SEMIOCHEMICAL-BASED COMMUNICATION IN INTERSPECIFIC INTERACTIONS BETWEEN *IPS PINI* (SAY) AND *PITYOGENES KNECHTELI* (SWAINE) (COLEOPTERA: SCOLYTIDAE) IN LODGEPOLE PINE

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Abstract

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The pine engraver, *Ips pini* Say, and *Pityogenes knechteli* Swaine often co-exist in lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann. We tested the hypotheses that *P. knechteli* produces an attractive pheromone and that the attraction of *P. knechteli* and *I. pini* to conspecifics is inhibited by the presence of the other species. *Pityogenes knechteli* males and females were attracted to bolts infested with conspecific males and to bolts infested with *I. pini* males; however, there was no significant cross-attraction of *I. pini* males or females to bolts infested with *P. knechteli* males. Attraction of *P. knechteli* and *I. pini* males and females to bolts infested with conspecific males was not inhibited in the presence of bolts infested with males of the other bark beetle species. *Pityogenes knechteli* has no potential for competitive displacement of *I. pini* but may enhance the adverse effect of *I. pini* on the mountain pine beetle, *Dendroctonus ponderosae* Hopkins.

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Résumé

Les scolytes *Ips pini* Say et *Pityogenes knechteli* Swaine cohabitent souvent dans des Pins de Murray *Pinus contorta* var. *latifolia* Engelmann. Nous avons éprouvé l'hypothèse selon laquelle *P. knechteli* produit une phéromone d'attraction et selon laquelle, chez *P. knechteli* aussi bien que chez *I. pini*, l'attraction entre les individus de la même espèce est inhibée par la présence de l'autre espèce. Les mâles et les femelles de *P. knechteli* étaient attirés vers des billes infestées de mâles de l'une ou l'autre espèce; cependant, les billes infestées de mâles de *P. knechteli* n'avaient pas d'attirance significative pour les mâles ou les femelles d'*I. pini*. L'attirance des mâles et des femelles des deux espèces pour les billes infestées de mâles de leur propre espèce n'était pas inhibée en présence de billes infestées par des mâles de l'autre espèce. *Pityogenes knechteli* n'a donc pas la capacité d'exclure *I. pini* par compétition, mais peut augmenter l'effet néfaste d'*I. pini* sur le Dendroctone du Pin ponderosa, *Dendroctonus ponderosae* Hopkins.

[Traduit par la rédaction]

Introduction

Trees are frequently attacked simultaneously by bark beetles of several species, resulting in potential competition for food and living space. The pine engraver, *Ips pini* Say, and *Pityogenes knechteli* Swaine often co-exist in lodgepole pines, *Pinus contorta* var. *latifolia* Engelmann. *Ips pini* usually infests logging slash, cull logs, and windthrown trees, but at high densities may attack and kill trees in unthinned young stands or the tops of older trees (Livingston 1979). *Pityogenes knechteli* is abundant in slash, fallen, and diseased trees, but is not economically important (Reid 1955; Jacobi 1993). The two species often colonize the same host tree and apparently partition the resource based on tree diameter, with *I. pini* associated with large-diameter and *P. knechteli* associated with small-diameter hosts. Beetles of the two species may establish successful galleries adjacent to each other, and their galleries commonly intermix (Poland 1993; Poland and Borden 1994).

Specificity in pheromone-based communication has been hypothesized to be an important mechanism in maintaining breeding isolation between sympatric Scolytidae (Birch 1978). In the genus *Ips*, sibling species are slightly attracted to one another's pheromones

but are able to discriminate between the pheromones of their own species and those of sibling species (Lanier and Wood 1975). Within this genus, cross-attraction decreases with taxonomic difference between species and cross-attractive species are seldom sympatric (Birch 1978). Sympatric species of bark beetles may enhance breeding isolation by inhibiting the response of competing beetles, thus imparting an adaptive advantage for the pioneer species through reserving scarce host material (Birch 1978).

