Evaluation of Frontalin and Exo-brevicomin as Kairomones to Control Mountain Pine Beetle (Coleoptera: Scolytidae) in Lodgepole Pine

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ABSTRACT Augmentation of entomophagous insects with synthetic attractants for control of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, was evaluated in lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, stands located in central Idaho and northeastern Oregon. The clerid predator, *Thanasimus undatulus* (Say), was the only species that responded to sticky traps baited with either frontalin or exo-brevicomin. Significantly more adults responded to frontalin, and exo-brevicomin was eliminated from subsequent tests. Frontalin was successful in augmenting *T. undatulus* adults on trees baited either before (May–mid-July) or during (mid-July–September) the mountain pine beetle flight period. Baiting before the bark beetle flight period was most effective in augmenting *T. undatulus*, because baiting was concurrent with peak flight activity of the clerid. Frontalin, in association with the host trees, also attracted mountain pine beetle when used during the latter's flight period. Augmentation of *T. undatulus* adults without aggregating mountain pine beetle was accomplished by removing the attractant before the flight period of the latter. Baiting brood trees in this manner increased the incidence of *T. undatulus* larvae 3-fold, and mortality of emerging mountain pine beetle adults by 7.1%, but did not significantly reduce pine beetle brood survival or consequent tree mortality. However, the influence of the substantially increased predator population may be synergistic with other control tactics, and the use of frontalin should be considered seriously within a pest management program.

PHEROMONES OF numerous insects have been isolated, identified, synthesized, and utilized successfully to manipulate pest populations (Birch 1974). Recent studies have shown that a great potential also exists for manipulating entomophagous insects with pheromones. In a discussion on the use of pheromones to promote action by beneficial insect parasites, Jones et al. (1976) noted that such chemicals enhanced the host-finding ability, increased the retention time (duration on host) and promoted egg release of two hymenopteran parasites of *Heliothis zea* (Boddie). Laboratory and field studies by the same workers have shown that enhancement of these characteristics produced substantial reductions in the pest population.

Several synthetic pheromones used primarily to manipulate bark beetle populations also attract certain entomophagous insects (Borden 1982). Adults of the predacious clerid, *Thanasimus undatulus* (Say), were strongly attracted to synthetic frontalin in stands of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, infested with the Douglas-fir beetle, *Dendroctonus pseudotsuga* Hopkins (Furniss and Schmitz 1971, Rudinsky et al. 1972, Borden 1977, Schmitz 1978). Schmitz (1978) suggested that frontalin could be used to concentrate predator populations on trees currently under attack by bark beetles. Similarly, exo-brevicomin has served as an effective attractant to *Temnochila chlorodia* (Mannerheim) in Douglas-fir (Pitman and Vité 1971) and ponderosa pine, *Pinus ponderosa* Laws., stands (Bedard et al. 1969).

The primary objective of this study was to evaluate the attractiveness of frontalin and exo-brevicomin to mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, and associated insects in lodgepole pine (LPP), *Pinus contorta* Douglass, stands. Corollary objectives were to determine the most effective frontalin-baiting period in which to augment predators and parasitoids of MPB under field conditions, and to evaluate the efficacy of this technique in reducing MPB survival and beetle-caused tree mortality.

Methods

The study was conducted during 1978 and 1979 in three LPP stands (McCall, Thorn Creek, and Paddy Flat) located in the Payette National Forest in central Idaho, and one stand in northeastern Oregon (McCubbin, Wallowa-Whitman National Forest). A preliminary study (Chatelain and Schenk 1983) showed that each stand supported an epidemic infestation of MPB, high populations of enmophagous insect species, and a sufficient num- of suitable host trees to sustain the infestations at least 2 more years.

Effectiveness of Baited Traps. Sticky bait-traps, structed of two white panels (45 by 90 cm) ounted back-to-back, were placed on stakes 0.9 above ground in the McCall stand. Three treat- ents, each consisting of either a racemic mixture of frontalin (1,5-dimethyl-6,8-dioxabicyclo [3.2.1] octane), exo-brevicomin (7-ethyl-5-methyl-6,8-dioxabicyclo [3.2.1] octane), or no-bait (control) treatments were assigned randomly to three traps in each of nine rows spaced at 20-m intervals on a grid system (randomized block design) in an × configuration. Both attractants were 96% pure.

