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Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera: Scolytidae)

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Abstract The bark beetles *Ips pini*, *I. perroti*, and *I. grandicollis* are sympatric in pine forests of the north-central United States. They share the same limited phloem resource and often coexist within the same host trees. We tested whether phloem resources are partitioned in time and space by measuring spatial and seasonal colonization of logs. Differences among species in flight phenology, development time, voltinism, and spatial colonization patterns within logs reduce, but do not eliminate, species overlap. The bark beetle species share predation by *Thanasimus dubius* (Cleridae) and *Platysoma cylindrica* (Histeridae), which exploit pheromone signals for prey location. We employed pheromone traps to test for chemical communication among bark beetle species. Heterospecific signals tend to be deterrents when they are added to conspecific signals but attractants when they are alone, indicating that the communication system can both reduce and increase species overlap in resource use depending upon relative abundance of the species. Deterrence by heterospecific signals is probably a result of selection for minimizing interspecific competition. However, individuals may sometimes benefit from joining aggregations of other species because of (1) predator swamping, (2) improved success in attacking live trees, and (3) location of suitable, recently dead, trees. These benefits should be greatest for males (which locate and colonize host trees before signalling females) and indeed

males tended to be more attracted than females by heterospecific signals. Shared resources, shared predators, and heterospecific pheromone communication all contribute to species interactions in this guild of bark beetles, but predicting whether the removal of one species will tend to increase or decrease the abundance of remaining species remains difficult. Species interactions are likely conditional and coexistence is probably promoted by benefits to rare species of multispecies associations.

Keywords Interspecific competition · Pheromones · Conditional interactions · Chemical communication · Information theory

Introduction

In forests throughout the world, bark beetles (Coleoptera: Scolytidae) lie at the center of complex communities that exploit the resources provided by dead and dying trees (Saveley 1939; Howden and Vogt 1951; Moser et al. 1971; Dajoz 1974; Wood 1982a; Herard and Mercadier 1996; Kaila et al. 1997; Amezaga and Rodriguez 1998). Multiple species of bark beetles frequently live and feed within the phloem of trees (Reid 1955; Birch et al. 1980; Paine et al. 1981; Flamm et al. 1987, 1989; Smith et al. 1990). Multispecies aggregations can be structured by airborne host volatiles and by insect pheromones (Birch 1978; Svirha et al. 1980; Wood 1982a; Savoie et al. 1998) which can convey multiple species-specific messages (Blum 1996). Interspecific responses to pheromones range from strong deterrence (Lanier and Wood 1975; Byers and Wood 1980; Borden et al. 1992; Miller and Borden 1992), suggesting an antagonistic relationship, to strong attraction (Hedden et al. 1976; Cane et al. 1990), which suggests the potential for mutualism (Svirha et al. 1980; Smith et al. 1990). Suitable phloem is frequently a limited resource for bark beetles (Berryman 1973; Anderbrandt et al. 1985) and competition among bark beetles can limit parental fecun-

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dity and reduce the survival and fecundity of progeny (Light et al. 1983; Kirkendall 1989; Rankin and Borden 1991; Gara et al. 1995; Robins and Reid 1997). However, offsetting benefits of interspecific attraction could accrue from increased success in mass attacks of trees, exploiting host material located by other species (De Jong and Sabelis 1988), or predator swamping.

Ips pini (Say) (Coleoptera: Scolytidae) occurs throughout pine forests of temperate North America. In Wisconsin, *Ips pini* coexists with *I. grandicollis* (Eichhoff) and *I. perroti* (Swaine). These three species can be found in mixed assemblages feeding on the same phloem resource within the same region of the tree bole. *I. pini* produces the pheromone ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol; Stewart 1975; Lanier et al. 1980), and the attractant synergist lanierone (Teale et al. 1991), which function in aggregation and mate attraction. *I. grandicollis* produces and is attracted to the related compound ipsenol (2-methyl-6-methylene-7-octen-4-ol; Vité and Renwick 1971). Pheromone production of *I. perroti* was analyzed as part of this study. Of the three species, *I. pini* is most frequently implicated in pine tree mortality (Sartwell et al. 1971; Goulding et al. 1988) but we have also observed *I. grandicollis* and *I. perroti* participating in attacks of live trees.

We conducted experiments to determine how these three species of *Ips* maintain sympatry while apparently sharing a single limited food resource and habitat. We tested for phenological and spatial segregation within and among trees, and evaluated whether semiochemical interactions promoted or reduced resource overlap. The absence of mechanisms for avoiding interspecific competition could imply that the species assemblage is unstable or that the species accrue benefits from association that offset the costs of competition. Determining whether these species interactions are antagonistic or beneficial is of considerable importance to forest managers who need to judge whether particular species should be considered pests or biological controls on congeneric species that are pests.

Materials and methods

Field experiments were conducted in pure red pine (*Pinus resinosa*) plantations in Dunn County, west central Wisconsin, USA. All study sites were planted between 1957 and 1967, had been thinned within the last 5 years, and were being maintained at a basal area of 27–46 m² ha⁻¹. All plantations had little or no undergrowth, and study sites were selected to avoid what little there was.

Pheromone production of *I. perroti*

I. perroti was collected in Dunn County, Wisconsin, in early May 1995. Because preliminary studies indicated that this species was attracted to the combination of ipsenol and ipsdienol, beetles were caught in Lindgren funnel traps baited with commercial formulations of both compounds (Phero Tech, Delta, Canada). After capture, 120 male beetles were placed on damp paper towelling and shipped overnight to Syracuse, N.Y. Volatiles were collected by

aerating a pooled sample of males feeding on red pine for 5 days (Teale et al. 1991). The adsorbent was extracted daily. A coupled gas chromatograph-mass spectrometer (Hewlett Packard models 5890 and 5971) fitted with a 30-m HP-Wax column was used to identify and quantify the components. The GC conditions were 0.5 min splitless injection at 209°C, oven 40°C for 1 min, ramp 5°C min⁻¹, 20 min at 210°C. The ipsdienol enantiomeric composition of individual males was determined by solvent extraction of frass followed by chiral GC-MS (Teale et al. 1994; Hager and Teale 1996).

Flight phenology and seasonal abundance

In 1994 and 1995, we used three-trap arrays of Lindgren funnel traps to assay the flight phenology, relative abundance, and pheromone preferences of wild insects. Within each array, traps were hung 2 m aboveground and configured as an equilateral triangle 20 m each side. Each array contained one trap baited with each of three pheromone lures: ipsdienol, ipsenol, or ipsdienol plus ipsenol. The ipsdienol was a 50% (+):50% (-) enantiomeric blend, which approximates the preferred blend for this population of *I. pini* (Herms et al. 1991; Seybold et al. 1995a). The pheromone lures were 20-mg bubblecaps with elution rates of 0.2 mg day⁻¹ (Phero Tech). In 1994, we used one three-trap array. In 1995, we repeated the trial with eight three-trap arrays: two in each of four plantations. Plantations were separated by 10–15 km. Arrays within plantations were separated by 200 m. Traps were emptied weekly from 15 April–15 October. The position of pheromone lures within trap arrays was rotated weekly to guard against spurious spatial effects. In two of the plantations, lanierone was added (elution rate 0.01 mg day⁻¹) to the ipsdienol and the ipsdienol+ipsenol lures at one array. The lanierone was alternated weekly between the two arrays within those plantations. No lanierone was used at the other two plantations.

A small parallel study was conducted in two pine plantations in west-central New Hampshire, USA, to test for regional stability in the interspecific patterns of pheromone preferences. From May–October 1995, we sampled *Ips* pheromone preferences with one three-trap array in each of two pine plantations separated by 2 km. Array configurations and sampling protocols were as in Wisconsin. Traps within each array were baited with either ipsdienol, ipsenol, or ipsdienol+ipsenol.

From 1989–1995, 5–18 funnel traps baited with 20-mg ipsdienol bubblecaps (elution rates of 0.2 mg day⁻¹) were emptied weekly from spring snow melt to the first snowfall. All scolytids and coleopteran predators were counted and identified. Daily high and low air temperatures were recorded from on-site thermometers.