Interspecific interactions may be exploited by mankind to deter attack by members of major pest species (Bakke 1981; Borden 1989; Paine and Hanlon 1991; Borden et al. 1992; Devlin 1992). We tested the hypotheses that *P. knechteli* produces an attractive pheromone and that the attraction of *P. knechteli* and *I. pini* to conspecifics is inhibited by the presence of the other species.

Methods and Materials

General Methods. Naturally infested logs from windthrown lodgepole pines containing *I. pini* and *P. knechteli* larvae and pupae were collected 40 km east of Princeton, B.C., on 19 June 1992. The cut ends of the logs were waxed to prevent desiccation of the phloem and the logs were placed in cages at 27°C. Emergent beetles were sexed (Bright 1976; Wood 1982) and held at 4°C. Fresh uninfested pine logs, approximately 1.5 m long and 12–14 cm in diameter, were collected from the same area, the cut ends waxed, and stored in shade. Each log was cut into six 20-cm-long bolts when needed for experiments.

Two field experiments were conducted in the same areas where the logs were collected in a forest of lodgepole pine 60–80 years old. Eight-unit multiple-funnel traps (Lindgren 1983) were baited with bolts hanging beside them in mesh bags. Bolts from the same tree were used for all treatments within each replicate.

Beetles were introduced into a bolt by drilling 50 holes, each 2 mm in diameter, in the bark and allowing the beetles to select their own attack sites. For treatments involving both sexes, females were introduced 24 h after the males. During the 2-day introduction period, dead beetles were replaced by healthy beetles of the same sex. Traps were baited with bolts within 24 h after the female beetles were introduced. Control bolts were treated as the experimental bolts, but had no beetles.

Test for Aggregation Pheromone in *P. knechteli*. Each of four replicates comprised five treatments (one treatment per trap) in a randomized complete block with 15 m between traps: (1) a bolt infested with 50 *I. pini* males; (2) a bolt infested with 50 *P. knechteli* males; (3) a bolt infested with 50 *P. knechteli* females; (4) a bolt infested with 50 male and 50 female *P. knechteli* (assumed to have formed mated pairs); and (5) an uninfested control bolt. One replicate was initiated per week on 17, 24, and 31 July, and 2 August 1992. All captured beetles were tallied at the end of 2 weeks for each replicate. The bolt infested with *I. pini* males tested the experimental technique and determined a standard level of response by beetles known to produce an aggregation pheromone.

Interspecific Communication between *I. pini* and *P. knechteli*. The attraction of male and female *I. pini* and *P. knechteli* to bolts infested with conspecific males alone and in the presence of bolts containing males of the other species was tested. Each of four replicates comprised four treatments (one per trap) in a randomized complete block design with 15 m between traps: (1) a bolt infested with 50 *I. pini* males; (2) a bolt infested with 50 *P. knechteli* males; (3) one bolt infested with 50 *I. pini* males and another with 50 *P. knechteli* males, both hung beside the same trap; and (4) an uninfested control bolt. For treatment 3, separate bolts were used for each species to ensure that pheromone production would be similar to that for the treatments with either species alone, because behavior and pheromone production in co-attacked logs were unknown. Replicates were initiated on 7, 13, 16, and 21 August 1992, and each replicate was terminated 2 weeks later.

Statistical Analysis. The data for each experiment were analyzed by a two-way analysis of variance with treatment and block as model factors. Data were transformed by $X' = \log (X + 1)$ to stabilize the variances between replicates and to normalize the data. Bonferroni *t*-tests were used to test a priori pairwise comparisons of responses to the different treatments (SAS Institute Inc. 1985). The level to reject the null hypotheses was ≤ 0.05.

