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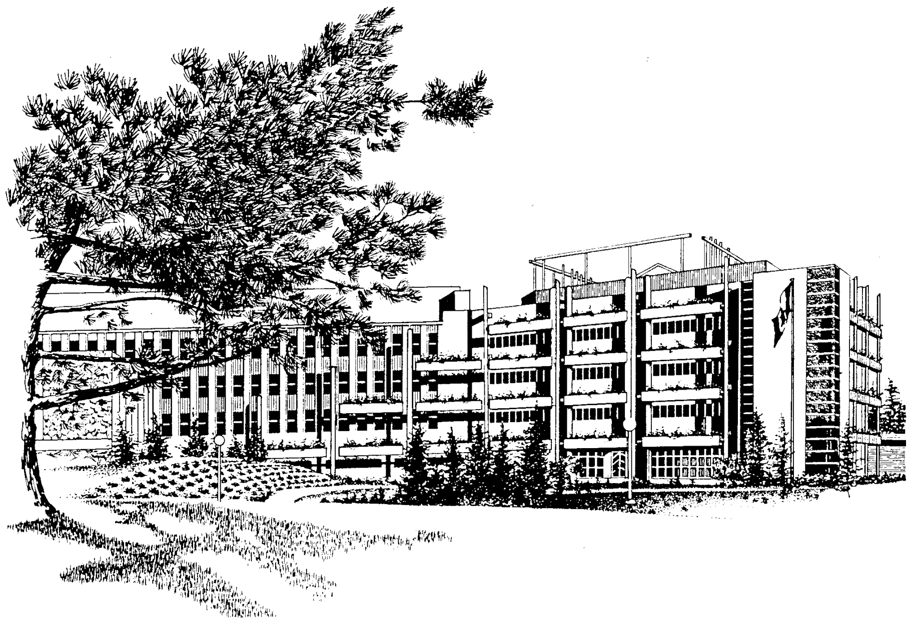

The Pacific Forestry Centre, Victoria, British Columbia

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Pest Management Methods Network

The protection of Canada's forest resource against damaging insects, disease-causing organisms, and competing vegetation is essential to sustainable development from both environmental and economic perspectives.

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The Pest Management Methods Network (PMMN) advances the development of cost-effective and ecologically acceptable methods for managing forest pests and contributes to the establishment of integrated pest management and sustainable forest development in partnership with other CFS networks and external clients and collaborators.

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Contents

Abstract

The effects of pheromone-induced competition from secondary bark beetle species on mountain pine beetle attack and brood production in mature lodgepole pine were investigated in south central British Columbia. The effects of delaying baiting for secondary species and of felling host trees (following mountain pine beetle attack) were also examined. The pine engraver (*Ips pini* (Say)) was the principal competitor in all experiments and three additional secondary species, *I. latidens* (LeConte) and *Dryocoetes affaber* Mannerheim were included in one experiment. Baiting simultaneously for mountain pine beetles and pine engravers significantly reduced mountain pine beetle attack density and brood production in one of two trials, due mainly to the repellent effects of the pine engraver bait. Use of pine engraver bait resulted in greater numbers of attacks and increased densities of that species hibernating in duff. Delaying baiting for pine engraver significantly increased their brood production, but usually not that of mountain pine beetle. Felling trees had no significant effect on attack or brood production. Baiting trees for *I. latidens* or *D. affaber* about one week after peak attack by mountain pine beetle caused marginal reductions in mountain pine beetle brood density and suggested that a strategy of simultaneous baiting should be explored. The complex interactions of the pine engraver and the mountain pine beetle in response to induced attacks by both species are illustrated using a hypothetical model.

Résumé

Les auteurs ont étudié dans le centre-nord de la Colombie-Britannique les effets de la compétition exercée sous influence phéromonale par des espèces de scolytes secondaires sur les taux d'attaque et la production de couvain par le dendroctone du pin ponderosa dans des pins tordus matures. Les effets provoqués par le report des essais avec appâts ciblant les espèces de scolytes secondaires et de l'abattage d'arbres hôtes (après une attaque par le dendroctone du pin ponderosa) ont également été examinés. Le scolyte du pin (*Ips pini* (Say)) était la principale espèce compétitrice dans toutes les expériences, mais trois autres espèces secondaires, soit *I. latidens* (LeConte) et *Dryocoetes affaber* Mannerheim, ont également été incluses dans une expérience. Dans un des deux essais, l'utilisation simultanée d'appâts contre le dendroctone du pin ponderosa et le scolyte du pin a entraîné une réduction significative de la densité des attaques et de la production de couvain par le dendroctone du pin ponderosa. L'effet répulsif de l'appât utilisé contre le scolyte du pin a été tenu comme la cause principale de ce phénomène. Les essais avec appât contre le scolyte du pin ont causé une augmentation de la densité des attaques par ce ravageur et des individus hibernant dans la litière. Le report des essais avec appât contre le scolyte du pin a entraîné une augmentation significative de la production de couvain par cette espèce mais, de façon générale, n'a pas entraîné d'effets prononcés chez le dendroctone du pin ponderosa. L'utilisation de billons d'appât contre *I. latidens* ou *D. affaber* environ une semaine après la phase d'attaque maximale par le dendroctone du pin ponderosa a provoqué des réductions marginales de la densité du couvain du dendroctone du pin ponderosa et démontré la pertinence d'explorer une stratégie d'appâtage simultané. Les interactions complexes entre le scolyte du pin et le dendroctone du pin ponderosa observées en réponse aux attaques induites par les deux espèces sont illustrées dans un modèle hypothétique.

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1. Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Col.: Scolytidae), is highly destructive in the mature pine forests of western North America (Safranyik et al. 1974). They kill trees that are subsequently attacked by a number of secondary wood-boring and phloem-feeding species. Of the phloem-feeding group, some less aggressive bark beetle species, such as the pine engraver (*Ips pini* (Say)) and *I. latidens* (LeConte) are commonly found in lodgepole pine (*Pinus contorta* var *latifolia* Engelm.) killed by mountain pine beetle (Furniss and Carolin 1977). During outbreaks of the mountain pine beetle, large populations of associated secondary species can develop, and occasionally kill large numbers of apparently healthy trees, usually in the smaller diameter classes.

The secondary species normally breed in weakened trees, windfall, logging residue, and the thin-barked or unutilized portions (including tops and limbs) of trees killed by primary bark beetles. In lodgepole pines killed by mountain pine beetle, attacks by secondary species may be dispersed among the mountain pine beetle attacks. Co-attacks by several secondary species are common (Safranyik et al. 1974). The pine engraver, which readily attacks the lower bole, is the secondary beetle most commonly associated with mountain pine beetle.

Attack by secondary bark beetle species can affect both the establishment and survival of mountain pine beetle broods. Mountain pine beetle attacks and attack success are negatively affected by semiochemical signals produced by some secondary species. Larvae of secondary species compete for food and space with mountain pine beetle larvae. The secondary species commonly associated with mountain pine beetle in lodgepole pine typically have higher attack densities, and are often bivoltine, with the parents re-emerging to establish second broods.

The general objective this work was to assess the effects of pheromone-induced competition by secondary bark beetles on mountain pine beetle attack behaviour and brood survival. The work involved four experiments, the specific objectives of which are described in later sections.

Our earlier work on competitive interactions between pine engraver and mountain pine beetle concentrated on increasing the mortality rate among mountain pine beetles in naturally attacked lodgepole pine (Safranyik et al. 1996). These later experiments differed in that we induced attacks with pheromones. This was done for two reasons: First, mountain pine beetles could be attracted to designated areas so most of the attacked trees could be easily located, and the brood destroyed, as in operational suppression programs. Second, trees could be baited simultaneously for both primary and secondary species in order to increase competition during the attack period and thus reduce the success of the primary species.

Baits for the secondary species were applied either simultaneously with the mountain pine beetle baits or following peak attack of the latter. We could thus compare competitive exclusion (preventing attack) with competitive displacement (causing brood mortality) (Poland 1997). In three experiments, we manipulated densities of the pine engraver as the principal competing species. In some cases we felled infested trees to determine the effects of felling on subsequent attack behaviour and brood development. The other experiment involved manipulation of the densities of the pine engraver, *I. latidens* and *D. affaber* Mannerheim and their effect on the mountain pine beetle.

2. Standard methods

Some of the methodology used in performing these experiments was standardized and used from year to year, sometimes with minor variations. The standard techniques will be described once and referred to by name in the following text. Variations will be described individually in the appropriate sections.

2.1 Sample tree selection

All experiments were carried out in mature (80+ years old) lodgepole pine forests. Sample trees were selected on the basis of size and spacing relative to one another. Candidate trees had to be larger than 15 cm diameter at 1.3 m

(DBH), of the dominant or co-dominant crown classes, with no sign of recent damage or insect activity, and 15 m or more from other sample trees. Treatments were assigned randomly or randomly within blocks, as dictated by the experimental designs. DBH of all sample trees was measured at the time of selection.

2.2 Pheromones

All of the pheromones used in these experiments were obtained commercially from Phero Tech Inc. (7572 Progress Way, Delta, B.C., Canada). The pine engraver bait consisted of two bubble caps containing ipsdienol and lanierone (release rate 0.2 mg/day and 0.02 mg/day, respectively). The standard ‘Mountain Pine Beetle Tree Bait’ (trans-verbenol, and exo-brevicomin) was used for the mountain pine beetle. Other pheromones used will be described in the text. ‘Control’ treatment consisted of application of mountain pine beetle bait to all sample trees at the time of plot establishment. Additional baits were placed at different times and heights as dictated by experimental design. Pheromones were always attached to the trees on the north side at roughly breast height (1.3 m), unless otherwise stated in the descriptions of individual experiments. Mountain pine beetle eggs, larvae (4 instars), pupae and adults were assigned indices of 0, 1- 4, 5, and 6, respectively, for calculating an average index of brood development. When secondary species baits were placed at the same time as mountain pine beetle baits, they will be referred to as ‘simultaneous’ baiting, baits placed at any later time will be referred to as ‘delayed’.