Development time

Freshly cut logs and emergence traps were used to compare generation times of the three *Ips* species under ambient field temperatures. On 16 May 1995, we induced synchronous colonization of 12 logs (0.5 m in length, 15–17 cm in diameter) by wrapping each log with screen to enclose 25–50 adults of either *I. pini*, *I. perroti*, or *I. grandicollis* (four logs per species). Logs were cut from mid bole of four codominant trees (three sequential logs from each tree starting 1 m aboveground) selected for uniform size and thick phloem. Bolts from all trees were mixed and then randomly assigned to species. Insects were taken from pheromone traps that day. Insects were not sexed, but concurrent pheromone captures showed a significant male bias (431 vs 272 for *I. pini*; 1,844 vs 226 for *I. perroti*; *I. grandicollis* not sexed) which assured that female oviposition would not be limited by availability of mates. Seven days after colonization, the screen was removed and logs were placed in emergence traps (20-cm diameter PVC tubing with four mesh-covered holes, 100 mm diameter, to provide air circulation). All traps from all sites were hung under a rain shelter in one of the study plantations. Insects emerging from the bolts were removed

and counted twice weekly. After 92 days, when emergence had largely ceased, the bark was peeled from all bolts to count living, unemerged *Ips*.

We compared development time of the three *Ips* species in the laboratory at 25°C by introducing adults into sections of fresh phloem (6×25 cm) sandwiched within plexiglass (Schmitz 1972) and monitoring the development of their progeny. Bark and phloem were peeled from freshly cut red pine logs. We introduced one adult male into each of three 3-mm holes in the plexiglass of each sandwich (four to ten sandwiches per species). After 24 h, two females were placed with each male that had begun a nuptial burrow. Each resulting progeny was individually monitored every 24 h through hatching, larval development, and pupation.

The egg volume for each species was estimated using a microscope micrometer (± 0.01 mm) to measure the length and width of 16–79 eggs from 6–24 mothers from each species (assuming a prolate spheroid). A subset of 20 eggs were measured, dried and individually weighed to allow a conversion to dry mass. Average adult dry mass was estimated from 30–40 adults per species.

Species associations

We tested for natural spatial separation of *Ips* species within entire felled trees. On 14 May 1994, we cut down seven red pines and mapped the subsequent colonization of logs by *Ips*. All trees were 13–18 m tall, 15–22 cm diameter at 1 m, and separated from the closest felled tree by 30–100 m. After 2 weeks, and at 3-day intervals for the next 2 weeks, *Ips* colonization galleries were counted and mapped on each tree. One month after felling, three 1-m-long sections were cut from each tree, one within 1 m of the butt, one just above the first live branch, and the third from midway between. The bark was peeled from these sections, and the colonizers identified. On 8 June, seven more trees were felled, and on 25 July, five galleries within each of three regions (butt, lower crown, and midpoint) on each tree were sampled.

We tested for spatial separation of *Ips* species among logs. Between 5 May and 6 July 1995, we peeled the bark from 61 logs that had been naturally colonized by *Ips* and determined the species occupying each gallery. All logs were 0.5–1.0 m long, 10–30 cm diameter, and separated from the nearest such log by >20 m.

Analyses

We compared the flight phenology of species with χ^2 -tests of the null hypothesis that equal proportions of each species would be captured each month. We used a one-way ANOVA to test for differences among species in egg development, larval development, pupation time, and adult mass, and a nested ANOVA to test for differences in egg volume among species and among individual mothers within species. Spatial patterns of colonization within felled trees were evaluated with (1) a general linear model that included tree as a class variable and distance from butt as a continuous variable and (2) a χ^2 -test of the hypothesis that equal proportions of all species occupied the butt, mid tree, and lower live crown regions of the bole. We evaluated species associations among logs with a *G*-test based on the null hypothesis that occupancy of a log by one species was independent of occupancy by other species.

Contingency analyses (CATMOD procedure; SAS 1990) were used to compare pheromone preferences of the three *Ips* species and to test for effects of season, lanierone, and sex on pheromone preferences. For each main effect and interaction, the null hypothesis was that the source had no effect on the proportion of beetles captured with ipsdienol versus ipsenol versus ipsdienol+ipenol. By design and necessity, the experiment was a partial factorial (because the effects of lanierone were only tested in two of the four pine plantations, and because it was impractical to sex one of the species, *I. grandicollis*). Consequently, we developed orthogonal contrasts to test each hypothesis for main effects and interac-

tions using the most data that could be applied while still retaining a balanced design structure. This involved four different statistical models. In model 1, we tested for differences among the three *Ips* species, effects of season (spring=1 May–14 June, mid summer=16 June–31 July, late summer=1 August–9 October), and species×season interactions ($n_{\text{total}}=6,619$ *Ips* captured in six three-trap arrays within four plantations; trap arrays with lanierone were excluded). In model 2, we tested for effects of lanierone and interactions of lanierone with season and species ($n_{\text{total}}=6,233$ *Ips* captured in four trap arrays within two plantations; two plantations without lanierone were excluded). In model 3, we tested for effects of sex, and interactions of sex with season and species ($n_{\text{total}}=5,784$ *Ips* captured in six trap arrays within four plantations; *I. grandicollis* and trap arrays with lanierone were excluded). In model 4, we tested for interacting effects of sex and lanierone ($n_{\text{total}}=5,926$ *Ips* captured in four trap arrays within two plantations; *I. grandicollis* and plantations without lanierone were excluded). This family of tests was controlled for experimentwise error with the Dunn-Šidák adjustment (Sokal and Rohlf 1995).

Results suggested that interspecific effects of one pheromone could depend upon other signals within the same pheromone plume (from other *Ips* species that might or might not be colonizing the same log). We summarized the response of each species to heterospecific pheromone signals as

$$R = \frac{N_{\text{with}} - N_{\text{without}}}{N_{\text{conspecific}}} \times 100 \quad (1)$$

where R =beetle response, N_{with} =number of captures with the heterospecific signal, N_{without} =number of captures without the heterospecific signal, and $N_{\text{conspecific}}$ =number of captures with conspecific signal alone. R can range from –100%, indicating high deterrence, to 0, indicating no effect, to 100%, indicating high attraction. This parameter is similar to that suggested by Lanier and Wood (1975) but more readily accounts for the possibility of both attraction and deterrence. For each species, R was calculated for each possible combination of heterospecific pheromones in both the presence and absence of the conspecific pheromones (values for N_{with} and N_{without} were either with or without the conspecific signal). Because we had not anticipated that a parameter such as R would be required, the present research lacked a treatment with unbaited funnel traps (the basis for calculating N_{without} in the absence of conspecific signals). However, we know from previous sampling at the same sites that *Ips* captures in unbaited traps are very rare (9 captures of *I. pini* in unbaited traps vs 1,289 captures in paired traps baited with racemic ipsdienol; Herms et al. 1991). So, for the purposes of calculating R in the absence of conspecific signals, we used this result (9 vs 1,289) to estimate expected captures in unbaited traps. We used χ^2 statistics to evaluate departures from the null hypothesis of no effect on captures of adding a heterospecific signal ($R=0$). Tests for effects of heterospecific signals in the absence of conspecific signals were approximate because they depended on previously collected data and, in the case of *I. perroti* and *I. grandicollis*, assumed that these species have the same probability as *I. pini* of being captured in unbaited traps. All other tests were statistically rigorous in being based on planned comparisons of treatment combinations within the present data. For each *Ips* species, we controlled for experimentwise error in the family of tests regarding responses to heterospecific pheromone signals (Dunn-Šidák adjustment; Sokal and Rohlf 1995).

