The enemy of my enemy is still my enemy: competitors add to predator load of a tree-killing bark beetle

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Abstract
The mountain pine beetle *Dendroctonus ponderosae* is a major tree-killing bark beetle in North America. We evaluated how the subsequent arrival of a competing bark beetle *Ips pini* influences the arrival of predators and their impact on both species. The predators *Temnochila chlorodia* and *Enoclerus sphageus* were strongly attracted to pheromones of *D. ponderosae*. By contrast, *Enoclerus lecontei* was mostly attracted to *I. pini* pheromones. The host compound myrcene synergized attraction of both *D. ponderosae* and *E. sphageus* to the pheromone of *D. ponderosae*. However, it inhibited attraction of both *I. pini* and *E. lecontei* to *I. pini*’s pheromone. *Dendroctonus ponderosae* were more attracted to trees than logs treated with its pheromones, whereas *I. pini* were more attracted to logs than trees treated with its pheromones. Some 78% of *T. chlorodia* were captured at hosts baited with *D. ponderosae* pheromones, whereas 83% of *E. lecontei* were captured at hosts baited with *I. pini* pheromones. We characterized the sequence of arrival to live trees baited with pheromones of *D. ponderosae* as: *D. ponderosae*, *T. chlorodia*, *E. sphageus*, *I. pini*, *E. lecontei*.

Various combinations of *I. pini* and predators were added to logs colonized by *D. ponderosae* in the above sequence of arrival observed in live trees baited with *D. ponderosae* aggregation pheromones. *Ips pini* reduced *D. ponderosae* adult brood production. However, the combination of *I. pini* and *E. lecontei* did not raise *D. ponderosae* brood production above that observed with only *I. pini* present. Similarly, the combination of *I. pini* and *T. chlorodia* did not reduce *D. ponderosae* brood production below that observed with *I. pini* alone. By contrast, the combination of *I. pini*, *T. chlorodia* and *E. lecontei* caused more brood loss to *D. ponderosae* than *I. pini* alone.

*Enoclerus lecontei* did not reduce brood production by *T. chlorodia*, whereas *T. chlorodia* substantially reduced brood production by *E. lecontei*.

Secondary bark beetles that exploit the resource created by primary tree-killing species exert negative effects through both competition and increased predator load. Implications to the population dynamics, ecology and evolution of tree-killing bark beetles are discussed.

Keywords Kairomones, mountain pine beetle, pine engraver, population dynamics, tritrophic interactions.

Introduction
Populations of some bark beetle (Coleoptera: Curculionidae: Scolytinae) species undergo dramatic outbreaks that exert important economic and ecological effects. However, a number of biotic and abiotic factors often constrain bark beetles from developing outbreaks and most generations are spent within an endemic, low-density state (Berryman, 1982; Raffa et al., 2005). Among biotic constraints, the most important factors are tree resistance (Raffa & Berryman, 1983; Franceschi et al., 2005), predation (Reeve, 1997; Turchin et al., 1999) and interspecific competition (Berryman, 1974; Coulson, 1979; Rankin & Borden, 1991).
Predators of bark beetles consist primarily of beetles in the Cleridae, Trogossitidae and Histeridae, and flies in the genus Medetera (Dolichopodidae) (Berryman, 1966; Bickel, 1991; Coulibaly, 1993). Predaceous beetles appear to be particularly important because they attack both the colonizing adults and the developing brood (Reeve, 1997). These predators are highly attracted to the pheromones that bark beetles produce to coordinate mass attacks and overcome tree defences (Dahlsten & Stephen, 1974; Stephen & Dahlsten, 1976; Wood, 1982; Billings & Cameron, 1984; Ross & Daterman, 1995; Zhou et al., 2001; Dahlsten et al., 2004; Fettig & Dabney, 2006). Attraction of predators to bark beetle pheromones has been observed in many systems, and typically lasts several days (Bowers & Borden, 1992; Poland & Borden, 1997; Gaylord et al., 2006; Hulcr et al., 2006). These predaceous beetles are considered habitat specialists but feeding generalists, in that they develop almost exclusively in trees killed by bark beetles, but feed on the diverse guild of insects within this resource (Person, 1940; Berryman, 1966; Erbilgin & Raffa, 2001).

Other species of bark beetles that are more typically associated with dead or severely stressed trees rapidly exploit the resource created by tree-killing species (Safranyik et al., 2000). Most of these beetles also produce aggregation pheromones when colonizing host tissue (Wood, 1982). When colonization by a tree-killing species is followed by a species more commonly associated with dead or severely stressed trees, the terms ‘primary’ and ‘secondary’ are commonly applied to designate this sequence (Amman & Safranyik, 1985; Rankin & Borden, 1991). This nomenclature is adopted in the present study, recognizing that these terms refer to the sequence of cohabitation, and not strict categories. The so-called ‘secondary beetles’ are generally considered more efficient competitors than species that kill vigorous trees (Rankin & Borden, 1991; Safranyik et al., 1996, 2000).

