KAIROMONAL RESPONSES BY FOUR *Monochamus* SPECIES (COLEOPTERA: CERAMBYCIDAE) TO BARK BEETLE PHEROMONES*

by
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ABSTRACT

I investigated the hypothesis that wood-boring beetles in the genus *Monochamus* Megerle (Cerambycidae) utilize pheromones of sympatric bark beetles as host-finding kairomones. All nine bark beetle pheromones tested electrophysiologically were antenally-active for both sexes of *M. scutellatus* (Say), *M. clamator* (LeConte) and *M. obtusus* Casey from southern British Columbia, but only six were antenally-active for male and female *M. scutellatus* from northern British Columbia. When field-tested with multiple-funnel traps (British Columbia) or cross-vane traps (Ontario), a blend composed of frontalin, ipsdienol, ipsenol and MCH, in combination with a blend of host volatiles attracted significant numbers of *M. clamator*, *M. obtusus*, *M. notatus* (Drury) and *M. scutellatus* to baited traps. Traps baited with host volatiles in combination with a second blend composed of *exo*- and *endo*-brevicomin, *cis*- and *trans*-verbenol and verbenone caught no more beetles than unbaited traps or traps baited with the host blend alone. In British Columbia, traps baited with the first blend alone or both blends together captured significantly more *M. scutellatus* and *M. clamator* than unbaited traps, demonstrating a response to bark beetle pheromones in the absence of host volatiles. When the components from the blend composed of frontalin, ipsdienol, ipsenol and MCH were tested individually in southern British Columbia the data were inconsistent, but traps baited with either or both ipsdienol or ipsenol attracted significant numbers of *M. clamator* and *M. scutellatus*. In northern British Columbia none of the above components alone attracted significant numbers of male *M. scutellatus*, but traps baited with the host blend and ipsenol caught more female *M. scutellatus* than traps baited with only the host blend. Neither *endo*-brevicomin, *exo*-brevicomin, *cis*-verbenol, *trans*-

verbenol nor verbenone attracted significant numbers of *Monochamus* spp. in either location. These results suggest that *Monochamus* spp. minimize foraging costs by using the pheromones of sympatric bark beetles as kairomones. This would be adaptive because: 1) the pheromones would indicate suitable host trees or logs; and 2) the pheromones may indicate the potential presence of bark beetle larvae which when preyed upon by *Monochamus* larvae may positively influence brood development.

ACKNOWLEDGEMENTS

I thank John Borden for taking a chance and retrieving the "crud" from the bottom of the ocean. I also thank Dave Boyle, James Burns, Sarah Butler, Leslie Chong, Peter de Groot, Kathy Hein, Dezene Huber, Peter Katinic, Rory McIntosh, Tristan Mennel, Deepa Pureswaren, Bob Setter and Ian Wilson for assistance, Dave Moore and Dean Morewood for critical reviews, Regina Gries for her GC-EAD expertise and Chris Hogan of Slocan Forest Products Ltd. – Tackama Division and Ken Veillette of Ainsworth Lumber Co. Ltd. for making their logyards available as research sites. This research was supported by the Natural Sciences and Engineering Research Council of Canada, the Science Council of British Columbia, Forest Renewal British Columbia, the Canadian Forest Service, Abitibi Consolidated Forest Products Inc., Ainsworth Lumber Co. Ltd., B.C. Hydro and Power Authority, Bugbusters Pest Management Inc., Canadian Forest Products Ltd., Crestbrook Forest Industries Ltd., Gorman Bros. Ltd., International Forest Products Ltd., Lignum Ltd., Manning Diversified Forest Products Ltd., Millar Western Forest Products Ltd., Phero Tech Inc., Riverside Forest Products Ltd., Slocan Forest Products Ltd., TimberWest Ltd., Tolko Industries Ltd., Weldwood of Canada Ltd., West Fraser Mills Ltd., Western Forest Products Ltd., and Weyerhaeuser Canada Ltd.

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INTRODUCTION

Most woodboring insects reproduce in stressed, dying or dead trees that are usually randomly distributed in space and time (Schroeder, 1992). The larvae feed under the bark in the phloem tissue, in the sapwood, and sometimes deep into the heartwood (Linsley, 1961), often boring long tunnels which weaken and degrade the wood and provide infection courts for wood-rotting fungi. Woodboring beetles have caused economic losses as high as 30% in British Columbia (B.C.) log yards (Safranyik and Raske, 1970). A southern interior B.C. mill, which converts 700,000 m^3 of coniferous timber into lumber annually, could expect annual degrade losses from all woodborers to total between $1.8 and 4.8 million (US)[1]. If these values were extrapolated to encompass all interior mills, annual losses would be $293 million (US), $43.6 million of which would be attributable to large woodborers. Woodborers in the genus *Monochamus* are large and are of particular economic significance, because in addition to causing significant physical damage (Parmelee, 1941; Gardiner, 1957, 1975) they are vectors of the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer, 1934) Nickle (Vallentgoed, 1991).

Coniferophagous woodborers use olfactory stimuli to locate hosts (Linsley, 1961) and many are attracted to host monoterpenes and ethanol (e.g. Chénier and Philogène, 1989). Consequently, commercial woodborer baits consist of host monoterpenes (usually α-pinene) and ethanol, to simulate the odor of a stressed or dying tree. Current

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[1]Phero Tech Inc. 7572 Progress Way, RR#5, Delta, BC. V4G 1E9, Canada. Damage Assessment of Woodborers in the Interior of BC. Unpublished Report. 1997.

understanding of the cues involved in host selection by woodborers is incomplete.

There is considerable overlap in pheromone components among sympatric scolytid beetles (Borden, 1982), facilitating kairomonal responses by entomophagous insects to trees or logs infested by bark beetles of numerous species (e.g. Vité and Williamson, 1970; Dixon and Payne, 1979; Bedard et al., 1980; Bakke and Kvamme, 1981; Raffa and Klepzig, 1989). Coniferophagous woodborers in the families Cerambycidae and Buprestidae often attack the same hosts at the same time as conifer-infesting bark beetles (e.g. Dahlsten and Stephen, 1974; Stephen and Dahlsten, 1976; Dixon and Payne, 1979; Coulson et al., 1976, 1980). Semiochemical-based interaction between bark beetles and woodboring beetles has long been hypothesized, but has been formally tested only twice (Billings and Cameron, 1984; Billings, 1985). A kairomonal response to bark beetle pheromones would be adaptive to host seeking woodboring beetles because it could aid them in locating suitable host material.

Sub-cortical interactions between bark beetles and woodboring beetles have been classified as competitive (e.g. Coulson et al., 1976, 1980; Schroeder and Weslein, 1994a,b) or commensal (Flamm et al., 1989). A decline in larval density or emergence of adult bark beetles was attributed primarily to competition between cerambycid and bark beetle larvae. A kairomonal response to bark beetle pheromones would be even more adaptive to host seeking woodborers if bark beetle larvae represent a food resource for woodborer larvae. Dodds et al. (2001) found that 74% of the sixspined ips, *Ips calligraphus* (Germar), larvae encountered by *Monochamus carolinensis* (Olivier) larvae in phloem sandwiches were attacked; 85% were killed, suggesting that cerambycid larvae may be facultative predators of bark beetle larvae. This result supports the earlier

observation by Schenk and Benjamin (1969) that in Wisconsin "up to 50% of a brood (of the pine engraver, *Ips pini* (Say)) in the egg and 1st instar was destroyed by cerambycid larvae; a single cerambycid larvae could reduce the available food supply by 3%." However, Flamm et al. (1989) found that foraging by *Monochamus titillator* (Fabricius) results in low mortality of the southern pine beetle *Dendroctonus frontalis* Zimmermann, because the larvae migrate to the outer bark before *M. titillator* foraging becomes significant. One possible explanation for the observed behaviour is co-evolution between *M. titillator* and *D. frontalis*, with larval *D. frontalis* migration to the outer bark being an adaptive response that would reduce mortality due to *M. titillator* predation.

Billings and Cameron (1984) and Billings (1985) reported a kairomonal response by the southern pine sawyer, *M. titillator*, to a blend of *Ips* spp. pheromones (ipsenol, ipsdienol and *cis*-verbenol). In one study, there was a synergistic interaction between this stimulus and blends of *endo*-brevicomin and verbenone, or *endo*- plus *exo*-brevicomin with verbenone, all of which are pheromones of *D. frontalis* (Billings and Cameron, 1984). In another study, this stimulus was synergized by loblolly pine, *Pinus taeda* L., turpentine (Billings, 1985). Raffa (1991) reported an undisclosed number of *M. carolinensis* captured in ipsdienol-baited traps. Miller and Borden (1990) captured *Monochamus clamator* (LeConte) in increasing numbers as the combined release rates of ipsdienol and (-)-ß-phellandrene increased.

The objectives of this study were to test the following hypotheses: 1) male and female *Monochamus* spp. can perceive sympatric bark beetle pheromones antennally; 2) multiple-funnel traps baited with host volatiles and bark beetle pheromones are

significantly more attractive than traps baited with host volatiles alone; and 3) multiple-funnel traps baited with bark beetle pheromones alone are significantly more attractive than unbaited traps.