2.3 Square samples

To assess initial attack and brood gallery establishment in the fall of the initial attack year, squares of bark, measuring 15 cm by 15 cm, were removed from the sample trees from the north and south sides at 1.3 m (breast height). In some experiments, additional samples were also taken from greater heights. Five-cm-wide chisels were used to cut the perimeter of each sample. The squares of bark were then carefully peeled from the tree using knives or narrower chisels, with as little disruption of underbark features as possible. All measurements of egg galleries, attacks, and other attributes were done in the field, using the wood surface as well as the inner and outer bark surfaces for identification and verification. Attack success was evaluated based on successful egg hatch and on the presence or absence of lethal resinosis in the egg galleries. The numbers of attacks and total gallery length were measured for mountain pine beetle and pine engravers.

2.4 Duff samples

Duff sampling was used to estimate numbers of pine engravers overwintering in duff at the bases of their host trees, which was the estimate of brood production. Duff was collected from the north and south sides of plot trees in late October or in November of the year of initial attack, after several days of frost, frequently from beneath snow. The samples were the width of the host tree at the ground, and 50 cm long, measured radially from the bark face; depth was to mineral soil. Each rectangle of duff was excised with a sharp, square-ended spade, separated from the mineral soil, and placed in a plastic bag for transport to Victoria where they were kept at 0°C until placed in the rearing room.

Rearing was done at 24°C during December and January. Duff samples were removed from the plastic bags and sealed individually into $38 \times 30 \times 25$ cm cardboard boxes with glass jars screwed into a 5-cm hole in one end. The boxes were stacked in rows with the jars facing a light source in the otherwise darkened room. As the duff samples warmed, the insects in them became active, and moved towards the light source into the jars. Insects were removed from the jars every 2-3 days until emergence ceased (usually 2-3 weeks). The total number of pine engravers captured was recorded for each sample. Sex determination of adults was made by examining the declivital spination under 10x magnification. Pronotal widths were determined using an ocular micrometer.

2.5 Disc samples

Disc samples were used to sample mountain pine beetle populations in trees after overwintering, in May or early June of the year following attack. Disc samples were cut from the north and south sides of each tree using a gas-powered drill and a 15-cm industrial hole saw. The saw kerf was cut to a depth of 1-1.5 cm into the wood 5-10 cm away from the square samples previously taken. The discs were then chiseled out, taking a thin layer of wood with the bark attached. The discs were then placed in individual plastic bags and transported to the laboratory for detailed examination. The attack variables recorded were the same as for square samples, with the addition of counts of larvae (sometimes by instar), pupae, and adults. In some years, counts of Clerid and *Medetera* larvae were also made. The proportion of bark disturbed by woodpeckers was estimated by viewing the bark sample through a 10 cm × 10 cm transparent plastic grid and counting the number of 1-cm squares covering bark that was damaged or searched by woodpeckers.

2.6 Statistical analysis

All analysis was done using SAS software (Statistical Analysis Systems Inc., Cary, N.C., USA). All counts, and measurements of egg gallery length, were converted to a per square metre (density) basis before analysis. Throughout this report, counts such as “attacks” or “brood” refer to “attacks per m^2” or “brood per m^2”, etc, and “gallery length” refers to “meters of gallery per m^2”. Treatment effects for all response variables were analyzed by analysis of variance. For analysis purposes, the fall measurements of attack variables were deemed more reliable because the inner bark surfaces of spring samples were often degraded by insect feeding. Count variables were transformed to (x+1) 0.5 prior to analysis. When treatment effects were significant, means were compared using Tukey’s test (unbalanced ANOVA) or the Ryan-Einot-Gabriel-Welsh multiple F (REGWF) test (balanced ANOVA). Comparisons were made at $p \leq 0.05$. Treatment interactions were generally not significant, and with a few exceptions, are not reported in the tables. The relation between mountain pine beetle brood density and the density of pine engravers emerging from duff was compared by regression analysis. Departures from these standard analyses are described for each experiment.

3. Experiments

3.1. Delaying pine engraver attacks

The objective of this experiment was to determine the effect of delaying pine engraver attacks on the establishment and survival of mountain pine beetle broods.

Field trials were conducted in 1992-93 at the following sites: Valentine Lake and Horse Lake Road near 100 Mile House, and in 1993-1994 at Chasm 1, Chasm 2, and Riske Creek, in the Cariboo Forest Region of British Columbia. Field trials included the following treatments:

Control:	Mountain pine beetle bait.
Treatment 1:	Simultaneous baiting. (Control +) pine engraver bait applied simultaneously.
Treatment 2:	Delay 1. (Control +) pine engraver bait applied approximately 1 week after mass attack of baited trees by mountain pine beetle.
Treatment 3:	Delay 3. (Control +) pine engraver bait applied approximately 3 weeks after mass attack of baited trees by mountain pine beetle

Treatments were assigned at random to 60 lodgepole pines. Mountain pine beetle baits were placed in early July. In late September, following establishment of mountain pine beetle and pine engraver attacks, square samples were taken. During late October, duff samples were taken. At Valentine Lake and Horse Lake Road, due to time and space limitations, duff samples were collected only from the north side of treatment trees. All trees were disc sampled in mid June of the year following beetle attack.

3.1.1. Results in 1992-1993

The average dbh (SE) was 29.9 cm (2.25), with no significant difference among treatments. Mean development index (SE) of mountain pine beetle brood sampled in the spring of 1993 was 2.34 (0.036). The treatments had a significant effect on the proportion of trees judged resistant following mountain pine beetle attack (χ^2_{3df} =10.05; $p \leq 0.05$) (Fig. 1).

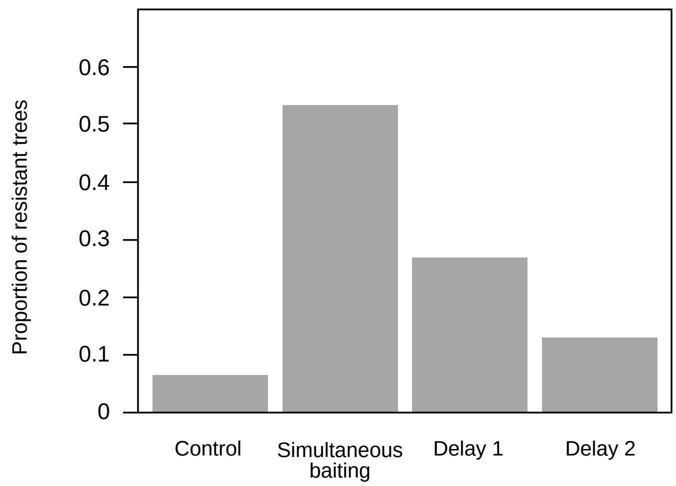

Figure 1. Proportion of resistant trees by treatment, Experiment 1, 1992-3. Treatments are described in Methods.

The analysis of variance of pine engraver and mountain pine beetle attack, egg gallery length, brood densities, and densities of *Medetera* larvae and clerid larvae by treatment and aspect are summarized in Appendix A, Table A1. For mountain pine beetle, egg gallery and brood densities differed among treatments (Table 1). With simultaneous baiting, egg gallery length and brood were significantly lower than in the control. Egg gallery length was also significantly lower than for the Delay 3 treatment. Although not significantly different, treatment means for attack followed the same pattern as for egg gallery length and brood, and averaged 105.63 per m^2.

No *Medetera* larvae were found in samples in the Delay 1 treatment. The mean densities for Control and Delay 3 (24.63 and 20.68 larvae per m^2, respectively) were both significantly different from the simultaneous baiting treatment (3.76 per m^2). There were no significant differences by treatment in the mean densities of clerid larvae, which averaged 10.34 per m^2. There was a significant interaction between treatment and aspect because the preponderance of clerid larvae in the control and simultaneous baiting treatments were located on the south aspect, whereas the reverse was true for the other two treatments.

During the first summer, no pine engraver attacks were found higher on the trees than the highest mountain pine beetle attacks. Mean densities of pine engraver attacks and brood are compared in Table 2. The trend of pine engraver emergence on treatment was opposite to that of mountain pine beetle (Table 1), because the simultaneous baiting and the control treatments had the highest and lowest density, respectively. Similarly, egg gallery length for simultaneous baiting was significantly greater than that of the control. Although not significantly different, the mean density of pine engraver attacks (37.8 per m^2) had the same trend as that of gallery length and brood.

3.1.2. Results 1993-1994

There was significant variation in tree dbh among sites ($F_{2,54}$=3.75), but not among treatments ($F_{3,54}$=1.08). The average dbh at Riske Creek (26.7cm) and Chasm 1 (26.7cm) were significantly greater than at Chasm 2 (22.6 cm). There was no significant difference in the proportion of resistant trees among treatments (χ^2_{3df}=5.59, $p>0.05$); the average proportion of resistant trees was 0.20.

The analysis of variance by site, treatment, and aspect in the densities of the following variables are summarized in Appendix A, Table A2: mountain pine beetle attack, brood, and gallery length, pine engraver attack, gallery length, emergent adults, *Medetera* larvae, and clerid larvae. For all variables but pine engraver brood, the data were from the spring 1994 sampling.

3.1.2.1. Mountain pine beetle

Average attack per m^2 at Riske Creek (129.02) was significantly different from the both the Chasm 1 (89.1) and Chasm 2 (75.0) sites, but there was no significant difference between the latter two sites. There were no significant differences in mean attack among treatments or aspects. Attack averaged 84.4, 74.1, 78.5, and 103.7 per m^2 for the control, simultaneous baiting, delay 1 and delay 3, and averaged 110.3 per m^2 on the north and 106.5 per m^2 on the south.

Gallery length differed significantly among all sites but not among treatments or aspects. Mean gallery length ranged from 10.1 m per m^2 at Chasm 2 to 31.2 m per m^2 at Riske Creek. Numerically, Simultaneous Baiting and Delay 1 had lower densities (13.3 and 20.1 m per m^2) than the Control and Delay 3 (23.4 and 27.0 m per m^2 treatments). Mean gallery length was 21.1 m per m^2 on the north and 20.8 m per m^2 on the south.

Mean brood development index (SE) was 3.58 (0.04), indicating that the preponderance of the brood were in the third (20%) and fourth (45%) larval stages. Brood density varied significantly between aspects, nearly significantly ($p \leq 0.06$) among treatments, but not among sites (Appendix A, Table A2). The north aspect had greater average density (352.5) than the south (217.8). Numerically, the Control and Simultaneous Baiting treatments had higher brood densities (362.2 and 503.6) than Delay 1 or Delay 3 (139.8 and 135.8). Mean brood density ranged from 258.6 at Chasm 2 to 335.3 at Riske Creek. Bark disturbance by woodpeckers varied significantly among sites but not among treatments or aspects. Bark disturbance was significantly higher at Riske Creek (22.0%) than at the other two sites (1.0 and 2.0%). Bark disturbance by treatment ranged from 6.3% to 10.5% and by aspect from 7.6% to 9.1%.