We currently have a limited understanding of how interactions among competitors and predators affect the population dynamics of eruptive bark beetles. In many insect systems, multispecies interactions yield outcomes that would not be predicted based on paired interactions alone (Price, 1997; Losey & Denno, 1998; Venzon et al., 2001; Denno et al., 2002). For example, if a predator preys more heavily on one of two competing species, it can reduce the superior competitors’ impacts on the less consumed species, a relationship termed ‘asymmetric apparent competition’ (Settle & Wilson, 1990; Holt & Lawton, 1994; Holt & Barfield, 2003). It is not known whether such interactions occur among bark beetles and their associates, from either a behavioural or population dynamics perspective.

The mountain pine beetle Dendroctonus ponderosae Hopkins is the major tree-killing bark beetle affecting ponderosa pine Pinus ponderosa and lodgepole pine Pinus contorta in the Rocky Mountains (Logan & Bentz, 1999; Carroll et al., 2004). As with other tree-killing bark beetles, most generations are restricted to stressed trees, a resource that is sparsely distributed and of relatively poor nutritional quality, and in which interspecific competition can be high (Carroll & Safranyik, 2004). During eruptions, however, mountain pine beetle escapes these constraints (Raffa et al., 2008), and can generate positive feedback through its mass attack behaviour. During initial phases of host tree colonization, mountain pine beetle primarily produces the pheromone components exo-brevicomin (Rudinsky et al., 1974) and trans-verbenol (Pitman et al., 1968), which attract both sexes. Attraction to these pheromones is synergized by a host compound, myrcene (Miller & Borden, 2000). Aggregation typically lasts 3–4 days (Wood, 1982; Amman & Cole, 1983).

Among the mountain pine beetle’s competitors is another bark beetle, the pine engraver Ips pini (Say) (Rankin & Borden, 1991; Safranyik et al., 1999, 2000). Extensive colonization by the pine engraver has often been observed in trees attacked by mountain pine beetle (Andrews, 1987; Humphreys & Ferris, 1987; Unger & Stewart, 1987). They partially partition the resource, with the pine engraver mostly colonizing the upper bole, and the mountain pine colonizing the lower (Furniss & Carolin, 1977). However, colonization by the pine engraver has been shown to substantially reduce mountain pine beetle brood survival and replacement rates (Furniss & Carolin, 1977; Amman & Safranyik, 1985; Rankin & Borden, 1991; Safranyik et al., 2000). The pine engraver produces the pheromone ipsdienol that attracts both sexes. In some regions, including Montana, it also produces lanierone, which is not attractive by itself but synergizes its attraction to ipsdienol (Miller et al., 1997; Steed, 2003).

The present study aimed to evaluate how: (i) attraction of a secondary beetle (I. pini) might affect the arrival of predators that also attack the primary tree-killing beetle (D. ponderosae) and (ii) interactions between secondary bark beetles and predators affect the reproductive success of the tree-killing beetle. Specifically, we evaluated the attraction of the three major coleopteran predators of bark beetles in Montana to pheromones of the mountain pine beetle and the pine engraver. We also compared how the overall assemblage varies under dynamic conditions (i.e. when responders to an initial source of volatiles can enter and likewise emit volatiles). Finally, we compared the effects of various combinations of competitors and predators on reproduction by the mountain pine beetle.

Materials and methods

Attraction of predators and bark beetles to synthetic lures

Experiments were conducted in a predominantly ponderosa pine Pinus ponderosa Douglas ex Lawson & C. Lawson forest at the University of Montana Lubrecht Experimental Forest in Greenough, Montana (46°53.30′N, 113°26.00′W). Preliminary assays conducted in 2003 demonstrated that D. ponderosae was present but at relatively low densities, identified the major predators and characterized seasonal flight patterns. Detailed information on the sites can be found at: http://nwmviewogc.cr.usgs.gov/viewer.htm?bbox = -113.555,46.826;113.302,46.965. A behavioural choice assay was conducted in 2004, consisting of six treatments: (i) Control: no lure; (ii) myrcene; (iii) 97% -(−)-ipsdienol and lanierone; (iv) 97% -(−)-ipsdienol,
lanierone plus myrcene; (v) *exo*-brevicomin plus *trans*-verbenol; and (vi) *exo*-brevicomin, *trans*-verbenol plus myrcene. The treatments were arranged in a randomized complete block design (RCBD) consisting of four sites with three blocks per site. Each block contained six twelve-unit multiple funnel traps (Lindgren, 1983) arranged in a line, with the collection cup approximately 75 cm from the ground. Each trap contained one randomly assigned treatment. Spacing was at least 10 m between traps within a block, 100 m between blocks and 500 m between sites. Overall, this yielded 12 replicates per treatment across all sites.

