to meet assumptions of normality and homogeneity of variances. Treatment means were subjected to Tukey's honestly significant difference (HSD) to determine pairwise differences. To examine the relationship between collection period and sex ratio, the proportion female of *D. jeffreyi* caught was determined for each trap at each collection period for the attractant treatments. Random coefficient regression analysis (with trap and trap*date linear viewed as random) was carried out separately for the lures in each experiment to test for linear effects of collection period on the proportion of *D. jeffreyi* caught that was female.

Table 2. Experiment 1. Mean catch of *D. jeffreyi* and associated insects by semiochemical treatment at Luther Pass, CA from 15 June to 18 July 2007 ($\bar{X} \pm 1$ SEM). Means within a column followed by different letters are significantly different by Tukey's HSD ($P < 0.05$). Columns without letters contain no significantly different means

Treatment[a]	No. or % caught (mean per trap ± 1 SEM)				
	D. jeffreyi[b]	% female[b]	*D. valens*	*T. chlorodia*	Cleridae
APT	252.8 ± 50.3	41.6 ± 7.6	9.6 ± 3.6a	4.4 ± 2.9b	2.0 ± 1.5
HRHH	163.6 ± 19.6	35.0 ± 6.0	3.0 ± 0.7ab	1.8 ± 1.1b	1.0 ± 0.4
HRHHE	154.4 ± 11.5	31.2 ± 1.8	4.0 ± 1.1ab	40.2 ± 16.2a	3.8 ± 3.6
LRHH	67.4 ± 21.4	55.4 ± 4.6	5.0 ± 1.7ab	3.0 ± 1.7b	0.4 ± 0.4
LRHHE	31.6 ± 4.8	58.2 ± 4.2	1.0 ± 0.5b	6.2 ± 1.7ab	1.4 ± 1.2

[a] APT = 95:5 n-heptane:l-heptanol (APTIV, Inc., Portland, OR; HRHH = high release heptanol, heptane bottle; HRHHE = high release heptanol, heptane bottle, *exo*-brevicomin; LRHH = low release heptanol, heptane bottle; LRHHE = low release heptanol, heptane bottle, *exo*-brevicomin (all Synergy Semiochemicals, Corp., Burnaby, BC, Canada). See Table 1 for release rates.

[b] Sex* treatment was significant in 2007 so treatment effects were not evaluated for total number or percentage female of total number caught.

The first collection of experiment 1 was a partial day collection, from the day of trap deployment, with one missing datum. To obtain trap sums, this single missing datum (HRHH treatment) was imputed by fitting a full model with treatment, sex, collection date, and trap as model factors. Single degrees of freedom contrasts were used when the experimental design allowed measurement of a semiochemical used in combination or at different rates. In experiment 1, this included the presence or absence of *exo*-brevicomin and the high or low release rate of l-heptanol. In experiment 4, contrasts were used to measure the disruptant effects on sex ratio of *D. jeffreyi* and the effect of frontalin on *D. valens* catch. All statistical analyses were conducted using SAS (version 9.2, SAS Institute, Cary, NC) or JMP (version 9.0.3, SAS Institute).

Results

In experiment 1 (2007), a total of 3,349 *D. jeffreyi* (1,397 females; 1,924 males; 28 indeterminate), 278 *Temnochila chlorodia*, 113 *D. valens*, and 43 Cleridae were captured (Table 2). Because the split-plot ANOVA revealed that sex*treatment was significant ($F_{4, 20} = 5.21$; $P = 0.0048$) for *D. jeffreyi*, treatment effects were analyzed separately by sex (Fig. 1). For females, semiochemical treatment significantly affected catch with the APT lure $\bar{X} = 117.6 \pm 33.2$; (mean ± 1 SEM, untransformed data) being highest, followed by HRHH (58.4 ± 15.4), HRHHE (46.4 ± 1.9), LRHH (38.2 ± 12.9), and LRHHE (18.8 ± 3.7). The only significant pairwise difference between treatment means was APT compared with LRHHE. However, lures that emitted high levels of heptanol (Table 1, APT, HRHH, HRHHE; $n = 15$) caught significantly more female *D. jeffreyi* than did low heptanol lures (LRHH and LRRHHE, $n = 10$; $\bar{X} = 74.1 \pm$