3.1.2.2. Pine engraver

Attack density did not vary significantly among sites, treatments, or aspects and averaged 71.2 per m^2. Pine engraver emergence from duff varied significantly by site and treatment (Appendix A, Table A2). Mean emergence for the Control (44.0 per m^2) was significantly lower than each of Simultaneous Baiting (128.60 per m^2), Delay 1 (219.8 per m^2), and Delay 3 (101.1 per m^2), but there were no significant differences among the pine engraver bait treatments. The mean emergence at Riske Creek (326.7 per m^2) was significantly greater than at the other two sites (25.5 per m^2 and 18.3 per m^2). The overall female: male ratio was 1.57 (n=2236). The female ratio was significantly greater on the north aspect than on the south aspect (1.70 vs. 1.43; χ^2_{1df} =3.81), and differed significantly among treatments (χ^2_{3df} =25.25). The female ratios for the Control, Simultaneous Baiting, Delay1 and Delay 3 were 1.06. 1.28, 1.69, and 1.63. There were no significant differences in female ratio by site (χ^2_{2df} =0.68).

3.1.2.3. Natural enemies

There were no differences in mean density of *Medetera* spp. or clerid spp. by treatment, aspect, or site (Appendix A, Table A2). The respective means (SE) were 7.54 (3.91) per m^2 and 4.64 (2.02) per m^2.

3.1.3. Discussion

3.1.3.1. 1992-1993

In 1992-93 the inhibitory effects of components of the pine engraver bait (Hunt and Borden 1988), when applied early in the flight season (Simultaneous Baiting and Delay 1), probably resulted in reduced mountain pine beetle activity, thus enabling a high proportion of trees to resist attack. The increased incidence of unsuccessful attacks due to resin production was mirrored by reduced gallery production and brood survival. Delay 3 was applied near the end of the mountain pine beetle attack period and thus had no significant effects (Table 1, Fig. 1). Therefore, though not statistically significant, the difference in brood density between the Control and Delay 3 in Table 1 (6.3%) is an estimate of the effects of competition from the pine engraver (competitive exclusion). The significantly higher *Medetera* densities in the Control and Delay 3 treatments suggest that their attacks tend to be concentrated in trees with high densities of mountain pine beetle brood. The significant treatment × aspect (T×A) interaction for clerid larvae, with most larvae found on the north aspect in the Delay 1 and 3 treatments, suggest that both bait type and location affected clerid oviposition.

The pine engraver is inhibited by components of mountain pine beetle pheromone (Hunt and Borden 1988). As all treatment trees in this experiment were initially baited for mountain pine beetle, the effect on pine engraver attack should be similar in all treatments. The observed differences in pine engraver attack and egg gallery length densities were thus mainly due to the timing of pine engraver bait placement relative to the beetles' flight activity. The density of pine engravers hibernating at the bases of trees is correlated with attack density near breast height (Safranyik et al. 1996). Since both tree resistance and pine engraver brood production were the highest with Simultaneous Baiting, baiting trees with pine engraver bait prior to mountain pine beetle flight is shown to be the most effective strategy explored in this experiment. During the summer of initial attack, no pine engraver attacks were found on the boles above the highest mountain pine beetle attacks.

3.1.3.2. 1993-1994

The repeat of the 1992 experiment in 1993-1994 gave inconclusive results. Even though there were no significant differences by treatment in either mountain pine beetle attack or egg gallery length density, both were numerically highest in the Delay 3 treatment and lowest in the Simultaneous Baiting treatment, corresponding with the lowest and highest values of the resistance index. These results were in general agreement with the findings from 1992-1993. However, contrary to the results from 1992-1993, brood density was numerically highest in the Simultaneous Baiting treatment. These inconclusive results were partially due to the low populations attacking at the Chasm sites, compared to a relatively high population at Riske Creek. At the Chasm sites, the majority of trees produced only a few beetles or none at all, whereas at Riske Creek, mountain pine beetle attacks overwhelmed all of the baited trees, resulting in high levels of brood production regardless of treatment.

The densities of *Medetera* and clerid larvae were much lower in this experiment than in 1992-1993 and partially explain the lack of significant differences among treatments, aspects and sites. Densities were numerically higher at Riske Creek in the Control and Delay 3 treatments; as in 1992-1993, there were no recorded *Medetera* from the other treatments. Woodpecker work was significantly greater at Riske Creek than at the other sites because the infestation at Riske Creek was an older and larger infestation. Woodpeckers are known to prefer feeding on trees with the heaviest broods in late stages of development.

Pine engraver attack density measured at 1.3 m did not vary significantly among treatments, although those treatments that were baited for pine engravers produced significantly greater adult emergence from duff. The highest (326.7 per m^2) occurred in the Delay 3 treatment, and indicates that the timing of bait placement with respect to the abundance of attacking populations had an effect on overall attacks per tree and subsequent brood production. The significantly greater pine engraver emergence at Riske Creek compared to the Chasm sites is explained by the older and larger mountain pine beetle infestation at Riske Creek which provided more breeding material for population increase. The significantly greater female ratio on the north aspect, and the female ratio increasing directly with density of beetles emerging from duff suggest that host condition and brood density may both affect the sex ratio (Safranyik 1976).

3.2. Dosages of pine engraver pheromone

The objective of this experiment was to determine the effects of different dosages of pine engraver bait on pine engraver attack and mountain pine beetle attack and brood density.

This experiment was carried out at Sunday Creek near Princeton, British Columbia, during 1992-1993. The treatments were:

Control:	Mountain pine beetle bait.
Treatment 1:	Delay 1×1: (Control +) one pine engraver bait placed approximately one week after mass attack by mountain pine beetle.
Treatment 2:	Delay 3×1: (Control +) one pine engraver bait placed approximately three weeks after mass attack by mountain pine beetle.
Treatment 3:	Delay 1×6: (Control +) six pine engraver baits placed at two heights approximately one week after mass attack by mountain pine beetle.
Treatment 4:	Delay 3×6: (Control +) six pine engraver baits placed at two heights approximately three weeks after mass attack by mountain pine beetle

Treatments were assigned at random to 60 lodgepole pines. Mountain pine beetle baits were placed on all plot trees in early July. The pine engraver bait for Treatments 1 and 2 was attached to trees at 1.3 m height on the north side and for Treatments 3 and 4 three baits were attached spaced equally around the bole at 1.3 m and three more at 3 m.

In late September, all trees were square sampled at breast height and at 3 m on both the north and south sides of the bole. In early November, duff samples were collected from the bases of the trees on the north sides only. During mid-June of the following year, disk samples were collected.

3.2.1. Results

The results of the analysis of variance by treatment (T), height on the bole (H) and aspect (A) of attack, gallery length and brood density for mountain pine beetle and pine engraver, and bark disturbance by woodpeckers are summarized in Appendix A, Table A3. Since the T×H, T×A, and T×H×A interactions were not statistically significant for any of the variables tested, they were not included in Table A3.

Thirty-nine percent of the trees were judged to be resistant: 5, 7, 8, 3, and 6 trees in the Control and Treatments 1-4, respectively. There was no significant difference among treatments in the proportion of resistant trees ($\chi^2_{5df} = 7.51$).

3.2.1.1. Mountain pine beetle

The mean densities of mountain pine beetle attacks, egg gallery lengths, and brood were all significantly higher ($p<0.05$) on the north sides of the trees and at the lower (1.3 m) sampling height. The height × aspect interactions were significant for all variables because mean responses by aspect from one height level to the other changed at different rates. Woodpeckers disturbed a significantly greater percentage of the bark at 3 m (11.1%) than at 1.3 m (2.9%).

The brood development index (SE) was 4.22 (0.048), and 49.9% of the brood were in the fourth larval instar at the time of the spring sampling. Neither the number of pine engraver baits nor the timing of bait placement nor the interactions among treatment, aspect and height on the bole produced any significant effect on mountain pine beetle attacks, egg gallery length, or brood. Mean densities of attacks, egg gallery lengths and broods are given in Table 3.

When the resistant trees were excluded from the analysis, mean attack densities for the Control and Treatments 1-4 were as follows: 164.1, 69.0, 82.3, 74.3 and 72.3. The corresponding egg gallery length densities were 15.4, 16.9, 21.8, 12.9 and 14.6 m per m^2, respectively. None of these were significantly different.

3.2.1.2. Pine engraver

Mean densities of pine engraver attack, egg gallery length and brood by treatment are given in Table 4, which also shows significant variation among treatments in the density of pine engravers emerged from duff. Significantly more adults emerged from those treatments with six pine engraver baits (Treatments 3 and 4) than from the Control and Treatment 2. The other treatment combinations were not significantly different.

The density of pine engraver emergence was significantly correlated with log (mountain pine beetle egg gallery per m^2+1)(r = 0.25, n = 75) and log (mountain pine beetle brood per m^2 +1)(r = 0.25, n = 75) at 3 m, but not with pine engraver attack or gallery length. At 1.3 m, none of these correlations were statistically significant.

3.2.2. Discussion

The significantly greater densities of mountain pine beetle attacks, egg gallery length and brood due to aspect found in this experiment have been shown previously (Safranyik 1968; Shepherd 1965). The circumferential distribution of attack is affected by the beetle's response to heat and light intensity during host colonization. The vertical attack density gradient, on the other hand, is the result of the distribution of suitable bark niches for attack initiation, and the height and density of the undergrowth.

The late emergence and slow accumulation of attacks by mountain pine beetle in 1992 resulted in relatively large numbers of lightly attacked resistant trees, regardless of treatment. After receiving an initial light attack during mid-August, about one-third of the treatment trees were heavily re-attacked in September, by which time all of the treatments were implemented. A bear destroyed mountain pine beetle baits on four trees. These events may have reduced variation among treatments, resulting in no significant differences for mountain pine beetle variables when all trees were included in the analysis. Even the numerical magnitudes of the variables were not related to either timing or dosage of pine engraver baits. On the other hand, when resistant trees were excluded, all treatments reduced attack density. In Treatments 3 and 4, which had six pine engraver baits, egg gallery length per m^2 was considerably reduced.