Results

Pheromone production of *I. perroti*

Of the 120 male beetles introduced to the red pine billet, 97 successfully bored in and excavated mating galleries. The average production of ipsenol was 4.7 $\mu\text{g male}^{-1} \text{day}^{-1}$ (range=3.3–7.6) and of ipsdienol was 1.0 $\mu\text{g male}^{-1} \text{day}^{-1}$ (range=0.7–1.7). The ipsenol:ipsdienol ra-

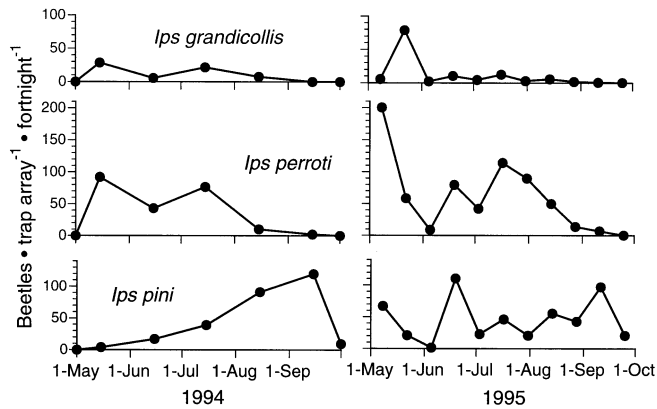


Fig. 1 Seasonal captures at pheromone baited funnel traps of *Ips grandicollis*, *I. perroti*, and *I. pini* in 1994 and 1995

tio increased from 3.9:1 on day 1 to 5.3:1 on day 5 and increased each day except for day 3 which was unchanged from day 2. The average enantiomeric composition of ipsdienol (\pm SE) was $11.6 \pm 1.7\%$ *R*-(-)-ipsdienol and ranged from 4.4 to 21.0% *R*-(-)-ipsdienol ($n=13$).

Flight phenology and seasonal abundance

Funnel traps captured a total of 1,133 *Ips* in 1994 and 10,350 in 1995 (Fig. 1). Of these, *I. pini*, *I. perroti*, and *I. grandicollis* constituted 49, 40 and 11%, respectively in 1994, and 39, 51, and 10%, respectively, in 1995. The phenological pattern varied among species (Fig. 1; $\chi^2=638.37$ for 1994 and 2,379.95 for 1995, $P<0.0001$, $df=8$ for both years). In both years *I. grandicollis* and *I. perroti* were most abundant in May but showed second peaks in July. Within this spring flight, *I. perroti* and *I. pini* tended to fly earliest, with high captures in the first week of May followed by 4 weeks of decline. In contrast, *I. grandicollis* captures were low until the third week of May, but 63% of total annual captures occurred in the next 2 weeks. Adult activity of all three species declined following the spring flight (minimum during the second week of June). Thereafter, the abundance of *I. grandicollis* adults remained low but measurable through September. The abundance of *I. perroti* rebounded in July to levels near those of the spring flight, but then declined throughout the remainder of the summer. In contrast, the abundance of *I. pini* adults remained quite stable from May through August and peaked in September.

Seven species of predator were captured in 1989–1995, five of Cleridae and two of Histeridae, but only one species from each family was abundant. In 1995, we captured 492 *Thanasimus dubius* (Cleridae) and 501 *Platysoma (= Cylistix) cylindrica* (Histeridae). The peak flights of both predators tended to occur in June, but in some years they were also abundant later in the summer (Fig. 2).

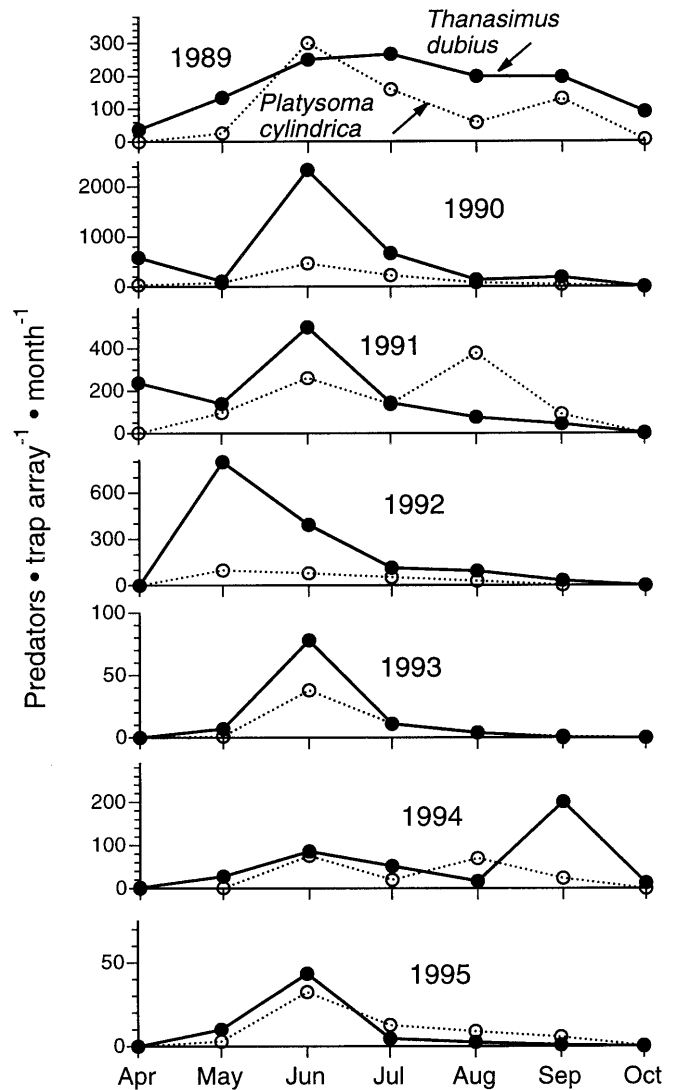


Fig. 2 Total monthly captures at pheromone-baited funnel traps of the two most abundant species of *Ips* predators. Traps in 1989–1993 were baited with ipsdienol only. Trap arrays in 1994–1995 also included ipsenol and ipsdienol+ipsenol

Development time

Under natural temperatures (mean \pm SD of daily temperatures= $19.4 \pm 3.8^\circ\text{C}$; maximum daily high= 36.6°C and minimum daily low= 0.2°C), the median development time of *I. pini* was 65 days, compared to 76 and 78 days for *I. grandicollis* and *I. perroti*, respectively ($n=630$, 131, and 82 adults, respectively). There were no living larvae after 92 days but 30% of the *I. perroti* adults still remained within the logs while all *I. pini* and *I. grandicollis* had emerged.

At constant temperatures, *I. pini* eggs hatched faster than *I. grandicollis*, and both hatched faster than *I. perroti* (mean \pm SE= 3.08 ± 0.05 , 3.60 ± 0.16 , 3.85 ± 0.08 days, respectively; $F_{2,136}=26.23$, $P=0.0001$; Fig. 3). Larval development was relatively rapid in *I. pini* and *I. grandicollis* compared to *I. perroti* (mean \pm SE= 9.59 ± 0.23 , 9.86 ± 0.23 ,

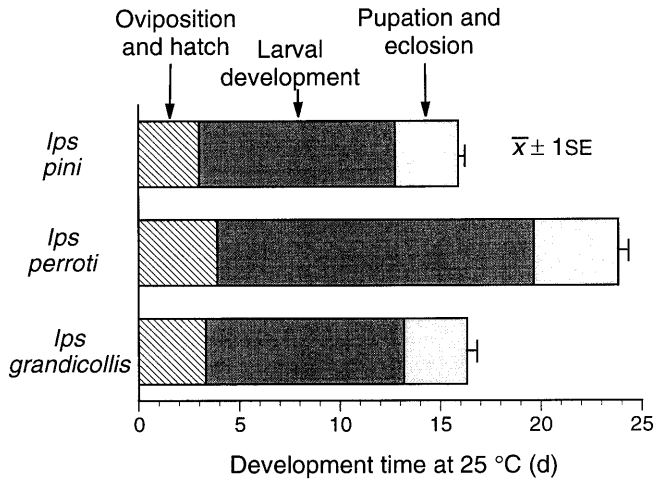


Fig. 3 Generation time at 25°C of *I. pini*, *I. perroti*, and *I. grandicollis*

15.61±0.43 days, respectively; $F_{2,81}=103.04$, $P=0.0001$). Similarly, pupal development time was nearly identical for *I. pini* and *I. grandicollis* and 35% longer in *I. perroti* (mean±SE=3.07±0.07, 3.09±0.06, 4.15±0.10 days, respectively; $F_{2,167}=56.02$, $P=0.0001$). Each larval molt was preceded by the insect reversing its orientation within the feeding chamber and compacting frass to seal the burrow behind it. Prior to pupation, larvae stopped feeding and spent 24–36 h thrashing in a manner that resulted in slow rotation within the feeding chamber and created a circular barrier of compacted frass around them. These pre-molting behaviors constituted a substantial proportion of development time. After eclosion, adults spent 1–2 days within their pupal chamber, then began wandering and feeding throughout the sandwich.