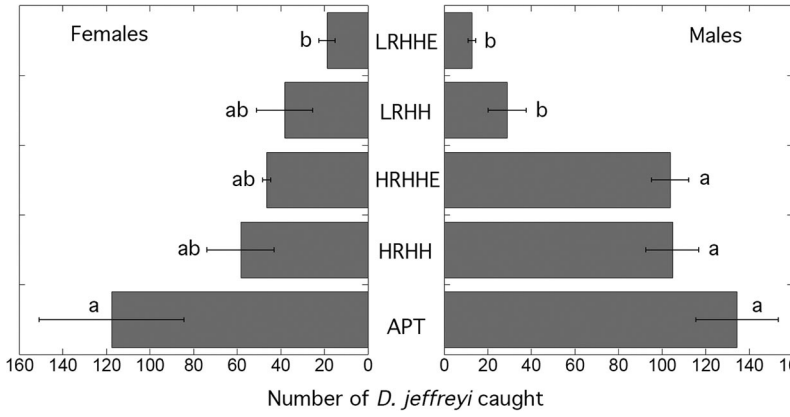

Fig. 1. Mean (±1 SEM) number of female (left) and male (right) *D. jeffreyi* caught at Luther Pass, CA in 2007 (experiment 1) by treatment. Letters near the top of bars indicate mean grouping as determined by Tukey's HSD ($P < 0.05$), which followed one-way ANOVA on square root transformed trap sums ($n = 25$ traps, five per treatment). APT = 95:5 n-heptane:l-heptanol (APTIV, Inc., Portland, OR); HRHH = high release heptanol, heptane bottle; HRHHE = high release heptanol, heptane bottle, *exo*-brevicomin; LRHH = low release heptanol, heptane bottle; LRHHE = low release heptanol, heptane bottle, *exo*-brevicomin (all Synergy Semiochemicals, Corp., Burnaby, BC, Canada).

14.0 versus 28.5 ± 7.1; $P = 0.006$). There was no significant effect observed for *exo*-brevicomin on female *D. jeffreyi* (*exo* present, $n = 10$, $\bar{X} = 32.6 \pm 5.0$ versus *exo* absent, $n = 15$, $\bar{X} = 71.4 \pm 14.0$, $P = 0.06$).

Males in experiment 1 also were affected by semiochemical treatment (Fig. 1). The APT lure caught the greatest number of male *D. jeffreyi* ($\bar{X} = 134.4 \pm 18.9$), followed by HRHH (104.8 ± 12.2), HRHHE (103.8 ± 8.6), LRHH (29.0 ± 8.8), and LRHHE (12.8 ± 1.7). Significant differences were found between each high heptanol treatment (APT, HRHH, and HRHHE) compared with each low heptanol treatment (LRHH and LRHHE), but no differences were found within either group. As with females, the contrast comparing high to low heptanol treatments was significant for males ($\bar{X} = 114.3 \pm 8.3$ versus 20.9 ± 5.0, $P < 0.0001$). Unlike females however, males were significantly affected by *exo*-brevicomin with fewer males being caught in traps with *exo*-brevicomin compared to traps without *exo*-brevicomin (*exo* present, $n = 10$, $\bar{X} = 58.3 \pm 15.7$ versus *exo* absent, $n = 15$, $\bar{X} = 89.4 \pm 14.0$, $P = 0.012$).

Semiochemical treatment significantly affected the number of *T. chlorodia* caught in experiment 1 ($F_{4, 20} = 5.6$, $P = 0.003$; Table 2). Treatment HRHHE caught by far the most *T. chlorodia*, followed by LRHHE, APT, LRHH, and HRHH (Table 2). As expected (Bedard et al. 1969), the presence of *exo*-brevicomin (with *exo*, $n = 10$, $\bar{X} = 23.2 \pm 9.5$) significantly increased catch of *T. chlorodia* compared with treatments without it (without *exo*, $n = 15$, $\bar{X} = 3.1 \pm 1.1$; df = 20, $t = 3.66$, $P = 0.002$). Treatment means, and an interaction plot depicting heptanol level and *exo*-brevicomin presence, suggest an important interaction because of a positive effect between the higher level of heptanol and presence of *exo*-brevicomin. On the square root scale (employed for analysis), the interaction was not as obvious but was significant ($t = 2.15$, df = 20, $P = 0.044$). Additional experiments are necessary to confirm the validity and magnitude of this interaction. Heptanol level (averaged over presence/absence of *exo*-brevicomin) did not affect catch of *T. chlorodia* (high, $n = 15$, $\bar{X} = 15.5 \pm 6.9$ versus low, $n = 10$, $\bar{X} = 4.6 \pm 1.2$; df = 20, $t = 1.29$, $P = 0.21$). For *D. valens*, mean catch was significantly higher with the APT lure ($\bar{X} = 9.6 \pm 3.6$) than with LRHHE ($\bar{X} = 1.0 \pm 0.5$) (Table 2). No other treatment differences were significant for *T. chlorodia* or *D. valens*.

In experiment 2 (2007 late), a total of 1,021 *D. jeffreyi* (277 females, 739 males, 5 indeterminate), 7 *D. valens*, 10 *T. chlorodia*, and 7 Cleridae were caught (Table 3). Because of the low numbers of associates caught, we subjected only *D. jeffreyi* data to inferential statistics. The combination of verbenone and the two-component GLV mixture significantly reduced catch of *D. jeffreyi* by ≈80% compared with the attractant alone ($t = 4.31$, df = 22; $P = 0.0003$). Ratio of females to males was unaffected by treatments ($t = 1.176$, df = 22, $P = 0.25$).