The attractant material was dispensed from a 0.5-dram glass vial placed inside a plastic 35 mm film canister with six holes (1.8 mm diam) on the bottom (Rudinsky et al. 1972). This provided an average elution rate of ca. 1 mg/day per vial. Each trap panel was baited with one canister on 14 June 1978 and examined weekly until 26 August 1978. Entrapped scolytids and entomophagous insects were removed from each trap, cleaned in xylene, and identified. The number of each species was recorded.

Data were subjected to an analysis of variance (split-plot in time design) to determine differences among treatments. Orthogonal comparisons of treatment means were conducted to determine statistical differences between treatments.

Effects of daily rainfall and temperature on response of *T. undatulus* to the attractants were determined by a comparison of weekly trap catches with weather data obtained from the U.S. Forest Service Ranger Station located 0.2 km north of the test stand. Sex ratios for *T. undatulus*, using descriptions by Schmitz (1978), were compared by date and attractant to determine response differences between sexes.

Effect of Baiting Trees During MPB Flight. *Entomophagous Insects.* During the early period of MPB emergence and flight in 1978 (late July), 16 recently infested (1978 attacks) and 16 noninfested sample trees were selected systematically at ca. 40-m grid intercepts within the Paddy Flat stand. Four trees of each infestation category were selected from each of four classes (5 cm diam; 17, 22, 27, 32 cm dbh). A tree was classed as recently infested if it had at least 10 fresh MPB attacks in the lower 2 m of the bole, and there were no more than three such trees within a 0.5-m radius, and none between a 0.5- and 20-m radius. This distance was selected to reduce the possibility of confounding treatment effects. Noninfested trees were devoid of MPB attacks, and no recently infested trees were present within a 20-m radius. Two recently infested and two noninfested trees were selected randomly from each diameter class and baited with frontalin between 25 July and 23 August 1978. Frontalin was dispensed from a film canister as previously described, but fastened to the bole 2 m above ground. An equal number of nonbaited trees served as checks. Exo-brevicomin, less effective than frontalin in attracting *T. undatulus*, was eliminated from further testing.

Entomophagous insect response to baited and nonbaited, recently infested and noninfested trees (32 trees) was determined by comparing the number of insects (by species) observed weekly on the lower 2 m of each tree bole. Observations were conducted between 0830 and 1130 hours to reduce the influences of diurnal activity of each insect species.

Mountain Pine Beetle. Response of MPB to trees baited during beetle flight was evaluated using the eight baited and eight nonbaited noninfested trees in Paddy Flat. A similar number of noninfested baited and nonbaited trees were examined in the Thorn Creek stand to obtain replication. The trees were examined for MPB attacks in August and the numbers of trees attacked by stand and treatment were compared by means of a 2 × 2 contingency table.

Tree Mortality. The influence of distance from source of attractant on beetle-caused tree mortality was evaluated in the Paddy Flat stand using the 16 baited and 16 nonbaited trees, each group containing 8 noninfested and 8 infested trees equally distributed among the classes of diameter at breast height. Using each of these trees as the center for a 10-m radius plot, four concentric subplots of 78.5 m² each were established with boundaries of 4.0, 7.1, 8.7, and 10.0 m, respectively, from each plot center. At a distance of ca. 150 m from each of the 16 baited trees, an additional noninfested or infested tree (at least 40 m from any other sample tree) was selected until an additional 8 trees (2/dbh class) were obtained in each infestation category (i.e., 16 trees). A series of concentric subplots was established as before around each of the additional sample trees. Thus, there were eight infested and eight noninfested plots baited with frontalin, eight of each plot type located ca. 30 m from baited trees, and eight of each plot type ca. 140 m from baited trees.

The number of trees infested and noninfested, and their mean diameter at breast height after baiting within each subplot, was recorded after MPB emergence in late August. The numbers attached in each class, plot, and subplot were compared by analysis of variance (repeated measures split-plot design) and orthogonal comparisons to determine the effects of frontalin and recently infested trees on MPB aggregation. Number and diameter at breast height of trees within each subplot were similarly compared to determine whether these factors were confounded with plot treatments, because both are known to affect MPB outbreaks (Amman 1978, Schenk et al. 1980).