Treatments were placed in the field 9 June and samples were collected at 4-day intervals for 11 weeks ending 23 August. The lures were re-randomized at each sampling period. The lures were removed and replaced with new ones on 18 July to ensure continuous delivery.

All lures were obtained from Pherotech International Inc. (Delta, British Columbia). *Trans*-verbenol (85–95% W/W) was dispensed from polyvinyl bubble-cap lures with a release rate of 2.0 mg/day at 24°C. *Exo*-brevicomin (96–98%, w/w) was dispensed from a 2.5-cm polyurethane flexlure in a PVC sleeve with a release rate of 0.3 mg/day at 20°C. Myrcene (90–92%, w/w) was dispensed from 20-mL low density polyethylene bottles with a release rate of 100 mg/day at 24°C. Ipsdienol and lanierone were formulated in 1,3-butanediol. Ipsdienol (94–97%, w/w) was dispensed from polyvinyl bubble-cap lures with a release rate of 0.2 mg/day at 24°C. The (–) stereoisomer was used because western populations of *I. pini* use this form (Birch et al., 1980). Lanierone (> 95%, w/w) was dispensed from polyvinyl bubble-cap lures with a release rate of 0.02 mg/day at 24°C.

The numbers of *I. pini*, *D. ponderosae* and coleopteran predators captured in traps were recorded. Data were pooled across sampling dates and analyzed according to a RCBD using proc GLM in SAS (SAS Institute, 2003). Data were log(*x* + 1) transformed prior to analyses to reduce heteroscedasticity, and suitability of the resultant models was judged by visual inspection of their residual plots and Levene’s test. Means separation using *t*-tests were performed where significant treatment effects occurred. Untransformed means are presented.

Arrival sequence of bark beetles and predators under dynamic conditions to hosts baited with various pheromones

This experiment was conducted in 2004, in the same general location as the semiochemical attraction tests. It was designed to characterize the arrival sequence and time intervals of bark beetles and coleopteran predators as a dynamic process beginning from various initial conditions.

This experiment included six treatments: (i) *P. ponderosa* log plus three male/female pairs of *I. pini*; (ii) *P. ponderosa* log plus three male/female pairs of *D. ponderosae*; (iii) *P. ponderosa* log plus *I. pini* two-component lure: 97% (−)-ipsdienol plus lanierone; (iv) *P. ponderosa* log plus *D. ponderosae* three-component lure: *trans*-verbenol, *exo*-brevicomin, plus myrcene; (v) living *P. ponderosa* tree plus *I. pini* two-component lure; and (vi) living *P. ponderosa* tree plus *D. ponderosae* three-component lure.

The treatments were arranged in a RCBD of five sites and three blocks per site. Each block contained six treatments, yielding 15 replicates per treatment. Spacing was at least 30 m between treatments, 100 m between blocks and 500 m between sites. Treatments were deployed in the field between 16 and 19 July to coincide with the beginning of the mountain pine beetle’s emergence flight. *Pinus ponderosa* trees approximately 20 cm in diameter at 1.4 m in height were used. For treatments requiring logs, one 16-unit funnel trap (Lindgren, 1983) and one panel trap (IPM Tech, Portland, Oregon) were suspended from ropes stretched over the log at 3.0 m height so that the collection cups were just above the log. The rope was attached to either neighbouring trees or aluminum poles placed in the ground. Treatments were administered the day after trees were felled. Treatments containing beetles received three pairs that were introduced by drilling small holes in the bark and phloem at 2.0, 2.5 and 3.0 m. At each entrance site, we placed one member of the host selecting gender (female: *D. ponderosae*: male: *I. pini*), followed by a mate. A 2 × 2 cm piece of window screening was placed over the hole and sealed with duct tape. For treatments involving standing trees, traps were suspended from ropes stretched between trees so that the collection cups were approximately 75 cm from the ground. Synthetic lures were in place for the first 5 days.

Arrival sequence was monitored by sampling insects collected in traps daily for 10 days. The species and numbers of predators and bark beetles were recorded, and live insects were retained for use in the controlled manipulation experiment. Insects caught in panel and funnel traps were pooled for analyses. Data were also pooled across sampling dates and analyzed according to a RCBD using proc GLM in SAS (SAS Institute, 2003). Data were log(*x* + 1) transformed for analyses. Mean separation using *t*-tests were performed where significant treatment effects occurred. Mean arrival date for each species within treatments was calculated by the equation:

\[
\left( \sum_{t=1}^{10} N_t \right) / N_{\text{total}}
\]

Where *t* is the day after treatment was applied (from 1–10 days), *N* *t* is the number of insects captured on day *t*, and *N* *total* is the total number of insects captured for the treatment.