In experiment 3 (2008), 4,506 *D. jeffreyi* (2,026 females; 2,469 males; 11 indeterminate), 127 *D. valens*, 113 *T. chlorodia*, and 22 Cleridae were caught (Table 4). *Dendroctonus jeffreyi* was significantly affected by

Table 3. Experiment 2. Mean catch of *D. jeffreyi* by semiochemical treatment at Luther Pass, CA from 19 July to 16 Aug. 2007 ($\bar{X}$ ± 1 SEM). Associates were not evaluated due to their low numbers caught. Means within a column followed by different letters are significantly different by Tukey's HSD ($P < 0.05$). Columns without letters contain no significantly different means

Treatment	No. or % caught (mean per trap ± 1 SEM)	
	D. jeffreyi	% female
Lure A[a]	70.7 ± 14.9a	27.7 ± 3.6
A + verbenone + GLV[b]	14.4 ± 3.1b	35.5 ± 5.5

[a] 95:5 n-heptane:l-heptanol released from 250-ml Nalgene bottle.
[b] Verbenone and GLV blend were released from separate pouches (BeetleBlock, Synergy Semiochemicals, Corp.).

Table 4. Experiment 3. Mean catch of *D. jeffreyi* and associated insects by semiochemical treatment at Luther Pass, CA from 24 June to 5 August 2008 ($\bar{X}$ ± 1 SEM). Means within a column followed by different letters are significantly different by Tukey's HSD ($P < 0.05$). Columns without letters contain no significantly different means

Treatment	No. or % caught (mean per trap ± 1 SEM)				
	D. jeffreyi	% female	*D. valens*	*T. chlorodia*	Cleridae
Lure A	445.4 ± 212.2a	51.0 ± 4.4	14.6 ± 4.6a	10.2 ± 4.4	0.6 ± 0.4
Lure B[a]	253.2 ± 40.4a	41.6 ± 4.0	9.6 ± 2.6a	4.8 ± 2.1	0.8 ± 0.6
A + verbenone	98.8 ± 19.6a	45.3 ± 8.4	1.0 ± 0.3b	2.4 ± 0.8	0.4 ± 0.2
A + verbenone + GLV	102.4 ± 14.8a	57.0 ± 2.7	0b	1.6 ± 1.1	1.4 ± 0.7
A + verbenone + GLV + 600-mg frontalin[b]	1.4 ± 0.9b	–	0.2 ± 0.2b	3.6 ± 1.2	1.2 ± 0.8

[a] 75:25 n-heptane:l-heptanol released from 250-ml Nalgene bottle.
[b] Southern pine beetle load, two microcentrifuge tubes (Synergy Semiochemicals, Corp.).

treatment, with Lure A catching the greatest number; however, the only significant differences were between treatments with and without frontalin (Table 4). *Dendroctonus valens* was the only associate for which treatment effect was significant ($F_{4, 20} = 13.7$, $P < 0.0001$): each treatment with verbenone caught significantly fewer individuals than did those without (Lure A and Lure B; Table 4). Sex ratio of *D. jeffreyi* was not affected by semiochemical treatments in experiment 3 ($F_{3, 16} = 1.61$, $P = 0.23$ [treatment with frontalin excluded because of the low number caught]; Table 4).

In experiment 4 (2009), total catch of *D. jeffreyi* was 1,092 (491 females, 600 males, and 1 indeterminate), with 143 *D. valens,* 53 *T. chlorodia,* and 28 Cleridae also being trapped (Table 5). Semiochemical treatment was highly significant for explaining the number of *D. jeffreyi* caught ($F_{3, 20} = 32.2$, $P < 0.0001$). All treatments with frontalin differed significantly from Lure A; however, there were no differences among the disruptant treatments (Table 5). For *D. valens,* only the disruptant that included verbenone and GLV resulted in a noticeably lower mean catch; the only significant difference was between this treatment and Lure A + 300 mg of frontalin. The contrast used to test the effect of presence or absence of frontalin (excluding the verbenone + GLV treatment) was NS (with frontalin, $n = 12$, $\bar{X} = 9.1 \pm 2.7$ versus without frontalin, $n = 6$, $\bar{X} = 5.7 \pm 2.6$; $t = 0.78$, df = 16, $P = 0.44$), indicating that frontalin was not attractive or disruptive to *D. valens.* Neither *T. chlorodia* nor the Cleridae were significantly affected by semiochemical treatments (Table 5) in experiment 4.

Disruptant treatments in experiment 4 were effective and caught too few *D. jeffreyi* to evaluate individual treatment effects on sex ratio; however, because the disruptants did not differ in catch of *D. jeffreyi*, and because it is important that disruptants affect the pioneering sex, we combined results to provide an indication of the impacts treatments had on sex ratio. To do this, we first excluded those traps that caught ≤2 individuals during the experiment ($n = 10$ traps), and then combined across disruptant treatments to provide $n = 8$ traps for measurement against our standard attractant. This resulted in a comparison between Lure A (46.0 ± 2.1% female, $n = 6$ traps) and the disruptant group (29.7 ± 5.6% female, $n = 8$ traps; unequal variance $t = 2.74$, df = 9, $P = 0.02$), which indicated that the disruptants, all of which contained frontalin, reduced the percentage of *D. jeffreyi* caught that was female.