METHODS AND MATERIALS

Adult *Monochamus obtusus* Casey, *Monochamus scutellatus* (Say) and *M. clamator* were collected on emergence from caged bolts of lodgepole pine, *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm., and ponderosa pine, *P. ponderosa* P. Laws. ex C. Laws. from the Lillooet Forest District and Okanagan Valley in the summer of 1999. Adult male and female *M. scutellatus* were collected in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, B.C. in July 2000. The species *M. notatus* is rare in British Columbia and consequently were not included in the GC-EAD analyses. Coupled gas chromatographic-electroantennographic detection (GC-EAD) analyses[2] were performed on the antennae of both male and female *M. clamator*, *M. scutellatus*, and *M. obtusus* emerging in the summer of 1999 and male and female *M. scutellatus* collected in July 2000 with an HP 5890 gas chromatograph equipped with a fused silica column (DB-5, 30 m x 0.32 mm ID, J&W Scientific, Folsom, California, 95630-4714) (Gries, 1995). Authentic samples of nine (1999) or eleven (2000) candidate bark beetle pheromones (ipsenol, ipsdienol, MCH, frontalin, *cis*-verbenol, *trans*-verbenol, *exo*-brevicomin, *endo*-brevicomin, and verbenone; MCOL and lineatin were included in the 2000 analyses) (e.g. Borden, 1985) were mixed in hexane solutions at concentrations

[2] GC-EAD analyses were conducted by Ms. Regine Gries, Department of Biological Sciences, Simon Fraser University.

of both 10 ng/µl and 100 ng/µl. These were analysed in 1 µl amounts by GC-EAD under splitless conditions with a temperature program of 60°C (1 min), 10°C/min to 220°C (1999) or 50°C (1min), 10°C/min to 80°C for five min then 4°C/min to 240°C (2000). The 1999 analyses were repeated with a temperature program of 50°C (1 min), 10°C/min to 90°C then 4°C/min to 240°C to separate ipsdienol and *trans*-verbenol.

Synthetic antennally-active pheromones were arbitrarily partitioned into two blends: blend 1 consisting of ipsenol, ipsdienol, MCH and frontalin, and blend 2 consisting of *cis*- and *trans*-verbenol, *exo*- and *endo*-brevicomin and verbenone (Table 1). These were tested in the field for behavioral activity with and without a host blend composed of ethanol and α-pinene (Experiment 1) or ethanol with a synthetic host blend (Table 1) composed of 10.7 % (-)-α-pinene, 0.4 % (+)-α-pinene, 13.7 % (-)-β-pinene, 7.3 % myrcene, 1.5 % 3-carene, 0.1 % α-phellandrene, 63.7 % (+)-β-phellandrene, 0.3 % γ-terpinene and 2.4 % terpinolene (Experiment 2, 3) (Table 1). These proportions represent an average of those found in subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. and Engelmann spruce, *Picea engelmannii* Parry ex Engelm (R.L. McIntosh, unpublished data). See table two for a description of the number of replicates, location, treatments, and dates of all field experiments.

Experiments 1 and 3-12 used 12-unit multiple-funnel traps (Lindgren, 1983) deployed in randomized complete blocks with traps ≥ 15m apart. A small block of Vapona No-Pest Strip (Green Cross, Fisons Horticulture Inc., Mississauga, Ontario) was placed in each collecting cup to minimize predation and cannibalism. Traps were hung from aluminum poles such that the top funnel was ca. 1.5 m above ground. Experiment 2 used cross-vane traps with collection bins containing soapy water, deployed as above

(de Groot and Nott, 2001).

Captured beetles were collected weekly and frozen until they could be identified and sorted by sex. *Monochamus* spp. were identified and sorted by sex using elytral, antennal, and sternite characters (Linsley and Chemsak, 1984). Voucher specimens for all species reported have been deposited at the Pacific Forestry Centre, Canadian Forest Service, Victoria, B.C.

Data for each sex of *Monochamus* spp. were transformed by $\log_{10}(x+1)$ to correct for non-normality and heteroscedasticity (Zar, 1984), and analyzed by ANOVA (GLM) and the Ryan-Einot-Gabriel-Welsch (REGW) multiple range-test (Day and Quinn, 1989) using SAS Institute Inc. software (SAS Institute Inc., 1988). In all cases $\alpha = 0.05$. For other woodborer species, the above analyses were run if the number of beetles captured was ≥ 50, providing sufficient numbers for analyses.

RESULTS

As shown in a representative example from a female *M. scutellatus* antenna (Figure 1), all nine pheromones were detected by the antennae of both male and female *M. scutellatus*, *M. clamator* and *M. obtusus* from Southern British Columbia, with no differences by species or sex in the level of response. For both male and female *M. scutellatus* from Northern British Columbia, only seven of the eleven pheromones tested were detected antenally (Figure 2). There were no differences by sex in the level of response.

In experiment 1, one or both sexes of *M. clamator* and *M. obtusus* were captured in significantly higher numbers in traps baited with the host blend plus pheromone blend

Table 1. Compounds and their source, chemical purity, release devices, enantiomeric composition and release characteristics of semiochemicals tested in field experiments as attractants for *Monochamus* spp.

Blend and compounds[a]	Source[b]	Chemical purity (%)	Release device[c]	Enantiomeric composition (+:-)	Release rate mg/(24hr)[d]
PHEROMONE BLEND 1					
ipsenol	Phero Tech	98	bubble cap	50:50	0.24
ipsdienol	Phero Tech	95.4	bubble cap	50:50	0.11
MCH	Phero Tech	98.8	bubble cap	50:50	4.5
frontalin	Phero Tech	99.9	closed 400µl Eppendorf tube	50:50	2.6
PHEROMONE BLEND 2					
endo-brevicomin	Phero Tech	99.1	closed 250 µl Eppendorf tube	50:50	0.28
exo-brevicomin	Phero Tech	99	closed 250 µl Eppendorf tube	50:50	0.28
cis-verbenol	Phero Tech	92.7 (5% *trans*-)	bubble cap	22:78	0.35
trans-verbenol	Phero Tech	75 (15% *cis*-)	bubble cap	18:82	1.5
verbenone	Phero Tech	98	bubble cap	18:82	5
SYNTHETIC HOST MONOTERPENE BLEND					
(-)-α-pinene	Aldrich	98	plastic sleeve	81:19	47.5
(+)-α-pinene	Aldrich	98	plastic sleeve	91:9	1.8
(-)-β-pinene	Aldrich	99	plastic sleeve	1:99	77.4
myrcene	Phero Tech	92.6	plastic sleeve	Not Chiral	88.1
3-carene	Aldrich	90	plastic sleeve	NA[f]	5.4
(-)-α-phellandrene	Fluka	59.6	plastic sleeve	NA[f]	15.8

(+)-β-phellandrene[c]	Liberty Natural Products	70	plastic sleeve	99:1	409.9
γ-terpinene	Aldrich	97	plastic sleeve	Not Chiral	16.9
terpinolene	Fluka	92.6	plastic sleeve	Not Chiral	36.3
HOST COMPOUNDS RELEASED SEPARATELY					
α-pinene	Phero Tech Inc.	>99	plastic sleeve	90-95:5-10	2187
ethanol	Phero Tech Inc.	95	plastic sleeve	Not Chiral	1200

[a]IUPAC names, if different from trivial name follow: ipsenol; 2-methyl-6-methylene-7-octen-4-ol: ipsdienol; 2-methyl-6-methylene-2,7-octadien-4-ol: MCH; 3-methylcyclohex-3-en-1-one: frontalin; 1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane: *endo*-brevicomin; *endo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane: exo-brevicomin; *exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane: (-)-α-pinene; (-)-2-pinene: (+)-α-pinene; (+)-2-pinene: (-)-β-pinene; 2(10)-pinene: 3-carene; 3,7,7-trimethyl-bicyclo[4.1.0]hept-3-ene: (-)-α-phellandrene; 2-methyl-5-(1-methylethyl)-1,3-cyclohexadiene: (+)-β-phellandrene; *p*-mentha-1(7),2-diene: γ-terpinene; 1-methyl-4-(1-methylethyl)-1,4-cyclohexadiene: terpinolene; 1-methyl-4-(1-methylethylidene)-cyclohexene.

[b]Phero Tech Inc., 7572 Progress Way, Delta, British Columbia, V4G 1E9, Canada; Aldrich Chemical Company, Sigma-Aldrich Canada Ltd., 2149 Winston Park Drive, Oakville, ON L6H 6J8; Fluka, Sigma-Aldrich Canada Ltd., 2149 Winston Park Drive, Oakville, ON L6H 6J8; Liberty Natural Products, 8120 SE Stark Street, Portland OR 97215.

[c]All release devices from Phero Tech Inc. For the host blend, ethanol and all other compounds were released from separate sleeves. All other compounds were released from separate devices.

[d]Release rates for ipsenol, ipsdienol, MCH, Frontalin, cis- and trans-verbenol, endo- and exo-brevicomin, and verbenone were determined at 20-23°C by Phero Tech Inc. Rates for(-) α-pinene, (+) α-pinene, (-) β-pinene, myrcene, 3-carene, (-) α-phellandrene, (-) β-phellandrene, γ-terpinene, terpinolene, α-pinene and ethanol were determined at 28-30°C at Simon Fraser University.

[e]Obtained from angelica seed oil (Liberty Natural Products, 8120 SE Stark Street, Portland, OR 97215). Enantiomeric determination after the field season revealed almost pure (+) enantiomer, the antipode of naturally-occuring β-phellandrene in conifers.