Effect of Baiting Trees Before Peak MPB Flight. *Entomophagous Insects.* Four infested (1979 brood) trees from each of the four classes were selected systematically at ca. 40-m grid intercepts within each of the Paddy Flat and McCubbin stands in 1979. Two trees in each of the four classes were baited and two trees in each class served as checks. Trees were baited from 13 May to 10 July in McCubbin and 6 June to 11 July in Paddy Flat coincident with the presence of a preponderance of late instar MPB larvae.

The outer surface area of the lower 2 m bole of each tree was examined for entomophagous insects (primarily *T. undatulus*) at weekly intervals from 17 July to 1 September in McCubbin and biweekly from 18 July to 28 August in Paddy Flat. The number present on baited and nonbaited trees was compared with a χ^2 test to determine the effects of baiting on these insects. The number present during baiting and after bait removal also was compared to assess the effects of bait removal.

Mountain Pine Beetle Brood Survival. The baited and nonbaited infested trees in Paddy Flat and McCubbin were felled and sampled in late September to determine whether attraction of entomophagous insects to baited trees had any significant effect on MPB brood survival.

Sample slabs (15 by 30 cm) were removed at (upper limits) 0.3, 1.3, 2.3, 6.3, 10.3, and 14.3 m along the north side of the tree bole. The following MPB brood characteristics were recorded for each slab: number of egg niches, larval mines, pupal chambers, callow adults, and emergence holes; and mortality of each stage by cause when evident. Numbers of entomophagous and other associated insects also were recorded by species and host, if ascertainable.

Numbers of missing individuals in the larval, pupal, and callow adult stages in each sample were calculated as follows:

$$ML = LM - (DL + PC) \qquad (1)$$
$$MP = PC - DP - (EH * 1.14) \qquad (2)$$

where: ML = missing larvae, LM = larval mines, DL = dead larvae, PC = pupal chambers, MP = missing pupae and callow adults (combined because sampling occurred after emergence), DP = dead pupae and callow adults, EH = emergence holes, and 1.14 = multiple emergence factor (Reid 1963).

Mortality by cause for each developmental stage was recorded as a percentage of the total number of egg niches present in each sample. Total mortality and mortality by developmental stage were compared between baited and nonbaited trees by analysis of variance (repeated measures split-plot design) to determine whether baiting increased MPB mortality. Mean numbers of predators, parasites, and other associates also were compared between baited and nonbaited trees to determine the effects of baiting on their abundance.

Mortality of Emerging MPB. The influence of frontalin on survival rates of emerging MPB was estimated using the eight baited and eight nonbaited trees in the McCubbin stand selected for the brood survival study.

Number of MPB adults killed by predators was determined using aprons to collect body fragments of partially eaten bark beetles. Each apron consisted of a cloth (1.5 m^2) wrapped around the base of each tree at ground level with the outer edges elevated 30 cm above ground level to reduce rodent access. Insect fragments were collected at weekly intervals from 4 June to 1 September 1979 and identified according to species. Each head, thorax, and elytron was assumed to represent one killed beetle, which eliminated the task of matching body parts and possibly compensated for elytral fragments not collected or lost in aprons as a result of high winds, etc. The total number of beetles that emerged from each tree was estimated from sample slabs using the following equations:

$$A_i = [(D_i - (2 * B_i)] * L_i * \pi / S_i \qquad (3)$$
$$H_i = A_i * E_i \qquad (4)$$
$$EB = 1.14 * \Sigma H_i \qquad (5)$$

where: A_i = inner bark surface area of i^{th} tree section represented by i^{th} sample slab, D_i = mean outer bark diameter (cm) of i^{th} tree section, B_i = mean bark thickness (cm) of i^{th} tree section, L_i = length (cm) of i^{th} tree section, S_i = inner bark surface area (450 cm^2) of sample slab, H_i = number of emergence holes in i^{th} tree section, E_i = number of MPB emergence holes in i^{th} sample slab, EB = total number of MPB adults that emerged from tree.