Within each year of the study, the percentage of catch that was female using the blended 95:5 lure (APT or Lure A) decreased from start to end of the experimental period. On average, our first collection in a year was 59% female, whereas our last was 34% (Fig. 2). In 2007, our standard attractant treatments in experiments 1 and 2 were nearly identical (Table 1), yet the former (15 June to 18 July) caught 42% females and the latter (19 July to 16 August) 27.7%. Examination of the sex ratio at each collection period showed that the percentage of *D. jeffreyi* caught that was female declined throughout experiment 1 and leveled off for experiment 2 through about day of year 222 (10 August in nonleap years; Fig. 2). The linear decrease in the percentage female *D. jeffreyi* caught in the blended attractant during experiment 1 was significantly related to date ($n = 25$; r-square = 0.33; $P < 0.001$), dropping from a high of 55% on 20 June (second collection) to a low of 23% on 18 July (final collection). The average percentage female caught by Lure A in experiment 2 was 27.7 ± 3.6%; collection

Table 5. Experiment 4. Catch of *D. jeffreyi* and associated insects by semiochemical treatment at Luther Pass, CA from 29 June to 17 August 2009 ($\bar{X}$ ± 1 SEM). Means within a column followed by different letters are significantly different by Tukey's HSD ($P < 0.05$). Columns without letters contain no significantly different means

Treatment	No. or % caught (mean per trap ± 1 SEM)				
	D. jeffreyi	% female	*D. valens*	*T. chlorodia*	Cleridae
Lure A	168.3 ± 33.9a	46.0 ± 2.1	5.7 ± 2.6ab	1.3 ± 1.0	0.8 ± 0.5
A + 300-mg frontalin[a]	8.0 ± 2.7b	–	10.0 ± 3.7a	2.3 ± 1.0	2.5 ± 0.8
A + 600-mg frontalin	4.0 ± 1.8b	–	8.2 ± 4.3ab	3.8 ± 1.2	1.3 ± 0.4
A + verbenone + GLV + 600-mg frontalin	1.7 ± 1.1b	–	0b	1.2 ± 0.6	1.1 ± 0.0

[a] One microcentrifuge tube (Synergy Semiochemicals, Corp.).

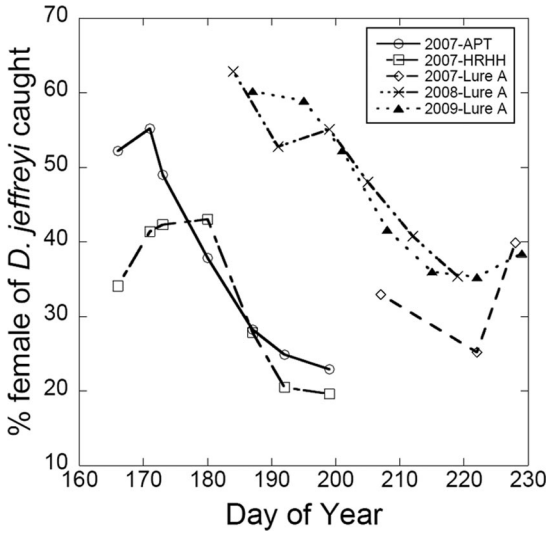

Fig. 2. Effect of year and day of year on the percentage female of *D. jeffreyi* caught at Luther Pass, CA during 2007–2009. Only similar attractant treatments are displayed to avoid interactions with time and treatment and because disruptant treatments frequently caught too few *D. jeffreyi* to reliably indicate sex ratio. Day of year 166 is usually 15 June and 229 is usually 17 August (Days of the year are one fewer after 29 February in leap years like 2008). All treatments were blended 95:5 n-heptane:1-heptanol except for 2007-HRHH, which released heptane and heptanol from separate containers (see Table 1).

period had no linear effect on this value ($n = 32$; r-square = 0.003; $P = 0.76$). Lure A in experiment 3 (2008) averaged 51.0 ± 4.4% female; the female percentage decreased significantly with collection date (linear effect, $n = 30$, r-square = 0.33; $P < 0.001$) from 62.9 ± 5.3% on 2 July to 35.4 ± 7.7% on 6 August. In experiment 4, Lure A averaged 46.0 ± 2.1% female and again varied by collection period (linear effect, $n = 41$, r-square = 0.25, $P < 0.001$), ranging from 60.2 ± 3.3% on 6 July to 35.3 ± 10.9% on 3 August 2009. Combining across experiments provides a pattern of declining females until day of year 210–220 (29 July to 8 August in nonleap years), after which the percentage of females caught stabilized or even increased (Fig. 2). Overall, for the attractant treatments, the percentage of catch that was female dropped 4–8% per week from initiation of our trapping through day of year 220.