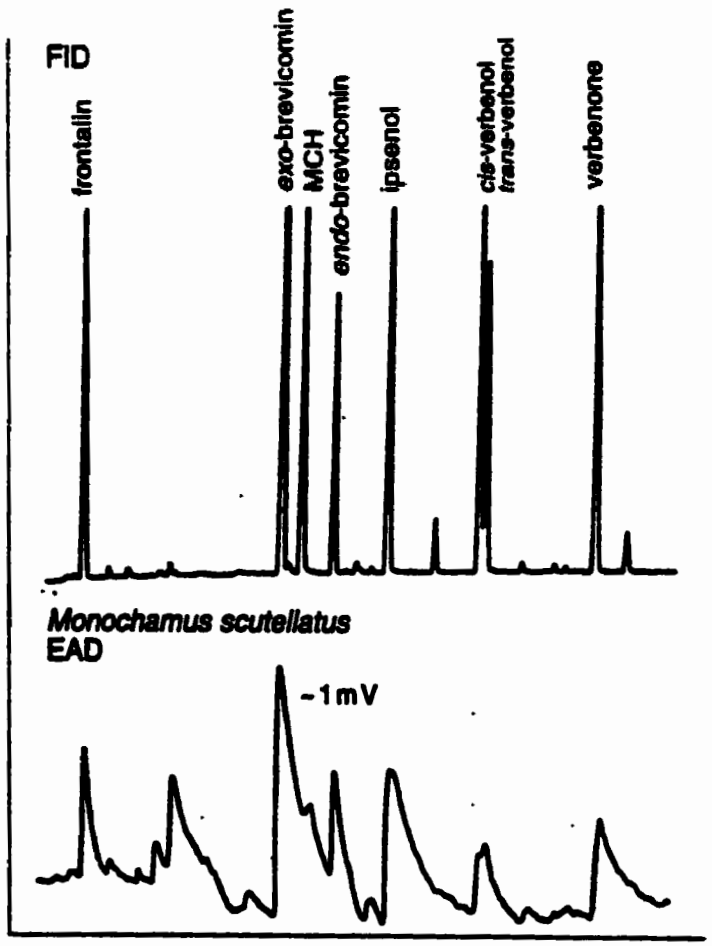
[f]Standards not available. Unable to determine.

Table 2. List of the date, number of replicates and location, and treatments for all experiments run in 1999 and 2000.

Experiment	Date	Number of replicates and location	Treatments
1	7-28 July 1999	9 replicates in the Gorman Bros. Ltd. millyard in Westbank, BC; 15 replicates in the Weyerhauser Canada Ltd. mill yard in Okanagan Falls, BC	1) unbaited control; 2) host blend (HB); 3) HB and pheromone blend 1 (B1); 4) HB and pheromone blend 2 (B2); 5) HB, B1, and B2
2	23 June-11 Aug. 1999	10 replicates in a recently thinned white pine stand north of Thessalon, Ontario	Same as experiment 1
3	19 July-14 Aug. 1999	8 replicates in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, BC	Same as experiment 1
4	29 June-31 July 1999	10 replicates in each of the Ainsworth Forest Products Ltd. mill yards in 100 Mile House and Chasm, BC	1) unbaited control; 2) pheromone blend 1 (B1); 3) pheromone blend 2 (B2); 4) B1 and B2
5	30 June-9 July 2000	19 replicates in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, BC	1) host blend (HB); 2) HB and frontalin; 3) HB and ipsdienol; 4) HB and ipsenol; 5) HB and MCH; 6) HB and pheromone blend 1
6	19-23 July 2000	20 replicates in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, BC	1) host blend (HB); 2) HB and *endo*-brevicomin; 3) HB and *exo*-brevicomin; 4) HB and *endo*- and *exo*-brevicomin
7	30 July-13 Aug. 2000	9 replicates in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, BC	1) unbaited control; 2) pheromone blend 1 (B1); 3) host blend and B1
8	13 Aug.-26 Sept.	10 replicates in the Slocan Forest Products Ltd., Tackama	1) host blend (HB); 2) HB, frontalin, ipsdienol, and

	2000	Division mill yard in Ft. Nelson, BC	ipsenol; 3) HB and pheromone blend 1
9	31 July-14 Aug. 2000	9 replicates with 4 and 5 replicates in the Ainsworth Forest Products Ltd. mill yards in Chasm and 100 Mile House, BC respectively	same as experiment 5
10	1-31 July 2000	10 replicates with 5 each in the Ainsworth Forest Products Ltd. mill yards in Chasm and 100 Mile House, BC respectively	1) host blend (HB); 2) HB and verbenone; 3) HB and *endo*- and *exo*-brevicomin; 4) HB and *cis*- and *trans*-verbenol; 5) HB and pheromone blend 2
11	14-21 Aug. 2000	9 replicates with 4 and 5 replicates in the Ainsworth Forest Products Ltd. mill yards in Chasm and 100 Mile House, BC respectively	1) host blend (HB); 2) HB and ipsenol; 3) HB and ipsdienol; 4) HB and ipsenol and ipsdienol
12	21 Aug.-25 Sept. 2000	5 replicates in the Ainsworth Forest Products Ltd. mill yard in Chasm, BC	1) unbaited control; 2) ipsenol; 3) ipsdienol; 4) ipsenol and ipsdienol; 5) host blend, ipsenol and ipsdienol

Figure 1. GC-EAD responses of female *Monochamus scutellatus* from Southern British Columbia to authentic samples of the bark beetle pheromones ipsenol, ipsdienol, MCH, frontalin, *cis*-verbenol, *trans*-verbenol, *exo*-brevicomin, *endo*-brevicomin and verbenone. Pheromones were analysed in 1 µl amounts under splitless conditions with a temperature program of 60°C (1 min), 10°C/min to 220°C (top) and 50°C (1 min), 10°C/min to 90°C then 4°C/min to 240°C (bottom) to separate ipsdienol and *trans*-verbenol.


FID
frontalin
exo-brevicomin
MCH
endo-brevicomin
ipsenol
cis-verbenol
trans-verbenol
verbenone
Monochamus scutellatus
EAD
~1mV

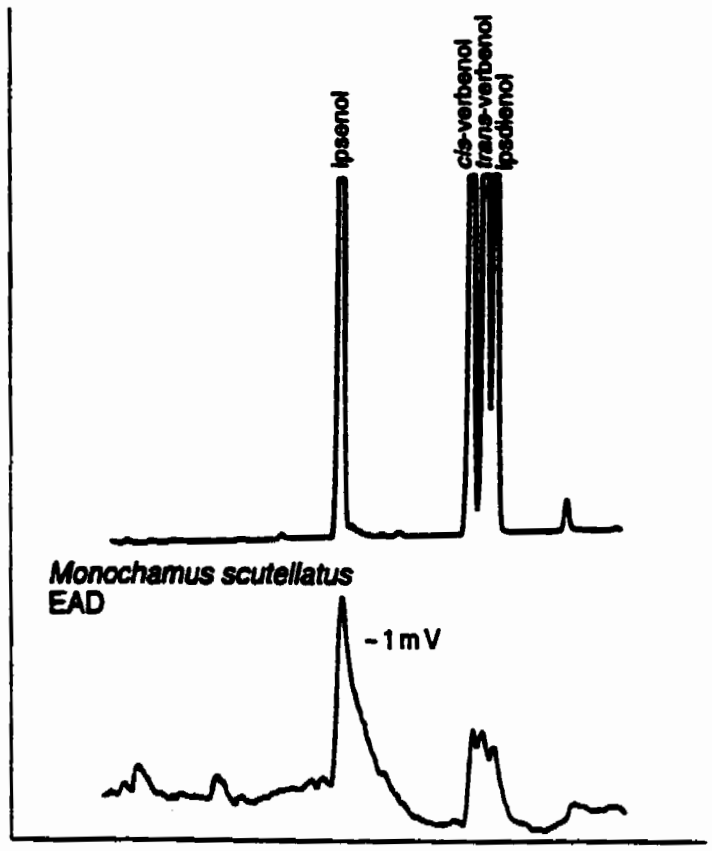
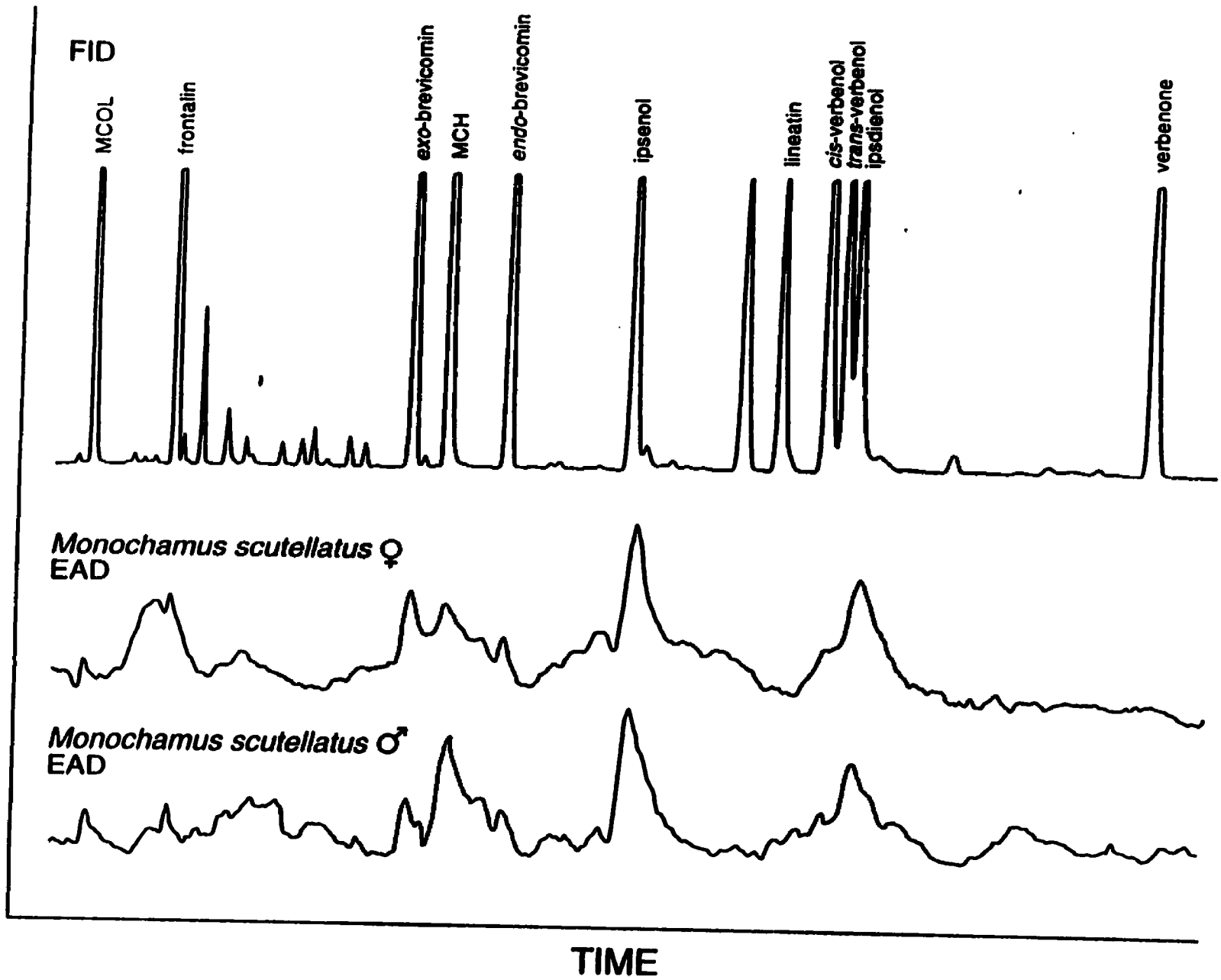