Application of pine engraver bait increased the number of engraver attacks and gallery production (Table 4), although the mean densities were not significantly different from the Controls. Based on these variables alone, no difference could be detected regarding the attractiveness of the two dosages (Treatments 1 and 2 vs. Treatments 3 and 4) or timing of bait placement (Treatments 1 and 3 vs. Treatments 2 and 4). However, the significantly greater brood production, as reflected by the density of emergence from duff, implied that the higher dosage (Treatments 3 and 4) induced more attacks. Pine engraver emergence was positively correlated with mountain pine beetle gallery density and brood production at 3 m, but was not correlated with pine engraver attack or gallery length at either of the two heights sampled. This implies that a) Much of the pine engraver attack and brood production must have occurred in the region of the bole above 3 m but below the highest mountain pine beetle attacks, and b) high mountain pine beetle brood density at 3.0 m or above increased pine engraver brood production. As stated earlier, pine engravers do not attack higher on the bole than mountain pine beetle during the year of initial attack.

Pine engraver attack density ranged from less than one-fifth to about half that of mountain pine beetle in the various treatments (Tables 3 and 4). Considering an average of two females per nuptial chamber and the same average number of eggs per female as mountain pine beetle (range 30-60, Sartwell et al. 1971), pine engravers may have produced a larval density ranging from 40% to equal that of mountain pine beetle. Based on the work of Rankin (1988), pine engraver densities of this magnitude would have had little or no effect on mountain pine beetle survival and brood production.

Overall, this experiment indicated that baiting trees with six pine engraver baits did not significantly increase pine engraver attack at the heights sampled, but did result in significantly increased engraver brood production over the entire bole area infested by mountain pine beetle. Pine engraver brood production was also increased by baiting simultaneously with mountain pine beetle bait irrespective of the dosage of pine engraver bait, although mountain pine beetle attack and brood production were not significantly affected. Host resistance, mainly due to slow accumulation of mountain pine beetle attacks, combined with low attack density by the pine engraver is the probable reason for this result.

3.3 Multiple competitor baiting

The objective of this experiment was to determine whether baiting for several species of secondary bark beetles one week after mountain pine beetle attack will reduce the density of mountain pine beetle broods.

This experiment was carried out at Sunday Creek, near Princeton during 1993-1994, and at Jug Lake on the Likely Road near Williams Lake during 1995-1996, and was comprised of the following treatments:

Control:	mountain pine beetle bait.
Treatment 1:	*Ips pini*: (Control +) pine engraver bait.
Treatment 2:	*Ips latidens*: (Control +) *Ips latidens* bait (+50/-50 ipsenol, 40 mg in bubble caps.
Treatment 3.	*Dryocoetes affaber*: (Control +) *Dryocoetes* bait (*exo*- plus *endo*-brevicomin mix, 250 mg in Eppendorf vial).
Treatment 4.	*Dryocoetes affaber*: (Control +) *Dryocoetes* bait (+50/-50 *endo*-brevicomin, 194 mg in Eppendorf vial).

The aggregation pheromone of *D. affaber* consists of a 1:2 mixture of (+) *exo*- and (+) *endo*-brevicomin (Camacho et al. 1994). The presence of (-) *exo*-brevicomin does not affect attraction of *D. affaber* but (-) *endo*-brevicomin is inhibitory. However, Poland (1997) used a 1:2 mixture (±) *exo*- and (±) *endo*-brevicomin to effectively induce attacks on spruce trap trees by *D. affaber*. Also, baits containing (±) *endo*-brevicomin induced significantly greater attack density on felled spruce trees by both *D. affaber* and *I. tridens* Mannerheim compared to unbaited trees or trees baited with a 1:1 mixture of (±) *exo*- and (+) *endo*-brevicomin (Poland 1997).

At Sunday Creek and Jug Lake, each treatment was assigned at random to 12 trees and 8 trees, respectively.

In late September, all treatment trees were square sampled for mountain pine beetle and pine engraver attack characteristics only. The resistance of each tree was judged on a five-point numeric scale based on the appearance of pitch tubes and boring dust:

1. No pitch tubes formed; quantities of dry, reddish boring dust in crevices and around base of tree.
2. Some attacks have sticky boring dust, usually with a visible entrance hole; dry boring dust in crevices and at base of tree.
3. Most attacks have sticky boring dust as above; in crevices and around base of tree there is a small amount of dry boring dust.
4. Most attacks have pitch tubes of moderate size; little or no overflow pitch; entrance hole usually visible in tube.
5. All attacks have pitch tubes, some overflowing with resin; fresh borings usually stuck on bark, red and shiny when wet with pitch.
6. Nearly all attacks have large pitch tubes, most with no entrance hole showing; frequently beetles may be seen encased in pitch; frequently tree will have low attack density.

In early November, duff samples were taken. In late May of the following year all trees were disc sampled. At Sunday Creek, disks were also taken at 3 m and 5 m heights from two randomly selected trees in each treatment. At Jug Lake, a second pair of disks was taken at the mid-point of the infested bole between the 3 m sample and the top of infestation of each treatment tree (referred to as “midpoint” in the following text). Attack, gallery length and brood data were collected only for mountain pine beetle and the pine engraver because of the low incedence of *I. latidens* and *D. affaber* and difficulty with reliable identification of their attack and gallery systems in the field.

3.3.1. Results 1993-1994

There was no significant variation among treatments in dbh ($F_{4, 55}$ = 0.91; the average dbh (SD) =27.1 (2.16) cm), or resistance scores using the Kruskal -Wallis test (χ^2_{4df} = 1.74; average resistance score (SD)= 2.96 (0.39)). A number of trees in each treatment group sustained light mountain pine beetle attacks due to late flight and low emergence rates.

The analysis of variance of mountain pine beetle and pine engraver attacks, egg gallery lengths and brood, density of *Medetera* larvae, and disturbance by woodpeckers by treatment and aspect are given in Table A4. Since there was no significant variation by height on the bole in any of the mountain pine beetle variables, Table A4 contains results from data taken at 1.3 m.

The average development index (SD) of mountain pine beetle broods was 3.79 (1.13), n=1499, at the time of the spring sampling and 31.8% of the brood were in the fourth larval instar.

Although there were no significant differences in the mean densities of any of the response variables among treatments (Table 5), mean attack and gallery length density were numerically lowest on trees baited for *I. latidens*. Mean brood density, however, was lowest on trees baited for *D. affaber* (Treatment 3 and Treatment 4), and highest in the Control trees. Trees baited for *I. latidens* (Treatment 2, Table 6) had no pine engraver attacks. Maximum mountain pine beetle attacks occurred in Treatment 4 (Table 5). The lowest mean mountain pine beetle brood densities, in Treatments 3 and 4, corresponded with the highest mean pine engraver emergence (Tables 5 and 6). Pine engraver emergence was significantly correlated with both pine engraver egg gallery length (r =0.70, n = 60) and mountain pine beetle egg gallery length (r = 0.49, n=60); the latter two variables were also significantly correlated (r = 0.43).

There was significant variation among treatments in the sex ratio of pine engraver adults from duff (χ^2_{4df} = 16.90). The female ratios for the Control and Treatments 1 to 4 were 1.03, 1.48, 1.00, 2.16, and 1.74, respectively.

There was no significant variation among treatments in the mean density of *Medetera* larvae (22.3 per m^2) or clerid larvae (1.0 per m^2), or in the amount (0.6%) of bark disturbed by woodpeckers (Appendix A, Table A4).

3.3.2. Results 1995-1996

The analysis of variance by treatment, height, and aspect of mountain pine beetle and pine engraver, attack, gallery length and brood are summarized in Table A5. Two-way interactions are not shown because none were statistically significant.

Forty-two percent of the mountain pine beetle brood was in pupal stage at the time of the spring, 1996, sampling. The treatments had no significant effect on any of the mountain pine beetle variables (Appendix A, Table A5), though numerically more brood was found in the Control and the *Ips pini* treatment (Table 7). Mean densities of all measured variables were significantly greater at 1.3 m than at 3 m. Gallery length was significantly greater on the north aspect of the bole than on the south (Appendix A, Table A5). There was significant variation among treatments in all measured pine engraver variables (Table A5). Treatment 1 had significantly more attacks and egg gallery length than all other treatments (Table 8). Significantly more pine engravers emerged from the Control and Treatment 1, which were different from all other treatments and from each other (Table 8). Other than for the *Ips pini* treatment, mean engraver attack, gallery length and brood were small fractions of the corresponding numbers for mountain pine beetle.

There was no significant variation among treatments in the percentage of bark disturbed by woodpeckers (1.9%) (Appendix A, Table A5). Nine trees were judged resistant; three trees in Treatment 3, three in Treatment 4 and one tree in each of the other treatments.

3.3.3. Discussion

This experiment produced essentially the same results in both years. Although treatment effects on mountain pine beetle brood production were not significant, the average attack density was numerically lower on trees baited for the pine engraver (Treatment 1), *I. latidens* (Treatment 2) and *Dryocoetes* (Treatment 3). Average brood densities were lowest in Treatments 2 to 4. Treatment 1 had the highest density of emerging pine engravers in 1993-1994 (Tables 6 and A4), but mountain pine beetle brood density was nearly the same as in the Controls in both years. Owing to the low pine engraver attack density in this treatment, competitive effects on mountain pine beetle brood were insignificant. In Treatments 1 to 4 the lower average mountain pine beetle brood densities were assumed to be the result of reduced mountain pine beetle attacks. No *I. latidens* were found in samples for this experiment, in agreement with Safranyik et al. (1996).

It is known that the pheromone produced by *Ips latidens* is repellent to the pine engraver (Furniss and Livingston 1979). In 1993-94, no pine engraver attacks were found on trees baited for *I. latidens* (Treatment 2, Table 6). In 1995-1996, pine engraver attack density in the *I. latidens* treatment was significantly different from the *Ips pini* treatment (Table 8). In 1993-1994, the *Dryocoetes* treatments (3 and 4) appeared to enhance pine engraver attack and brood production over the Control and *Ips pini* treatments, but not in 1995-1996, possibly because of the very low pine engraver population in 1996. The positive correlation of pine engraver emergence with mountain pine beetle gallery length indicates that pine engravers preferred to attack trees already successfully colonized by mountain pine beetle. Such trees cannot produce resin in response to the later attacks, which enhances the success of pine engraver brood establishment and survival. Pine engraver gallery length was correlated with brood density (indexed by emergence from duff). The significant variation among treatments in the sex ratio of pine engravers appeared to be related to density. Higher densities (Table 6) tended to have higher female ratios. This suggests that survival by sex may be density related.