Tree section lengths represented by each sample were 65, 105, 205, 400, 400 cm, and x (x = 1,215 − infestation height in cm), respectively, depending on each sampling height from ground to crown level. D_i and B_i of each tree section were determined from midsection measurements conducted during field sampling.

The proportion of emerging adult beetle mortality was estimated by dividing the number of MPB fragments found in the apron by EB. The effects of frontalin and tree diameter on mortality were determined by analysis of variance (randomized block design). Two separate analyses of variance (repeated measures split-plot design) were used to compare the H_i and number of MPB fragments at each observation period to determine the effects of frontalin on emergent beetle mortality.

Tree Mortality. The baited and nonbaited trees within the 10-m plots and concentric subplots in the Paddy Flat and McCubbin stands also were used to determine the influence of frontalin-augmented *T. undatulus* populations on MPB-caused tree mortality. The number of recently infested and noninfested trees in each subplot and their mean diameter at breast height were recorded after MPB emergence in September.

Numbers of trees attacked in each plot, subplot, and diameter at breast height class after the frontalin was removed from the stand were compared by an analysis of variance (repeated measures split-plot design) to determine the effects of baiting before MPB emergence on MPB aggregation. Mean diameter at breast height and number of trees

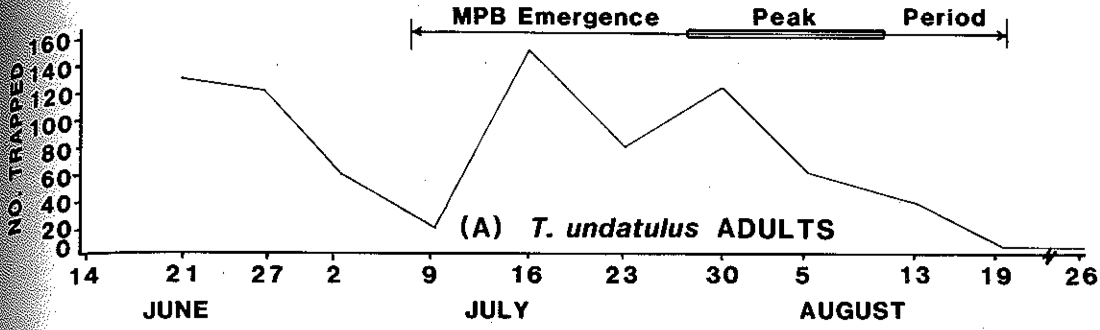

Fig. 1. Trap catches of adult *T. undatulus* on sticky traps baited with frontalin.

within each subplot were similarly compared to determine whether these variables confounded treatment effects.

Results and Discussion

Effectiveness of Baited Traps. Only *T. undatulus* showed a significant response to either frontalin or exo-brevicomin (Table 1). Differences in the numbers of adult *T. undatulus* caught between nonbaited traps (six adults) and those baited (784 adults) with either attractant were highly significant ($P < 0.01$). This confirms earlier reports of the attractiveness of synthetic frontalin to adult *T. undatulus* (Dyer 1975) and appears to be the first record of a verified response of this species to exo-brevicomin. Frontalin, however, was significantly ($P < 0.05$) more effective than brevicomin; ca. 60% of trapped clerids were on frontalin-baited traps.

The significance of *T. undatulus* utilization of two different compounds as kairomones is unclear. However, this behavior may aid *T. undatulus* in locating more than one host species, which would be important to its survival during endemic conditions when populations of one or more host species are low. For example, in addition to MPB, *T. undatulus* is a predator of *Ips* spp. in lodgepole pine slash (Reid 1957), the spruce beetle (*D. rufipennis* Kirby) and associated scolytids infesting Englemann spruce (*Picea engelmanni* Parry) (Knight 1961), the fir engraver (*Scolytus ventralis* Le Conte) infesting *Abies* species (Struble 1957) and the Douglas-fir beetle, *D. pseudotsugae* Hopkins in Douglas-fir, *Pseudotsugae menziesii* (Mirb.) Franco (Cowan and Nagel 1965). Frontalin has been isolated and identified from the hindguts of *D. pseudotsugae* and *D. rufipennis* (Pitman and Vité 1970) and from air samples drawn over *D. ponderosae* (Ryker and Libbey 1982). Pitman et al. (1969) identified brevicomins from hindguts of *D. ponderosae.*