Reproduction of mountain pine beetle in logs containing varying mixtures of pine engravers and predators

The controlled manipulation experiment consisted of five treatments in *P. ponderosa* logs: (i) *D. ponderosae* alone; (ii) *D. ponderosae* plus *I. pini*; (iii) *D. ponderosae*, *I. pini* plus *Tettnochila chlorodia* (Mannerheim); (iv) *D. ponderosae*, *I. pini* plus *Enoclerus lecontei* (Wolcott); and (v) *D. ponderosae*, *I. pini*, *T. chlorodia* plus *E. lecontei*. Densities of beetles and sex ratios were selected to emulate field conditions: *D. ponderosae*: 68 females/m², 1:1 female:male (Raffa & Berryman, 1983); *I. pini*: 100 males/m², 1:2 male:female.
(Rankin & Borden, 1991). For each predator species, eight individuals were used. At least three females were used in each treatment. The gender of the predators was determined by observing mating. The predator treatments were selected based on the results of preliminary studies conducted in 2003 indicated that three species were the predominant predators, and the two field experiments in 2004 (see Results).

Live uninfested ponderosa pine trees approximately 25 cm in diameter at 1.4 m in height were felled on 28 July and cut into 50-cm sections. Within the next 2 days, the ends were sprayed with 10% sodium hypochlorite solution to prevent microbial contamination. The solution was allowed to dry, and the ends were sealed by dipping them in paraffin wax. Logs were stored indoors under a tarp for approximately 1 week at ambient temperatures (unheated room) to protect them from colonization by wild beetles until they were placed in a rearing chamber. The rearing chambers consisted of 60 × 40.6 cm diameter Fastform (Boyd Lumber & Design Center, Missoula, Montana) cardboard concrete form tubes. The ends were covered with aluminum window screening, which was then covered with opaque black cloth to block light from entering the chamber. A collection cup was fastened to one end of the chamber by cutting the base off of a 473-mL clear plastic cup leaving approximately 5 cm of the top of the cup to be taped with duct tape to a hole cut in the end of the chamber. The cup was then covered with a second intact cup to capture emerging beetles. The cup contained paper tissue that provided a surface on which the beetles could walk. The rearing room was maintained at 18–20°C under 24 h light to promote emergence.

Insects for each treatment were introduced into the rearing chamber over a 9-day period to simulate the arrival sequence that we observed in the treatment emulating D. ponderosae attacking live trees in the arrival sequence experiment. The sequence and number of beetles introduced was: day 1: D. ponderosae females (26); day 2: D. ponderosae males (26); day 4: T. chlorodida (8); day 6: I. pini males (40); day 7: I. pini females (80), and day 9: E. lecontei (8). The beetles were introduced by placing them on a piece of tissue paper and placing the paper on the log within the chamber. The treatments were administered as a completely randomized design with four replications of treatments two to five and five replications of treatment one. Because there were only four replicates for most treatments, no correction for experiment-wide error was used.

The treatments began 5 August and one replicate of each treatment was initiated each day for 4 days. During the insect introductions, the holes for the collection cups were sealed with dark cloth to prevent beetles from escaping by flying towards light. After 1 week, the cloth was removed and the collection cups were monitored every other day for approximately 11 weeks. The logs were then dissected beginning 26 October. The number of adults, immatures, and gallery structures were recorded for each beetle species. Some data were log(x + 1) transformed prior to analyses to reduce heteroscedasticity, and suitability of the resultant models was judged by visual inspection of their residual plots. The numbers of dark and tenereal adults were pooled, and data were analyzed using proc GLM in SAS (SAS Institute, 2003) and mean separation using t-tests were performed where significant differences occurred.

Results

Attraction of predators and bark beetles to synthetic lures

The most common predators were T. chlorodida (819), Enoclerus sphegeus (448) and E. lecontei (280). Temnochila chlorodida had two major peaks, 23–27 June and 14–18 July. Enoclerus sphegeus peaked from 18–27 June. Enoclerus lecontei peaked from 4–7 August.

Overall, E. lecontei was more attracted to the I. pini lure (Fig. 1A), whereas T. chlorodida and E. sphegeus were more attracted to the D. ponderosae lure (Fig. 1B, C). Attraction by E. lecontei to 97%-(-)-ipsdienol plus lanierone was reduced by 42.2% when myrcene was added to this combination. By contrast, its attraction to trans-verbenol plus exo-brevicomin was not affected by myrcene. Enoclerus sphegeus showed the opposite pattern of E. lecontei. Attraction by E. sphegeus to trans-verbenol plus exo-brevicomin increased 24.1% with the addition of myrcene to trans-verbenol plus exo-brevicomin. However, its attraction to ipsdienol plus lanierone was not affected by myrcene. Temnochila chlorodida was not affected by the presence of myrcene. No predators were attracted to myrcene alone.