The results of these experiments indicate that baiting trees for any of the four species of secondary bark beetles one week or so following onset of mass attack by mountain pine beetle is ineffective in significantly reducing survival of mountain pine beetle broods. The marginal reduction of mountain pine beetle brood in trees baited for *I. latidens*, *Dryocoetes* and *Pityogenes* was mainly related to reduction of mountain pine beetle attacks. Since these trees were baited after the start of attack, the strategy of co-baiting trees for mountain pine beetle and one of these secondary species should be investigated further.

3.4. Felling and competitive interaction

The objective of this experiment was to determine the combined effects of felling and pine engraver bait on mountain pine beetle in lodgepole pine.

Experiments were carried out in stands at two locations in each of two years, 1994-1995 and 1995-1996, at Saturday Creek located near Princeton, and at Jug Lake. Thirty-six uninfested trees were selected and baited for mountain pine beetle in a 15-m to 20-m grid at each location prior to the flight period. Pine engraver bait was applied to 12 randomly selected trees as follows:

Control:	Mountain pine beetle bait.
Treatment 1:	Simultaneous. (Control +) pine engraver bait applied simultaneously.
Treatment 2:	Delay 2. (Control +) pine engraver bait applied approximately two weeks later.

Half of the trees in each treatment were felled at the time Treatment 2 was applied.

All trees were square sampled in mid-September and duff was sampled in early November. In mid-May of the following year, all trees were disc sampled as in the multiple competitor baiting experiment (section 3.3).

3.4.1. Results Saturday Creek 1994-1995

There was no significant variation in dbh among treatments; the average dbh (SE) was 25.55 (0.35) cm. By the time of the spring 1995 sampling, 36.5% of the brood had become adults. The plot trees were lightly attacked by mountain pine beetle (Table 9); consequently, 22 of the 36 trees were resistant - seven trees were resistant in the controls, eight in Treatment 1 and seven in Treatment 2.

The analysis of variance of response variables by treatment, height on the bole, and felling, is given in Appendix A, Table A6. Only those treatments and interactions where statistically significant variation was found are shown.

Baiting had no significant effect on the attack, egg gallery length or brood density of mountain pine beetle (Appendix A, Table A6 and Table 9). Although not statistically significant, mean brood density was numerically lowest in the Control and highest in the two pine engraver bait treatments (Table 9). Attack and gallery length were both significantly higher on felled trees than on standing trees and at 1.3 m height than at the midpoint. For attack, the bait × felling interaction was also significant because standing trees in the Delay 2 treatment received higher attack density than the felled trees. There was no significant variation by bait, felling, height on the bole, or aspect, in the percentage of bark disturbed by woodpeckers (1.2%).

Neither pine engraver attack nor gallery length were affected by treatment, felling, aspect, or height (Appendix A, Table A6). Mean densities for both were numerically lowest for simultaneously baited trees (Table 10). No adult engravers emerged from the duff samples in the Control and there was no significant difference in mean brood density between Treatments 1 and 2.

3.4.2. Saturday Creek 1995-1996

There was no significant variation in dbh among treatments; the average (SE) dbh was 25.5 (0.32) cm. At the time of the spring 1996 sampling 23.85% of the mountain pine beetle brood were in the pupal stage. Two trees each of 12 in Treatments 1 and 2 were judged resistant.

Analysis of variance showed that the treatments had no significant effects on any of the mountain pine beetle response variables (Appendix A, Table A7 and Table 11). Attack density was significantly greater on the north aspect, at 1.3 m, and on standing trees, than on the south aspect, at the midpoint, on felled trees. The same pattern was evident for brood but not for gallery length. On the north aspect, attacks declined at a significantly greater rate with height than on the south. Except for simultaneously baited trees, felled trees had significantly greater brood density than standing trees. The percentage of bark disturbed by woodpeckers was significantly higher on the north aspect ($F_{1,24}$=6.33), but height on the bole, felling, and baiting, had no significant effect. The average intensity of woodpecker disturbance was 0.55%.

Bait and height had significantly increased pine engraver attack and gallery length (Appendix A, Table A7). Felling trees significantly lowered pine engraver emergence. Attack and gallery length were significantly lowest in the Controls and in the midpoint samples (Table 12). The pine engraver attacks and emergence were significantly correlated (r_{46}=0.43). There was no significant correlation between mountain pine beetle attack and pine engraver emergence (r_{46}= -0.16). There was a significant interaction between the bait treatments and sex ratio (χ^2_{2df} = 6.81, n=611). The male ratios for the Control and the Simultaneous and Delay 2 treatments were 0.71, 0.64 and 0.41, respectively. There was no significant treatment effect on the pronotal width of adults but males (average pronotal width = 1.52 mm, n = 72) were significantly larger than females (average pronotal width = 1.50 mm, n = 84).

3.4.3. Likely Road 1994-1995

Eight trees were resistant, one from the Control, four in Treatment 1, and three in Treatment 2. At the time of the spring 1995 sampling 86.95% of the mountain pine beetle brood were adults. There was no significant variation by treatment in the percentage of bark disturbed by woodpeckers, which averaged 9.14%. Bark disturbance was significantly greater on standing than on felled trees.

The analyses of variance for mountain pine beetle and the pine engraver are summarized in Appendix A, Table A8. Attack density by mountain pine beetle was significantly greater at 1.3 m than at the mid-point. Gallery length was significantly higher on the north aspect. Although not statistically significant, attack, gallery length and brood density were all numerically lowest in Treatment 2 (Table 13).

Pine engraver activity was light, as indicated by the low attack, gallery length and brood densities (Table 14). The density of pine engravers emergence was significantly highest for Delay 2, but as neither attack nor egg gallery length showed a relationship to treatment, these large numbers may have resulted from attacks made above the highest samples.

3.4.4. Likely Road 1995-1996

The analysis of variance for mountain pine beetle and the pine engraver are summarized in Appendix A, Table A9. There was no statistically significant variation by treatment in dbh (mean 28.9 cm; SE=0.74). At the time of the spring 1996 sampling, 76.5% of the brood were larvae, 21.3% were pupae, and 0.2% were adults. Four trees were resistant, two trees each in the Control and in Treatment 1. The low mountain pine beetle attack density resulted in sustained resin production with consequent brood mortality, and reduced attacks by the pine engraver.

Felled trees, and mid-point samples had significantly less mountain pine beetle attack and gallery length than standing trees and samples at 1.3 m. Gallery length was significantly lowest in the Delay 2 treatment (Table 15). Attack and brood were also lowest in Delay 2, but not significantly so. Overall, brood density was significantly lower at mid-point than at 1.3 m. On average, 3.46% of the bark was disturbed by woodpeckers, with no significant variation by bait, felling, height, or aspect.

For the pine engraver attacks, the aspect × bait interaction was significant because the Control and Delay 2 attacks were higher on the south aspect whereas the reverse held true for Simultaneous baiting. The mean pine engraver emergence was significantly greater in Treatment 2 (Table 16). There was no significant interaction between sex and bait treatment ($\chi^2_{2df} = 4.22$); the overall male ratio was 35.05%.

3.4.5. Discussion

Simultaneous baiting numerically (but not significantly) reduced mountain pine beetle attack density. It also reduced egg gallery length, but the reduction was significant in one trial. With the exception of the earlier trial at Saturday Creek, the number of resistant trees was not a good indicator of the effects of resinous response by the host on beetle attacks, reproduction, and survival. In all cases, mountain pine beetle attack was light and mean attack densities were lower or close to that considered adequate for successful host colonization. In both trials on the Likely Road, mountain pine beetle brood varied with treatment in the same way as attack and egg gallery length. Pine engraver densities at Likely Road were very low in comparison with Saturday Creek. At Saturday Creek, mean density of mountain pine beetle brood increased directly with density of pine engravers from duff, regardless of treatment. Although not statistically significant, these results suggest that pine engraver bait may reduce mountain pine beetle attack and brood survival in some cases. Under other conditions, however, perhaps through accelerating the death of host cells in the upper parts of the infested bole, increasing pine engraver activity may result in enhanced mountain pine beetle survival.

Felling had differing effects, as it significantly increased mountain pine beetle attack and gallery length in one trial, significantly decreased attack in another, and had no significant effects in the balance of the trials. Brood was significantly increased in felled trees in one of the four trials in all but the Simultaneous Baiting treatment. This indicates that at least some trees were attacked after felling, behaviour previously described by Amman (1983). Woodpecker predation was generally light, and not significantly different among treatments in most of the trials. The highest mean bark disruption (9.14%) was found in the only case in which the mean percentage of bark disturbed by woodpeckers on standing trees was significantly greater than on felled trees, Pine engraver brood density was generally higher in the Delay 2 treatment than in the Control. Attack density was affected similarly in two trials, although differences among treatments were not always statistically significant. In one trial each at Saturday Creek and Likely Road, the numerically lowest attack density occurred with Simultaneous baiting, mainly because of light mountain pine beetle attack and more effective host resistance. Two weeks delay resulted in the highest attack and brood densities because trees were baited for pine engraver after their resistance had largely been overcome by the mountain pine beetle mass attack, thus increasing the chances of successful engraver brood establishment. Where significantly different, attack and egg gallery density were greater at 1.3 m than at midpoint, indicating that during the year of host colonization, pine engraver attacks tended to be concentrated in areas with the greatest numbers of mountain pine beetle attacks.

Duff emergence figures from standing and felled trees are not directly comparable. Samples taken from below standing trees are an index of brood production over the entire height of the tree whereas samples from below felled trees index only the portion of the population in the area of the bole immediately above where the sample was taken. Felling had no statistically significant effect on attack density, which is a more suitable measure of brood productivity in this case.

In the Saturday Creek 1995-1996 trial, which produced a relatively high density of pine engravers from duff, bait treatment had a significant effect on the male ratio, which was highest in the Control and lowest in the Delay 2 treatment. In contrast, in the Likely Road 1995-1996 trial, where pine engraver density was very low, there was no significant treatment effect on the male ratio (35%), which was lower than the lowest male ratio at Saturday Creek (41% in Delay 2). These results suggest that host condition and competitive interactions cause differential mortality in male and female pine engraver brood.