ipsenol
cis-verbenol
trans-verbenol
ipsdienol
Monochamus scutellatus
EAD
~1mV
TIME

Figure 2. GC-EAD responses to female (middle trace) and male (bottom trace) *Monochamus scutellatus* from Northern British Columbia to authentic samples of the bark beetle pheromones ipsenol, ipsdienol, MCH, frontalin, *cis*-verbenol, *trans*-verbenol, *exo*-brevicomin, *endo*-brevicomin and verbenone. Pheromones were analysed in 1µl amounts under splitless conditions with a temperature program of 50°C (1 min), 10°C/min to 80°C for 5 min then 4°C/min to 240°C.


FID
MCOL
frontalin
exo-brevicomin
MCH
endo-brevicomin
ipsenol
lineatin
cis-verbenol
trans-verbenol
ipsdienol
verbenone
Monochamus scutellatus ♀
EAD
Monochamus scutellatus ♂
EAD
TIME

1 than in traps baited with the host blend alone (Figure 3). Fewer *M. obtusus* of both sexes were captured in traps baited with the host blend plus both bark beetle pheromone blends. In no case were there significantly more beetles of either sex captured in traps baited with the host blend plus pheromone blend 2 than in either unbaited traps or traps baited with the host blend alone. Only male *M. obtusus* were significantly more attracted to traps baited with the host blend than to the unbaited control traps.

In experiment 2, both sexes of *M. scutellatus* and *M. notatus* were captured in significantly higher numbers in traps baited with the host blend plus pheromone blend 1. Both sexes of *M. scutellatus* and female *M. notatus* were captured in significantly higher numbers in traps baited with the host blend plus both pheromone blends than in other traps (Figure 3). Similarly, both sexes of *M. scutellatus* and female *M. notatus* were captured in higher numbers in traps baited with the host blend plus pheromone blend 2 or the host blend alone than to unbaited traps. In experiment 3 both sexes of *M. scutellatus* were caught in significantly higher numbers in all baited traps than in unbaited control traps (Figure 3).

In experiment 4, male and female *M. clamator* and *M. scutellatus* were captured in significantly higher numbers in traps baited with pheromone blend 1 alone or combined with pheromone blend 2 than in unbaited traps or traps baited with pheromone blend 2 alone (Figure 4).

In experiment 5, both sexes of *M. scutellatus* were captured in significantly higher numbers in traps baited with the host blend and pheromone blend 1 than in traps baited with the host blend alone (Figure 5). For both male and female *M. scutellatus*, traps baited with the host blend and pheromone blend 1 caught significantly more beeltes than

Figure 3. Catches of *Monochamus clamator, M. obtusus, M. notatus* and *M. scutellatus* in experiments 1 (run from 7-28 July 1999 in dryland sorts in Westbank and Okanagan Falls, BC), 2 (run from 23 June-11 August 1999 in a recently thinned white pine stand north of Thessalon, ON) and 3 (run from 19 July-14 August 1999 in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, BC). The host blend (HB) consisted of (ethanol and α-pinene in experiment 1, and ethanol and a synthetic host blend composed of 10.7% (-)-α-pinene, 0.4% (+)-α-pinene, 13.7% (-)-β-pinene, 7.3% myrcene, 1.5% 3-carene, 0.1% α-phellandrene, 63.7% (+)-β-phellandrene, 0.3% γ-terpinene and 2.4% terpinolene in experiments 2 and 3); pheromone blend 1 (B1) consisted of ipsenol, ipsdienol, MCH and frontalin; pheromone blend 2 (B2) consisted of *cis*- and *trans*-verbenol, *exo*- and *endo*-brevicomin and verbenone. Data was transformed by $\log_{10}(x+1)$ to correct for non-normality and heteroscedasticity, and analysed by ANOVA (GLM) and the REGW multiple range-test using SAS Institute Inc. software. In all cases $\alpha=0.05$. Treatments with different letters are significantly different.

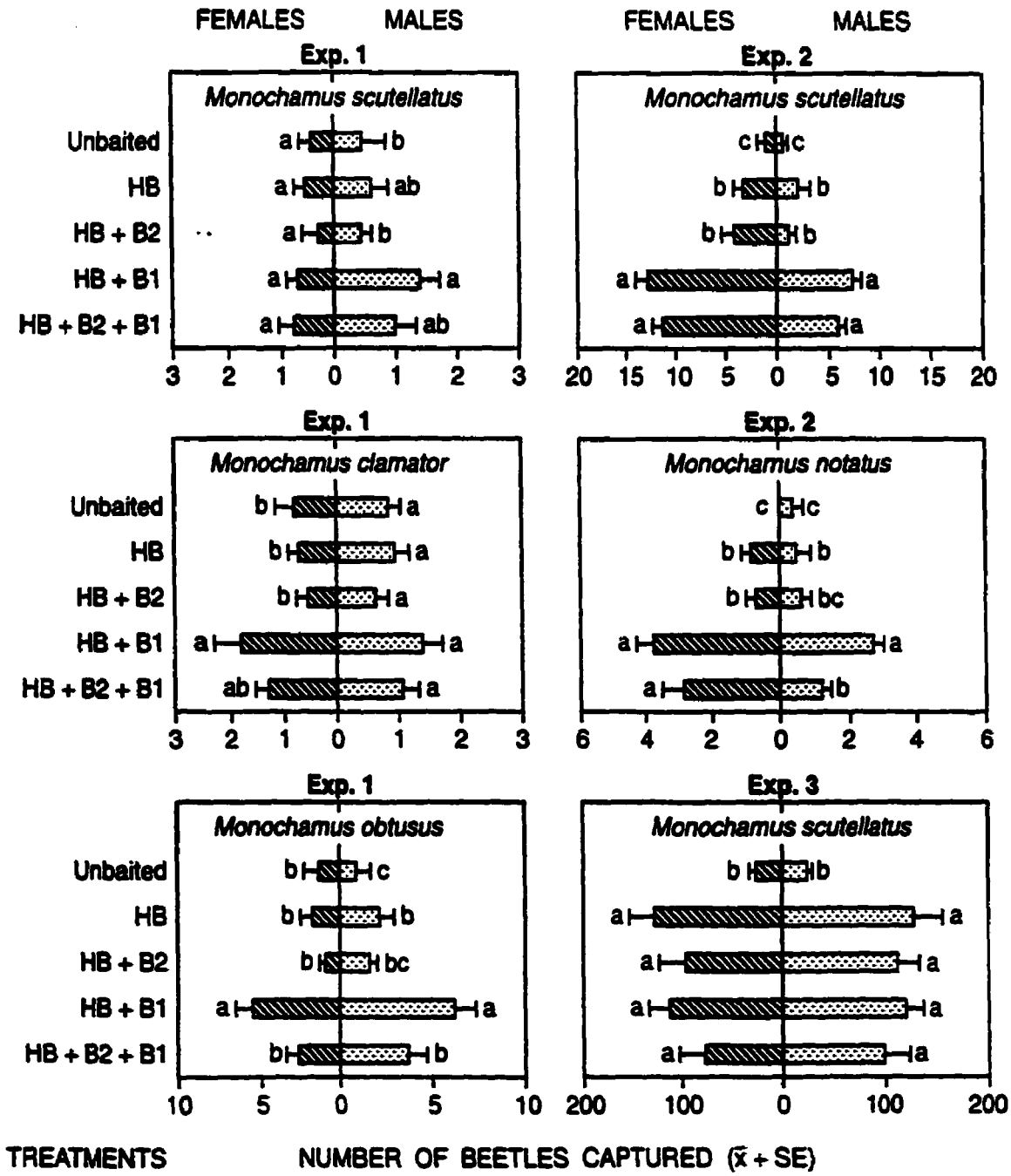
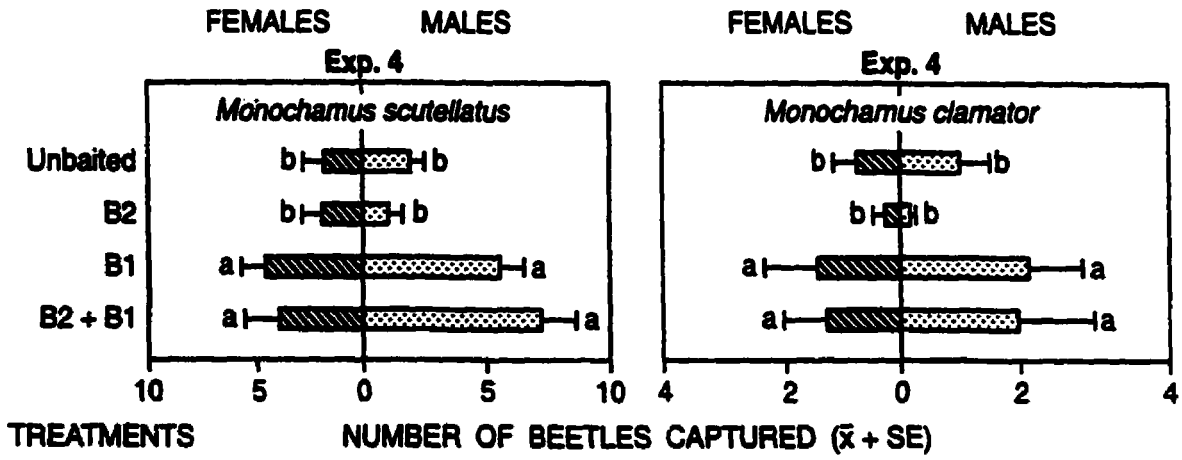