A total of 2320 D. ponderosae and 2849 I. pini were captured. As expected, D. ponderosae was attracted to trans-verbenol plus exo-brevicomin plus myrcene and I. pini was attracted to ipsdienol plus lanierone. Their responses to the host compound myrcene were markedly different. Addition of myrcene increased the attraction of D. ponderosae to its pheromone by 78.1%, whereas it reduced the attraction of I. pini to its pheromone by 96.3% (Fig. 2).

Arrival sequence of bark beetles and predators under dynamic conditions to hosts baited with various pheromones

Results from the field experiment in which various sources of beetle pheromones were applied to logs or trees, and arriving insects could generate additional sources of attraction, are shown in Tables 1 and 2. A total of 1555 D. ponderosae, 11957 I. pini, 328 E. lecontei, 274 E. sphegeus and 211 T. chlorodida were captured. The number of arriving I. pini was 18.2-fold higher when its lures were attached to logs rather than to trees (Table 1). By contrast, the number of D. ponderosae was 1.9-fold higher when its lures were attached to trees rather than to logs. Enoclerus lecontei was most attracted to logs baited with I. pini lures, and in particular was 22.1-fold more attracted to logs baited with I. pini lures than to trees baited with I. pini lures. Enoclerus sphegeus likewise was most attracted to logs baited with I. pini lures. By contrast, the highest number of T. chlorodida arrived at trees and logs that had been baited with D. ponderosae lures.

The various bark beetle and predator species showed distinct patterns of arrival with each treatment (Table 2). Ips pini arrived at logs with D. ponderosae lures at a mean of 4.3 days and a peak at 2 days, whereas it did not arrive at trees with the same treatment until after a mean 7 days and a peak of
Competitors add to predator load

8 days. Dendroctonus ponderosae generally arrived more quickly than *I. pini*, but showed little variation among treatments. *Enoclerus lecontei* arrived more rapidly to trees with *I. pini* than *D. ponderosae* lures, but equally to logs with these sources, apparently responding to the early arrival of *I. pini* to logs. *Temnochila chlorodia* generally arrived more quickly to sources that included either *D. ponderosae* or trees than *I. pini* or logs. All logs were eventually colonized by *I. pini*. All trees were attacked by *D. ponderosae* but not in numbers required to kill the tree.

The sequence of arrival to *D. ponderosae* pheromones on a live tree was: (i) *D. ponderosae*, which peaked on day 2 post-placement of pheromones with a mean arrival date of 3.8 days; (ii) *T. chlorodia*, which peaked on day 2 with a mean arrival date of 4.3 days; (iii) *E. sphegeus*, which peaked on day 5 with a mean arrival date of 5.4 days; (iv) *I. pini*, which peaked on day 8 with a mean arrival date of 7.0 days; and (v) *E. lecontei*, which peaked on day 8 with a mean arrival date of 7.5 days. This sequence was used to guide the introduction sequence in the controlled manipulation experiment.
Reproduction of mountain pine beetle in logs containing varying mixtures of pine engravers and predators

In the controlled manipulation assay, the total number of brood adult *D. ponderosae* was reduced by the addition of *I. pini*, either predator alone with *I. pini*, and by both predators with *I. pini* (Fig. 3). The interspecific competition effect due to the presence of *I. pini* reduced the number of *D. ponderosae* adults by approximately 22.2%. The addition of both *I. pini* and the predator attracted to *D. ponderosa*, *T. chlorodia*, reduced the adult brood production of *D. ponderosae* by 25.8%, relative to when *D. ponderosae* developed alone. The combination of *I. pini* and the predator responding to pheromones of *I. pini*, *E. lecontei*, did not raise reproduction of *D. ponderosae*, but rather resulted in the same reduction as *I. pini* alone or *I. pini* plus *T. chlorodia*. By contrast, the addition of *E. lecontei* to the combination of *I. pini* and *T. chlorodia* was the only treatment that reduced *D. ponderosae* reproduction below that resulting from the competitive effect of *I. pini*. Logs with *T. chlorodia*, *E. lecontei* and *I. pini* yielded 32.5% fewer *D. ponderosae* adults than did those with *D. ponderosae* alone, and 15.7% fewer than with *D. ponderosae* plus *I. pini*. This reduction in the replacement rate of *D. ponderosae* was largely cumulative across stages, but appeared to result mostly from mortality during the transition from pupal to adult stages (Table 3).