In summary, simultaneous baiting consistently (but not significantly) reduced mountain pine beetle attack and egg gallery length. These reductions, however, were not consistently or significantly reflected in reduced mountain pine beetle brood. The highest mountain pine beetle brood production was associated with the highest pine engraver emergence in two trials which suggests that pine engraver densities in this study were not high enough to affect mountain pine beetle brood mortality through competitive exclusion. Pine engraver attack and brood production were increased in trees baited following mass attack by mountain pine beetle. In general, felling treated trees did not affect the attack or brood production by either species. Baiting in combination with host condition appeared to differentially affect the survival of male and female pine engravers.

4. Summary and synthesis of results

4.1. Effects of mountain pine beetle on pine engraver brood production

Based on combined data from the first three experiments, mean density of mountain pine beetle brood (MPBB) at 1.3 m on the bole was a humpbacked function of attack density (A) (Figure 2) which reached a maximum between 88 and 177 attacks per m^2 and was described by the equation:

$$MPBB=11.43(A+20)e^{-0.085(A+20)}$$

This equation was fitted in the form Y=ln(mpb/(A+c)) vs. X=(A+c) by linear least squares, and for c=20 and n=8, the correlation coefficient was 0.86. The form of the relationship Figure 2 is similar to that shown by Berryman (1976) and results from the composite effects on brood survival of host resistance and intraspecific competition among larvae.

On average, pine engraver emergence from duff (I) was linearly and positively related to mountain pine beetle attack density (A) at 1.3 m (Fig. 3), and the relationship is described by the equation:

$$I=44.96+0.51A, n=6, r=0.96.$$

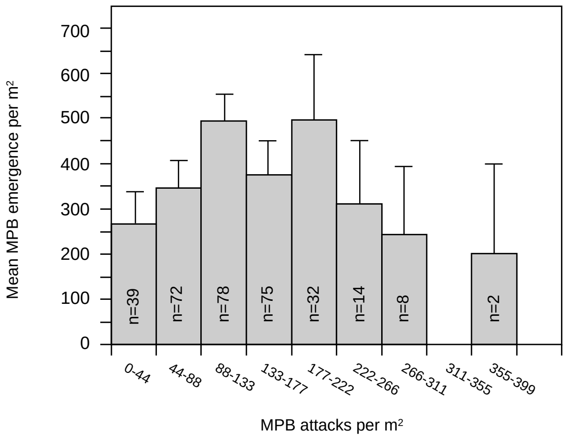

Figure 2. The relationship between attack and brood density of mountain pine beetle at 1.3 m. Combined data from Experiments 1 to 3. Vertical lines indicate 1 S. D.; N=sample size.

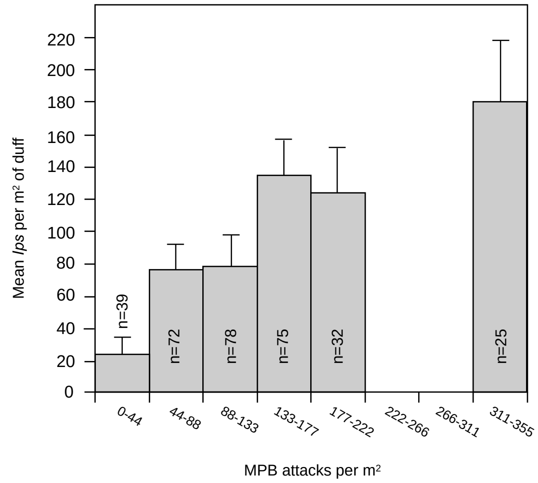

Figure 3. The relationship between the mean density of pine engravers from duff and mean attack density of mountain pine beetle at 1.3 m. Combined data from Experiments 1 to 3. Vertical lines indicate 1 S. D.; N= sample size.

This relationship occurred for the following reasons: a) we have shown previously (Safranyik et al. 1996) that attack densities of pine engraver and the mountain pine beetle along the bole are inversely related; b) the density of emerged pine engravers from duff is an index of total brood production in the entire tree; and c) host resistance is a main factor determining pine engraver attack success and brood survival. Hence, the relationship in Fig. 3 indicates that trees with high attack density by mountain pine beetle in the lower bole, pine engraver attack success was enhanced due to reduced host resistance. Also, since pine engraver attacks were inversely related to mountain pine beetle attacks, most of the pine engraver brood production occurred in the regions of the bole which sustained moderate to light mountain pine beetle attacks.

On average, the density of pine engravers from the duff and mountain pine beetle brood density at 1.3 m were inversely related (Figure 4). Low mountain pine beetle brood densities at 1.3 m occurred at both low and high mountain pine beetle attack densities (Figure 2). However, because of the relationship in Fig.3, on average, pine engraver production in trees increased with increasing density of mountain pine beetle attacks and decreasing density of mountain pine beetle brood at 1.3 m. This could occur at moderate to high densities of mountain pine beetle attacks at 1.3 m (Figure 2). Pine engraver density from duff declined with increasing mountain pine beetle density at 1.3 m (x); the maxima (R) of pine engraver density (Figure 4) were approximated by the function:

$$R=1800e^{-0.000845x}$$

As a consequence of the above relationships, the effect of pine engraver density on mountain pine beetle survival would be expected to be greatest at moderate mountain pine beetle attack densities. At high densities of mountain pine beetle attack, intra-specific competition is a major mortality factor. At low attack densities, pine engraver establishment and survival are reduced due to host resistance.

4.2. Effects of pine engraver on mountain pine beetle brood production

Mainly because of the relationships in Figures 2 and 3, the density of mountain pine beetle brood in the lower bole and that of pine engravers from duff were inversely related (Figure 4). Pine engravers tend to attack bark areas not

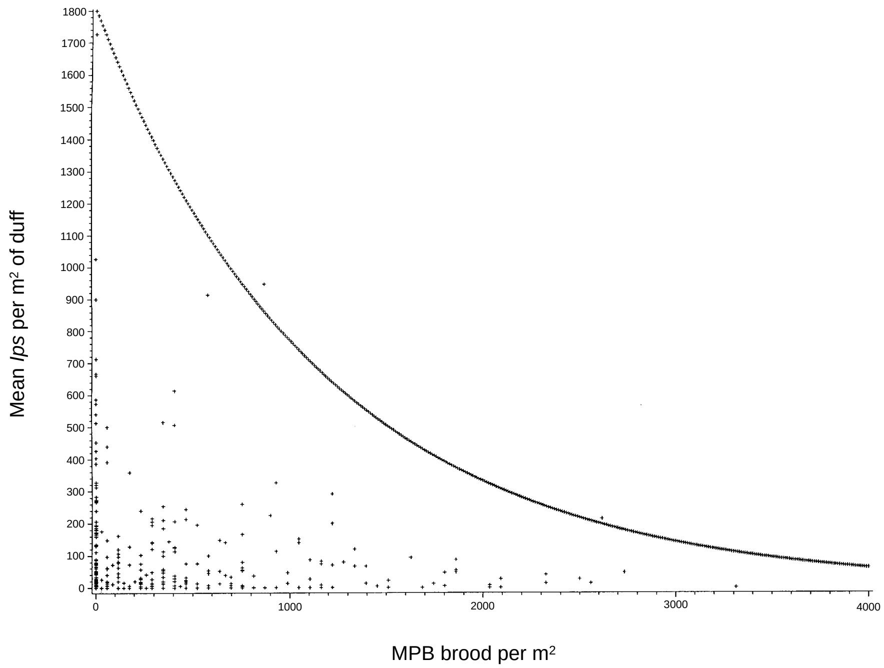

Figure 4. The relationship between the densities of pine engraver from duff and mountain pine beetle brood at 1.3 m. Combined data from Experiments 1 to 3. The maxima (R) of pine engraver density (solid curve) on MPB density (x) were described by the equation $R=1800e^{-0.000845x}$.

occupied by mountain pine beetle, and thus had little effect on mountain pine beetle survival in the lower bole (i.e., where the largest concentration of mountain pine beetle attacks and brood are located).

4.3. A hypothetical model of the mountain pine beetle - pine engraver interaction

Our understanding of the effects of simultaneous mountain pine beetle and pine engraver bait treatments is illustrated in Figure 5. This figure illustrates the effects of the bait treatments on interactions by the two species and survival probability for mountain pine beetle as a function of attack density. The general shape of the survival probability curves were modeled after Berryman (1994). Indirect effects of the baits on mountain pine beetle survival through induced changes in the natural enemy complex are not considered. Figure 5 depicts several scenarios:

4.3.1. Natural vs. induced mountain pine beetle attack

Under natural conditions, the probability of mountain pine beetle survival from egg to adult is a humpbacked function of attack density (Berryman 1974) due to the opposing effects of attack density on host resistance and intraspecific competition among larvae. Baiting trees for mountain pine beetle should result in brood survival at lower attack densities than in naturally attacked trees, due to more rapid accumulation of attacks and consequent reduced effectiveness of host defenses (primary and secondary resinosis). Consequently, in baited trees the rate of increase in brood survival at low to moderate attack density would be higher, and would peak at a higher density, compared to unbaited trees (curve A vs. B, Figure 5). Pine engravers attack after a tree’s defenses have been severely reduced or eliminated by mountain pine beetle attacks. Hence, average reduction in mountain pine beetle brood survival brought about by competition from pine engravers would be about the same whether or not trees were baited. Consequently, on average, mountain pine beetle brood survival in baited trees is expected to be greater than in naturally attacked trees irrespective of competition from the pine engraver.

4.3.2. Simultaneous baiting for mountain pine beetle and pine engraver

Baiting trees simultaneously for the two species may lower mountain pine beetle brood survival (curve C1, Figure 5) even if no significant interspecific competition occurs, for the following reasons: a) slow accumulation of mountain pine beetle attacks and the consequent increased effect of host resistance and, b) reduced mean attack density due to the repellent effect of the pine engraver bait. Pine engraver bait induces more pine engraver attack than would occur naturally, especially in bark areas lightly to moderately attacked by mountain pine beetle. Greater numbers of attacks usually result in increased pine engraver brood density and interspecific competition with mountain pine beetle broods. This changes the mountain pine beetle survival curve (curve C2, Figure 5) as interspecific competition will reduce the survival probability to a level below that caused by a reduction of mountain pine beetle attack density alone due to the repellent effect of pine engraver bait. The magnitude of the competitive reduction will depend largely on the size of the resident pine engraver population.