Table 1. Mean number of insects by species caught in frontalin or brevicomin-baited and unbaited traps in a LPP stand infested with MPB, McCall, Idaho, 1978

Insect species	Mean no. trapped[a]			Total (n)	Orthogonal comparison[b]	
	Frontalin I	Brevicomin II	Unbaited III		I, II vs. III	I vs. II
T. undatulus	1.32 (6.23)	0.88 (2.48)	0.04 (0.07)	790	**	*
E. sphegeus	0.04 (0.07)	0.03 (0.04)	0.01 (0.01)	11	NS	NS
Rhaphidia sp.	0.08 (0.14)	0.06 (0.10)	0.06 (0.10)	31	NS	NS
D. ponderosae	0.02 (0.03)	0.02 (0.03)	0.01 (0.10)	7	NS	NS

[a] Data based on 90 observations (9 rows × 10 dates) per treatment. Differences in variance were adjusted by a transformation of $\ln(x + 1)$ of each observation. Actual means are in brackets.

[b] NS, Not significant ($P > 0.05$); *, significant ($P < 0.05$); **, highly significant ($P < 0.01$).

Adult *T. undatulus* were present in the McCall stand throughout the summer, but with apparent peaks occurring in mid- to late June and mid- to late July (Fig. 1). Schmitz (1978) reported similar peak activity periods for adult *T. undatulus* when associated with the Douglas-fir beetle in Douglas-fir stands in northern Idaho.

Equal numbers of male and female adult *T. undatulus* were trapped with both attractants during each trapping period which is similar to results reported by Schmitz (1978).

No response was detected by MPB to either frontalin or exo-brevicomin baited sticky traps. Ryker and Libbey (1982) reported that frontalin reduced MPB numbers on sticky traps baited with the aggregation pheromone *trans*-verbenol and host terpenes, which suggested frontalin to be an antiaggregation pheromone. Our subsequent field tests, however, revealed that frontalin actually aggregated MPB populations when associated with the host tree during the flight period of MPB. Failure of sticky traps alone to detect the aggregating effects on MPB populations may be due to a multitude of factors, including the absence of certain semiochemicals. For example, Pitman and Vité (1969) reported that *trans*-verbenol in the absence of host odors showed no apparent attractive prop-

Table 2. Mean total number and diameter of all LPP, and mean number of pine beetle attacked trees within plots at various distances from frontalin baited and/or infested center trees, Paddy Flat, 1978[a]

Variables tested	Plot distance to bait source (m)						Orthogonal comparisons[b]				
	≈10		≈30		≈140						
	(I) Infested baited	(II) Non-infested baited	(III) Infested unbaited	(IV) Non-infested unbaited	(V) Infested unbaited	(VI) Non-infested unbaited	Baited vs. unbaited plots I, II vs. III, IV V, VI	Infested vs. non-infested plots I, III, V vs. II, IV, VI	≈30 m vs. ≈140 m plots III, IV vs. V, VI	Test for synergism I vs. II, III	Baited infested vs. unbaited infested plots I vs. III
Mean number of trees	4.94	4.56	4.34	4.50	3.22	3.19	NS[c]	NS	NS	NS	NS
Mean dbh (cm)	21.85	20.69	23.82	23.17	20.24	18.48	NS	NS	NS	NS	NS
Mean number of attacked trees	2.72	0.81	1.28	0.31	1.03	0.03	**	**	NS	**	NS

[a] Data based on 32 observations (2 replicates × 4 dbh classes × 4 subplots)/treatment.

[b] NS, Not significant ($P > 0.05$); **, highly significant ($P < 0.01$).

[c] Mean comparisons were not conducted because F was insignificant in analysis of variance.

erties in field or laboratory bioassays, but in the presence of host volatiles (e.g., α-pinene) was highly attractive to field populations of MPB females.

Effect of Baiting Trees During MPB Flight. *Entomophagous Insects.* Although very few adult *T. undatulus* were trapped, a slightly stronger response (three adults) to baited-infested than to baited-noninfested trees was indicated. No *T. undatulus* adults were found on nonbaited check trees. The low numbers collected may be attributable in part to monitoring *T. undatulus* subsequent to its peak flight period (Fig. 1). No other entomophagous species were trapped.