We measured semiochemical release rates in the field whenever possible, preferring these data over those generated in the laboratory. In experiment 1, the blended lure, APT, gave the highest release rate of n-heptane (estimated to be ≈0.96 g/d at 26.2°C). However, all three high release heptanol treatments (APT, HRHH, and HRHHE) were estimated to have had similar release rates of 1-heptanol (Table 1). In experiment 1, the average measured loss of mass for field deployed n-heptane and 1-heptanol components in the HRHH and HRHHE lures was 550 mg/d after 17 d (at which time they were refilled) for n-heptane and 80 mg /d for 27 d for 1-heptanol. We estimate that the low heptanol treatments (LRHHE and LRHH) released ≈6 mg/d over the same 27-d period in experiment 1. In experiment 2, the attractant blend (Lure A; 95:5 vol:vol, n-heptane: 1-heptanol) was released from 250-ml bottles that began with 100 ml of mixture. Mean lost volume at the end of deployment was 42.7 ml, providing an average release rate of ≈1.5 ml (≈1 g) per day for the 29-d experiment (Tables 2–5). Release of verbenone, GLV, and frontalin was not measured at our study site, however, companion field trials were conducted in Missoula, MT and Pineville, LA during 2007 to provide field-based semiochemical release information (Table 1). Rates of ≈66 mg/d for verbenone, 97 mg/d for GLV, and 6.8 mg/d for frontalin (600-mg load) were determined in Missoula in full sun at temperatures similar to those experienced at Luther Pass in the trapping portion of this study (Missoula mean temperature = 20°C; www.fs.fed.us/foresthealth/technology/elutionrate/lure.htm; Table 1).

Discussion

Commercially available racemic frontalin lures were potent disruptants of the *D. jeffreyi* host selection process at the host or trap finding step. In experiments with frontalin over 2 yr, released at an estimated 6.8 mg/d from 600-mg lures and with or without verbenone and GLV, we caught 0.3 and 3.4% of the attractant-alone treatment. In addition, females were affected equally or to a greater degree compared with males. This level of disruption is rare with bark beetles, especially with the pioneering sex and a single disruptant (but see below for effects of MCH on *D. psuedotsugae*), and it suggests that successful protection of *P. jeffreyi* may be achievable with a disruptant semiochemical.

Synthetic n-heptane and 1-heptanol lures were effective for capturing *D. jeffreyi* in areas with elevated levels of host mortality. In each experiment, traps baited with the most effective attractant, a blend consisting of 95% heptane and 5% heptanol (vol:vol), caught at minimum 845 *D. jeffreyi* (experiment 2) and up to 2,227 (experiment 3). Previous studies with *D. jeffreyi* report best-lure catches of 56 in 6 wk (two traps per treatment; Renwick and Pitman 1979) or a range of two to 50 per day (duration and trap numbers unreported; Paine et al. 1999). In our study, the greatest numbers of *D. jeffreyi* were caught in traps that released the most semiochemical (blended lure); however, differences were not significant among the three treatments that released high levels of heptanol in 2007 (estimated at 51–60 mg/d). The high heptanol treatments did, however, catch more *D. jeffreyi* than the low heptanol treatments, supporting the finding of Paine et al. (1999) that increasing the release of heptanol may increase catch. In 2008, however, our blend of 75:25 heptane:heptanol (Lure B) did not catch more *D. jeffreyi* (in fact 57% fewer) than the 95:5 blend (Lure A), suggesting that the effects of heptanol release are complicated by other factors.

Semiochemical treatments with *exo*-brevicomin did not significantly affect total catch of *D. jeffreyi* or the catch of females, but the number of males caught was reduced. The laboratory release rate of *exo*-brevicomin from the bubble caps used in this experiment was 125 μg at 20°C (Synergy Semiochemicals, Corp.; Table 1). Paine et al. (1999) found that *exo*-brevicomin released at 0.1% increased catch of females, but we do not know their quantitative release rate. Regardless, in our study, attractant blends were equally effective for attracting *D. jeffreyi* with or without *exo*-brevicomin.

Catch of *D. jeffreyi* insect associates was largely unaffected by our semiochemical treatments (Tables 2–5). Exceptions were attraction of *T. chlorodia* to *exo*-brevicomin and disruption of *D. valens* by verbenone and verbenone + GLV. Both of these effects were expected (Bedard et al. 1969, Gillette et al. 2001, Fettig et al. 2005, Zhang et al. 2007), but it is of interest to note that the disruption of *D. valens* was significant despite the differences between our *D. jeffreyi* attractant and the typical host monoterpenes used to attract *D. valens* (Zhang et al. 2007). For *T. chlorodia*, interaction plots suggest that the combination of heptanol release rate and *exo*-brevicomin presence were involved in attraction. This result was marginally significant and needs additional evaluation before their combined role will be clearer. The attraction of *T. chlorodia* to *exo*-brevicomin suggests that this compound should be deployed only after considering potential effects on this species.