FEMALES
MALES
Exp. 1
Monochamus scutellatus
Unbaited
HB
HB + B2
HB + B1
HB + B2 + B1
3 2 1 0 1 2 3
Exp. 2
Monochamus scutellatus
20 15 10 5 0 5 10 15 20
Exp. 1
Monochamus clamator
3 2 1 0 1 2 3
Exp. 2
Monochamus notatus
6 4 2 0 2 4 6
Exp. 1
Monochamus obtusus
10 5 0 5 10
Exp. 3
Monochamus scutellatus
200 100 0 100 200
TREATMENTS
NUMBER OF BEETLES CAPTURED (x̄ + SE)

Figure 4. Catches of *Monochamus clamator* and *M. scutellatus* in experiment 4 (run from 29 June-31 July 1999 in the Ainsworth Forest Products Ltd. mill yards in 100-Mile House and Chasm, BC). Pheromone blend 1 (B1) consisted of ipsenol, ipsdienol, MCH and frontalin; pheromone blend 2 (B2) consisted of *cis*- and *trans*-verbenol and *endo*- and *exo*-brevicomin and verbenone. Data was transformed by $\log_{10}(x+1)$ to correct for non-normality and heteroscedasticity, and analysed by ANOVA (GLM) and the REGW multiple range-test using SAS Institute Inc. software. In all cases $\alpha=0.05$. Treatments with different letters are significantly different.


FEMALES
MALES
Exp. 4
Monochamus scutellatus
Unbaited
B2
B1
B2 + B1
b
b
b
b
a
a
a
a
10
5
0
5
10
TREATMENTS
FEMALES
MALES
Exp. 4
Monochamus clamator
b
b
b
b
a
a
a
a
4
2
0
2
4
NUMBER OF BEETLES CAPTURED (x̄ + SE)

traps baited with the host blend and each of the pheromone components of blend 1 individually, except traps baited with the host blend and ipsenol. Traps baited with the host blend and ipsenol caught significantly more female *M. scutellatus* than traps baited with the host blend alone.

In experiment 6 there was no significant difference between the number of male and female *M. scutellatus* captured in traps baited with the host blend alone or the host blend and either or both *endo*-brevicomin and *exo*-brevicomin (Figure 5).

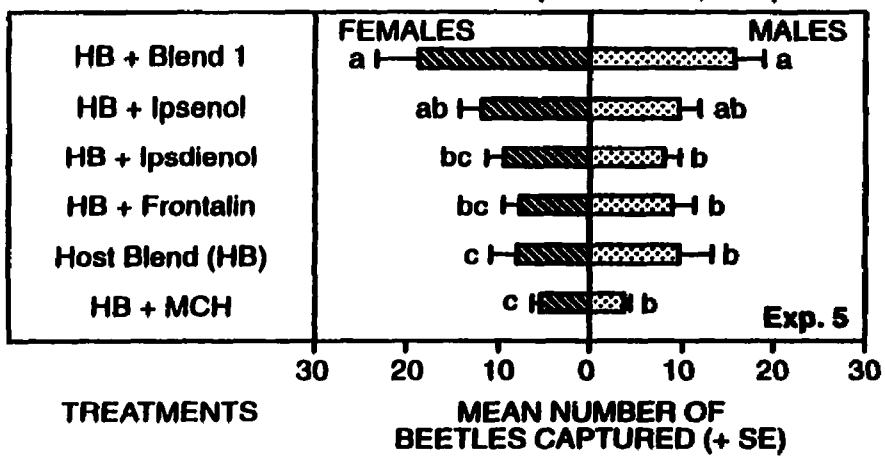
Both male and female *M. scutellatus* were captured in significantly higher numbers in traps baited with pheromone blend 1 or the host blend and pheromone blend 1 than in unbaited traps in experiment 7 (Figure 5). There was no difference in the mean number of male or female *M. scutellatus* captured in traps baited with the host blend and pheromone blend 1 or pheromone blend 1 alone.

In experiment 8 traps baited with frontalin, ipsenol, ipsdienol and the host blend or the host blend and pheromone blend 1, both caught significantly more male and female *M. scutellatus* than unbaited traps (Figure 5). There was no difference in the mean number of male or female *M. scutellatus* captured in traps baited with the host blend, frontalin, ipsenol and ipsdienol or the host blend and pheromone blend 1.

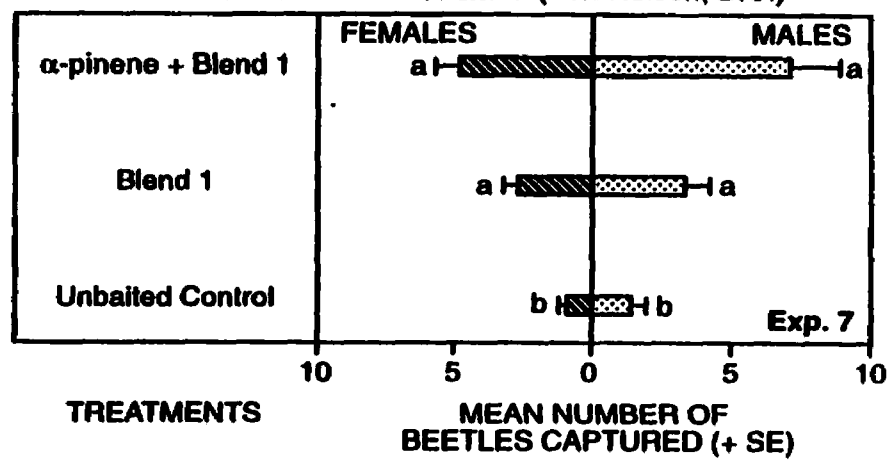
In experiment 9 there were no significant differences in the mean number of male and female *M. scutellatus* and female *M. clamator* caught by any of the treatments (Figure 6). Male *M. clamator* were captured in greater numbers by traps baited with the host blend and ipsenol than in traps baited with the host blend and MCH, with an intermediate capture in traps baited with the host blend and pheromone blend 1, the host blend and ipsdienol or frontalin and the host blend alone.

Figure 5. Catches of *Monochamus scutellatus* in experiments 5-8 run in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, BC. Experiment 5 was run from 30 June-9 July 2000; experiment 6 was run from 19-23 July 2000; experiment 7 was run from 30 July-13 August 2000 and experiment 8 was run from 13 August-26 September 2000. The host blend (HB) consisted of α-pinene and ethanol (experiment 5) or α-pinene alone (experiments 6-8). Pheromone blend 1 (B1) consisted of ipsenol, ipsdienol, MCH and frontalin. Data was transformed by $\log_{10}(x+1)$ to correct for non-normality and heteroscedasticity, and analysed by ANOVA (GLM) and the REGW multiple range-test using SAS Institute Inc. software. In all cases $\alpha=0.05$. Treatments with different letters are significantly different.