Results and Discussion

Test for Aggregation Pheromone in *P. knechteli*. Both male and female *P. knechteli* were significantly attracted to bolts infested with *I. pini* males, *P. knechteli* males, and *P. knechteli* pairs compared with uninfested control bolts or bolts infested with *P. knechteli* females (Fig. 1). *Ips pini* males and females were significantly attracted to bolts infested with conspecific males but to no other treatments. *Pityogenes knechteli* trap catch was significantly affected by both replicate and treatment, probably caused by declining numbers of flying beetles over time.

We conclude that *P. knechteli* males produce a pheromone that is attractive to both male and female conspecifics. This conclusion is supported by the existence of a similar pheromone in other *Pityogenes* spp. (Francke et al. 1977; Byers et al. 1989, 1990; Birgersson et al. 1990). The significant response to *P. knechteli* pairs suggests that the polygamous male continues to produce the pheromone while tending the first arriving female. Termination of pheromone production, or production of an antiaggregation pheromone when each male is joined by only one of up to five potential mates, would be disadaptive. For *I. paraconfusus*, attraction to frass declined progressively when males were joined by one, two, or three females (Borden 1967). Similarly, responses to mated male four-eyed spruce bark beetles, *Polygraphus rufipennis* Kirby, were significantly lower than to males alone (Bowers and Borden 1990). Responses of *I. grandicollis* and *I. calligraphus* were significantly reduced when bolts were infested with beetles of both sexes compared with bolts infested with pioneer beetles alone (Svihra 1982).

More females of *P. knechteli* and *I. pini* were caught than males. The ratios of males to females caught in traps baited with conspecific males were 1:4.02 for *P. knechteli* and 1:2.38 for *I. pini*, corresponding to reported ratios of four to six and two to four females joining each male per gallery for *P. knechteli* and *I. pini*, respectively (Reid 1955; Thomas 1961).

Interspecific Communication between *I. pini* and *P. knechteli*. *Pityogenes knechteli* males and females were attracted at statistically similar levels to bolts infested with conspecific males alone and in the presence of bolts infested with *I. pini* males (Fig. 2). Both male and female *P. knechteli* were apparently attracted to bolts infested with *I. pini* males alone, but the response was not significantly different from that to control traps, probably due to declining numbers over time causing a significant effect of replicate.

Significantly more *I. pini* of both sexes were caught in traps baited with *I. pini*-infested bolts alone and in the presence of *P. knechteli*-infested bolts than in traps baited with *P. knechteli*-infested bolts alone or uninfested control bolts (Fig. 2). The apparent but nonsignificant increase in attraction for *I. pini* males and females when *P. knechteli*-infested bolts were present was caused by an anomalously high catch in one replicate.

The hypothesis of mutual inhibition of attraction between *I. pini* and *P. knechteli* should be rejected. However, *P. knechteli* exploited the aggregation pheromone of *I. pini* to aid in host location (Figs. 1, 2). The relative response of male *P. knechteli* to *I. pini* males was higher than that of females, given a 1:5 sex ratio (Table 1). Thus kairomonal exploitation of the pheromone produced by *I. pini* may be more important for male *P. knechteli*, the pioneer sex in host location, than for females, whereas the aggregation pheromone produced by *P. knechteli* may be more important to *P. knechteli* females for mate location. There was a relatively greater response by male than female *I. pini* to *P. knechteli* males in one instance