In North America, the most successful example of tree protection with a semiochemical against a *Dendroctonus* bark beetle is the intraspecific pheromone MCH (3-methylcyclohex-2-en-1-one) with *D. pseudotsugae* (Ross et al. 2002, 2006). Although rigorous multiyear or multilocation field studies during outbreaks are needed to prove treatment efficacy (Shea et al. 1984, Progar 2005), there are similarities between the frontalin-*D. jeffreyi* system and that of MCH-*D. pseudotsugae* that provide optimism. In trapping bioassays that preceded the development of specific methods for tree protection, MCH reduced trap catch of both sexes of *D. pseudotsugae* to 0 when deployed at 10 or 100% concentrations (estimated release rates of 5 and 50 mg/d, respectively; Rudinsky 1973). Our results with *D. jeffreyi* are similar, showing near complete disruption (both sexes) at the 6.8 mg/d level of frontalin. In *D. pseudotsugae*, MCH is produced by females who increase production in response to male stridulation (Rudinsky et al. 1973). At low concentrations MCH increases attraction; only at higher concentrations does it act as a disruptant of host selection. Thus, although produced by females, the disruptant functioning of MCH depends also on the presence of males. Frontalin is produced by male *D. jeffreyi* (Paine et al. 1999, Hall et al. 2002), as it is in *D. ponderosae* (Ryker and Libbey 1982, Pureswaran et al. 2000), and its disruptant effects may relate to attack cessation or shifting to another tree (Renwick and Vité 1970).

Frontalin is an attractant for several species of *Dendroctonus*, making nontarget effects (e.g., attracting other beetles to target or nearby trees) a consideration in its deployment. We are not aware that *P. jeffreyi* is a host for other aggressive, tree-killing bark beetles, relegating nontarget impacts primarily to other hosts such as *P. ponderosa* Dougl. ex Laws, *P. monticola* Dougl. ex D. Don, *P. lambertiana* Dougl., or *Pseudotsuga menziesii* (Mirbel) Franco. Frontalin is a component of semiochemical attractants for both *D. brevicomis* and *D. pseudotsugae* (Vité and Pitman 1969, Pitman and Vité 1970), but in both cases it is only a portion of a more complex semiochemical bouquet. Frontalin is not an attractant, and may be a disruptant, for *D. ponderosae* (Ryker and Libbey 1982, Pureswaran et al. 2000), so deployment should not promote undesirable attacks by this species. Field-testing under mixed stand conditions is necessary before the importance of these potential interactions will be understood. In this study we did not catch either *D. brevicomis* or *D. pseudotsugae* in our traps despite the elution of frontalin; we do not know if they were present in the area or not. We did, however, catch *D. valens*, a species for which the role of frontalin in its chemical ecology is uncertain or variable. Furniss and Schmitz (1971) working in Idaho characterize frontalin as a low level attractant, whereas Zhang et al. (2009) report significant disruptant effects in China. Regardless, frontalin did not impact our catch of *D. valens* in the presence of *D. jeffreyi* attractant (Tables 4–5).

This study shows that semiochemicals can impact behavior of *D. jeffreyi* in environments with ongoing tree mortality. The attractant blend of 95% n-heptane and 5% 1-heptanol consistently caught beetles over the 3 yr of our experiments, suggesting that it is a reasonable lure for monitoring this species. However, the seasonality of female catch in traps that we observed with this lure should be considered, especially when measuring possible control measures. Females are the pioneering sex and must be affected if preventing attacks is a goal; they responded to our traps in greater proportions early in the season. We do not know if the observed sex ratios in our traps were accurate indicators of the flying beetle populations or if there was a lure response interaction between date and sex. With *D. ponderosae*, Rasmussen (1974) working in the field, found that sex ratio was biased toward females by ≈6% at the beginning of the emergence period, increasing to ≈11% after 1 wk and falling to 2% after 18 d. Amman and Cole (1983) found a similar pattern in the laboratory. In both studies, sex ratio of emerging *D. ponderosae* favored females with the relative proportions changing during the emergence period but not dipping below ≈1:1. More research is necessary with *D. jeffreyi* before interactions among time of emergence, response to lures, and sex are understood.

Frontalin was a strong disruptant for *D. jeffreyi* in this study when deployed alone, or in combination with verbenone and the two-component GLV blend of *cis*-3-Hexenol and 1-Hexanol (trap catches of nearly 0). A potential advantage of deploying the three-component blend is the possibility of also disrupting *D. valens*, a pest that is usually of minor importance in the

range of Jeffrey pine. However, disadvantages to operational use include the difficulties associated with registering multiple components with the USEPA (Gillette et al. 2006). Future studies will measure protection of high-value individual or groups of *P. jeffreyi;* however, until those studies are completed, frontalin (with or without verbenone and GLV) may be the best option for those areas where *D. jeffreyi* is threatening individual trees or groups, but synthetic insecticides cannot be used.