*Ips pini* also showed significant responses to predator treatments. Production of brood adults was reduced more by *E. lecontei* than *T. chlorodia*, and most strongly by the combination (Table 3). The greatest impact occurred during establishment of ovipositional galleries, which were reduced by 72% when both predators were present compared with when both were absent. Additional reduction due to predators occurred in larval galleries, pupal chambers, pupae, tentorial adults and hardened adults.

### Table 1 Response (mean ± SE) of bark beetles and predators to host plants treated with various sources of beetle pheromones in western Montana, 2004

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ips pini</th>
<th><em>Dendroctonus ponderosae</em></th>
<th><em>Enoclerus lecontei</em></th>
<th><em>Enoclerus sphageus</em></th>
<th><em>Temnochila chlorodia</em></th>
<th>Total predators</th>
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<tr>
<td>Log + <em>Ips pini</em> beetles</td>
<td>66.6 ± 21.65&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.33 ± 0.48&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2.2 ± 0.98&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.9 ± 0.27&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>1.5 ± 0.58&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>4.5 ± 1.15&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Log + <em>Dendroctonus ponderosae</em> beetles</td>
<td>1.8 ± 0.63&lt;sup&gt;c&lt;/sup&gt;</td>
<td>6.33 ± 1.56&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.0 ± 0.39&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.5 ± 0.22&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.3 ± 0.61&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>2.9 ± 0.99&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Log + <em>Ips pini</em> lures</td>
<td>676.7 ± 75.17&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.2 ± 0.90&lt;sup&gt;d&lt;/sup&gt;</td>
<td>14.7 ± 1.67&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.9 ± 5.20&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.1 ± 0.68&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>26.7 ± 6.77&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>Log + <em>Dendroctonus ponderosae</em> lures</td>
<td>7.5 ± 3.25&lt;sup&gt;c&lt;/sup&gt;</td>
<td>30.0 ± 5.45&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.2 ± 0.58&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>3.7 ± 1.61&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.1 ± 1.07&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>9.0 ± 2.21&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td>Tree + <em>Ips pini</em> lures</td>
<td>37.2 ± 9.67&lt;sup&gt;b&lt;/sup&gt;</td>
<td>5.67 ± 2.52&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0.7 ± 0.33&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.3 ± 0.16&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.4 ± 0.19&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>1.4 ± 0.43&lt;sup&gt;d&lt;/sup&gt;</td>
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<tr>
<td>Tree + <em>Dendroctonus ponderosae</em> lures</td>
<td>7.4 ± 4.46&lt;sup&gt;c&lt;/sup&gt;</td>
<td>58.1 ± 7.04&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.1 ± 0.73&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2.9 ± 8.56&lt;sup&gt;b&lt;/sup&gt;</td>
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<th><em>F</em>&lt;sub&gt;.78&lt;/sub&gt;</th>
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<td>39.25</td>
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Means within a column followed by different superscript letters are significantly different (*p < 0.05*).
Table 2 Arrival sequence of bark beetles and predators, expressed as days after treatment applied

<table>
<thead>
<tr>
<th>Species</th>
<th>Peak</th>
<th>Mean</th>
<th>Peak</th>
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<tr>
<td>Log + Ips pini beetles</td>
<td>2</td>
<td>4.13</td>
<td>5</td>
<td>4.21</td>
<td>2</td>
<td>4.58</td>
<td>2</td>
<td>4.08</td>
<td>9</td>
<td>6.35</td>
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<td>Log + Dendroctonus</td>
<td>1</td>
<td>2.89</td>
<td>2</td>
<td>2.32</td>
<td>2</td>
<td>3.73</td>
<td>7</td>
<td>6.38</td>
<td>8</td>
<td>5.55</td>
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<tr>
<td>Log + Ips pini lures</td>
<td>2</td>
<td>4.75</td>
<td>2</td>
<td>2.72</td>
<td>8</td>
<td>5.23</td>
<td>9</td>
<td>6.30</td>
<td>9</td>
<td>7.81</td>
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<tr>
<td>Log + Dendroctonus</td>
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<td>4.29</td>
<td>2</td>
<td>3.00</td>
<td>5</td>
<td>4.22</td>
<td>2</td>
<td>5.50</td>
<td>2</td>
<td>3.95</td>
</tr>
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<tr>
<td>Tree + Ips pini lures</td>
<td>3</td>
<td>4.63</td>
<td>2</td>
<td>2.26</td>
<td>2</td>
<td>3.00</td>
<td>1</td>
<td>4.40</td>
<td>1</td>
<td>4.00</td>
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<tr>
<td>Tree + Dendroctonus</td>
<td>8</td>
<td>7.02</td>
<td>2</td>
<td>3.76</td>
<td>8</td>
<td>7.45</td>
<td>5</td>
<td>5.39</td>
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<td>4.29</td>
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</table>

Predator reproduction also varied among treatments (Table 3). Enoclerus lecontei and T. chlorodia performed equally well when introduced alone. Addition of E. lecontei did not reduce brood production by T. chlorodia. By contrast, T. chlorodia reduced brood production of E. lecontei by 68%.

