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Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*

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Abstract. Bark beetles, *Ips typographus* and *Pityogenes chalcographus*, attracted by synthetic or natural pheromone to Norway spruce logs, *Picea abies*, preferred to colonize uninfested logs rather than logs occupied by these beetles, probably as a means of avoiding intra- and interspecific competition. The aggregation pheromone components of *P. chalcographus*, chalcogran and methyl (E, Z)-2,4-decadienoate, inhibited the attraction response of *I. typographus* to its pheromone components (methyl butenol and *cis*-verbenol), while the converse was not true. However, verbenone released from colonized bark inhibited pheromonal response of *P. chalcographus*.

Key words. Semiochemical; pheromone; host selection; competition; Coleoptera; Scolytidae.

Intraspecific competition is a genetic selection force that can be expected to shape the evolution of a species through sexual selection, stabilizing selection, and competitive selection[1,2]. Similarly, interspecific competition involves a genetic selection influencing speciation and character displacement[3,4]. During competitive interactions, animals increase their expenditure of energy reserves and also incur greater risks of physical damage and mortality. Thus the avoidance of competition is advantageous whenever possible. Bark beetles (Coleoptera, Scolytidae) must compete for food and space in which to reproduce within the relatively thin phloem layer of their host tree. It has been found that as the number of bark beetle attacks in a bark area increases (attack density), the effects of competition cause a decrease in the number of offspring produced per parent[5-7].

The six-spined spruce bark beetle, *Pityogenes chalcographus*, and the eight-spined spruce bark beetle, *Ips typographus*, are the most serious pests of Norway spruce trees, *Picea abies*, in Europe. Male *P. chalcographus* bore into the host tree and produce two pheromone components, chalcogran (CH) and methyl (E, Z)-2,4-decadienoate (MD), that act synergistically to cause an aggregation of both sexes[8-10]. *I. typographus* also aggregates on Norway spruce in response to male-produced pheromone components, 2-methyl-3-buten-2-ol (MB) and (4S)-*cis*-verbenol (cV)[11]. The two species can be found alone or together in colonized trees, but when they occur together, *P. chalcographus* usually segregates in the top, smaller-diameter areas[12]. Experiments have shown that intra- and interspecific competition by these bark beetles for the phloem of their host tree can be severe (Byers, unpublished). The objective here was to determine whether host-seeking *I. typographus* and *P. chalcographus* avoid recently colonized bark areas of either species, and if so, whether olfactory semiochemical mechanisms are responsible for the avoidance.

The first experiment in the field tested the preference of *I. typographus* for logs previously infested with conspecifics compared with uninfested logs of the same age. A Norway spruce tree was felled and four logs (20 cm diam. × 50 cm) were sawn from the trunk. Two of the logs (A and B) were exposed side by side for 3.5 days to *I. typographus* attracted to a standard pheromone bait (50 mg MB/day and 1 mg cV/day)[13], while two other logs (C and D) were caged to prevent attacks. At noon on 10 June, attacks by males on the exposed logs were marked and counted. Logs C and D were then taken from the cage and all four logs exposed together for another 4.5 days at which time new attacks were counted. As seen in figure 1, logs A and B received about 60 attacks each during the first period but only 0 to 6 attacks in the second period, while the previously

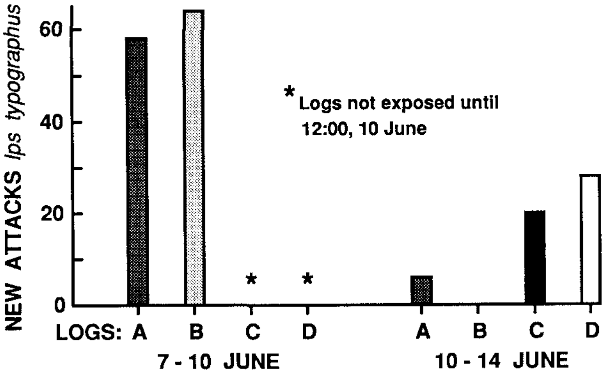

Figure 1. Attacks of *Ips typographus* on four Norway spruce logs (20 cm diam. × 50 cm) during two periods (7–10 and 10–14 June 1983, Skien, Norway). Logs A and B were exposed together to natural populations of bark beetle from 7–10 June in a forest clearcut, while logs C and D were unexposed until placed with logs A and B at 12.00 h on 10 June. Synthetic pheromone was used to attract beetles into the area. Logs C and D received significantly more new attacks than A and B during the second period ($p < 0.01$, χ^2).

unexposed logs C and D received the majority of new attacks. This indicates that *I. typographus* males avoided colonizing areas with higher densities of attack, where intraspecific competition would be more intense, and chose sites relatively free of competitors. The mechanisms for avoidance may be due, at least in part, to inhibition of the olfactory response by verbenone and ipsenol[14]. Verbenone has been shown to be released from individual entrance holes[15] and ipsenol is present in low amounts in males after nuptial chamber construction[16]. Other compounds may be involved as well as physical interactions between beetles.