Insect development time is partly a function of the growth that must be accomplished from neonate to adult (Ayres and Scriber 1994). *I. grandicollis* adults were the largest of the three species (mean±SE=2.17±0.07 mg dry mass, $n=50$). Males were larger than females in both *I. pini* (mean±SE=1.99±0.07 vs 1.77±0.06 mg; $t=2.44$, $P<0.01$, $df=58$) and *I. perroti* (mean±SE=1.45±0.04 vs 1.11±0.05 mg, $t=5.21$, $P<0.001$, $df=54$). Egg volumes of *I. pini* and *I. grandicollis* were larger than those of *I. perroti* (mean±SE=0.111±0.004, 0.104±0.006, and 0.073±0.008 mm³, respectively; $F_{2,30}=7.87$, $P=0.0023$). There was additional variation in egg size among galleries within species ($F_{30,137}=4.68$, $P=0.0001$). The average dry mass for eggs of *I. pini*, *I. grandicollis*, and *I. perroti* was 27.9, 24.5, and 18.7 µg, respectively. Thus, larval development in *I. pini* and *I. perroti* requires an increase in biomass of 59- to 64-fold, compared to 88-fold for *I. grandicollis*.

Species associations within logs

In June 1994, 3 weeks after trees had been felled, the number of colonizing female adults per tree equaled, in

Table 1 Associations of *Ips pini*, *I. perroti*, and *I. grandicollis* in 61 logs that were naturally colonized in summer 1995

<i>Ips</i> species present	Number of logs	
	Observed	Expected ^a
<i>I. pini</i> alone	32	28.5
<i>I. perroti</i> alone	2	2.0
<i>I. grandicollis</i> alone	11	4.9**
<i>I. pini</i> and <i>I. perroti</i>	6	6.3
<i>I. pini</i> and <i>I. grandicollis</i>	7	15.0**
<i>I. perroti</i> and <i>I. grandicollis</i>	2	1.1
All three <i>Ips</i> species	1	3.3

^a Based on the null hypothesis of no association between species
 ** $P<0.01$ (G -tests)

rank order, 1, 23, 25, 47, 52, 89, and 326 ($F_{5,78}=45.67$, $P<0.0001$ for effect of tree, excluding the tree with only one colony). Colonization was densest at the stump end and decreased toward the crown ($F_{1,78}=135.25$, $P<0.0001$), especially on trees with the most *Ips* galleries ($F_{5,78}=20.76$, $P<0.0001$ for distance×tree interaction: slopes±SE=−2.96±0.29 vs −0.32±0.08 galleries m^{−1} for trees with 326 vs 23 colonies). We identified 225 colonizing adults (109 *I. pini*, 71 *I. grandicollis*, and 45 *I. perroti*). Species overlapped within the logs, but differed in their relative abundance along the length of the logs ($\chi^2=58.92$, $df=4$, $P<0.001$). The majority of *I. grandicollis* colonies were near the butt of the log (59% compared to 25% in the mid bole and 15% at the lower live crown). One-third (35%) of *I. pini* colonies occurred near the butt of the logs, 61% in the mid bole, and 5% at the lower live crown. Only 2% of the *I. perroti* colonies were in the butt, compared to 62% in the mid bole and 36% in the lower live crown. Thus *I. perroti* and *I. grandicollis* tended to be spatially separated within trees, while *I. pini* overlapped extensively with the other two species. In July 1994, we identified *Ips* from 90 galleries in three zones of seven trees felled on 8 June: all were *I. pini*, with the exception of two *I. grandicollis* (both located in the basal region), and one *I. perroti* (located in the crown).

Species associations among logs

Of 61 logs that were naturally colonized in 1995, 45 were colonized by *I. pini*, 21 by *I. grandicollis*, and 10 by *I. perroti*. Fifteen bolts were colonized by two species and one was colonized by all three species (Table 1). *I. grandicollis* was significantly more likely to occur alone and less likely to occur with *I. pini* than would be expected by chance (Table 1). *I. pini* co-occurred with *I. perroti* at about the frequency expected by chance (6 vs 6.3 logs). Logs were rarely shared equally; in all but four logs, a single species comprised >85% of the colonizing population.

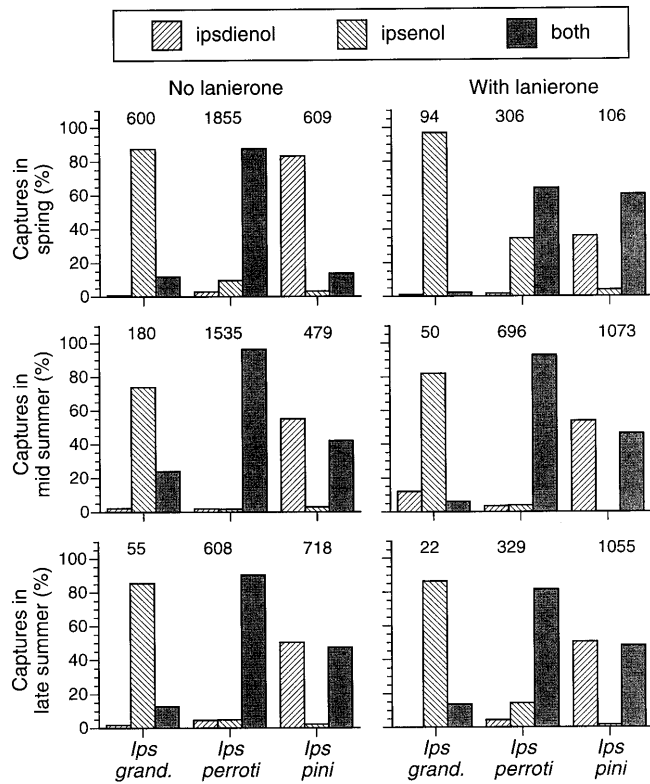


Fig. 4 Relative preferences of three *Ips* species for ipsdienol alone, ipsenol alone, and ipsdienol+ipsenol. Percent captures at each blend are shown for spring, mid summer, and late summer, without and with the presence of lanierone. Values above each set of bars indicate total captures of each species in each season with no lanierone (six trap arrays) or without lanierone (two trap arrays) (*Ips grand.* *I. grandicollis*). See Table 2 for corresponding analyses

Pheromone interactions

Species differed strongly in their pheromone preferences (Fig. 4, Table 2). Each species was most attracted to the pheromone signal produced by that species: *I. grandicollis* to ipsenol alone, *I. pini* to ipsdienol+lanierone, and *I. perroti* to ipsenol+ipsdienol. However, there were interactions with season, and the effects of any particular pheromone signal often depended upon the presence or absence of other signals (Table 2, Figs. 4, 5). With three *Ips* species, there are seven possible permutations of species within a tree, which gives rise to four possible composite signals that might be encountered by an individual beetle searching for host material. In general, beetles were attracted to heterospecific signals in the absence of their conspecific signal, but were deterred if the heterospecific signal was added to the conspecific signal (Fig. 5).

