Interspecific Variation in Host-Finding Cues of Parasitoids of the Southern Pine Beetle (Coleoptera: Scolytidae)[1]

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Abstract Experiments were performed with host-associated olfactory attractants of the larval parasitoids of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, to elucidate both their biological origin and their chemical composition. Sticky-screen traps were erected in an active *D. frontalis* infestation and baited with parts of *D. frontalis*-infested loblolly pines (*Pinus taeda* L.) or their extracts. The diversity of parasitoid species landing on trees infested with larval *D. frontalis* was substantially greater than that attracted to traps baited with wood and bark taken from similar, infested trees. Females of four parasitoid species, *Spathius pallidus* (Ashmead), *Roptrocerus xylophagorum* (Ratzeburg), *Dinotiscus dendroctoni* (Ashmead), and *Eurytoma tomici* Ashmead, were attracted to bark infested with *D. frontalis* larvae. Two of these species, *R. xylophagorum* and *S. pallidus,* were attracted to debarked wood from host-infested trees although this tissue was free of hosts and host frass. *Spathius pallidus* were more attracted to the excised bark (containing *D. frontalis* larvae and frass) than the debarked wood from *D. frontalis*-infested pine bolts, while *R. xylophagorum* were attracted in similar numbers to both materials. When traps were baited with steam/water-distilled extracts of *D. frontalis*-infested bark, *R. xylophagorum* strongly preferred extracts from bark containing early-instar larvae over extracts from bark infested with either younger (egg-stage) or older (late-instar larval and pupal) brood. In contrast, *S. pallidus* responded significantly only to extracts of late larval/pupal bark. Coupled gas chromatograph/mass spectrometer (GC-MS) analyses of the bark extracts revealed that the concentrations of numerous extract constituents correlated positively with trap catch of *S. pallidus,* but no such relationships were identified for *R. xylophagorum.* These data provide further evidence that members of the parasitoid complex associated with *D. frontalis* differ in their strategies for locating trees infested with susceptible hosts.

Key Words Scolytidae, *Dendroctonus frontalis,* parasitoids, Pteromalidae, Braconidae, host location, semiochemicals, pine

A guild of at least seven common species of hymenopterous parasitoids utilize the larvae of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, as hosts (Bushing 1965, Franklin 1969, Moore 1972, Berisford 1980). The larval parasitoids of bark beetles (including those of *D. frontalis*) are trapped predominantly on trees infested specifically with late-instar larvae (Berisford 1969, Camors and Payne 1973, Stephen and Dahlsten 1976, Dixon and Payne 1979, Ohmart and Voigt 1982) sug-

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gesting that they have an efficient mechanism for host habitat location and host life-stage discrimination during flight. While pheromones of bark beetle adults have been identified as important prey location cues for a large number of bark beetle predators (Vite and Williamson 1970, Billings and Cameron 1984, Payne 1989, Miller et al. 1989, Raffa and Dahlsten 1995, Erbilgin and Raffa 2001), pheromones probably do not play a comparable role in host finding by larval parasitoids of bark beetles. Pheromone production by attacking adult bark beetles terminates prior to the development of beetle larvae and the arrival of parasitoids (Berisford 1969, Camors and Payne 1972, Sullivan 1997), and larval parasitoids are attracted weakly or not at all to synthetic bark beetle pheromones, in contrast to their predatory counterparts (Camors and Payne 1972, Dixon and Payne 1980, Kudon and Berisford 1981). Volatile compounds associated specifically with larvae-infested tree tissue, especially oxygenated monoterpenes, apparently play an important role in attracting parasitoids to bark beetle-infested trees (Pettersson et al. 2000, 2001, Sullivan et al. 2000, Pettersson 2001a, b). However, synthetic blends of oxygenated monoterpenes have not equaled the biological activity of naturally-derived parasitoid attractants (Sullivan et al. 1997, Pettersson et al. 2000, 2001, Pettersson 2001a), and the composition of host location cues has not been completely characterized for any single parasitoid species.

In previous experiments, pine bark infested with *D. frontalis* brood and essential oil extracts of such bark were attractive to two larval parasitoids, *Roptrocerus xylophagorum* (Ratzeburg) (Pteromalidae) and *Spathius pallidus* (Ashmead) (Braconidae) (Sullivan et al. 1997). *Roptrocerus xylophagorum* was more strongly attracted to bark infested with early-instar *D. frontalis* larvae than bark infested with late-instar larvae and pupae. *Spathius pallidus* showed the reverse preference. We conducted the following research to (1) investigate whether attractants are produced solely within the microhabitat of the host (i.e., the bark) or more generally in the bole of infested trees, and (2) determine whether parasitoid discrimination of host life stages can be attributed to the presence of specific chemical cues in infested bark tissue.