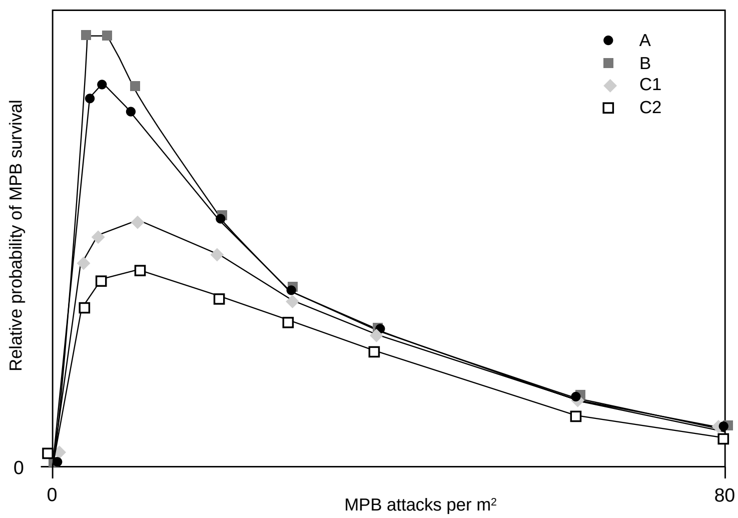

Figure 5. A hypothetical, graphical model of the effect of baiting individual lodgepole pines with mountain pine beetle and pine engraver bait on mountain pine beetle survival probability as a function of average attack density per tree (see text for detail). A = No baiting, B = baited with mountain pine beetle bait, C1 = baited simultaneously with mountain pine beetle and pine engraver bait; illustrates effect of pine engraver bait on reducing the rate of accumulation of mountain pine beetle attacks, C2 = same as C1 but includes the effect of induced attacks by pine engraver. In each of the four scenarios (A, B, C1 and C2), we assumed constant population sizes for the two bark beetle species and identical host defense capability.

4.3.3. Impact of competitive interactions in trees baited simultaneously with mountain pine beetle and pine engraver bait

Mountain pine beetle attack and brood densities are inversely related to height on the infested bole (Safranyik, 1968). On the other hand, pine engraver attacks and brood are directly related to height on the infested bole during the year of mountain pine beetle attack (Safranyik et al. 1996), when interspecific competition has the largest potential impact. Hence, assuming that host defenses have been overcome, competition will have the greatest impact in areas of the infested bole which contain the lowest densities of mountain pine beetle brood. Consequently, interspecific competition from induced pine engraver attacks is expected to have less impact on mountain pine beetle brood survival than reduction in mountain pine beetle attack density due to the repellent effect of pine engraver bait. The effect of either factor will be greater at moderate to light mountain pine beetle attack densities, which are normally realized in small to medium sized infestations and higher on the infested bole in individual trees. In large infestations, mass attack by mountain pine beetle tends to overwhelm the repellent effect of the pine engraver bait. Hence, in these situations most of the effects on mountain pine beetle brood survival are expected to result from induced pine engraver attacks. However, pine engraver attacks are also reduced in areas of the bole containing the highest densities of mountain pine beetle brood. Conversely, in spot infestations involving only a few trees, there are often not large enough populations of pine engravers to impact on mountain pine beetle survival.

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Tables

Table 1. Mean densities per m^2 of mountain pine beetle egg gallery length (m) and brood by treatment at Valentine Lake and Horse Lake Road, 1992-1993.

	Control	Treatment 1	Treatment 2	Treatment 3
Egg gallery	41.50a	11.38b	23.42ba	41.37a
Brood	509.55a	124.56b	354.72ab	375.67ab

Means designated by the same letter within rows are not significantly different; p>0.05.

Table 2. Mean densities per m^2 of pine engraver egg gallery length and brood emerged from duff at Valentine Lake and Horse Lake Road, 1992-1993.

	Control	Treatment 1	Treatment 2	Treatment 3
Egg gallery	0.99b	3.57a	1.53ab	1.83ab
Brood	9.41b	54.83a	48.48ab	34.24ab

Means within rows designated by the same letters are not significantly different; p>0.05

Table 3. Mean densities per m^2 of mountain pine beetle attacks, egg gallery lengths and brood by treatment at Sunday Creek, 1992-1993.

	Control	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Attack	80.42a	75.57a	87.20a	81.33a	72.67a
Egg gallery	19.72a	18.23a	22.47a	13.01a	15.46a
Brood	109.49a	106.59a	138.57a	137.59a	63.95a

Means within rows designated by the same letter are not significantly different; p>0.05.

Table 4. Mean density per m^2 of pine engraver attack, egg gallery length and brood by treatment at Sunday Creek, 1992-1993.

	Control	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Attack	14.53a	33.91a	31.98a	40.70a	16.47a
Egg gallery	1.16a	3.38a	4.72a	3.18a	2.48a
Brood[1]	40.17a	88.52ab	51.60a	151.81b	173.80b

Means within rows designated by the same letter are not statistically significant, p>0.05.
[1] Adults emerged from duff.

Table 5. Mean mountain pine beetle attacks, egg gallery lengths and brood per m^2 by treatment. Sunday Creek, 1993-1994.

Variable	Control	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Attack	88.1a	68.5a	63.8a	64.8a	98.1a
Egg gallery	18.2a	14.8a	12.4a	16.3a	15.0a
Brood	651.6a	552.4a	419.1a	217.0a	227.7a

Means within rows designated by the same letter not statistically significant; $p > 0.05$

Table 6. Mean pine engraver attacks, egg gallery lengths and brood per m^2 by treatment. Sunday Creek, 1993-1994.

Variable	Control	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Attack	7.4a	7.4a	0.0a	11.1a	16.7a
Egg gallery	4.1a	3.3a	0.0a	3.9a	9.4a
Brood[1]	80.0a	93.4a	23.3a	205.6a	213.4a

[1] Adults emerged from duff
Means within rows designated by the same letter are not statistically significant; $p > 0.05$.

Table 7. Mean mountain pine beetle attack, egg gallery length and brood per m^2 by treatment. Likely Road, 1995-1996.

Variable	Control	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Attack	103.8a	72.3a	83.2a	82.6a	93.0a
Egg gallery	20.1a	28.4a	21.47a	20.2a	20.52a
Brood	198.1a	190.6a	113.2a	106.7a	86.9a

Means designated by the same letter are not significantly different, $p>0.05$

Table 8. Mean pine engraver attack, egg gallery length and brood per m2 by treatment. Likely Road, 1995-1996.

Variable	Control	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Attack	6.3b	33.0a	7.1b	6.4b	3.9b
Egg gallery	0.07b	1.33a	0.28b	0.16b	0.17b
Brood[1]	14.3c	266.4a	1.0b	4.0bc	3.5bc

Means designated by the same letter are not significantly different, $p>0.05$
[1] Adults emerged from duff

Table 9. Mean mountain pine beetle attacks, egg gallery lengths and brood per m^2 by treatment at Saturday Creek, 1994-1995.

Variable	**Control**	**Treatment 1**	**Treatment 2**
Attack	50.61a	40.74a	53.08a
Egg gallery (m)	7.11a	5.34a	10.04a
Brood	120.02a	173.93a	182.08a

Means within rows designated by the same letter are not significantly different (p> 0.05)

Table 10. Mean pine engraver attacks, egg gallery lengths and brood per m^2 by treatment at Saturday Creek, 1994-1995.

Variable	**Control**	**Treatment 1**	**Treatment 2**
Attack	19.75a	1.23a	12.34a
Egg gallery (m)	0.11a	0.03a	0.24a
Brood[1]	0.00b	62.86a	91.43a

Means within rows designated by the same letter are not significantly different (p>0.05)
[1] Adults emerged from duff

Table 11. Mean mountain pine beetle attacks, egg gallery lengths and brood per m^2 by treatment at Saturday Creek, 1994-1995.

Variable	**Control**	**Treatment 1**	**Treatment 2**
Attack	62.95a	49.37a	50.61a
Egg gallery (m)	20.29a	16.50a	16.27a
Brood	109.82a	192.17a	235.99a

Means within rows designated by the same letter are not significantly different (p>0.05)

Table 12. Mean pine engraver attacks, egg gallery length and brood per m^2 by treatment at Saturday Creek, 1994-1995.

Variable	**Control**	**Treatment 1**	**Treatment 2**
Attack	4.94b	58.01a	80.23a
Egg gallery (m)	0.16b	1.94a	2.57a
Brood[1]	15.41b	77.91a	75.53a

Means within rows designated by the same letter are not significantly different (p>0.05)
[1] Adults emerged from duff

Table 13. Mean mountain pine beetle attacks, egg gallery lengths and brood per m^2 by treatment at the Likely Road, 1994-1995

Variable	Control	Treatment 1	Treatment 2
Attack	53.08a	41.97a	92.58a
Egg gallery (m)	16.81a	13.02a	16.30a
Brood	227.72a	181.37a	189.97a

Means within rows designated by the same letter are not significantly different ($p>0.05$)

Table 14. Mean pine engraver attacks, egg gallery length and brood per m^2 by treatment at the Likely Road, 1994-1995.

Variable	Control	Treatment 1	Treatment 2
Attack	1.61a	0a	0a
Egg gallery (m)	0.15a	0.088a	0a
Brood[1]	1.48a	12.51a	37.08b

Means within rows designated by the same letter are not significantly different ($p>0.05$)
[1] Adults emerged from duff

Table 15. Mean mountain pine beetle attacks, egg gallery lengths and brood per m^2 by treatment at the Likely Road, 1995-1996

Variable	Control	Treatment 1	Treatment 2
Attack	64.19a	33.33a	43.20a
Egg gallery (m)	14.15a	6.67b	14.76a
Brood	214.79a	124.47a	218.24a

Means within rows designated by the same letter are not significantly different ($p>0.05$)

Table 16. Mean pine engraver attacks, egg gallery lengths and brood per m^2 by treatment at the Likely Road, 1995-1996.