Mountain Pine Beetle. Significantly more baited (11) than nonbaited (3) trees were attacked by MPB in both Thorn Creek and Paddy Flat stands ($P < 0.05$). No nonbaited trees were attacked in Thorn Creek. In Paddy Flat, only the larger diameter (>25 cm), nonbaited trees were attacked, but the smaller (ca. 16 cm) baited trees also were attacked. This suggests that frontalin may be used to induce MPB attacks. Thus, frontalin possibly could be used to lure MPB to smaller trees, resulting in smaller broods and reduced populations, as suggested by Amman (1978) for *trans*-verbenol. Significantly more trees (ca. 4-fold) were attacked in Paddy Flat than Thorn Creek ($P < 0.05$), probably reflecting the substantial differences in MPB population levels between stands at the time of baiting, rather than habitat differences.

Tree Mortality. Mean diameter at breast height and number (density) of trees did not vary significantly among strata (Table 2) ($P > 0.05$). These were tested because both have been shown to be related to MPB outbreaks (Amman 1978, Mahoney 1978, Schenk et al. 1980). Although other factors also may be involved, many are related to tree diameter and stand density. Thus, the differences among treatments in number of trees affected after baiting may be assumed to be due to the presence or absence of baited or infested trees. Presence of either frontalin or recently infested (1979 attack) trees significantly increased the incidence of attacked trees ($P < 0.01$). Differences in the number of attacked trees were insignificant between baited and infested plots ($P > 0.05$). Thus, baiting trees was as effective in aggregating MPB populations within a 10-m radius as were natural attractants emanating from infested trees. Synergistic effects on MPB aggregation occurred when infested center trees were baited with frontalin.

The effective distance from a frontalin source apparently is less than 30 m at the concentration used, as manifested in the insignificant differences

Table 3. Orthogonal comparison of number of LPP trees attacked by MPB after baiting during beetle flight, Paddy Flat, Idaho, 1978

Treatment[a]	Mean no. of recently attacked trees/subplot[b] Distance to center tree (m)				Orthogonal comparison[c]		
	(I) 0–5.0	(II) 5.0–7.1	(III) 7.1–8.7	(IV) 8.7–10.0	I vs. II, III, IV	II vs. III	I, II, III vs. IV
Bait + infested	3.38	2.50	3.38	1.63	*	NS	**
Bait + noninfested	0.50	1.25	0.88	0.63	NS	NS	NS
No bait + infested	2.25	1.00	1.50	0.38	**	NS	**
No bait + noninfested	0.13	0.25	0.13	0.75	NS	NS	NS

[a] No bait trees were ca. 30 m distance from baited trees.

[b] Data based on eight observations per subplot (2 trees × 4 dbh classes).

[c] *, Significant at $P < 0.05$; **, significant at $P < 0.01$.

Table 4. Effect of baiting trees before MPB flight period on abundance of insects, by species, associated with MPB in LPP. McCubbin stand (Oregon) and Paddy Flat stand (Idaho), 1979

Species	Mean number ± SE			
	Paddy Flat		McCubbin	
	Baited	Nonbaited	Baited	Nonbaited
Parasites				
Coeloides rufovariegatus	—	0.051 ± 0.036	0.083 ± 0.083	1.036 ± 0.495
Rhopalicus pulchripennis	—	—	—	0.018 ± 0.018
Predators				
Anthocoridae	0.095 ± 0.066	0.026 ± 0.026	0.167 ± 0.123	0.055 ± 0.031
Cucujus clavipes	0.024 ± 0.024	—	0.333 ± 0.149	0.200 ± 0.098
Enoclerus sphegeus	0.024 ± 0.024	0.026 ± 0.026	0.028 ± 0.028	0.018 ± 0.018
Rhaphidia sp.	—	—	—	0.018 ± 0.018
Thanasimus undatulus	0.190 ± 0.061	0.051 ± 0.036	0.083 ± 0.047	0.036 ± 0.026
Xylophagus sp.	—	—	—	0.026 ± 0.057
Miscellaneous associates				
Aleorharinae	—	0.026 ± 0.026	—	—
Epuraea sp.	0.048 ± 0.033	0.026 ± 0.026	—	—
Lasconotus spp.	—	0.026 ± 0.026	—	0.018 ± 0.018
Lepidoptera	0.024 ± 0.024	0.026 ± 0.026	0.056 ± 0.056	0.036 ± 0.026
Competitors[a]				
Ips mexicanus	0.024 ± 0.024	0.026 ± 0.026	0.028 ± 0.028	—
Ips pini	5.939 ± 4.453	1.744 ± 0.983	1.028 ± 0.437	4.418 ± 1.884
Pityogenes knechteli	1.429 ± 1.290	0.513 ± 0.394	—	0.109 ± 0.109
Pityphthorus confertus	1.952 ± 1.330	0.077 ± 0.077	1.472 ± 0.805	6.164 ± 1.937