Materials and Methods

Experiment 1. Sticky-screen cylinders (31 cm high, 19 cm diam, 0.64 cm mesh hardware cloth coated with Stikem Special®) were baited either with (1) a loblolly pine bolt (10 to 14 cm diam, 30 cm long) infested with late-instar larval *D. frontalis* brood, (2) the bark excised from such a bolt, (3) the debarked bolt, (4) baits two and three together, or (5) nothing (blank trap). The bolts were cut from a naturally infested pine felled immediately before the tests. To provide a uniform visual profile among treatments, we enclosed baits in cylindrical cages (37 cm high, 16 cm diam) of black plastic hardware cloth. Blank traps had an empty cage. Any residual insect frass or bark fragments clinging to the exposed sapwood surface in treatment 3 were carefully removed. Parasitoid attraction to bait treatments was assayed within nine replicates in a randomized complete block design. Traps were erected on 2 m-long posts positioned at least 5 m apart, and 2 to 3 complete blocks were set up at one time within an active *D. frontalis* infestation. Treatment positions within blocks were assigned at random, and then treatments were rotated four times (every 45 min) for a total of 3.75 h. In addition, three standing trees infested with late-instar *D. frontalis* larvae and adjacent to the traps were wrapped with sticky screen cylinders (as above) at 2 m height. Screens were left in place for the duration of the trap rotations. The experiment

was performed during daylight hours on 17 and 22 July and 29 August 1996 in the Oconee National Forest, GA.

Experiment 2. Bark infested with one of three different beetle life stages was extracted by steam/water distillation (Guenther and Althausen 1948), and the extracts were both tested in the field for parasitoid attraction and analyzed by coupled gas chromatography/mass spectrometry (GC-MS). Bark was steam/water-distilled with an apparatus (Fig. 1) modified from that described in Sullivan et al. (1997). Extracted bark had either (1) adult beetles constructing egg galleries and the majority of brood in the egg stage, (2) early-instar larvae feeding in filamentous larval mines (Bridges et al. 1984), or (3) late-instar larvae and pupae present predominantly in the outer, corky bark. Bark was collected from standing infested pines, placed into plastic bags, transported to the laboratory on ice, and stored frozen. Bark from 2 to 3 trees was distilled together, and 3 to 5 such distillations using bark from different sets of trees were performed separately for each of the above three bark categories.

The composition of the extracts from each distillation was analyzed semiquantitatively with a Hewlett-Packard GCD G1800A GC-MS system equipped with an HP-FFAP fused-silica capillary column (Hewlett-Packard Corp., Avondale, PA) (50 m × 0.2 mm i.d.; 0.33 μm film thickness). The temperature program was 32°C for 1 min, then 15°C/min to 75°C, then 6°C/min to 220°C held 12 min. Carrier gas flow was 0.7 ml/min helium. Pure extract was diluted 1:300 in pentane and injected (1 μl) with a split ratio of 1:30. Approximate percent concentrations for individual components were obtained by dividing the raw ion abundances for individual peaks by the total ion abundances for the entire sample.

Extracts were combined within each life-stage category, and sticky-screen cylinder traps as described in experiment 1 were each baited with 4.5 ml of one of the three extract types or left unbaited (blank trap). Parasitoid attraction to these four treatments was compared within ten replicates in a randomized complete block design. Extract was applied to a cellulose sponge (8 × 5 × 0.2 cm) suspended inside each trap. Total trapping time was 5 h, and trap positions were rotated every 1.25 h. Trapping was performed within active *D. frontalis* infestations at the Oconee National Forest on 1 and 2 October, and at the Ft. Benning Military reservation, GA, on 11 and 19 October 1995. In all other respects, trapping procedures were identical to those used in experiment 1.

After completion of trapping, parasitoids were removed manually from sticky screens, cleaned in solvent, and stored in 70% alcohol for later sexing and identification. Voucher specimens were deposited with the University of Georgia Museum of Natural History, Athens, GA.

Data analyses. All statistical analyses were performed using Sigma Stat™ 2.03 software (SPSS 1997). Raw catch numbers were transformed with $log_{10}(X+1)$ to remove heteroscedasticity, and treatment effects were identified with a two-way analysis of variance (ANOVA) using block and treatment of the randomized complete block design as model factors. The relative proportions of species trapped by different treatments were compared using either a chi-square test or a Fisher exact test. Differences in the percent concentrations of individual constituents of the bark oils were compared using a one-way ANOVA on the $arcsin(\sqrt{X})$ transformed data. Pairwise comparisons of treatment means for all ANOVAs were performed with the Student-Newman-Keuls (SNK) procedure ($\alpha = 0.05$). The degree of correlation between mean trap catch for each bark extract and the concentration of individual extract constituents was determined with a Pearson Product Moment Correlation ($\alpha = 0.10$).