Another test used three sets of three spruce logs (10 cm diam. × 29 cm freshly cut from a tree) artificially infested with 30 *I. typographus* males, 30 *P. chalcographus* males, or uninfested. Uniformly spaced holes were drilled into the phloem and males introduced two days prior to placing the logs in a forest clearcut. The three logs of a set were arranged in an equilateral triangle 30 cm on a side, and each set was spaced about 20 m from any other. After seven days the number of new attacks by these species were counted. Both species made new attacks but the differences between logs were not statistically significant, although the log with 30 male *I. typographus* received the least new attacks from *P. chalcographus* and the uninfested log had the most new *I. typographus* attacks (fig. 2, test A). The moderate initial density of male attacks (3.3/dm^2) apparently did not appreciably hinder new attacks. In test B, four sets of logs of the same diameter but half as long were artificially infested in the same way with either 5 or 48 male *I. typographus* or uninfested. These logs were placed in the same way in the field but this time baited with synthetic pheromone (MB + cV) to attract higher numbers of *I. typographus*. In this case, the number of new attacks of *P. chalcographus* significantly declined with density of *I. typographus*, and new attacks of *I. typographus* were significantly reduced at the highest density (10.5/dm^2, fig. 2, test B). These results indicate that both species avoid higher densities of *I. typographus* in order to reduce intra- and interspecific competition. *Ips* beetles may avoid intraspecific competition by an olfactory mechanism, in which males avoid higher concentrations of male-produced pheromone[17]. *I. typographus* males are relatively less attracted than females to higher releases of MB + cV odors[18, 19]. Aggregation pheromone components of bark beetles have also been shown to play a role in avoidance of interspecific competition. Both *I. pini* and *I. paraconfusus* avoid the colonized logs of the opposite species by means of an olfactory mechanism which includes inhibition by (+)-ipsdienol from *I. paraconfusus* and (−)-ipsdienol from *I. pini*[20–22]. Similarly, *I. paraconfusus* and *Dendroctonus brevicomis* preferred landing on logs colonized by their own species to landing on logs colonized by both species[23]. In this olfactory mechanism, verbenone from male *D. brevicomis* inhibits *I. paraconfusus* response to aggregation pheromone, while the aggregation pheromone components of *I. paraconfusus* (ipsenol, ipsdienol and cV) inhibit *D. brevicomis* aggregation response[24]. Similar semiochemical mechanisms might be present in *I. typographus* and *P. chalcographus*.

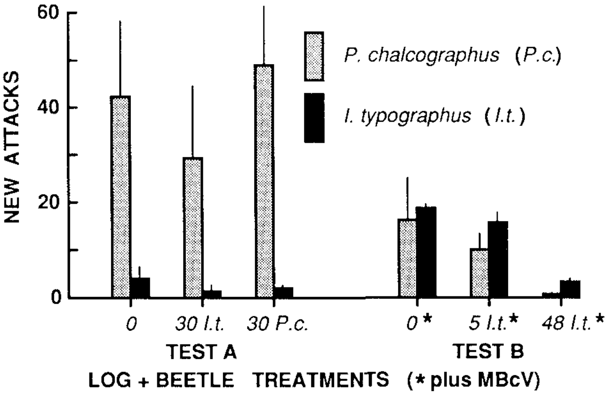

Figure 2. Mean number of new attacks of *Ips typographus* (I.t., n = 4) or *Pityogenes chalcographus* (P.c., n = 3) on Norway spruce logs (see text) artificially infested with different numbers of beetles (tests from 8–14 June 1983, Skien, Norway). Synthetic pheromone was used to attract *I. typographus* in test B. Vertical lines +SEM.

This was examined in test C (fig. 3) by three pipe traps with funnel[9, 18], spaced 11 m apart in a line, and releas-