I. pini was somewhat more likely to be captured in traps baited with the heterospecific signals of *I. grandicollis* (ipsenol) than in unbaited traps (captures with ipsenol=69 compared to 16 expected under the hypothesis of no effect, $R=2.3$ in Fig. 5, $\chi^2=20.27$). Conspecific signals from *I. perroti* (or *I. perroti*+*I. grandicollis*) were even

Table 2 Contingency analysis comparing the pheromone preferences of three *Ips* species in three seasons (spring, mid summer, and late summer), with and without the presence of lanierone. For each line of the table, the null hypothesis is that the source had no effect on the proportion of beetles captured with ipsdienol vs ipsenol vs ipsdienol+ipsenol. Data are summarized in Fig. 4

Source	df	χ^2
Species	2	3,423.10**
Season	2	182.51**
Lanierone	1	7.31
Species×season	4	191.96**
Species×lanierone	2	11.22
Season×lanierone	2	11.22
Species×season×lanierone	4	63.91**
Sex	1	0.00
Sex×species	1	8.02
Sex×season	2	0.13
Sex×lanierone	1	0.50
Sex×species×season	2	4.33
Sex×species×lanierone	1	2.11
Sex×season×lanierone	2	6.23
Sex×species×season×lanierone	2	3.63

** $P<0.01$; controlled for experimentwise error with Dunn-Šidák adjustment for 15 tests

more attractive to *I. pini* (624 captures vs 12 expected if there was no effect, $R=54.4$ in Fig. 5, $\chi^2=551.04$). *I. pini* females were deterred by signals from *I. grandicollis* and/or *I. perroti* if the plume already contained their conspecific signal ($R=-20.4$, $\chi^2=16.68$ for 574 captures vs 721), while males were unaffected or even attracted by addition of the same signal ($R=16.6$, 484 captures vs 416; χ^2 for difference between sexes=19.01). With lanierone, captures of *I. pini* were about fivefold higher during the spring and mid summer than in replicate arrays without lanierone (106 vs 23 captures in spring and 1,053 vs 271 captures in mid summer). During late summer, captures were still higher with lanierone than without (1,055 vs 460 captures), but the effect of lanierone was significantly reduced relative to earlier in the summer (χ^2 for season×lanierone interaction=36.18). χ^2 statistics in this paragraph were all significant at $P<0.05$ when controlled for experimentwise error with a Dunn-Šidák adjustment for five post hoc tests.

Compared to *I. pini*, *I. grandicollis* was less attracted by heterospecific pheromone signals in the absence of conspecific signals and more deterred by heterospecific signals in the presence of conspecific signals (Fig. 5). This matches the pattern of stronger segregation in naturally colonized logs (Table 1). By itself, ipsdienol+lanierone was barely any more attractive to *I. grandicollis* than an unbaited funnel trap ($R=1.2$). However, ipsdienol was a strong deterrent when added to a pheromone plume that already contained ipsenol ($R=-84.9$ for addition of signal from *I. perroti*, $\chi^2=536.24$ for 151 captures vs 684). *I. grandicollis* was similarly deterred by the addition of a signal from *I. pini* which added lanierone as well as ipsdienol ($R=-91.7$ for signals 3 or 4 in Fig. 5).

In the absence of its own pheromone signal, *I. perroti* was somewhat attracted by the signal of *I. pini* (Fig. 5;

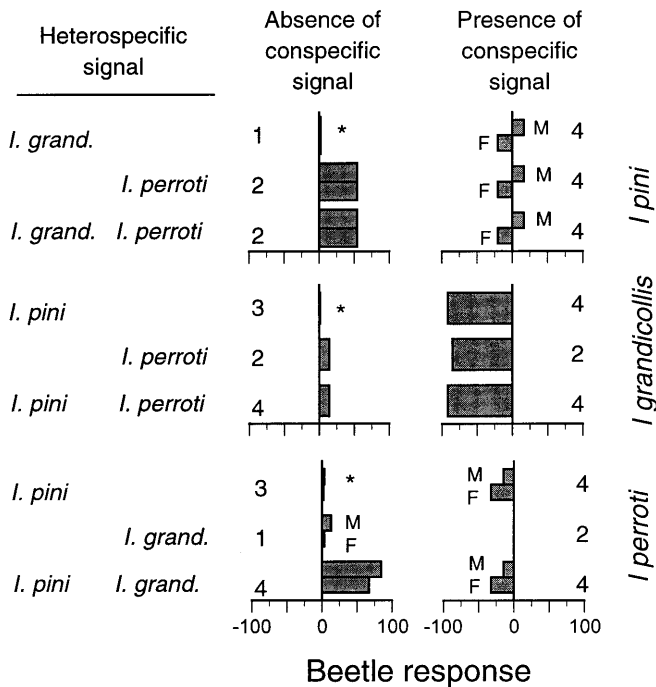


Fig. 5 Response of *I. pini*, *I. grandicollis*, and *I. perroti* to heterospecific semiochemicals in the presence and absence of conspecific signals. Beetle response is expressed as numbers of beetles relative to that attracted by the conspecific signal alone (Eq. 1). Values can range from strong deterrence (–100) to strong attraction (100), with a value of 0 indicating no effect. Numbers to the left and right of each bar indicate the composite pheromone signal: 1 ipsenol, 2 ipsenol+ipsdienol, 3 ipsdienol+lanierone, 4 ipsenol+ipsdienol+lanierone. Asterisks indicate three cases where the bars are very small but *R* is significantly positive (*M* males, *F* females)

$R=2.5$ for responses to signal 3, $\chi^2=23.81$; 153 captures with ipsdienol+lanierone vs 35 captures expected if $R=0$). In the absence of their own signal, *I. perroti*, especially males, were also attracted by the signal of *I. grandicollis* ($R=13.0$ and 3.1 for males and females, respectively; $\chi^2=146.78$ and 29.60 for male and female captures, respectively, of 320 and 92 vs expected captures of 19 and 17 if $R=0$; $\chi^2=121.06$ for contrast between sexes). Lanierone tended to deter *I. perroti*, especially females (captures with and without lanierone=701 vs 1,035 for females, and 451 vs 528 for males; $\chi^2=64.26$ for females, not significant for males). Consequently, the combined signal of *I. pini* and *I. grandicollis* was not quite as attractive as the conspecific signal ($R=85$ and 67 for males and females in Fig. 5, lower left), and the addition of a signal from *I. pini* to the conspecific signal tended to reduce captures of *I. perroti* ($R=-15$ and -32 for males and females, respectively; Fig. 5, bottom right; note that the signal from *I. grandicollis* is qualitatively redundant with the conspecific signal, so again $R=-15$ and -32). *I. perroti* was less discriminating earlier in the season, with significantly more choosing either ipsenol or ipsdienol over the combination in the spring than in the summer (322 of 1,331 vs 343 of 3,978; $\chi^2=161.00$). χ^2 statistics in this paragraph

were all significant when controlled for experimentwise error with a Dunn-Šidák adjustment for six post hoc tests.

Patterns of pheromone attraction and deterrence were similar in New Hampshire except that we captured no *I. perroti*. Ipsenol had little or no deterrent effect on *I. pini* responses to traps already baited with ipsdienol (812 vs 914 *I. pini* at one site and 89 vs 80 *I. pini* at the other site), but ipsdienol was a strong deterrent to *I. grandicollis* (captures of *I. grandicollis* with ipsenol alone vs ipsenol+ipsdienol=38 vs 4 at one site and 19 vs 2 at the other site).

Predator responses to *Ips* pheromones

Both *T. dubius* and *P. cylindrica* were more attracted to the combination of ipsenol and ipsdienol than to either by itself (captures during 1995 with ipsenol, ipsdienol, and ipsenol+ipsdienol=101, 164, and 227, respectively, for *T. dubius*, and 88, 129, and 284, respectively, for *P. cylindrica*; χ^2 for differences among signals=48.4 and 1,501.36). Lanierone had little or no effect on responses of *T. dubius* but appeared to increase captures of *P. cylindrica*: captures in paired arrays with and without lanierone=101 versus 124 for *T. dubius*, and 109 versus 161 for *P. cylindrica* ($\chi^2=10.01$). χ^2 statistics in this paragraph were significant at $P<0.05$ when controlled for experimentwise error with a Dunn-Šidák adjustment for three post hoc tests.