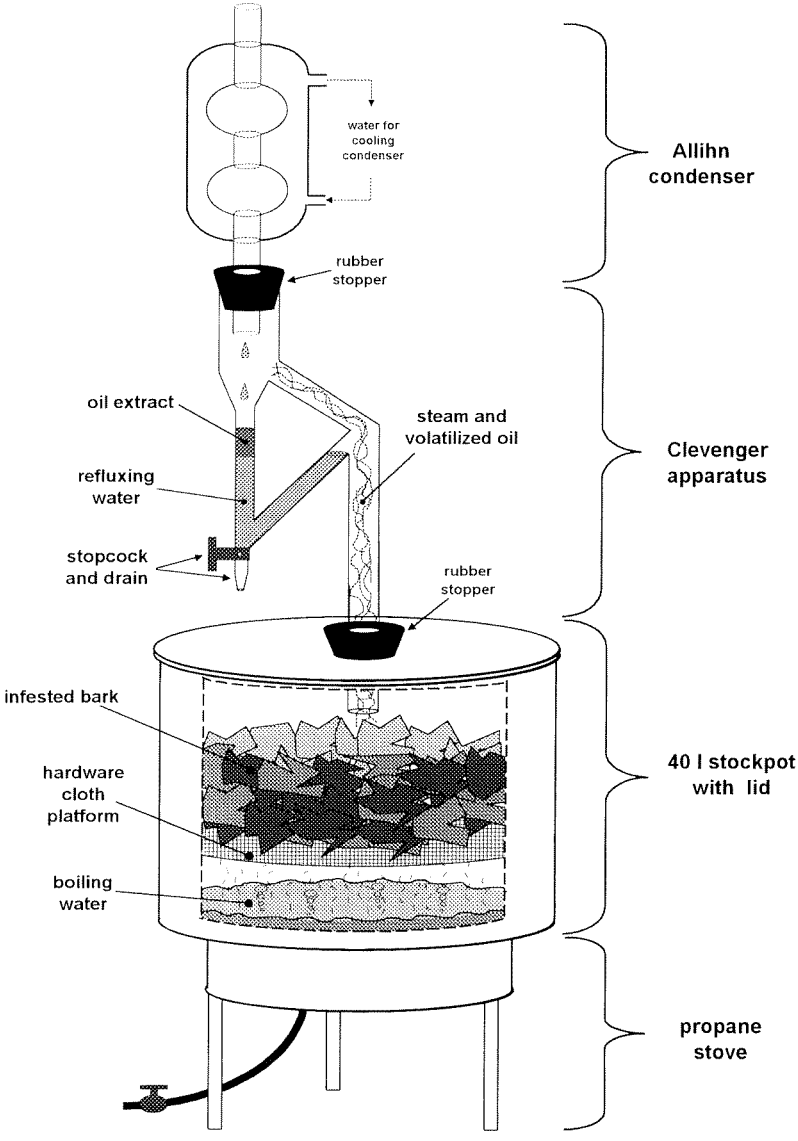

Fig. 1. Schematic diagram of the steam/water distillation apparatus used to extract essential oils from *D. frontalis*-infested bark. A propane stove heated a layer of water in the bottom of a large stockpot to boiling, forcing steam through pieces of infested bark suspended above the water on a hardware cloth platform. Steam and volatilized essential oil from the stockpot was condensed and the oil separated from water with a Clevenger apparatus (as in Geunther and Althausen 1948, but constructed in double-scale) attached at its top to a large Allihn condenser. Two to six kg of bark were extracted during each 3 h distillation.

For correlation analyses, concentrations of extract components in blank traps were assigned a value of zero.

Results

Experiment 1. Females of four parasitoid species, *R. xylophagorum, S. pallidus, Eurytoma tomici* Ashmead (Eurytomidae), and *Dinotiscus dendroctoni* (Ashmead) (Pteromalidae), were attracted to traps baited with *D. frontalis* larvae-infested bark in significantly greater numbers than to blank traps (Fig. 2). In addition, *S. pallidus* and *R. xylophagorum* responded to whole bolts infested with *D. frontalis* larvae, infested bolts with bark removed, and infested bark/debarked bolt combinations. These two species also significantly preferred host-infested bark/debarked bolt combinations to unaltered host-infested bolts. *Spathius pallidus* preferred excised, infested bark to debarked bolts, while *R. xylophagorum* was similarly attracted to both. The proportions of *S. pallidus* and *R. xylophagorum* females responding to these two baits differed significantly ($P = 0.0002$, chi-square test).

The frequency distribution of parasitoid species caught on bark and wood-baited traps differed significantly from that trapped on adjacent, infested trees ($P < 0.0001$, chi-square test). Relative to adjacent, naturally-infested trees, baited traps attracted a greater proportion of *R. xylophagorum* and *S. pallidus* and a lower proportion of *E. tomici, D. dendroctoni, Heydenia unica* Cook and Davis (Pteromalidae), and *Coeloides pissodis* (Ashmead) (Braconidae) (Fig. 3).

Experiment 2. Females of two parasitoid species, *R. xylophagorum* and *S. pallidus,* responded to the extracts of *D. frontalis*-infested bark (Fig. 4). Extract of bark