[a] Number of competitors, by species, was determined from egg gallery counts.

obtained between unbaited plots located 30 and 140 m from the source (Table 2) ($P > 0.05$).

Distribution patterns of attacked trees resulting from a frontalin source differed from the pattern produced by the natural attraction of MPB infested trees (Table 3). Attacked trees tended to be concentrated within a 5-m radius of infested trees, but were more equally distributed within noninfested plots. However, reducing the elution rates and duration of baiting may result in aggregation patterns more similar to that caused by infested trees. A greater proportion of attacked trees occurred in each subplot when infested trees were baited, suggesting that synergistic effects were produced throughout a 10-m radius. Borden et al. (1983) reported a similar concentration of MPB attacked trees in lodgepole stands around trees baited with the attractant semiochemicals myrcene, *trans*-verbenol, and exo-brevicomin and suggested that dispersal of MPB could be inhibited by baiting.

Synthetic *trans*-verbenol, a principal volatile component in the hindguts of *Dendroctonus* spp., in combination with α-pinene is highly attractive to MPB (Pitman et al. 1969). Attempts have been made to reduce MPB populations by placing this mixture on trees treated with insecticides (Pitman 1971) or containing phloem too thin for normal brood development (Rasmussen 1972). These attempts have been unsuccessful largely because this mixture promotes attacks on many nontarget trees. Studies by Rasmussen (1972) showed that the number of newly attacked trees increased for a distance of 60 m from the nearest infested tree baited with *trans*-verbenol. This problem may be alleviated with the use of frontalin at low elution rates, which would tend to aggregate MPB populations in areas <30 m from the bait source.

Our original intent for baiting trees during the flight period of MPB was to reduce tree mortality by increasing predation against attacking MPB on susceptible trees. Baiting trees during this period under MPB epidemic conditions resulted in augmenting *T. undatulus* populations, but it also attracted MPB and increased tree mortality in the immediate area of the source.

Effect of Baiting Trees Before Peak MPB Flight. *Entomophagous Insects. T. undatulus* was again the only entomophagous insect species that showed a response to frontalin. Significantly more *T. undatulus* adults were found on baited (18) than nonbaited trees (2) ($P < 0.01$). No significant interaction was found between baiting and stand location ($P > 0.05$), although a greater number of adults was observed on trees baited in the Paddy Flat stand than in the McCubbin stand. More *T. undatulus* adults were observed on trees baited during this period, which coincided with their peak flight period (May–July) than when trees were baited during the MPB flight period (July–September).

An obvious reduction in the number of adult *T. undatulus* occurred in both stands after the bait was removed. However, a few adults were found in baited trees as late as ca. 4 weeks after bait removal, whereas none was observed on unbaited

Table 5. MPB brood mortality by cause in frontalin-baited LPP stands at two locations, 1979