Variable	Control	Treatment 1	Treatment 2
Attack	6.17a	4.93a	15.43a
Egg gallery (m)	0.17a	0.10a	0.75a
Brood[1]	1.22a	5.23a	24.12b

Means within rows designated by the same letter are not significantly different ($p>0.05$)
[1] Adults emerged from duff at bases of treated trees.

Appendix

Analysis of variance tables

All treatments, heights and aspects are described in Methods.

Table A1. Analysis of variance by treatment and aspect on the bole, of mountain pine beetle and pine engraver attacks, brood, mountain pine beetle egg gallery lengths, and brood of some natural enemies at Valentine Lake and Horse Lake Road, 1992-1993. (Attacks and egg gallery lengths were sampled in September, 1992; brood was sampled in June, 1993.)

Variable	Treatment (T)		Aspect (A)		TxA	
	F	**P**[1]	**F**	**P**	**F**	**P**
			Mountain pine beetle			
Attack	**1.70**	**0.18**	0.29	0.59	2.84	0.05
Egg gallery	7.17	0.0004	0.01	0.93	4.61	0.006
Brood	2.77	0.05	**0.22**	0.64	0.26	0.85
			Pine engraver			
Attack	1.06	**0.37**	0.24	0.61	0.77	0.69
Gallery	4.65	**0.012**	2.01	0.163	1.23	0.40
Brood[2]	2.20	0.098	-	-	-	-
			***Medetera* sp.**			

Table A2. Analysis of variance by site, treatment, and aspect of mountain pine beetle and pine engraver attack , egg gallery length and brood densities, percent woodpecker bark disturbance, and larval densities of clerids and *Medetera* sp. in lodgepole pine. Chasm and Riske Creek, 1993-1994. Fully resistant trees were excluded from analysis.

Variable	**Site(Block)**		**Treatment(T)**		**Aspect(A)**	
	F	**P**[1]	**F**	**P**	**F**	**P**
			Mountain Pine Beetle			
Attack	15.15	**0.008**	0.61	0.63	0.95	**0.33**
Gallery	19.52	0.004	0.73	0.57	0.46	0.50
Brood	2.07	0.22	4.90	0.06	14.42	0.0004
			Pine Engraver Beetle			
Attack	1.02	**0.42**	0.68	0.60	0.38	**0.54**
Brood[2]	64.63	0.000	5.97	0.001	0.41	0.52
			***Medetera* larvae**			
Brood	2.33	**0.17**	2.00	0.21	0.28	**0.60**
			Clerid larvae			
Brood	0.72	0.52	0.38	0.77	.32	**0.57**
			Bark disturbed by woodpeckers			

Table A3. Analysis of variance by treatment height on the bole and aspect of attack variables and brood density for mountain pine beetle and the pine engraver, and of percent bark disturbed by woodpeckers at Sunday Creek, 1992-1993.

Variable:	**Treatment**		**Height**		**Aspect**		**HxA**	
	F	**P**[1]	**F**	**P**	**F**	**P**	**F**	**P**
				Mountain pine beetle				
Attack	0.63	0.64	4.36	**0.04**	21.2	**0.0001**	9.27	**0.003**
Egg gallery	0.78	0.54	28.63	0.0001	7.23	0.008	3.55	0.062
Brood	0.44	0.78	3.73	**0.058**	23.17	0.0001	8.68	0.004
				Pine engraver				
Attack	1.22	0.31	1.91	**0.17**	1.67	**0.12**	0.69	**0.16**
Egg gallery	0.96	0.44	1.02	**0.31**	1.61	0.20	0.70	0.15
Brood[2]	3.47	0.012	-	-	-	-	-	-
				Bark disturbed by woodpeckers				
Bark disturbed	0.46	0.76	34.67	**0.0001**	3.49	**0.065**	1.14	**0.29**

Table A4. Analysis of variance by treatment and aspect at 1.3 m of response variables measured for mountain pine beetle, pine engraver, *Medetera* sp. and percent bark disturbance by woodpeckers. Sunday Creek, 1993-1994.

Variables:	**Treatments**		**Aspect**	
	F	**P**[1]	**P**	**F**
		Mountain Pine Beetle		
Attack	0.51	0.73	0.50	1.32
Egg gallery	1.48	**0.25**	0.34	0.92
Brood	0.8	0.57	0.14	2.01
Pine engraver				
Attack	1.14	0.35	0.62	0.43
Egg gallery	1.92	0.13	0.18	0.67
Brood[2]	1.36	0.27	5.87	0.02
		***Medetera* sp.**		
Brood	0.99	0.42	0.38	0.54
		Woodpecker bark disturbance		
Bark disturbed	1.25	**0.30**	2.28	0.14

[1] Prob. >F.

Table A5. Analysis of variance by treatment, height on the bole and aspect of attack and brood variables for mountain pine beetle and the pine engraver. Likely Road, 1995-1996.

Variable	Treatment (T)		Height (H)		Aspect (A)		AxHxT	
	F	P[1]	F	P	F	P	F	P
Mountain Pine Beetle								
Attack	0.38	0.82	5.04	0.034	1.14	0.29	3.00	**0.026**
Egg Gallery	0.70	0.60	3.90	0.060	8.46	0.0052	0.32	0.86
Brood	1.06	0.39	10.11	0.0040	1.19	0.28	1.78	0.15
Pine engraver								
Attack	2.98	0.034	2.93	0.10	0.10	0.76	4.44	**0.0034**
Egg gallery	4.17	0.0081	**2.89**	0.10	0.22	0.64	5.00	0.0016
Brood[2]	13.01	0.0000	-	-	-	-	-	-

[1] Prob. >F.

[2] Pine engraver adults emerging from duff at bases of treatment trees.

Degrees of freedom (Treatment, error): T=(4,31); H=1, 24; A=1, 57: A×H×T=5,57.

Table A6. Analysis of variance by bait treatment, height on the bole and felling of attack, egg gallery length and brood densities for mountain pine beetle and the pine engraver at Saturday Creek, 1994-1995.

Variable	Treatment (T)		Felling (F)		Height (H)		TxF	
	F	P[1]	F	P	F	P	F	P
			Mountain pine beetle					
Attack	0.64	0.54	7.73	0.017	18.50	0.0010	4.40	0.037
Egg Gallery	0.99	0.40	6.39	0.027	10.81	0.0065	1.07	0.37
Brood	0.68	0.51	0.001	0.99	1.61	0.21	2.24	0.13
			Pine engraver					
Attack	1.32	0.30	**0.19**	0.67	3.11	0.10	0.03	0.96
Egg gallery	1.14	0.35	0.54	0.47	2.23	0.16	0.05	0.95
Brood[2]	1.08	0.35	-	-	-	-	-	-

[1] Prob. >F.

[2] Pine engraver adults emerging from duff at bases of treatment trees.

Degrees of freedom: T=2,12; f=1,12; H=1,12; T×F=2,12.

Table A7. Analysis of variance by treatment, felling, height and aspect of response variables for mountain pine beetle and the pine engraver at Saturday Creek, 1994-1995.

Variable	Treatment		Felling (F)		Height (H)		Aspect (A)		FxA		FxH	
	F	P [1]	F	P	F	P	F	P	F	P	F	P
Mountain pine beetle												
Attack	0.49	0.62	8.27	0.0074	3.71	0.066	14.65	0.0006	6.48	0.016	0.11	0.97
Egg gallery	0.42	0.66	2.55	0.12	0.22	0.64	19.42	0.0001	3.07	0.092	4.94	0.016
Brood	0.21	0.81	5.09	0.031	42.43	0.001	6.69	0.015	0.18	0.67	13.86	0.001
Pine engraver												
Attack	8.08	0.002	2.06	0.16	2.31	0.14	2.90	0.10	4.05	0.053	3.69	0.040
Egg gallery	7.53	0.0022	3.24	0.082	7.85	0.010	0.73	0.40	2.21	0.15	0.02	0.90
Brood[2]	4.53	0.019	6.61	0.015	-	-	0.01	0.92	-	-	-	-

[1] Prob. >F.

[2] Adults emerged from duff; duff samples were not taken from felled trees

Degrees of freedom (treatment, error: T=2,30; F=2,30; H=1,30; H=1,24 A=1,30; F*×A=1,30; F×H=1,24.

Table A8. Analysis of variance by treatment, felling, height and aspect of response variables for mountain pine beetle and the pine engraver at the Likely Road, 1994-1995.

Variable	Treatment (T)		Felling (F)		Height (H)		Aspect (A)	
	F	P[1]	F	P	F	P	F	P
Mountain pine beetle								
Attack	1.27	0.31	0.002	0.95	10.16	0.0078	0.17	0.68
Egg gallery	0.14	0.87	0.42	0.53	0.00	0.98	22.77	0.0001
Brood	0.17	**0.84**	3.23	0.086	3.53	0.030	0.33	0.57
Pine engraver								
Attack[2]	-	-	-	-	-	-	-	-
Egg gallery	0.56	0.58	2.19	0.16	0.01	0.91	2.19	0.15`
Brood[3]	5.11	0.0089	-	-	-	-	0.31	0.58

[1] Prob. >F.

[2] Attacks were recorded only for Treatment 1.

[3] Adults emerged from duff at bases of treated trees; duff samples were not taken from felled trees

Degrees of freedom (treatment, error): T=2,12; F=1,12; H=1,30; H=1,24 A=1,24.

Table A9. Analysis of variance by treatment, felling, height and aspect of response variables for mountain pine beetle and the pine engraver at the Likely Road, 1995-1996.

Variable	Treatment (T)		Felling (F)		Height (H)		Aspect x T	
	F	P[1]	F	P	F	P	F	P
Mountain pine beetle								
Attack	2.45	0.10	5.83	0.022	9.12	0.0059	0.32	0.73
Egg gallery	**4.64**	0.017	5.91	0.021	14.67	0.0008	0.71	0.50
Brood	2.07	0.14	0.93	0.34	12.38	0.0018	2.65	0.087
Pine engraver								
Attack	1.53	0.23	2.02	0.16	0.55	0.46	3.85	0.033
Egg gallery	**3.15**	0.057	0.45	0.50	0.35	0.55	1.46	0.24
Brood[2]	**4.81**	0.016	6.70	0.015	-	-	0.11	0.89

[1] Prob. >F.

[2] Adults emerged from duff at bases of treated trees.

Degrees of freedom (treatment, error): T=2,30; F=1,30; H=1,24; A×T=2,30.