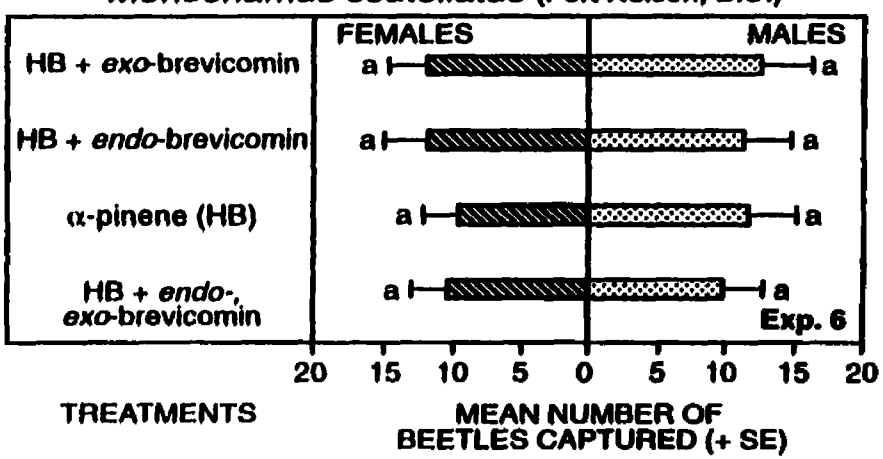
Monochamus scutellatus (Fort Nelson, B.C.)



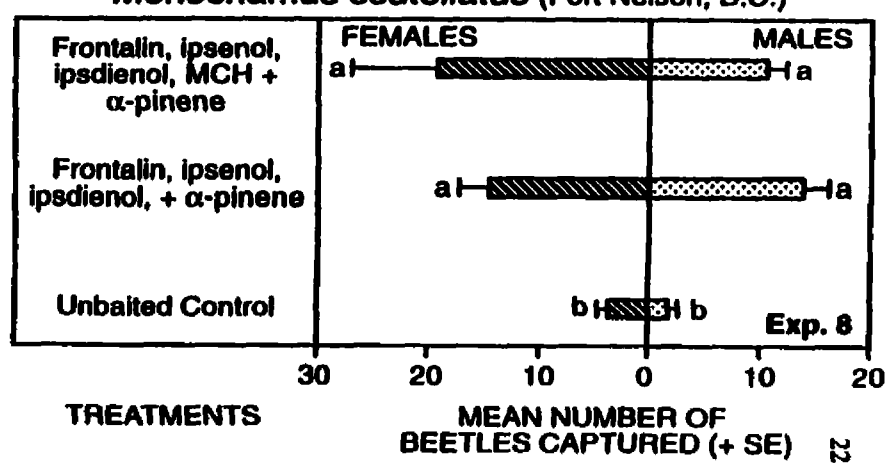
Monochamus scutellatus (Fort Nelson, B.C.)



Monochamus scutellatus (Fort Nelson, B.C.)



Monochamus scutellatus (Fort Nelson, B.C.)

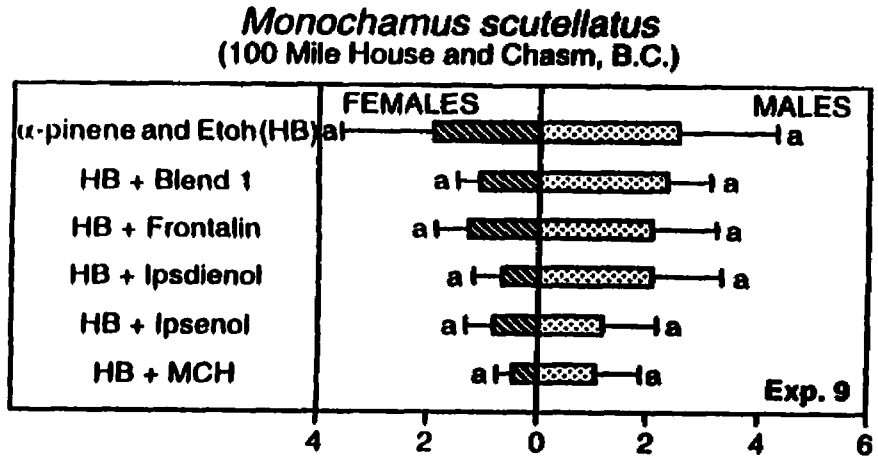


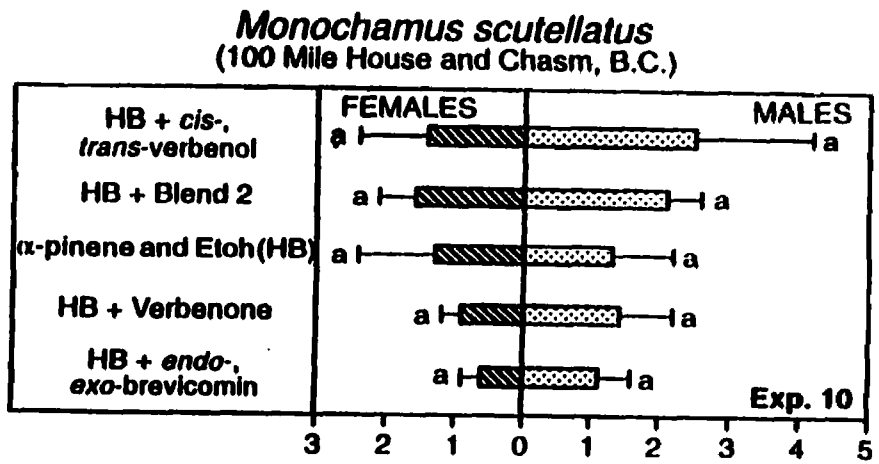
In experiment 10 there were no significant differences in the mean number of male and female *M. scutellatus* and *M. clamator* caught by any of the treatments (Figure 6).

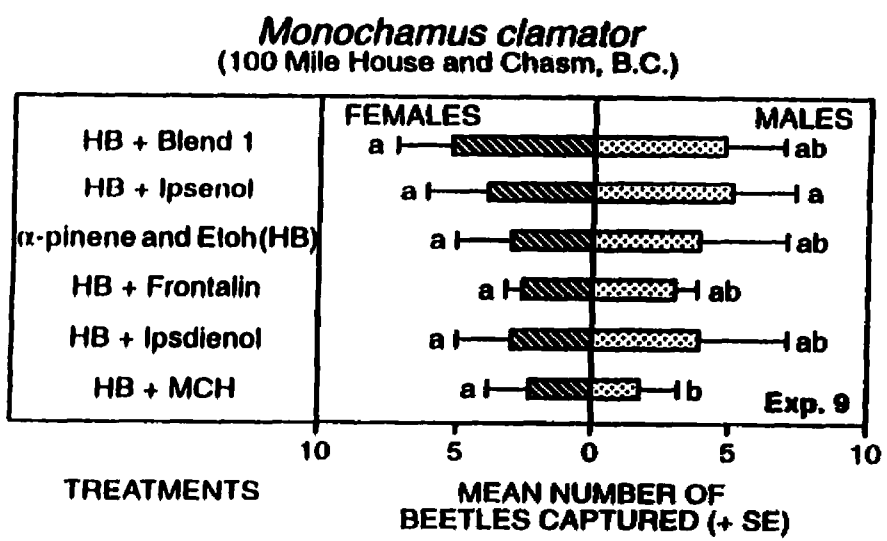
In experiment 11 there was no significant difference in the mean number of female *M. scutellatus* or male *M. clamator* caught by any of the treatments (Figure 7). Significantly more male *M. scutellatus* were captured in traps baited with the host blend, ipsenol and ipsdienol or the host blend and ipsenol than in traps baited with the host blend alone, with an intermediate capture in traps baited with the host blend and ipsdienol. Female *M. clamator* were captured in greater numbers in traps baited with the host blend, ipsenol and ipsdienol than in traps baited with the host blend alone, with an intermediate level of response to traps baited with the host blend and ipsdienol or the host blend and ipsenol.

In experiment 12 there was no significant difference in the mean number of female *M. scutellatus* caught by any of the treatments (Figure 7). Significantly higher numbers of male *M. scutellatus* were caught by traps baited with the host blend, ipsenol and ipsdienol than by unbaited traps or traps baited with ipsenol and ipsdienol. Similarly, traps baited with ipsenol caught significantly more male *M. scutellatus* than unbaited traps. An intermediate level of response was observed for male *M. scutellatus* to traps baited with ipsenol and ipsdienol or ipsdienol alone. Female *M. clamator* were captured in significantly higher numbers by traps baited with the host blend, ipsenol and ipsdienol, ipsenol and ipsdienol or ipsdienol alone than by unbaited traps. Male *M. clamator* were captured in greater numbers by traps baited with the host blend, ipsenol and ipsdienol than by traps baited with ipsenol alone or by unbaited traps, with an intermediate

Figure 6. Catches of *Monochamus clamator* and *M. scutellatus* in experiments 9 (run from 31 July-14 August 2000) and 10 (run from 1-31 July 2000) in the Ainsworth Forest Products Ltd. mill yards in 100-Mile House and Chasm, BC. Pheromone blend 1 (Blend 1) consisted of ipsenol, ipsdienol, MCH and frontalin; pheromone blend 2 (Blend 2) consisted of *cis*- and *trans*-verbenol and *endo*- and *exo*-brevicomin and verbenone. Data was transformed by $\log_{10}(x+1)$ to correct for non-normality and heteroscedasticity, and analysed by ANOVA (GLM) and the REGW multiple range-test using SAS Institute Inc. software. In all cases $\alpha=0.05$. Treatments with different letters are significantly different.