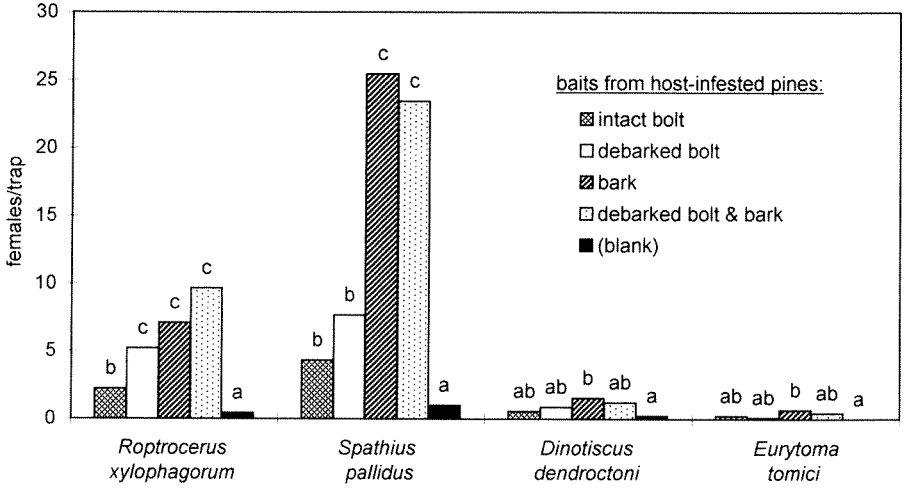

Fig. 2. Responses of female parasitoids to sticky traps baited with parts from the bole of loblolly pines infested with late instar *D. frontalis* larvae: (1) a bolt (10-14 cm diam., 30 cm long), (2) a similar bolt, debarked, (3) the excised bark, (4) baits two and three together, or (5) nothing (blank). Within species, means associated with the same letter were not significantly different, $\alpha = 0.05$, SNK test.

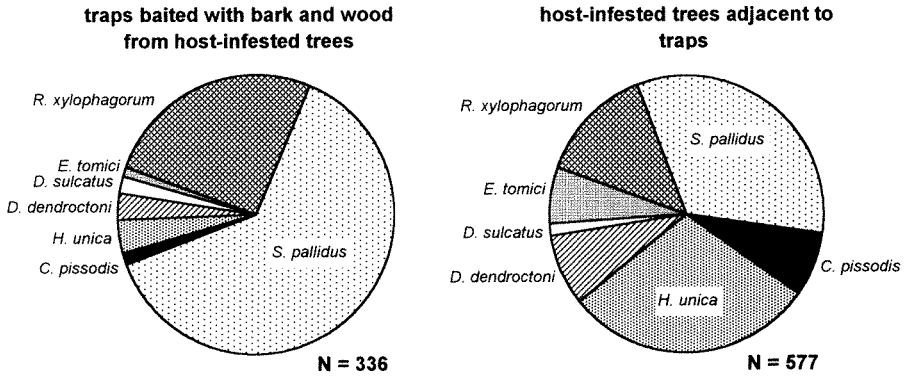

Fig. 3. The distribution of parasitoid species caught on sticky traps baited with bark and wood from pines infested with late-instar *D. frontalis* larvae (a), and sticky screens attached to similarly infested standing pines adjacent to the traps (b). Trapped species included *Roptrocerus xylophagorum, Eurytoma tomici, Dendrosoter sulcatus* Muesbeck, *Dinotiscus dendroctoni, Heydenia unica, Coeloides pissodis,* and *Spathius pallidus.*

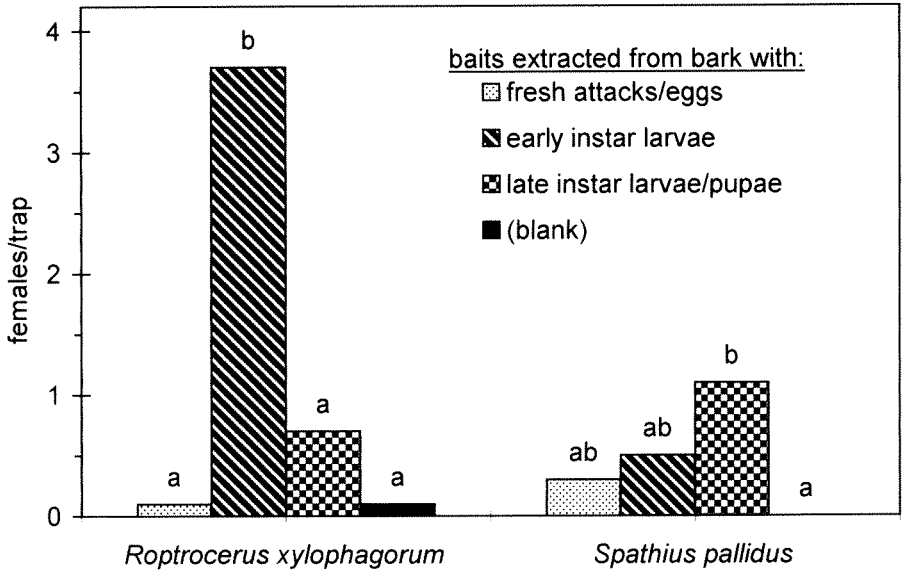

Fig. 4. Responses by female parasitoids to sticky traps baited with steam/water distillates of loblolly pine bark infested with one of three categories of *D. frontalis* brood development. Within species, means associated with the same letter were not significantly different, $\alpha = 0.05$, SNK test.

infested with early instar *D. frontalis* larvae attracted significantly more *R. xylophagorum* than any other bait, and extract of bark infested with either younger or older beetle brood did not trap significantly more *R. xylophagorum* than the blank. Extract of bark infested with late-instar larvae and pupae was the only bait which attracted *S. pallidus* in significantly greater numbers than the blank, but *S. pallidus* did not exhibit a significant preference for this extract over extracts of bark with younger brood stages. However, *S. pallidus* differed significantly from *R. xylophagorum* in the proportion of individuals responding to extracts of bark infested with either early-instar larvae or late-instar larvae and pupae ($P = 0.0002$; Fisher exact test).