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References Cited

Amman, G. D., and W. E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II: Population dynamics. Gen. Tech. Report INT-GTR-145. U.S. Department of Agriculture–Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Bedard, W. D., P. E. Tilden, D. L. Wood, R. M. Silverstein, R. G. Brownlee, and J. O. Rodin. 1969. Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. Science 164: 1284–1285.

Borden, J. H. 1993. Strategies and tactics for the use of semiochemicals against forest insect pests in North America, pp. 265–279. *In* R. D. Lumsden and J. L. Vaughn (eds.), Pest management: biologically based technologies. Am. Chem. Soc., Washington, DC.

Borden, J. H., I. M. Wilson, R. Gries, L. J. Chong, H. D. Pierce, Jr., and G. Gries. 1998. Volatiles from the bark of trembling aspen, *Populus tremuloide*s Michx. (Salicaceae) disrupt secondary attraction by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Chemoecology 8: 69–75.

Egan, A., D. Fournier, H. Safford, J. Sloughter, T. Cardoso, P. Trainor, J. Wenz. 2011. Assessment of a Jeffrey pine beetle outbreak from 1991–1996 near Spooner Junction, Lake Tahoe basin. FHP Report #SS11–09. U.S. Department of Agriculture, Forest Service, Forest Health Protection, Sonora, CA. 24 pp.

Fettig, C. J., S. R. McKelvey, and D.P.W. Huber. 2005. Nonhost angiosperm volatiles and verbenone disrupt response of western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae), to attractant-baited traps. J. Econ. Entomol. 98: 2041–2048.

Fettig, C. J., K. K. Allen, R. R. Borys, J. Christopherson, C. P. Dabney, T. J. Eager, K. E. Gibson, E. G. Hebertson, D. F. Long, A. S. Munson, et al. 2006. Effectiveness of bifenthrin (Onyx) and carbaryl (Sevin SL) for protecting individual, high-value conifers from bark beetle attack (Coleoptera: Curculionidae: Scolytinae) in the western United States. J. Econ. Entomol. 99: 1691–1698.

Furniss, M. M., and R. F. Schmitz. 1971. Comparative attraction of Douglas-fir beetles to frontalin and tree volatiles. Res. Pap. INT-96. U.S. Department of Agriculture–Forest Service. Intermountain Forest and Range Experiment Station, Ogden, UT.

Gillette, N. E., J. D. Stein, D. R. Owen, J. N. Webster, G. O. Fiddler, S. R. Mori, and D. L. Wood. 2006. Verbenone-releasing flakes protect individual Pinus contorta trees from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae). Agric. For. Entomol. 8: 243–251.

Gillette, N. R., D. R. Owen, and J. D. Stein. 2001. Interruption of semiochemical-mediated attraction of *Dendroctonus valens* (Coleoptera: Scolytidae) and selected nontarget insects by verbenone. Environ. Entomol. 30: 837–841.

Hall, G. M., C. Tittiger, G. J. Blomquist, G. L. Andrews, G. S. Mastick, L. S. Barkawi, C. Bengoa, and S. J. Seybold. 2002. Male Jeffrey pine beetle, *Dendroctonus jeffreyi,* synthesizes the pheromone component frontalin in anterior midgut tissue. Insect Biochem. Mol. Biol. 32: 1525–1532.

Haverty, M. I., P. J. Shea, J. T. Hoffman, J. M. Wenz, and K. E. Gibson. 1998. Effectiveness of esfenvalerate, cyfluthrin, and carbaryl in protecting individual lodgepole pines and ponderosa pines from attack by *Dendroctonus* spp. Res. Pap. PSW-RP-237. U. S. Department of Agriculture–Forest Service, Pacific Southwest Research Station, Albany, CA.

Hopkins, A. D. 1909. The genus *Dendroctonus.* Technical Series Part I. U.S. Department of Agriculture–Bureau of Entomology, Washington, DC.

Jenkinson, J. L. 1990. *Pinus jeffreyi* Grev. & Balf., pp. 359–369. *In* R. M. Burns and B. H. Honkala (tech. cords.), Silvics of North America, vol. 1, conifers. Agriculture Handbook 654. U.S. Department of Agriculture–Forest Service, Washington, DC.

Kennedy, J. S. 1965. Mechanisms of host plant selection. Proceedings of the Association for Applied Biology. 56: 317–322.

Kogan, M. 1994. Plant resistance in pest management, pp. 73–128. *In* R. L. Metcalf and W. H. Luckmann (eds.), Introduction to insect pest management. Wiley, New York.

Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. 115: 395–410.

Lyon, R. L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. Can. Entomol. 90: 582–584.

Miller, J. R., and K. L. Strickler. 1984. Finding and accepting host plants, pp. 127–157. *In* W. J. Bell and R. T. Cardé (eds.), Chemical ecology of insects. Sinauer, Sunderland, MA.

Paine, T. D., J. G. Millar, C. C. Hanlon, and J. S. Hwang. 1999. Identification of semiochemicals associated with Jeffrey pine beetle, *Dendroctonus jeffreyi.* J. Chem. Ecol. 25: 433–453.