Monochamus scutellatus
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
α-pinene and Etoh(HB)
HB + Blend 1
HB + Frontalin
HB + Ipsdienol
HB + Ipsenol
HB + MCH
a
Exp. 9
4 2 0 2 4 6


Monochamus scutellatus
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
HB + cis-, trans-verbenol
HB + Blend 2
α-pinene and Etoh(HB)
HB + Verbenone
HB + endo-, exo-brevicomin
a
Exp. 10
3 2 1 0 1 2 3 4 5


Monochamus clamator
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
HB + Blend 1
HB + Ipsenol
α-pinene and Etoh(HB)
HB + Frontalin
HB + Ipsdienol
HB + MCH
a
ab
b
Exp. 9
10 5 0 5 10
TREATMENTS
MEAN NUMBER OF BEETLES CAPTURED (+ SE)

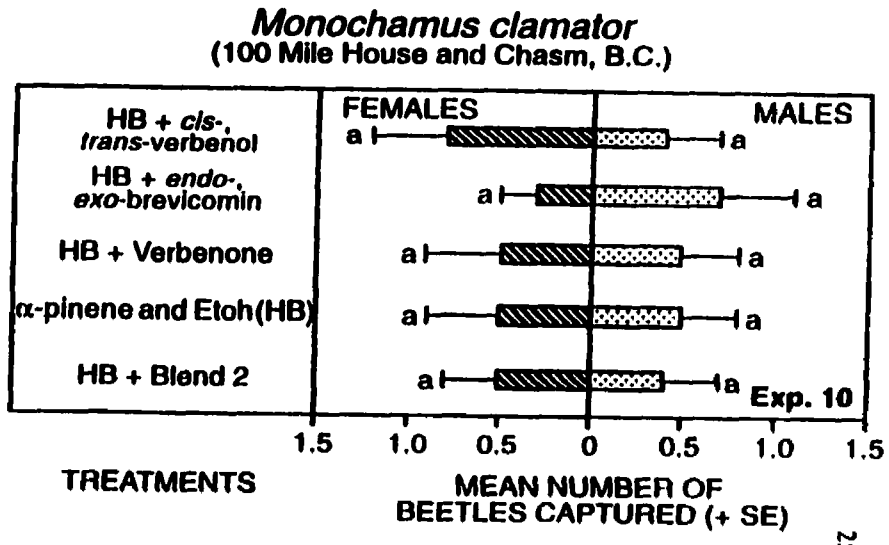
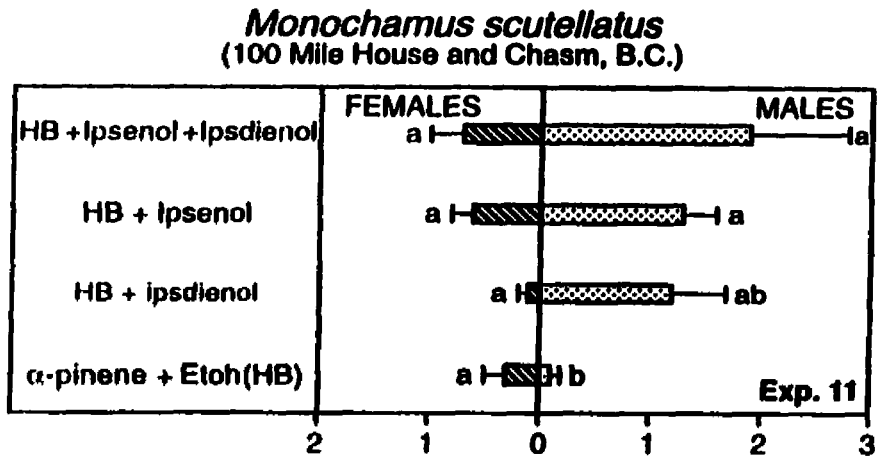
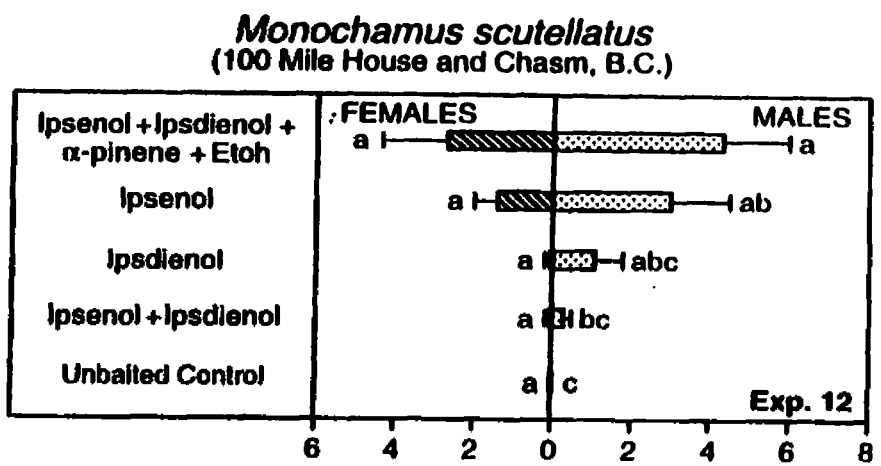
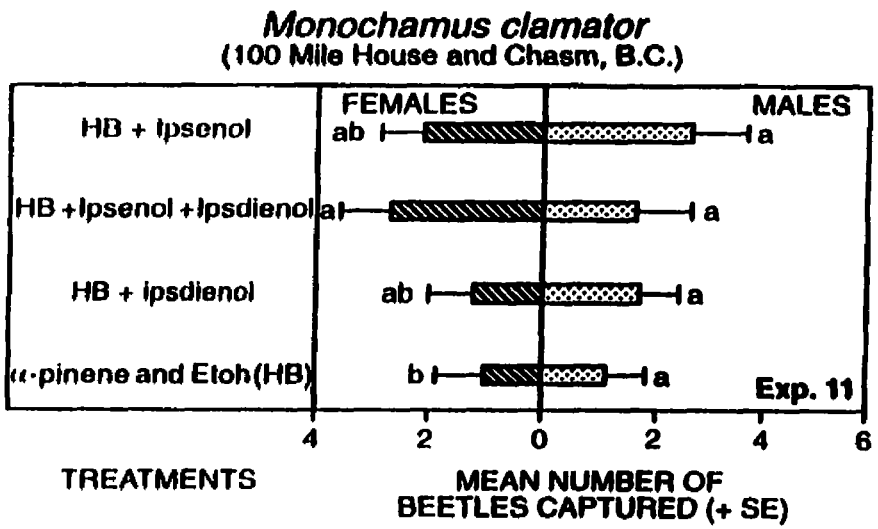
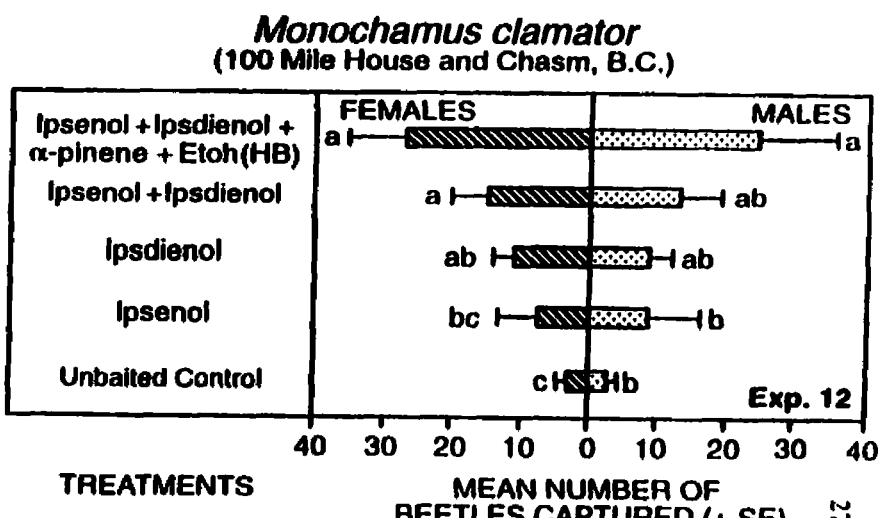

Monochamus clamator
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
HB + cis-, trans-verbenol
HB + endo-, exo-brevicomin
HB + Verbenone
α-pinene and Etoh(HB)
HB + Blend 2
a
Exp. 10
1.5 1.0 0.5 0 0.5 1.0 1.5
TREATMENTS
MEAN NUMBER OF BEETLES CAPTURED (+ SE)

Figure 7. Catches of *Monochamus clamator* and *M. scutellatus* in experiments 11 (run from 14-21 August 2000) and 12 (run from 21 August-25 September 2000) in the Ainsworth Forest Products Ltd. mill yards in 100-Mile House and Chasm, BC. Data was transformed by $\log_{10}(x+1)$ to correct for non-normality and heteroscedasticity, and analysed by ANOVA (GLM) and the REGW multiple range-test using SAS Institute Inc. software. In all cases $\alpha=0.05$. Treatments with different letters are significantly different.