Distillates of bark infested with different *D. frontalis* life stages diverged significantly in their composition (Table 1). Nineteen compounds increased significantly in concentration with increasing beetle brood age. These included seven hydrocarbon monotepenes (α-fenchene, camphene, α-terpinene, γ-terpinene, *p*-cymene, terpinolene and 2,4-dimethylstyrene), eleven oxygenated monoterpenes (fenchone, camphor, isopinocamphone, fenchyl alcohol, terpinen-4-ol, myrtenal, *trans*-pinovarveol, α-terpineol, borneol, verbenone, and *p*-cymen-8-ol) and one unidentified compound. One hydrocarbon monoterpene (β-pinene) decreased significantly with increasing beetle brood age. Eighteen compounds were significantly ($\alpha = 0.1$) positively correlated with trap catch of *S. pallidus* (Table 1). Generally, these correlating compounds were the same as those that increased significantly with *D. frontalis* brood development. In contrast, *R. xylophagorum* trap catch did not correlate with the concentration of any extract constituent ($P > 0.28$ for all compounds).

Discussion

Previous studies have shown that the *D. frontalis* parasitoids *S. pallidus* and *R. xylophagorum* are attracted to odors of host-infested pine bark (Sullivan et al. 1997, 2000). The present study indicates that two additional species, *D. dendroctoni* and *E. tomici,* share this behavior. The present study also replicates previous observations that excision of bark from *D. frontalis* larvae-infested bolts increased its attractiveness to parasitoids (Sullivan et al. 1997). Bark excision exposes infested phloem and beetle frass to the air and undoubtedly increases the rate at which volatiles are released.

The mines and frass of *D. frontalis* adults and brood are confined to the phloem and corky bark of infested trees. Hence, *R. xylophagorum* and *S. pallidus* were responding to tree parts that were free of either hosts or obvious host products when they were attracted to debarked wood of infested trees. Previous research showed that host-damaged bark tissue remains highly attractive to *R. xylophagorum* after all hosts and host frass are removed (Sullivan et al. 2000), indicating that attractive cues are present in the phloem tissue itself. Our data further suggest that cues attractive to flying parasitoids are present also within the xylem and are not confined merely to those tissues specifically infested by beetles. Semiochemical attractants may have diffused from the phloem into the xylem or may have been produced in the xylem itself, possibly by bark beetle associated fungi that had penetrated into the wood (Dahlsten and Berisford 1995, B. T. Sullivan, unpubl. data). Discoloration from the *D. frontalis*-associated bluestain fungus *Ophiostoma minus* was visible in the wood baits.

Presumably host-seeking female *R. xylophagorum* showed a strong preference for volatile essential oils from bark infested specifically with early-instar *D. frontalis* lar-

Table 1. Percent composition* of bark extracts produced from loblolly pines infested with one of three different developmental stages of southern pine beetle brood

#	Compound name	Fresh attack/egg stage mean ± 95% conf.	Early larval stage mean ± 95% conf.	Late larval/pupal stage mean ± 95% conf.	Correlation coefficient with trap catch *R. xylophagorum*	Correlation coefficient with trap catch *S. pallidus*
1	Tricyclene	0.40 ± 0.02	0.48 ± 0.06	0.49 ± 0.09	0.47	0.81
2	α-Pinene	65.45 ± 0.96	71.49 ± 9.00	53.46 ± 11.1	0.51	0.60
3	α-Fenchene	0.15 ± 0.04a†	0.39 ± 0.10b	1.19 ± 0.20c	0.13	0.99‡
4	Camphene	1.13 ± 0.08a	1.25 ± 0.10a	1.52 ± 0.10b	0.38	0.84
5	β-Pinene	14.76 ± 3.68b	7.68 ± 4.86ab	6.20 ± 2.49a	0.06	0.12
6	Unknown	0.08 ± 0.03a	0.09 ± 0.03ab	0.18 ± 0.03b	0.29	1.00‡
7	Myrcene	1.77 ± 0.62	2.43 ± 1.29	1.21 ± 0.36	0.70	0.42
8	α-Terpinene	0.06 ± 0.05a	0.08 ± 0.01a	0.24 ± 0.04b	0.12	0.99‡
9	Limonene	1.91 ± 0.51	2.85 ± 2.71	2.46 ± 0.22	0.59	0.72
10	β-Phellandrene**	0.40 ± 0.05	0.33 ± 0.12	0.40 ± 0.08	0.27	0.63
11	γ-Terpinene	0.06 ± 0.03a	0.09 ± 0.01a	0.27 ± 0.04b	0.10	1.00‡
12	*p*-Cymene	0.12 ± 0.01a	0.21 ± 0.03b	0.64 ± 0.09c	0.09	0.99‡
13	Terpinolene	0.35 ± 0.03a	0.54 ± 0.11a	1.63 ± 0.50b	0.12	1.00‡
14	Fenchone	0.02 ± 0.01a	0.06 ± 0.02a	0.41 ± 0.15b	−0.03	0.95‡
15	2,4-Dimethylstyrene**	0.10 ± 0.01a	0.19 ± 0.03a	0.98 ± 0.36b	0.02	0.97‡
16	Camphor	0.12 ± 0.03a	0.22 ± 0.02a	1.49 ± 0.40b	−0.05	0.95‡

Table 1. Continued.