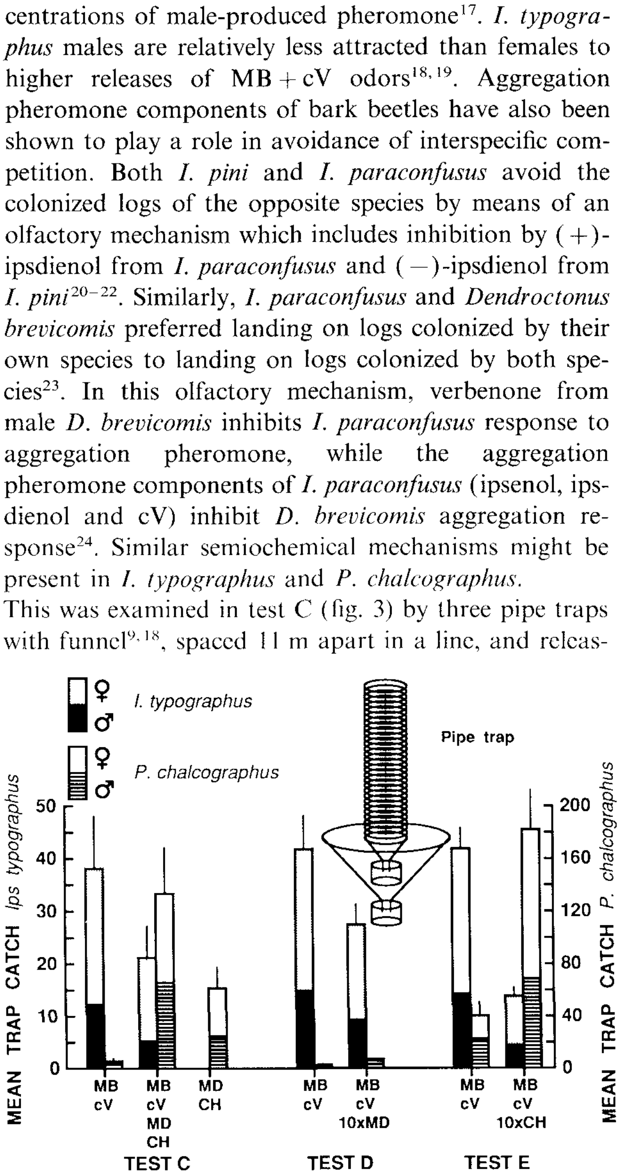

Figure 3. Catches of *Ips typographus* and *Pityogenes chalcographus* in pipe traps releasing various mixtures of the pheromone components of either *I. typographus* (MB, methyl butenol, and cV, *cis*-verbenol) or *P. chalcographus* (MD, methyl decadienoate, and CH, chalcogran) or both species (test C from 12 May–14 June and tests D and E from 14–17 June 1986, Hillerød, Denmark). Vertical lines above bars represent +SEM (n = 16–18). MB was released at 50 mg/day and cV at 1 mg/day as described previously[18], while MD was released at 18 µg/day (>99.5% pure) and CH at 1 mg/day (46% E:54% Z, >98% pure)[9]. Wilcoxon sign rank tests indicated that MD + CH, 10 × MD, or 10 × CH inhibited response of both sexes of *I. typographus* to MB + cV (tests C–E), while MB + cV increased response of both sexes of *P. chalcographus* to MD + CH in test C (all comparisons $p < 0.01$). The pipe traps with funnel used to catch beetles consisted of a vertically oriented black plastic cylinder (1.35 m × 12 cm diam. with 900, 2-mm diam. holes uniformly spaced over the surface[18] that was centered over a 33-cm diam. funnel.

ing MB + cV (*I. typographus*), MD + CH (*P. chalcographus*) or MB + cV + MD + CH in two clearcut areas (Grib Skov, Denmark, 12 May–14 June 1986; traps randomized after each replicate, n = 18). The attraction of *I. typographus* to its aggregation pheromone was significantly reduced by pheromone components of *P. chalcographus*. However, the response of *P. chalcographus* was not inhibited by the aggregation components of *I. typographus*; in fact there was a significant enhancement of attraction, as observed previously[25]. The *P. chalcographus* components, MD and CH, that together inhibited response of *I. typographus* in test C were tested separately at higher release rates to determine if either alone was active. In tests D and E (fig. 3, 14–17 June 1986; design as in test C, n = 16), the attraction of both sexes of *I. typographus* to their pheromone MB + cV was significantly reduced by odors of either MD or CH (each released at 10 times the rate of their release together in test C).

The pipe trap collects beetles separately either in the funnel or when entering the pipe, allowing comparisons between the male/female sex ratios responding to the pheromone baits (table 1). In *P. chalcographus*, a higher ratio of males to females caught was observed in baits where *I. typographus* components were released. Only 7.6% of the *P. chalcographus* males and females entered the pipe when their pheromone components were released, but significantly more (21–33%) were induced to enter holes by MB + cV (all comparisons $p < 0.001$, χ^2). Host monoterpenes such as α-pinene, β-pinene, and 3-carene have also been shown to induce *P. chalcographus* to enter holes in pipe traps[9]. In *I. typographus*, the male/female ratio caught on control MB + cV baits decreased on the baits containing both *P. chalcographus* components ($p < 0.05$), but no significant differences were found for MD or CH components alone (table 1). However, significantly fewer males than females of *I. typographus* entered the pipe than were caught in the funnel. Previously it has been shown that *I. typographus* males are more likely to be caught in the funnels than in the pipe[18,19]. This is consistent with reports that males of both species, and *I. paraconfusus* (California, USA), are more diffuse in their orientation to pheromone than females[9,13,17–19], probably in order to avoid areas of high attack density and intraspecific competition.