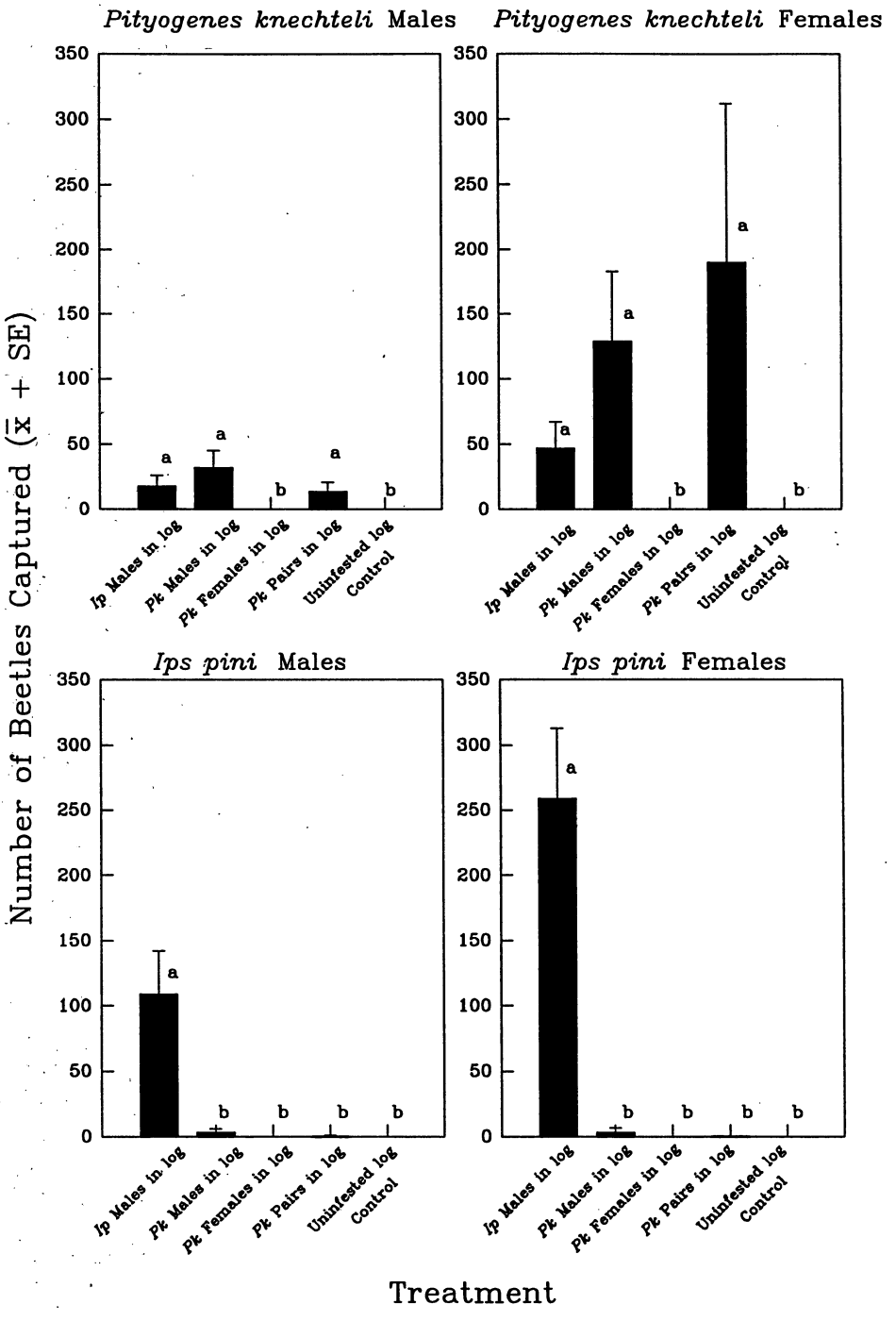

FIG. 1. Numbers of *Pityogenes knechteli* and *Ips pini* caught in multiple-funnel traps baited with lodgepole pine bolts infested by either species. For each responding species and sex, bars topped by the same letter are not significantly different, Bonferroni *t*-tests on data transformed by $X' = \log(X + 1)$, $P < 0.05$, $n = 4$.