#	Compound name	Fresh attack/egg stage mean ± 95% conf.	Early larval stage mean ± 95% conf.	Late larval/pupal stage mean ± 95% conf.	Correlation coefficient with trap catch *R. xylophagorum*	Correlation coefficient with trap catch *S. pallidus*
17	Isopinocamphone	trace	0.06 ± 0.03a	0.31 ± 0.11b	0.06	0.96‡
18	Fenchyl Alcohol	0.15 ± 0.0a	0.15 ± 0.04a	0.44 ± 0.12b	0.07	0.98‡
19	Terpinen-4-ol	1.04 ± 0.13a	2.90 ± 0.10b	9.00 ± 1.06c	0.11	0.98‡
20	Caryophyllene	1.64 ± 1.40	1.15 ± 1.74	2.64 ± 2.28	0.06	0.65
21	Myrtenal	0.04 ± 0.01a	0.11 ± 0.02b	0.19 ± 0.06b	0.51	0.94‡
22	*trans*-Pinocarveol	0.11 ± 0.03a	0.15 ± 0.02a	0.51 ± 0.17b	0.11	1.00‡
23	4-Allylanisole	5.26 ± 2.29	2.76 ± 0.42	3.49 ± 1.63	0.06	0.30
24	α-Humulene	0.41 ± 0.33	0.39 ± 0.43	0.66 ± 0.58	0.00	0.64
25	α-Terpineol	2.41 ± 0.04a	1.94 ± 0.24a	4.91 ± 1.54b	0.07	0.93‡
26	Borneol	0.36 ± 0.03a	0.32 ± 0.10a	0.76 ± 0.25b	0.13	0.94‡
27	Verbenone	0.17 ± 0.06a	0.50 ± 0.07b	0.45 ± 0.11b	0.72	0.82
28	Myrtenol	0.13 ± 0.04	0.12 ± 0.03	0.23 ± 0.07	0.24	0.91‡
29	*p*-Cymen-8-ol	0.03 ± 0.01a	0.10 ± 0.02b	0.29 ± 0.06c	0.13	0.98‡

* The compound's total ion abundance as a percentage of the summed ion abundances for all compounds in the chromatograms.
** Compound identified by mass spectrum only; retention time data was not available.
† For each compound, means followed by the same letter were not significantly different (α = 0.05), SNK test.
‡ Correlation was significant (α = 0.10), Pearson Product Moment Correlation.

vae, a preference observed in a previous study in which traps were baited with the bark itself (Sullivan et al. 1997). *Roptrocerus xylophagorum* parasitises predominantly late-instar bark beetle larvae (Samson 1984, Berisford and Dahlsten 1989), hence this parasitoid's ability to discriminate among odors associated with different *D. frontalis* life stages is apparently unrelated to its parasitism preferences. The preference of *R. xylophagorum* for essential oils from early larval bark could not be readily attributed to chemical composition, since no constituents of the bark extracts correlated quantitatively with attraction of this parasitoid. Coupled gas chromatographic-electroantennographic detection (EAD) studies of *R. xylophagorum* indicate that this species is especially sensitive to the oxygenated monoterpene components in attractive distillates of *D. frontalis* infested bark, and a blend of seven EAD-active oxygenated monoterpenes is moderately attractive to this species (Pettersson et al. 2000). Most of these oxygenated monoterpenes were present in substantially greater abundance in extracts from late-instar larvae/pupae-infested bark than bark with earlier stages, and other studies similarly indicate a continuous increase in the concentration of these compounds in infested trees as the brood of conifer-infesting bark beetles complete development (Birgersson et al. 1992, Sullivan 1997, Pettersson 2001b). While much evidence suggests that oxygenated monoterpenes mediate the attraction of *R. xylophagorum* to its host's habitat, it is clear from our results that these compounds do not act independently in a simple dose-dependent or additive fashion. Rather, *R. xylophagorum* may respond to oxygenated monoterpenes only when present in specific proportions or when combined with other oil constituents, ones possibly not detected by our analyses. The enantiomeric composition of individual oxygenated monoterpenes in the extracts was unknown and may have influenced extract activity as well.