Discussion

Spatial and temporal overlap among species

Differences among species in the timing of spring emergence, development rate, and number of annual generations reduce, but do not eliminate, interspecific competition for phloem. Of the three species, *I. pini* has the largest egg size and most rapid development. *I. pini* in this system is multivoltine, as are other populations (Reid 1955; Schenk and Benjamin 1969). *I. grandicollis* is multivoltine in the southern United States (Coulson et al. 1986) and *I. perroti* has been reported to be bivoltine in Alberta (Reid 1955), but we found very few *I. perroti* or *I. grandicollis* colonizing trees or bolts after June in either 1994 or 1995, suggesting that they are chiefly univoltine in our system. A small second peak in flight activity in July (Fig. 1) suggests that some fraction may initiate a second generation, but some *Ips* still respond to aggregation pheromones after reproduction has ceased for the season (Teale and Lanier 1991), so this second flight may also represent some poorly understood post-reproductive behavior. It makes sense that *I. grandicollis* and *I. perroti* would be univoltine because of their relatively long development time. Annual degree day accumulations (10°C base) from 1989 to 1995 reached their midpoint from 11–20 July. In 1995, the date of median

adult emergence from the first generation was near midsummer for *I. pini* (20 July), but after midsummer for *I. grandicollis* and *I. perroti* (31 July and 3 August, respectively), so multivoltinism only appears to be viable for *I. pini* (immatures of any species are unlikely to survive the winter; Clemens 1916; Reid 1955; Lombardero et al. 2000). Temporal overlap among species is increased by intraspecific variation in reproductive phenology. Although most of the mating and oviposition in *I. perroti* and *I. grandicollis* was during early May and mid May, respectively, there was additional flight activity, host colonization, and mating in both species during June (apparently from animals that had overwintered, because the first adult progeny did not appear until mid July). The relatively late spring flight of *I. grandicollis* (Fig. 1) further increases temporal overlap with *I. pini*. Similarly, *I. perroti* continues to compete for phloem resources throughout the summer even though it is univoltine. *I. perroti* has the slowest relative growth rate and longest larval development time of the three species. Furthermore, *I. perroti* adults continue feeding within the phloem for weeks after eclosion (perhaps to acquire energy reserves for overwintering or to become inoculated with mutualistic fungi). The relatively small larval galleries of *I. perroti* suggested a nutritional dependency upon fungi (Ayres et al. 2000), which would make them unique within this community.

Resource overlap between *Ips* species is reduced by partial spatial segregation on trees, as has been reported for some other bark beetle communities (Birch 1978; Svirha et al. 1980; Paine et al. 1981; Wagner et al. 1985; Hui and Xue-Song 1999). *I. grandicollis* most often colonized the base of the tree, while *I. perroti* tended to colonize near the crown, and *I. pini* colonized the mid bole. Spatial colonization patterns are flexible (presumably mediated by pheromones) because *I. pini* spread themselves evenly throughout the tree in late summer, when *I. grandicollis* and *I. perroti* were absent.

Pheromone communication among species

Interspecific responses to pheromones can both reduce and increase species overlap in resource use. A pheromone from a congener can act as a deterrent when added to a conspecific signal, or as an attractant when alone (Fig. 5, compare left and right panels). The deterrence must contribute to segregation of species within and among resource patches (logs), while the attraction must contribute to species overlap. Interspecific chemical communication is ubiquitous in bark beetle communities (Birch et al. 1980; Wood 1982a; Cane et al. 1990; Smith et al. 1990; Borden et al. 1992; Savoie et al. 1998), even though it is seldom reported in other taxa (London and Jeanne 1996; Chivers et al. 1997). *I. pini* in the western United States is deterred by ipsenol (Furniss and Livingston 1979; Borden et al. 1992), which is produced by sympatric populations of *I. paraconfusus* (Lanier), and *I. paraconfusus* are deterred by R(-)-ipsdienol which is

produced by sympatric populations of *I. pini* (Birch and Wood 1975). Similarly, the attraction of *I. latidens* to its pheromone, ipsenol, is inhibited by the ipsdienol produced by *I. pini* (Miller and Borden 1992). Conversely, *I. avulsus* (Eichhoff), *I. calligraphus* (Germar), *I. hoppingi* (Lanier), *I. montanus* (Eichhoff), *Dendroctonus frontalis* (Zimmermann), *Hylastes gracilis* (LeConte), and *Pityogenes knechteli* (Swaine) are all attracted to pheromones produced by sympatric species of bark beetles (Lanier and Wood 1975; Hedden et al. 1976; Svirha et al. 1980; Cane et al. 1990; Smith et al. 1990; Poland and Borden 1994). Ours seems to be the first report of heterospecific responses switching from attraction to deterrence depending upon the presence of conspecific signals. This indicates that the information content of a pheromone plume is more complex than predicted from the additive effects of individual pheromones. This increases the information that can be transferred with a limited number of signals (in this case, ipsdienol, ipsenol, and lanierone), and therefore represents an example of semiochemical parsimony (sensu Blum 1996). In terms of information theory, the *Ips* communication system has higher entropic properties (McCowan et al. 1999). The information content of a pheromone plume may be even greater because additional information is probably transmitted by pheromone quantity (Renwick and Vite 1969; Birgersson et al. 1984), the enantiomeric composition of ipsdienol (Teale et al. 1994; Miller et al. 1996), and undiscovered pheromones or synergists that are produced in low quantity (Miller et al. 1991).

Presumably, the potential for species interactions is increased when there is overlap between species in pheromone production. In our system, lanierone is the only chemical signal that is unique to a single species; ipsenol is produced by both *I. grandicollis* and *I. perroti*, and ipsdienol is produced by both *I. pini* and *I. perroti*. Signal overlap within bark beetle guilds is relatively common (Wood 1982a). It is also common for bark beetle species to have chemoreceptors that detect compounds they do not use as pheromones. For example, the antennae of both *I. pini* and *I. grandicollis* respond to numerous volatile molecules that function as pheromones in other species of bark beetle (Mustaparta et al. 1977; Ascoli-Christensen et al. 1993). Species overlap in pheromone production and response is probably enhanced because pine-feeding bark beetles share a limited set of suitable precursors in their host plants (chiefly monoterpenes) and share common biochemical pathways by virtue of common descent (Francke et al. 1995; Seybold et al. 1995b). Nonetheless, the family Scolytidae employs at least 20 different molecules as pheromones (Wood 1982a; Francke et al. 1995), so even species-rich guilds could be organized to eliminate overlap in pheromones. Species with pheromone signals that overlap most with sympatric species (e.g., *I. perroti*) should tend to experience the strongest interspecific interactions.

Are there benefits of multispecies aggregations?

The *Ips* community that we studied occurs in pine forests across a broad geographic area, suggesting that it is a stable assemblage. Indeed, most coniferous forests harbor diverse communities of bark beetles with very similar ecological requirements (Wood 1982b). Such communities would be more likely to persist if there were sometimes benefits of multispecies associations that mitigate the costs of competition. Adaptive explanations for communication systems have to be reconciled with benefits to the individuals that are producing the signals and/or those that are responding (Alcock 1982). Unlike eusocial insects, bark beetles derive no benefit from conspecific aggregations (beyond mating opportunities) that would not also be accrued from heterospecific aggregations. Sometimes, bark beetle individuals will suffer less from competition with heterospecifics than from an equivalent number of conspecifics (e.g., if the heterospecifics develop at a slower rate). Furthermore, there are at least three mechanisms by which bark beetle individuals could benefit from multispecies associations: predator swamping, group attack, and host location. The *Ips* species share a guild of predators (Fig. 2; Raffa and Klepzig 1989; Raffa 1991), so per capita survival is probably higher on logs where the total number of bark beetles is higher (Reeve et al. 1995). Abrams et al. (1998) described a similar situation as apparent mutualism. When bark beetles attack live trees, per capita reproductive success is enhanced by high attack rates (Raffa and Berryman 1983). Potential attack rates are greater for multispecies aggregations, so presumably per capita reproduction can sometimes be enhanced if beetles produce and respond to heterospecific signals. *Ips* species also depend upon locating recently dead host material. All three species exploit this same ephemeral resource, so pheromone plumes from any species will indicate suitable host material, and individuals that can orient to heterospecific pheromones should have an increased probability of finding food resources. In this context, the responding beetle is a parasite or commensalist. The attraction of *Ips* for heterospecific pheromones could result from selection to exploit these benefits. Differences among species could be the result of asymmetrical competition (e.g., weaker cross-specific attraction and stronger cross-specific deterrence in *I. grandicollis* suggests that it may suffer more from competition with other species than other species suffer from competition with *I. grandicollis*).