Discussion

Exploitation of trees killed by D. ponderosae by I. pini appears to add to the predator load experienced by D. ponderosae. The chemical signals produced by I. pini are highly attractive to E. lecontei, which otherwise might not locate and predate on D. ponderosae to the extent observed. Overall, 65% of the E. lecontei that arrived were in traps containing ipsdienol (Fig. 1). Moreover, the later arrival of pine engravers to trees (Table 2), and its longer flight season (Rankin & Borden, 1991; Safranyik et al., 1996, 2000), can extend the period during which trees colonized by mountain pine beetle are attractive to predators. Mountain pine beetle brood require a full season or more to develop under natural conditions, and hence are susceptible to predators that track the pheromones of I. pini, which often arrives substantially after D. ponderosae has ceased producing pheromones (Rankin & Borden, 1991; Safranyik et al., 1999).

The additional predators recruited by I. pini reduce reproduction by D. ponderosae. Overall, I. pini reduced D. ponderosae reproduction by approximately 22.2% due to competition, and an additional 12.5% due to competitor–predator interactions. This interaction of predators and competitors supports the rationale of Safranyik et al. (1996) for considering manipulation of I. pini as a tactic for reducing D. ponderosae reproduction.

Direct and indirect effects of competitors appear to be more severe on D. ponderosae when it colonizes dead rather than live hosts. For example, I. pini arrived only 1.3 days after D. ponderosae on logs baited with D. ponderosae pheromones, compared with 3.3 days after D. ponderosae in trees (Table 2). Likewise, E. lecontei arrived only 1.2 days after D. ponderosae in logs, compared with 3.7 days after D. ponderosae in live trees. Furthermore, the total number of predators per D. ponderosae was 0.30 in logs, compared with only 0.17 in trees (Table 1). Predator load can be an important factor in whether species such as D. ponderosae surpass the eruptive threshold beyond which they generate self-amplifying dynamics.

Figure 3 Emergence of adult Dendroctonus ponderosae from Pinus ponderosa logs containing various treatments of Ips pini, Temnochila chlorodia and Enoclerus lecontei ($F_{4,12} = 13.17$, $P = 0.0002$). Means with the same letter are not significantly different ($\alpha = 0.05$).
Table 3 Mean ± SE of various life stages of bark beetles and predators in the presence of competitors and/or predators in western Montana, 2004

<table>
<thead>
<tr>
<th>Variable</th>
<th>Dendroctonus ponderosae alone</th>
<th>+ Ips pini</th>
<th>+ Temnochila chlorodia</th>
<th>+ Enoclerus lecontei</th>
<th>+ Enoclerus lecontei</th>
<th>F_{4,12}</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovipositional galleries</td>
<td>20.40 ± 1.29</td>
<td>15.00 ± 1.47</td>
<td>16.75 ± 1.65</td>
<td>16.75 ± 1.38</td>
<td>14.50 ± 2.02</td>
<td>1.74</td>
<td>0.205</td>
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<tr>
<td>Gallery length (cm)</td>
<td>532.6 ± 25.4</td>
<td>524.6 ± 40.6</td>
<td>540.5 ± 41.2</td>
<td>509.8 ± 27.9</td>
<td>522.6 ± 67.6</td>
<td>0.12</td>
<td>0.972</td>
</tr>
<tr>
<td>Pupae chambers</td>
<td>334.6 ± 14.6</td>
<td>274.0 ± 12.4</td>
<td>257.8 ± 25.4</td>
<td>347.3 ± 25.3</td>
<td>317.3 ± 11.4</td>
<td>2.56</td>
<td>0.093</td>
</tr>
<tr>
<td>Larvae</td>
<td>79.4 ± 12.9</td>
<td>53.0 ± 4.26</td>
<td>46.25 ± 6.38</td>
<td>64.5 ± 6.55</td>
<td>59.3 ± 10.3</td>
<td>1.72</td>
<td>0.210</td>
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<tr>
<td>Pupae</td>
<td>82.4 ± 7.43</td>
<td>70.0 ± 1.58</td>
<td>68.75 ± 7.79</td>
<td>77.5 ± 7.08</td>
<td>65.3 ± 19.9</td>
<td>0.38</td>
<td>0.819</td>
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<tr>
<td>Teneral adults</td>
<td>121.6 ± 5.42</td>
<td>103.0 ± 6.52</td>
<td>91.5 ± 4.11</td>
<td>88.25 ± 2.84</td>
<td>79.8 ± 10.7</td>
<td>4.27</td>
<td>0.022</td>
</tr>
<tr>
<td>Hardened adults</td>
<td>109.4 ± 9.88</td>
<td>82.0 ± 6.87</td>
<td>80.0 ± 2.48</td>
<td>85.25 ± 5.2</td>
<td>76.25 ± 3.47</td>
<td>6.96</td>
<td>0.004</td>
</tr>
</tbody>
</table>

Means followed by a different superscript letter within a row are significantly different (α = 0.05).