In contrast, *S. pallidus* exhibited a strong dose-correlated response to the presence in extract baits of several oxygenated monoterpenes and certain minor hydrocarbon monoterpene constituents of loblolly pine resin. Previous studies have shown that many of these compounds are characteristically present in elevated concentrations in trees infested with late-instar bark beetle larvae, the life stage typically preferred for parasitism (Birgersson et al. 1992, Sullivan 1997, Pettersson 2001b). *Spathius pallidus* has demonstrated EAD sensitivity to numerous oxygenated monoterpenes (B. T. Sullivan, unpubl. data), including a majority of those that exhibited a dose relationship with *S. pallidus* attraction in the present study. *Spathius pallidus* was not attracted in field trials to synthetic mixtures which included these compounds (Sullivan et al. 1997, B. T. Sullivan unpubl. data), but this could have resulted from the accidental omission of necessary synergists or the inclusion of unrecognized inhibitors in the mixtures. Antennal sensitivity and/or attraction to oxygenated monoterpenes have been reported for several other species of bark beetle parasitoids including two other braconids (Salom et al. 1991, 1992, Pettersson et al. 2000, 2001, Pettersson 2001a).

Our study revealed several instances of interspecific variability in the host finding cues and behaviors utilized by parasitoids attacking *D. frontalis*. The parasitoid assemblage caught in traps baited with host-infested bole tissue did not reflect the diversity of species landing on nearby host-infested trees, with two species, *R. xylophagorum* and *S. pallidus*, responding to these traps in disproportionately high numbers. This apparent species-selectivity of traps might have resulted form interspecific variation in parasitoid sensitivity to tree bole-like visual cues (which were largely lacking from free-standing traps) or olfactory cues quantitatively altered during

manipulation of the tree-derived baits. Our results also complement previous evidence that *S. pallidus* and *R. xylophagorum* utilize host-finding cues that differ in their chemical composition (Sullivan et al. 1997). Further, our results show that these cues may differ also in their site of origin within host-infested trees. Attractants for *S. pallidus* were concentrated in infested bark, while attractants for *R. xylophagorum* were present similarly in both the bark and wood of infested trees. Relative to *R. xylophagorum*, host-seeking *S. pallidus* may rely more heavily on cues arising directly from hosts or their products than cues arising from the tree itself. Parasitoids utilizing the same host species in the same habitat can potentially reduce interspecific competition by using different host location cues, thereby specializing on portions of the host population more closely associated with the cues (van Dijken and van Alphen 1998). Interspecific differences in the host finding strategies used by parasitoids of *D. frontalis* may thus promote the stability of this rather large parasitoid complex.

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References Cited

Berisford, C. W. 1969. Attack sequence of *Ips grandicollis* (Coleoptera: Scolytidae) and some associated hymenopterous parasites. J. Georgia Entomol. Soc. 4: 93-96.

1980. Natural enemies and associated organisms, Pp. 31-54. *In* R. C. Thatcher, J. L. Searcy, J. E. Coster and G. D. Hertel [eds.], The southern pine beetle, U.S.D.A. Forest Service Science and Education Administration Tech. Bull. 1631.

Berisford, C. W. and D. L. Dahlsten. 1989. Biological control of *Ips grandicollis* (Eichoff) (Coleoptera: Scolytidae) in Australia—a preliminary evaluation, Pp. 81-93. *In* D. L. Kulhavy and M. C. Miller [eds.], Potential for biological control of *Dendroctonus* and *Ips* bark beetles. Univ. of Texas Press. Austin, TX.

Billings, R. F. and R. S. Cameron. 1984. Kairomonal responses of Coleoptera, *Monochamus titillator* (Cerambycidae), *Thanasimus dubius* (Cleridae), and *Temnochila virescens* (Trogositidae) to behavioral chemicals of southern pine bark beetles (Coleoptera: Scolytidae). Environ. Entomol. 13: 1542-1548.

Birgersson, G., M. J. Dalusky, K. E. Espelie and C. W. Berisford. 1992. Isolation and identification of kairomones utilized by southern pine beetle parasitoids, p. 30. *In* D. Allen and L. P. Abrahamson [eds.], Proceedings: North American forest insect work conference, 25-28 March 1991, Denver, CO. U.S.D.A. Forest Service General Tech. Report PNW-GTR-294.

Bridges, J. R., J. E. Marler and B. H. McSparrin. 1984. A quantitative study of the yeasts and bacteria associated with laboratory-reared *Dendroctonus frontalis* Zimm. (Coleopt., Scolytidae). J. Appl. Entomol. 97: 261-267.

Bushing, R. W. 1965. A synoptic list of the parasites of Scolytidae (Coleoptera) in North America north of Mexico. Can. Entomol. 97: 449-492.

Camors, F. B., Jr. and T. L. Payne. 1972. Response of *Heydenia unica* (Hymenoptera: Pteromalidae) to *Dendroctonus frontalis* (Coleoptera: Scolytidae) pheromones and a host tree terpene. Ann. Entomol. Soc. Am 65: 31-33.

1973. Sequence of arrival of entomophagous insects to trees infested with the southern pine beetle. Environ. Entomol. 2: 267-270.

Dahlsten, D. L. and C. W. Berisford. 1995. Diversity of bark beetle natural enemies, Pp.

184-201. *In* F. P. Hain, S. M. Salom, W. F. Ravlin, T. L. Payne and K. F. Raffa [eds.], Behavior, Population Dynamics and Control of Forest Insects: Proc. International Union of Forestry Research Organizations, Joint Conference, 6-11 February 1994, Maui, HI.