Several bark beetle species in the genera *Dendroctonus*, *Tomicus* and *Ips*, including *I. typographus*, are inhibited by verbenone, a compound contained in large amounts in hindguts of some of these species (*Dendroctonus*) but in low amounts (*Tomicus*) or nearly absent in others (*Ips*)[16,26–30]. Verbenone may also be produced by microorganisms, but it is certain that it is released increasingly by aging logs of spruce and pine colonized by bark beetles[15,30]. The effect of verbenone on attraction response of *P. chalcographus* was tested with a pair of sticky traps separated by 6 m and rotated slowly at 2 rph[31]. Each trap released aggregation pheromone components of *P. chalcographus* (MD + CH) but one trap also released (−)-verbenone, and this latter trap caught only 48% as many beetles (table 2).

If verbenone is a consistent signal of microbial activity in decaying hosts, then this could have been used initially by evolving bark beetles as a kairomone to avoid less suitable hosts. Later during evolution verbenone

Table 1. Male/female sex ratios of catches of *Pityogenes chalcographus* and *Ips typographus* caught in funnel or entering pipe (total catches of 16–18 replicates in parentheses) during attraction to MD + CH (methyl decadienoate and chalcogran, pheromone components of *P. chalcographus*), MB + cV (methyl butenol and *cis*-verbenol, pheromone components of *I. typographus*), or various combinations (test C: 12 May –14 June, tests D and E: 14–17 June 1986, Hillerød, Denmark). Descriptions of the pipe traps with funnel and chemical release rates are given in figure 3.

Test) Bait chemicals	Male/female sex ratio (n) Funnel	Entering pipe	% Entering pipe
P. chalcographus			
C) MD + CH	0.68 (1022)***[a]	0.68 (84)	7.6***
C) MD + CH + MB + cV	0.97 (1861)	1.00 (538)	22.4
D) MB + cV	12.00 (26)**	1.33 (7)	21.4
D) MB + cV + 10 × MD	1.23 (49)	1.67 (24)	32.9
E) MB + cV	1.26 (436)***	1.33 (207)***	32.2**
E) MB + cV + 10 × CH	0.61 (2149)	0.59 (762)	26.2
I. typographus			
C) MB + cV	0.60 (391)*[***][b]	0.34 (295)	43.0
C) MD + CH + MB + cV	0.40 (225)	0.24 (156)	40.9
D) MB + cV	0.81 (334)[***]	0.31 (251)	42.9
D) MB + cV + 10 × MD	0.74 (236)[***]	0.24 (148)	38.5
E) MB + cV	0.68 (374)[***]	0.35 (295)	44.0**
E) MB + cV + 10 × CH	0.63 (147)[**]	0.24 (73)	33.0

[a] Sex ratios (percentages entering pipe) were significantly different between chemical baits in the same test, column, and species with *, **, or *** indicating $p < 0.05$, 0.01, or 0.001, respectively (χ^2).

[b] Sex ratios were significantly different between funnel and entering pipe in the same row with [*], [**], or [***] indicating $p < 0.05$, 0.01, or 0.001, respectively (χ^2).

Table 2. Effect of (−)-verbenone on the attraction of *Pityogenes chalcographus* to their pheromone components MD + CH (methyl decadienoate plus chalcogran, chemicals released from a pair of sticky traps, 6 m apart, mechanically rotated at two rph[31] during the afternoon; Hillerød, Denmark)

Bait chemicals	Sticky trap Males	Females	Catch, total
13 May 1988			
MD + CH	139	400	539
MD + CH	160	422	582
17 May 1988			
MD + CH + verbenone	100[a,b]	174[b]	274[b]
MD + CH	165	409	574

[a]Male/female ratio significantly greater than corresponding ratio on MD + CH ($p < 0.05$, χ^2).
[b]Catches on paired traps (within the column) were significantly different than expected assuming equal proportions ($p < 0.001$, χ^2).
MD and CH release as in figure 3. Verbenone was >99% pure, $[\alpha]_D^{20} = -246°$, 99.2% e.e. (Bedoukian) and released at 0.25 mg/day[30].

could, in addition, serve as a pheromone to avoid intraspecific competition and as an allomone to avoid interspecific competition. Verbenone production in beetles would coevolve in several species since the same chemical could serve as the signal for all three beneficial messages (kairomone, pheromone, and allomone). *I. typographus* avoidance of areas colonized by *P. chalcographus* is due at least in part to inhibition by MD, CH and verbenone, while *P. chalcographus* avoids verbenone (probably released from older colonized substrates of both species).

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