Monochamus scutellatus
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
HB + Ipsenol + Ipsdienol
HB + Ipsenol
HB + Ipsdienol
α-pinene + Etoh(HB)
a
a
a
a
a
a
ab
b
Exp. 11
2
1
0
1
2
3


Monochamus scutellatus
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
Ipsenol + Ipsdienol + α-pinene + Etoh
Ipsenol
Ipsdienol
Ipsenol + Ipsdienol
Unbaited Control
a
a
a
a
a
a
ab
abc
bc
c
Exp. 12
6
4
2
0
2
4
6
8


Monochamus clamator
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
HB + Ipsenol
HB + Ipsenol + Ipsdienol
HB + Ipsdienol
α-pinene and Etoh(HB)
ab
a
a
a
ab
a
b
a
Exp. 11
4
2
0
2
4
6
TREATMENTS
MEAN NUMBER OF BEETLES CAPTURED (+ SE)


Monochamus clamator
(100 Mile House and Chasm, B.C.)
FEMALES
MALES
Ipsenol + Ipsdienol + α-pinene + Etoh(HB)
Ipsenol + Ipsdienol
Ipsdienol
Ipsenol
Unbaited Control
a
a
a
a
ab
ab
bc
b
c
b
Exp. 12
40
30
20
10
0
10
20
30
40
TREATMENTS
MEAN NUMBER OF BEETLES CAPTURED (+ SE)

response to traps baited with ipsdienol and ipsenol or ipsdienol alone. In experiments 1, 3, 4 and 6-12 significant responses to treatments occurred for males or females of seven other woodborer species (Table 3). Despite ≥50 beetles being captured, no significantly greater responses to treatment *versus* control traps in any experiment were found for the following: *Arhopalus* spp. and *Asemum* spp. (Cermabycidae); *Dicerca tenebrosa, Buprestis nutalli, Buprestis laeviventris, Buprestis maculativentris*, and *Chrysobothris* spp. (Buprestidae).

DISCUSSION

My results demonstrate that *M. clamator, M. obtusus* and *M. scutellatus* can perceive sympatric bark beetle pheromones electrophysiologically and that *M. clamator, M. notatus, M. obtusus*, and *M. scutellatus* are attracted by pheromones in combination with host volatiles. For two species, *M. scutellatus* and *M. clamator*, they demonstrate also that a response can occur to bark beetle pheromones in the absence of host volatiles, supporting the results of Billings and Cameron (1984), but not Billings (1985) for *M. titillator*. These findings strongly suggest that these *Monochamus* spp. use heterospecific pheromones as kairomones during host selection. The ability to respond to both sympatric bark beetle pheromones and host volatiles would minimize the energy spent in foraging to locate hosts, exposure to predation or environmental extremes (Dahlsten, 1982), and the opportunity cost of time lost for other biologically important activities (Campbell, 1996) in both the presence and absence of mass-attacking primary

and secondary bark beetles. Although inconclusive my results also suggest that ipsenol and/or ipsdienol may be the components responsible for the observed kairomonal responses.

The blends tested contained two antiaggregation pheromones, MCH and verbenone. Positive orientation toward sources of both aggregation and antiaggregation pheromones should be adaptive for *Monochamus* spp. as long as they indicate the presence of a suitable host. However, the lack of a response to pheromone blend 2 alone or combined with the host blend, as well as reduced responses by *M. obtusus* when it was combined with pheromone blend 1 in experiment 1, suggest that one or more of its components, possibly verbenone, could actually be repellent. The production of verbenone by microorganisms (Leufven et al., 1984; Hunt and Borden, 1990) after a host has been overcome by aggressive bark beetles may provide a signal to *Monochamus* spp. of hosts that are no longer acceptable. Microorganisms associated with larval woodborers may also produce verbenone. In the summer of 2000 the components from both pheromone blends were tested individually. The results suggest that neither verbenone nor MCH are behaviorally active for *Monochamus* spp.

The occurrence of intraguild predation is well documented in many terrestrial and aquatic communities (e.g. Polis et al., 1989). Dodds et al. (2001) recently found that *M. carolinensis* is a facultative, intra-guild predator of bark beetle larvae. This would reduce brood survivorship and consequently the number of host seeking bark beetles in the next generation. This may reduce the number of bark beetle killed hosts from which bark beetle produced kairomones (pheromones) would be released. As a result host-seeking *Monochamus* beetles may experience increased foraging costs, predation risk, exposure

Table 3. Significant responses by woodborers other than *Monochamus* spp. when numbers captured was ≥ 50 males and females.

Family	Species, sex and number	Response
Buprestidae	*Buprestis subornata*, females, N=89	Captured in greater numbers in unbaited traps in Exp. 1, than in traps baited with the host blend and pheromone blend 2. Intermediate response to the host blend with pheromone blends 1 or pheromone blend 1 and 2.
	B. lyrata, females, N=46	In Exp. 4 captured in higher numbers in traps baited with pheromone blend 2 than pheromone blend 1. Intermediate responses to all other treatments.
	Chalcophora virginiensis, females, N=158	In Exp. 4 captured in greater numbers in traps baited with pheromone blend 1 alone or with pheromone blend 2 than in all other traps.
	Dicerca tenebrica, males, N=482	In Exp. 4 captured in higher numbers in traps baited with either pheromone blend than in unbaited control traps. Intermediate response to both pheromone blends combined.
	D. tenebrica, females, N=1288	Captured in greater numbers in traps baited with blend 1 in Exp. 4 than in traps baited with both blends combined and unbaited traps. Intermediate response to pheromone blend 2.
Cerambycidae	*Xylotrechus undulatus*, males and females, N=62 and N=34 respectively	In Exp. 8 captured in greater numbers in traps baited with the host blend and pheromone blend 1, or the host blend, frontalin, ipsenol and ipsdienol than by unbaited traps.
	X. longitarsus, males and females, N=161 and N=78 respectively	In Exp. 12 captured in higher numbers in traps baited with the host blend, ipsenol and ipsdienol than in all other traps.
Siricidae	*Urocerus flavicornis*, females, N=51	In Exp. 12 captured in greater numbers in traps baited with the host blend, ipsenol and ipsdienol than in all other traps.

to environmental extremes and opportunity costs of time lost for other biologically important activities. This represents an apparent conflict. Cerambycid larvae may gain an adaptive advantage by feeding on bark beetle larvae (i.e. improved nutrition) however this benefit may be reduced by the cost of reduced bark beetle survivorship and consequently increased costs and risks for host-seeking adult *Monochamus*. I hypothesize that *M. clamator*, *M. notatus*, *M. obtusus* and *M. scutellatus* are intraguild predators, and thus gain an additional adaptive advantage from being able to orient to bark beetle pheromones. Evolution of a kairomonal response by *Monochamus* spp. to the pheromones of numerous species of sympatric bark beetles would be facilitated by overlapping host ranges and similar larval requirements. The absence of one or both of these may explain why the majority of other woodborers captured, mainly buprestids, did not respond to either the host or pheromone blends. If *Monochamus* spp. gain a significant adaptive advantage by preying on the larvae of bark beetles, they would inevitably be in competition with entomophagous insects that use the same compounds as kairomones (Borden, 1982).

In Ft. Nelson, population levels during experiment 3 were very high and it is possible that high numbers of responding beetles obscured responses by *M. scutellatus* to different stimuli. Alternatively, the Ft. Nelson population of *M. scutellatus* may represent a behavioral ecotype that is associated with different bark beetle pheromones than those in southern B.C. or Ontario. This hypothesis is supported by the differing GC-EAD profiles of male and female *M. scutellatus* from Northern and Southern British Columbia. Male and female beetles from the south perceive *cis*-verbenol, *trans*-verbenol and verbenone, while male and female beetles from the north do not (Figures 1, 2). None of

the bark beetles known to occur in Northern British Columbia produce *cis*-verbenol, *trans*-verbenol or verbenone (Mayer and McLaughlin, 1991).

Geographic variation in pheromone communication systems has been documented for several insects (e.g. the European corn borer, *Ostrinia nubilalis* (Hübner) [Sorenson et al. 1992], the pine engraver, *Ips pini* [Miller et al. 1997]). Several studies have found a genetic basis for variation in pheromone production and response (e.g. Baker and Cardé 1979; Klun and Huettel 1988; Hager and Teale 1996). Collins and Cardé (1989) selected for altered amounts of pheromone production or shifted ratios of pheromone components and demonstrated that the traits pheromone production and response are heritable. They also demonstrated that rapid evolution of these traits can occur under some selection regimes. This may be significant for large scale mating disruption and mass trapping programs which rely on the broadcast application of incomplete formulated synthetic pheromone blends. The observed geographic variation for the white-spotted sawyer suggests that pest management programs for it, as well as other pest insects, may need to be regionally-specific.

Kairomonal responses by *Monochamus* spp. may have practical application in pest management. If further research results in simplified, and thus inexpensive, kairomonal blends composed of both host volatiles and bark beetle pheromones, an improved trap (McIntosh et al., 2001; de Groot and Nott, 2001) baited with a more potent, attractive lure might be used effectively in operational monitoring and mass trapping programs. These in turn could lead to reduced lumber degrade losses and (where pine-wilt disease occurs) curtailment of the spread or infection rate of the pine wood nematode.

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