Pitman, G. B., and J. P. Vité. 1970. Field response of *Dendroctonus pseudotsug*ae (Coleoptera: Scolytidae) to synthetic frontalin. Ann. Entomol. Soc. Am. 63: 661–664.

Pitman, G. B., J. P. Vité, G. W. Kinzer, and A. F. Fentiman, Jr. 1969. Specificity of population-aggregating pheromones in *Dendroctonus.* J. Insect Physiol. 15: 363–366.

Progar, R. A. 2005. Five-year operational trial of verbenone to deter mountain pine beetle (*Dendroctonus ponderosae;* Coleoptera: Scolytidae) attack of lodgepole pine (*Pinus contorta*). Environ. Entomol. 34: 1402–1407.

Pureswaran, D. S., R. Gries, J. H. Borden, and H. D. Pierce, Jr. 2000. Dynamics of pheromone production and communication in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). Chemoecology 10: 153–168.

Rasmussen, L. A. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. Res. Note INT-RN-180. U. S. Department of Agriculture–Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Renwick, J.A.A., and G. B. Pitman. 1979. An attractant isolated from female Jeffrey pine beetles, *Dendroctonus jeffreyi.* Environ. Entomol. 8: 40–41.

Renwick, J.A.A., and J. P. Vité. 1970. Systems of chemical communication in *Dendroctonus.* Contributions from Boyce Thompson Institute 24: 283–292.

Ross, D. W., G. E. Daterman, and K. E. Gibson. 2002. Elution rate and spacing of antiaggregation pheromone dispensers for protecting live trees from *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). J. Econ. Entomol. 95: 778–781.

Ross, D. W., K. E. Gibson, and G. E. Daterman. 2006. Using MCH to protect trees and stands from Douglas-fir beetle infestation. U.S. Department of Agriculture–Forest Service, FHTET-2001–09. Forest Health Technology Enterprise Team, Morgantown, WV.

Rudinsky, J. A. 1973. Multiple functions of the Douglas fir beetle pheromone 3-methyl-2-cyclohexen-1-one. Environ. Entomol. 2: 579–585.

Rudinsky, J. A., M. Morgan, L. M. Libbey, and R. R. Michael. 1973. Sound production in Scolytidae: 3-methyl-2-cyclohexen-1-one released by the female Douglas fir beetle in response to male sonic signal. Environ. Entomol. 2: 505–509.

Ryker, L. C., and L. M. Libbey. 1982. Frontalin in the male mountain pine beetle. J. Chem. Ecol. 8: 1399–1409.

Ryker, L. C., and K. L. Yandell. 1983. Effect of verbenone on aggregation of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) to synthetic attractant. Z. Angew. Entomol. 96: 452–459.

Shea, P. J., M. I. Haverty, and R. W. Hall. 1984. Effectiveness of fenitrothion and permethrin for protecting ponderosa pine from attack by the western pine beetle. J. Georgia Entomol. Soc. 19: 427–433.

Shepherd, W. P., D.P.W. Huber, S. J. Seybold, and C. J. Fettig. 2008. Antennal responses of the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Curculionidae), to stem volatiles of its primary host, *Pinus ponderosa*, and nine sympatric nonhost angiosperms and conifers. Chemoecology. 17: 209–221.

Smith, R. H. 1982. Log bioassay of residual effectiveness of insecticides against bark beetles. Res. Pap. PSW-168. U.S. Department of Agriculture–Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Smith, R. H. 2000. Xylem monoterpenes of pines: distribution, variation, genetics, function. Gen. Tech. Report PSW-GTR-177. U. S. Department of Agriculture–Forest Service, Pacific Southwest Research Station, Albany, CA.

Smith, S. L., R. R. Borys, and P. J. Shea. 2009. Jeffrey pine beetle. Forest Insect and Disease Leafl. 11. Revised June 2009. U.S. Department of Agriculture–Forest Service, Pacific Northwest Region (R6), Portland, OR.

Vité, J. P., and G. B. Pitman. 1969. Aggregation behaviour of *Dendroctonus brevicomis* in response to synthetic pheromones. J. Insect Physiol. 15: 1617–1622.

Wilson, I. M., J. H. Borden, R. Gries, and G. Gries. 1996. Green leaf volatiles as antiaggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). J. Chem. Ecol. 22: 1861–1875.

Zhang, L., N. E. Gillette, and J. Sun. 2007. Electrophysiological and behavioral responses of *Dendroctonus valens* to non-host volatiles. Ann. For. Sci. 64: 267–273.

Zhang, L., S. R. Clarke, and J. Sun. 2009. Electrophysiological and behavioral responses of *Dendroctonus valens* (Coleoptera: Curculionidae: Scolytinae) to four bark beetle pheromones. Environ. Entomol. 38: 472–477.

Zhang, Q., and F. Schlyter. 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. Agric. For. Entomol. 6: 1–19.

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