	Paddy flat (Idaho)				McCubbin (Oregon)				PR > F[a]	
	Frontalin-baited		Nonbaited		Frontalin-baited		Nonbaited			
	Mean no./sample	Mortality (%)	Mean no./sample	Mortality (%)	Mean no./sample	Mortality (%)	Mean no./sample	Mortality (%)	Frontalin-baited vs. nonbaited	McCubbin vs. Paddy flat
Egg niches	162.78		168.30		196.00		200.54			
Resinosis		53.50		40.69		36.99		39.35		
Unknown		12.34		14.71		15.70		14.78		
Total		65.84		55.40		52.69		54.13	0.2312	0.0844
Larval mines	59.19		77.20		99.06		97.40			
Fungus		—		—		0.04		0.38		
Parasitized		—		0.01		0.44		0.46		
Desiccated		0.40		—		0.84		0.27		
Missing		23.73		31.36		30.47		25.03		
Total		24.13		31.37		31.39		26.15	0.5874	0.7460
Pupal chambers	16.94		20.13		32.43		38.46			
Desiccated		—		0.07		—		—		
Callow adults (emerged)	3.89		2.84		4.74		6.35			
Desiccated		0.20		0.02		0.02		0.33		
Missing (pupa and adults)		7.77		11.68		13.30		15.89		
Total		7.97		11.70		13.32		16.22	0.1901	0.0149
Total mortality		97.84		98.47		97.40		96.50	0.4764	0.1002

Data based on 128 observations (2 locations × 2 treatments × 4 diameter classes × 5 samples/trees × 2 trees). Only infested samples were used.

[a] Values <0.05 are significant; >0.05 are insignificant.

trees at that time. This suggests that *T. undatulus* populations may remain in the vicinity of baited trees for some time even after bait removal.

MPB Brood Survival. In the process of determining the influence of baiting on MPB brood survival, the numbers of individuals of other insect species found in the sample slabs also were recorded (Table 4). Although the mean numbers per slab were quite low in most cases, the overall insect community beneath the bark did not vary substantially between baited and nonbaited trees. However, the mean numbers of *T. undatulus* in both stands was slightly greater in the baited trees (0.14 per slab) than in the nonbaited trees (0.04 per slab), although a χ^2 test failed to reveal a significant difference ($P > 0.05$).

Frontalin had little or no effect in reducing MPB brood survival when applied to infested trees before MPB flight. Percentage of generation mortality, as well as percentage of mortality of each life stage, of MPB did not differ significantly between baited and unbaited trees (Table 5) ($P > 0.05$).

Considerable variation in MPB brood mortality as well as in populations of associated insect species was encountered among the sample heights within trees, suggesting the need for a larger sample.

Mortality of Emerging MPB. No significant difference in the number of emergence holes was found between baited and nonbaited trees ($P < 0.05$). However, estimated mortality of emerging MPB was 9.40 and 2.25% for baited and nonbaited trees, respectively. Although baiting increased mortality of emerging MPB by ca. 7%, these differences were slightly less than significant ($P > 0.50$).

Fragments used to estimate MPB mortality consisted of elytra (87.2%), heads (12.5%), and thoraces (0.3%). The use of each fragment to represent one predator-eaten beetle could result in overestimating mortality. However, many fragments, especially those falling from several meters up the bole, probably were lost to wind, or deposited on various tree parts not examined. Thus, the reported predator-caused mortality rates for emerging MPB adults probably represents an underestimate of the actual mortality.

Fragments of other bark beetle species, *Ips pini* (Say) (five) and *Pityophthorus confertus* Swaine (seven), also were collected. Although significantly more fragments of both species were found on baited than nonbaited trees ($P < 0.05$), the numbers were insufficient to determine the effects of baiting on their survival rates.

Tree Mortality. No significant difference in the number of trees infested by MPB was found between baited and nonbaited plots ($P > 0.05$). Also, the extraneous effects of tree diameter and density did not influence these results, since neither of these varied significantly between baited and nonbaited plots. Frontalin augmented *T. undatulus* populations, without aggregating MPB populations, when removed before MPB emergence. However, the augmented populations were ineffective in reducing MPB populations to levels low enough to reuce tree mortality. Greater benefits may be obtained if *T. undatulus* populations were augmented under pre-epidemic situations where higher prey: predator ratios are usual.

Frontalin-induced augmentation of *T. undatulus* populations may be synergistic with other preventative tactics, such as thinning or maintenance of species diversity, and should be given consideration within an integrated pest management program for the mountain pine beetle. Frontalin also should be tested against other bark beetles—e.g., Douglas-fir beetle and spruce beetle—that have emergence periods that closely coincide to peak flight periods of *T. undatulus*.

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