(Reeve, 1997; Turchin et al., 1999; Raffa et al., 2005). The combined direct competitive effects and indirect predator-attracting effects of *I. pini* on *D. ponderosae* reproduction (Fig. 3) support the view that the tree-killing strategy in bark beetles evolved in part as an escape from competition (Raffa & Berryman, 1987; Rankin & Borden, 1991; Raffa et al., 1993). That is, poorly defended trees reduce risks associated with colonization, but can increase risks to competitors and their associates.

These results yield further insights into how predators exploit pheromones and host tree volatiles associated with bark beetles. The host monoterpenic myrcene strongly synergized the attraction of mountain pine beetle to its pheromones (Miller & Borden, 2000), but strongly inhibited attraction of *I. pini* to its pheromones. Predators tended to respond accordingly. That is, attraction of *E. sphægus* to the pheromone of *D. ponderosae* was synergized by myrcene, but its attraction to the pheromones of *I. pini* was unaffected. Likewise, attraction of *E. lecontei* to pheromones of *I. pini* was reduced by myrcene, but its attraction to pheromones of *D. ponderosae* was unaffected. Predators use of host plant volatiles to track bark beetle pheromones (Erbilgin & Raffa, 2000, 2001) may be advantageous when the prey modifies enantiomeric ratios and synergists (Aukema et al., 2000; Dahlsten et al., 2003).

These results also suggest that predators of secondary bark beetles face risks arising from predators of the tree-killing beetle. *Enoclerus lecontei* experienced substantially lower reproduction in the presence of *T. chlorodia*, due to competition, intraguild predation, or both. Evidence of intraguild predation (i.e. partially consumed *E. lecontei*) was observed when logs were dissected, but it is unknown when this occurred or which species consumed them. This unidirectional relationship is likely due to the earlier introduction of *T. chlorodia* in our laboratory manipulations, that likewise emulated the earlier arrival of *T. chlorodia* in the sequential arrival experiment (Table 2), and its attraction to *D. ponderosae* pheromones (Fig. 1) in the field. Selective pressures resulting from the sequence of arrival could partially explain why *E. lecontei* prefers logs to trees with *I. pini* lures when given a choice (Table 1). In logs, there were only 0.15 *T. chlorodia* per *E. lecontei* but, in trees, this rose to 0.57.

The mechanism by which *I. pini* locates trees colonized by *D. ponderosae* is not known (Amman & Safranyik, 1985;
Rankin & Borden, 1991; Safranyik et al., 2000). We did not find evidence for attraction to pheromones of *D. ponderosae* (Fig. 2). Post-landing detection of chemical cues associated with weakened trees is known to be an important component of host selection by *I. pini* (Klepzig et al., 1996; Wallin & Raffa, 2000), and so may be involved in detecting trees successfully attacked by *D. ponderosae*.

We currently have little data on how competitors and predators interact with important abiotic factors such as temperature to affect bark beetle populations. However, the available information suggests they may be augmentative. *Dendroctonus ponderosae* has a facultative diapause, requiring 1 year for development under warm conditions but 2 years under cooler conditions (Bentz & Mullins, 1999; Bentz et al., 2001). In cases with semivoltinism, trees containing *D. ponderosae* brood can be colonized by *I. pini* not only during the year of attack, but also the next year (Rankin & Borden, 1991; Safranyik et al., 1999), thus adding further to the predator load of *D. ponderosae*. However, with recent warming trends, *D. ponderosae* is now univoltine in many regions with historically semivoltine development (Carroll et al., 2004; Hicke et al., 2006). In some of these areas, the mountain pine beetle is now causing unprecedented levels of mortality. A shortened window of opportunity for predators responding to secondary beetles could potentially benefit *D. ponderosae* survival by adding to the effects of reduced freezing mortality and accelerated development in temperature-driven population releases (Bentz & Mullins, 1999; Hicke et al., 2006).

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**References**


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Competition add to predator load

(Coleoptera: Cleridae) to traps with different semiochemicals. *Journal of Economic Entomology*, **88**, 106–111.


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