That males, the colonizing sex in these three species, would be more strongly attracted to heterospecific signals than females makes sense because they derive the most benefit from participating in mass attacks and from pirating previously located host material. Females would not normally accrue these benefits, but would suffer the negative effects of interspecific competition among larvae. If heterospecific attraction has been favored by natural selection, then it should be strongest among sympatric species, where it may tend to counteract selection for

reproductive isolation (Lanier and Wood 1975). An alternative hypothesis is that heterospecific attraction is an evolutionary anachronism or a biochemical artifact of coincidental overlap in signalling molecules and chemoreceptors (Lewis and Cane 1990).

Regardless of whether or not heterospecific attraction is an evolved attribute of bark beetle communities, the effect is to strengthen interactions among species. Predicting whether removing a species from our system would increase or decrease the abundance of remaining species remains difficult. This question has practical as well as theoretical value because it determines whether a species-specific control program (e.g., Bakke 1989) would tend to increase or decrease the abundance of other bark beetle species. The effect of changing the abundance of one species could depend upon the abundance of shared predators, the severity of food limitations, reliance on attacking live trees, and the relative abundance of the different bark beetle species. This would be an example of conditional interactions (Abrams 1987) such as reported for some communities of plants and fungi (Bronstein 1994a, 1994b; Callaway and Walker 1997; Johnson et al. 1997; Brooker and Callaghan 1998). Rare species are likely to accrue the strongest benefits of interspecies associations. For example, an individual of species A would receive greater benefits from species B (in predator swamping and mass attacks) if the former is without conspecifics than if it is associated with many conspecifics (with conventional assumptions regarding functional responses of predators and mortality responses of trees). If so, this frequency dependence of conditional interactions would tend to stabilize the community by increasing the reproductive success of rare relative to common species. Conditional interactions mediated by pheromone communication provide a promising hypothesis to explain the persistence and prevalence in coniferous forests of diverse guilds of bark beetles with very similar resource requirements.

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References

- Abrams PA (1987) On classifying interactions between populations. *Oecologia* 73:272–281
- Abrams PA, Holt RD, Roth JD (1998) Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology* 79:201–212
- Alcock J (1982) Natural selection and communication among bark beetles. *Fla Entomol* 65:17–32
- Amezaga I, Rodriguez MA (1998) Resource partitioning of four sympatric bark beetles depending on swarming dates and tree species. *For Ecol Manage* 10:127–135

- Anderbrandt O, Schlyter F, Birgersson G (1985) Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos* 45:89–98
- Ascoli-Christensen A, Salom SM, Payne TL (1993) Olfactory receptor cell responses of *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) to intra- and interspecific behavioral chemicals. *J Chem Ecol* 19:699–712
- Ayres MP, Scriber JM (1994) Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecol Monogr* 64:465–482
- Ayres MP, Wilkens RT, Ruel JJ, Lombardero MJ, Vallery E (2000) Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi (Coleoptera: Scolytidae). *Ecology* 81:2198–2210
- Bakke A (1989) The recent *Ips typographus* outbreak in Norway – experiences from a control program. *Holarctic Ecol* 12:515–519
- Berryman AA (1973) Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). I. Analysis of population behavior and survival from 1964 to 1971. *Can Entomol* 105:1465–1488
- Birch MC (1978) Chemical communications in pine bark beetles. *Am Sci* 66:409–419
- Birch MC, Wood DL (1975) Mutual inhibition of the attractant pheromone response by two species of *Ips* (Coleoptera: Scolytidae). *J Chem Ecol* 1:101–113
- Birch MC, Svihra P, Paine TD, Miller JC (1980) Influence of chemically mediated behavior on host tree colonization by 4 cohabiting species of bark beetles. *J Chem Ecol* 6:395–414
- Birgersson G, Schlyter F, Lofqvist J, Bergstrom G (1984) Quantitative variation of pheromone components in the spruce bark beetle *Ips typographus* from different attack phases. *J Chem Ecol* 10:1029–1056
- Blum MS (1996) Semoiochemical parsimony in the Arthropoda. *Annu Rev Entomol* 41:353–374
- Borden JH, Devlin DR, Miller DR (1992) Synomones of sympatric species deter attack by the pine engraver, *Ips pini* (Coleoptera Scolytidae). *Can J For Res* 22:381–387
- Bronstein JL (1994a) Conditional outcomes in mutualistic interactions. *Trends Ecol Evol* 9:214–217
- Bronstein JL (1994b) Our current understanding of mutualism. *Q Rev Biol* 69:31–51
- Brooker RW, Callaghan TV (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81:196–207
- Byers JA, Wood DL (1980) Interspecific inhibition of the response of the bark beetles *Dendroctonus brevicomis* and *Ips paraconfusus* to their pheromones in the field. *J Chem Ecol* 6:149–164
- Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965
- Cane JH, Merrill LD, Wood DL (1990) Attraction of pinyon pine bark beetle *Ips hoppingi* to conspecific and *Ips confusus* pheromones (Coleoptera Scolytidae). *J Chem Ecol* 16:2791–2798
- Chivers DP, Kiesecker JM, Wildy EL, Anderson MT, Blaustein AR (1997) Chemical alarm signalling in terrestrial salamanders: intra- and interspecific responses. *Ethology* 103:599–613
- Clemens WA (1916) The pine bark beetle. Cornell University Agricultural Experiment Station Bulletin 383
- Coulson RN, Flamm RO, Pulley PE, Payne TL, Rykiel EJ, Wagner TL (1986) Response of the southern pine bark beetle guild (Coleoptera: Scolytidae) to host disturbance. *Environ Entomol* 15:850–858
- Dajoz R (1974) Les insectes xylophages et leur role dans la degradation du bois mort. In: Pesson P (eds) *Ecologie forestiere*. Gautiers-Villars, Paris, pp 257–307
- De Jong MCM, Sabelis MW (1988) How bark beetles avoid interference with squatters: an ESS for colonization by *Ips typographus*. *Oikos* 51:88–96
- Flamm RO, Wagner TL, Cook SP, Pulley PE, Coulson RN, Mcardle TM (1987) Host colonization by cohabiting *Dendroctonus frontalis*, *Ips avulsus*, and *Ips calligraphus* (Coleoptera Scolytidae). *Environ Entomol* 16:390–399
- Flamm RO, Coulson RN, Beckley P, Pulley PE, Wagner TL (1989) Maintenance of a phloem-inhabiting guild. *Environ Entomol* 18:381–387
- Francke W, Bartels J, Meyer H, Schroder F, Kohnle U, Baader E, Vité JP (1995) Semoiochemicals from bark beetles: new results, remarks, and reflections. *J Chem Ecol* 21:1043–1063
- Furniss MM, Livingston RL (1979) Inhibition by ipsenol of pine engraver attraction in northern Idaho USA. *Environ Entomol* 8:369–372
- Gara RI, Werner RA, Whitmore MC, Holsten EH (1995) Arthropod associates of the spruce beetle *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae) in spruce stands of south-central and interior Alaska. *J Appl Entomol* 119:585–590
- Goulding HA, Hall DJ, Raffa KF, Martin AJ (1988) Wisconsin woodlands: identifying and managing pine pests in Wisconsin. Agricultural Bulletin G3428, University of Wisconsin-Extension, Madison, Wis
- Hager BJ, Teale SA (1996) Genetic correlation of pheromone production and response in the pine engraver beetle, *Ips pini*. *Heredity* 77:100–107
- Hedden R, Vite JP, Mori K (1976) Synergistic effect of a pheromone and a kairomone on host selection and colonization by *Ips avulsus*. *Nature* 261:696–697
- Herard F, Mercadier G (1996) Natural enemies of *Tomicus piniperda* and *Ips acuminatus* (Col.; Scolytidae) on *Pinus sylvestris* near Orleans, France: temporal occurrence and relative abundance, and notes on eight predatory species. *Entomophaga* 41:183–210
- Hermes DA, Haack RA, Ayres BD (1991) Variation in semiochemical-mediated prey-predator interaction: *Ips pini* (Scolytidae) and *Thanasimus dubius* (Cleridae). *J Chem Ecol* 17:1705–1714
- Howden HF, Vogt GB (1951) Insect communities of standing dead pine (*Pinus virginiana* Mill.). *Ann Entomol Soc Am* 44:581–585
- Hui Y, Xue-Song D (1999) Impacts of *Tomicus minor* on distribution and reproduction of *Tomicus piniperda* (Col., Scolytidae) on the trunk of living *Pinus yunnanensis* trees. *J Appl Entomol* 123:329–333
- Johnson NC, Graham JH, Smith FA (1997) Functioning and mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol* 135:575–586
- Kaila L, Martikainen P, Puntila P (1997) Dead trees left in clearcuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodivers Conserv* 6:1–18
- Kirkendall LR (1989) Within-harem competition among *Ips* females: an overlooked component of density-dependent larval mortality. *Holarctic Ecol* 12:477–487
- Lanier GN, Wood DL (1975) Specificity of response to pheromones in the genus *Ips* (Coleoptera: Scolytidae). *J Chem Ecol* 1:9–23
- Lanier GN, Classon A, Stewart T, Piston JJ, Silverstein RM (1980) *Ips pini*: the basis for inter populational differences in pheromone biology. *J Chem Ecol* 6:677–688
- Lewis EE, Cane JH (1990) Pheromonal specificity of southeastern *Ips* pine bark beetles reflects phylogenetic divergence (Coleoptera: Scolytidae). *Can Entomol* 122:1235–1238
- Light DM, Birch MC, Paine TD (1983) Laboratory study of interspecific and intraspecific competition within and between two sympatric bark beetle species, *Ips pini* and *I. paraconfusus*. *Z Angew Entomol* 96:233–241
- Lombardero MJ, Ayres MP, Ayres BD, Reeve JD (2000) Cold tolerance of four species of bark beetle (Coleoptera: Scolytidae) in North America. *Environ Entomol* 29:421–432
- London KB, Jeanne RL (1996) Alarm in a wasp-wasp nesting association: do members signal cross-specifically? *Insectes Soc* 43:211–215
- McCowan B, Hanser SF, Doyle LR (1999) Quantitative tools for comparing animal communication systems: information theory applied to bottlenose dolphin whistle repertoires. *Anim Behav* 57:409–419
- Miller DR, Borden JH (1992) (s)-(+)-ipsdienol – interspecific inhibition of *Ips latidens* (Leconte) by *Ips pini* (Say) (Coleoptera – Scolytidae). *J Chem Ecol* 18:1577–1582