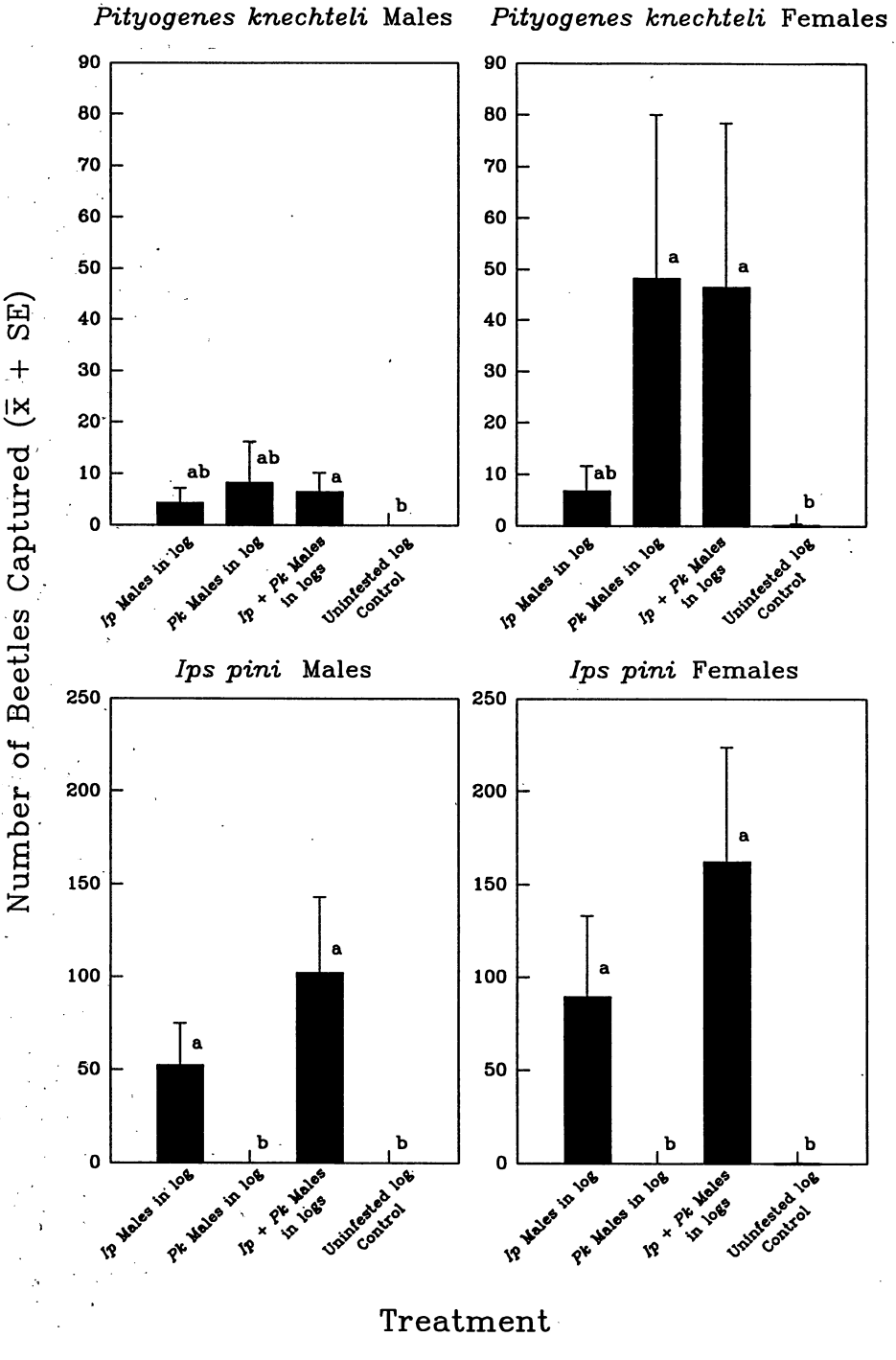

FIG. 2. Numbers of *Pityogenes knechteli* and *Ips pini* caught in multiple-funnel traps baited with a lodgepole pine bolt infested with either species, or two bolts, one infested with *P. knechteli* males and the other infested with *I. pini* males. For each responding species and sex, bars topped by the same letter are not significantly different, Bonferroni *t*-tests on data transformed by $X' = \log(X + 1)$, $P < 0.05$, $n = 4$.