Dixon, W. N. and T. L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Texas Agric. Exp. Sta. Bull. MP-1432.

1980. Attraction of entomophagous and associate insects of the southern pine beetle to beetle- and host tree-produced volatiles. J. Georgia Entomol. Soc. 15: 378-389.

Erbilgin, N. and K. F. Raffa. 2001. Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. Oecologia 127: 444-453.

Franklin, R. T. 1969. Hymenopterous parasites of the southern pine beetle in Georgia. J. Georgia Entomol. Soc. 4: 119-122.

Guenther, E. and D. Althausen. 1948. The essential oils. D. Van Nostrand Company, Inc., Princeton, NJ.

Kudon, L. H. and C. W. Berisford. 1981. An olfactometer for bark beetle parasites. J. Chem. Ecol. 7: 359-366.

Miller, M. C., M. McGregor, J. C. Grégoire, Z. Jia-xi, R. A. Werner, Y. S. Chow, D. C. Tovar, R. C. Balanos and Z. Mendel. 1989. Responses of insect associates of allied species to *Dendroctonus* and *Ips* (Coleoptera: Scolytidae) aggregation pheromones: A search for biological control agents., Pp. 213-230. *In* D. L. Kulhavy and M. C. Miller [eds.], Potential for biological control of *Dendroctonus* and *Ips* bark beetles. Univ. of Texas Press, Austin, TX.

Moore, G. E. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. Environ. Entomol. 1: 58-65.

Ohmart, C. P. and W. GH. Voigt. 1982. Temporal and spatial arrival patterns of *Ips plastographus maritimus* (Coleoptera: Scolytidae) and its insect associates on freshly felled *Pinus radiata* in California. Can. Entomol. 114: 337-348.

Payne, T. L. 1989. Olfactory basis for insect enemies of allied species, Pp. 55-69. *In* D. L. Kulhavy and M. C. Miller [eds.], Potential for biological control of *Dendroctonus* and *Ips* bark beetles. Univ. of Texas Press, Austin, TX.

Pettersson, E. M. 2001a. Volatile attractants for three pteromalid parasitoids attacking concealed spruce bark beetles. Chemoecology 11: 89-95.

2001b. Volatiles from potential hosts of *Rhopalicus tutela,* a bark beetle parasitoid. J. Chem. Ecol. 27: 2219-2231.

Pettersson, E. M., G. Birgersson and P. Witzgall. 2001. Synthetic attractants for the bark beetle parasitoid *Coeloides bostrichorum* Giraud (Hymenoptera: Braconidae). Naturwissenschaften 88: 88-91.

Pettersson, E. M., B. T. Sullivan, P. Anderson, C. W. Berisford and G. Birgersson. 2000. Odor perception in the bark beetle parasitoid *Roptrocerus xylophagorum* exposed to host associated volatiles. J. Chem. Ecol. 26: 2507-2525.

Raffa, K. F. and D. L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. Oecologia 102: 17-23.

Salom, S. M., A. Ascoli-Christensen, G. Birgersson, T. L. Payne and C. W. Berisford. 1992. Electroantennogram responses of the southern pine beetle parasitoid *Coeloides pissodis* (Ashmead) (Hym., Braconidae) to potential semiochemicals. J. Appl. Entomol. 114: 472-479.

Salom, S. M., G. Birgersson, T. L. Payne and C. W. Berisford. 1991. Electroantennogram responses of the southern pine beetle parasitoid *Dinotiscus dendroctoni* (Ashmead) (Hymenopters: Pteromalidae) to potential semiochemicals. J. Chem. Ecol. 17: 2527-2538.

Samson, P. R. 1984. The biology of *Roptrocerus xylophagorum* (Hym.: Torymidae), with a note on its taxonomic status. Entomophaga 29: 287-298.

SPSS. 1997. SigmaStat® 2.0 for Windows® User's Manual. SPSS Inc., Chicago, IL.

Stephen, F. M. and D. L. Dahlsten. 1976. The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. Can. Entomol. 108: 283-304.

Sullivan, B. T. 1997. The chemical ecology of host habitat location by larval parasitoids of the southern pine beetle, *Dendroctonus frontalis* Zimmermann: Olfactory cues and their possible sources. Ph.D. Diss., Univ. Georgia, Athens.

Sullivan, B. T., C. W. Berisford and M. J. Dalusky. 1997. Field response of southern pine beetle parasitoids to some natural attractants. J. Chem. Ecol. 23: 837-856.

Sullivan, B. T., E. M. Pettersson, K. C. Seltmann and C. W. Berisford. 2000. Attraction of the bark beetle parasitoid *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae) to host-associated olfactory cues. Environ. Entomol. 29: 1138-1151.

van Dijken, M. J. and J. J. M. van Alphen. 1998. The ecological significance of differences in host detection behavior in coexisting parasitoid species. Ecol. Entomol. 23: 265-270.

Vite, J. P. and D. L. Williamson. 1970. *Thanasimus dubius*: prey perception. J. Insect Physiol. 16: 233-239.