- Miller DR, Gries G, Borden JH (1991) E-Myrcenol; a new pheromone for the pine engraver *Ips pini* (Say) (Coleoptera: Scolytidae). *Can Entomol* 122:401–406
- Miller DR, Borden JH, Slessor KN (1996) Enantiospecific pheromone production and response profiles for populations of pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), in British Columbia. *J Chem Ecol* 22:2157–2172
- Moser JC, Thatcher RC, Pickard LS (1971) Relative abundance of southern pine beetle associates in east Texas. *Ann Entomol Soc Am* 64:72–77
- Mustaparta H, Angst ME, Lanier GN (1977) Responses of single receptor cells in the pine engraver beetle *Ips pini* (Coleoptera: Scolytidae) to its aggregation pheromone ipsdienol and the aggregation inhibitor ipsenol. *J Comp Physiol A* 121:343–348
- Paine TD, Birch MC, Svihra P (1981) Niche breadth and resource partitioning by 4 sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia* 48:1–6
- Poland TM, Borden JH (1994) Semiochemical-based communication in interspecific interactions between *Ips pini* (Say) and *Pityogenes knechteli* (Swaine) (Coleoptera: Scolytidae) in lodgepole pine. *Can Entomol* 126:269–276
- Raffa KF (1991) Temporal and spatial disparities among bark beetles, predators, and associates responding to synthetic bark beetle pheromones: *Ips pini* (Coleoptera: Scolytidae) in Wisconsin. *Environ Entomol* 20:1665–1679
- Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecol Monogr* 53:27–49
- Raffa KF, Klepzig KD (1989) Chiral escape of bark beetles from predators responding to a bark beetle pheromone. *Oecologia* 80:566–569
- Rankin LJ, Borden JH (1991) Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. *Can J For Res* 21:1029–1036
- Reeve JR, Ayres MP, Lorio PL Jr (1995) Host suitability, predation, and bark beetle population dynamics. In: Cappuccino N, Price PW (eds) *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, pp 339–357
- Reid RW (1955) The bark beetle complex associated with lodgepole pine slash in Alberta. *Can Entomol* 87:311–323
- Renwick JAA, Vite JP (1969) Bark beetle attractants: mechanism of colonization by *Dendroctonus frontalis*. *Nature* 224:1222–1223
- Robins GL, Reid ML (1997) Effects of density on the reproductive success of pine engravers: is aggregation in dead trees beneficial? *Ecol Entomol* 22:329–334
- Sartwell C, Schmitz RF, Buckhorn WJ (1971) Pine engraver, *Ips pini* in the western states. *Forest Pest Leaflet* 122. USDA Forest Service, Washington, DC
- SAS (1990) SAS/Stat user's guide: version 6, 4th edn. SAS Institute, Cary, NC
- Savely HE (1939) Ecological relations of certain animals in dead pine and oak logs. *Ecol Monogr* 9:321–385
- Savoie A, Borden JH, Pierce HD Jr, Gries R, Gries G (1998) Aggregation pheromone of *Pityogenes knechteli* and semiochemical-based interactions with three other bark beetles. *J Chem Ecol* 24:321–337
- Schenk JA, Benjamin DM (1969) Notes on the biology of *Ips pini* in central Wisconsin jack pine forests. *Ann Entomol Soc Am* 62:480–485
- Schmitz RF (1972) Behavior of *Ips pini* during mating, oviposition, and larval development (Coleoptera: Scolytidae). *Can Entomol* 104:1723–1728
- Seybold SJ, Ohtsuka T, Wood DL, Kubo I (1995a) Enantiomeric composition of ipsdienol: a chemotaxonomic character of North American populations of *Ips* spp. in the *pini* subgeneric group (Coleoptera: Scolytidae). *J Chem Ecol* 21:995–1016
- Seybold SJ, Quilici DR, Tillman JA, Vanderwel D, Wood DL, Blomquist GJ (1995b) De novo biosynthesis of the aggregation pheromone components ipsenol and ipsdienol by the pine bark beetles *Ips paraconfusus* Lanier and *Ips pini* (Say) (Coleoptera: Scolytidae). *Proc Natl Acad Sci USA* 92:8393–8397
- Smith MT, Payne TL, Birch MC (1990) Olfactory-based behavioral interactions among five species in the southern pine bark beetle group. *J Chem Ecol* 16:3317–3332
- Sokal RR, Rohlf FJ (1995) *Biometry*. Freeman, San Francisco
- Stewart TE (1975) Volatiles isolated from *Ips pini*: isolation, identification, enantiomeric composition, biological activity. PhD thesis, State University of New York, Syracuse, NY
- Svihra P, Paine TD, Birch M C (1980) Interspecific olfactory communication in southern pine beetles. *Naturwissenschaften* 67:518–529
- Teale SA, Lanier GN (1991) Seasonal variability in response of *Ips pini* (Coleoptera: Scolytidae) to ipsdienol in New York USA. *J Chem Ecol* 17:1145–1158
- Teale SA, Webster FX, Zhang A, Lanier GN (1991) Lanierone: a new pheromone component from *Ips pini* (Coleoptera: Scolytidae) in New York USA. *J Chem Ecol* 17:1159–1176
- Teale SA, Hager BJ, Webster FX (1994) Pheromone-based assortative mating in a bark beetle. *Anim Behav* 48:569–578
- Vité JP, Renwick JAA (1971) Population aggregating pheromone in the bark beetle *Ips grandicollis*. *J Insect Physiol* 17:1699–1704
- Wagner TL, Flamm RO, Coulson RN (1985) Strategies for cohabitation among the southern pine bark beetle species: Comparisons of life-process biologies. *USDA For Serv Gen Tech Rep SO-56:87–101*
- Wood DL (1982a) The role of pheromones, kairomones and allomones in the host selection and colonization behavior of bark beetles. *Annu Rev Entomol* 27:411–446
- Wood SL (1982b) The bark beetles and ambrosia beetles of North America and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Nat Mem* 6