TABLE 1. Male to female sex ratios for *Ips pini* and *Pityogenes knechteli* caught in multiple-funnel traps baited with lodgepole pine bolts infested with conspecific or heterospecific males

Responding species	Expt. No.	Stimulus	Total number captured		Male:female ratio	χ^2	*P*
			Males	Females			
I. pini	1	*I. pini* males	435	1037	1:2.38		
		P. knechteli males	13	14	1:1.08	4.376	0.036
	2	*I. pini* males	209	358	1:1.71		
		P. knechteli males	1	0	1:0	1.708	0.191
P. knechteli	1	*I. pini* males	74	187	1:2.53		
		P. knechteli males	128	514	1:4.02	7.566	0.006
	2	*I. pini* males	17	27	1:1.60		
		P. knechteli males	33	193	1:5.85	14.10	<0.0001

(Table 1), suggesting that *I. pini* males may weakly exploit the presence of *P. knechteli* males in selecting a host.

These results agree with those for the six-spined spruce bark beetle, *Pityogenes chalcographus* (L.), and the eight-spined spruce bark beetle, *Ips typographus* (L.), in European spruce trees (*Picea* spp.). *Pityogenes chalcographus* was attracted to Pheroprax, the commercial pheromone preparation for *I. typographus* consisting of 2-methyl-3-buten-2-ol (2MB), ipsdienol, and (*S*)-*cis*-verbenol. The male to female sex ratio for captured *P. chalcographus* was much higher than the natural sex ratio; mostly males were captured (Benz et al. 1986; Zuber and Benz 1992). Traps baited with the commercial pheromone preparation for *P. chalcographus*, Chalcoprax, a blend of chalcogran (2-ethyl-1,6-dioxaspiro[4,4]nonane), *E,Z*-2,4-methyl decadionate (MD), and 2MB, captured almost exclusively *P. chalcographus*, of which 60–70% were females. Traps baited with Pheroprax attracted mainly *I. typographus*, but also a fair number of *P. chalcographus* of which only 20–30% were females (Zuber and Benz 1992). Both species attack windthrown or weakened spruce trees, and resource partitioning could be mediated by the preference of the larger *I. typographus* for the thick bark of the lower two-thirds of the bole, and of *P. chalcographus* for younger trees or the crown region of larger trees (Benz et al. 1986).

A lack of mutual inhibition and evidence for cross-attraction as found for *P. knechteli* and *I. pini* is likely to occur wherever sympatric species of bark or ambrosia beetles commonly co-infest the same host tree. Mutual inhibition of each other's pheromones would be important in delineating breeding areas for sympatric bark beetles that do not co-infest the same host tree. To avoid competition, bark beetles that commonly co-infest the same tree would probably not interfere excessively with adjacent galleries of heterospecific beetles, but most competition would be avoided by partitioning the resource. Specificity of pheromones, and possible repellancy, may become important at close range as an aid in partitioning the resource. Mutual inhibition in host selection between *I. pini* and *P. knechteli* does not appear to be necessary, in part because the beetles are able to establish successful adjacent galleries, but primarily because they partition the resource on the basis of host diameter (Poland 1993; Poland and Borden 1994).

Pityogenes knechteli would be of limited value in causing competitive displacement of *I. pini* because of the lack of mutual inhibition between these two species and the ability of *P. knechteli* to co-exist successfully with *I. pini*. The amount of uncolonized phloem in co-attacked trees would be very low because *P. knechteli* occupies portions of the co-attacked phloem that are not utilized by *I. pini* (Poland 1993; Poland and Borden 1994). Attacks by

I. pini have been found to reduce progeny production by mountain pine beetles, *Dendroctonus ponderosae* Hopkins; rapidity of resource exploitation by *I. pini* was probably the main competitive factor (Rankin and Borden 1991). Competitive displacement of the mountain pine beetle might be enhanced through induction of attack by both *P. knechteli* and *I. pini*.

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