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INTERSPECIFIC INHIBITION OF THE RESPONSE OF THE BARK BEETLES, *Dendroctonus brevicomis* AND *Ips paraconfusus*,[1] TO THEIR PHEROMONES IN THE FIELD

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Abstract—Ponderosa pine logs infested with *Ips paraconfusus* males inhibited the attraction of *Dendroctonus brevicomis* in the field to either attractive logs cut from a ponderosa pine tree under attack by *D. brevicomis* or to their synthetic pheromones, *exo*-brevicomin, frontalin, and myrcene. Logs cut from trees under attack by *D. brevicomis* inhibited the response of *I. paraconfusus* to logs infested with male *I. paraconfusus*. *Exo*-brevicomin, frontalin, and myrcene did not inhibit their response but verbenone did. Verbenone was found in male *D. brevicomis* dissected from attractive logs under attack during the same time the response of *I. paraconfusus* was inhibited by these logs. *Trans*-verbenol and *exo*-brevicomin were found in female *D. brevicomis* while verbenone, *trans*-verbenol, and frontalin were found in male *D. brevicomis* in relatively large amounts near the beginning of the aggregation phase of host colonization. All of these compounds had decreased at a similar rate 5 days later. This gradual decrease in *exo*-brevicomin and frontalin probably caused the observed reduction in attraction. The ecological significance of these compounds in relation to termination of the aggregation phase of *D. brevicomis* and reduction of interspecific competition is discussed.

Key Words—*Dendroctonus brevicomis*, *Ips paraconfusus*, *Pinus ponderosa*, bark beetle, *exo*-brevicomin, frontalin, myrcene, verbenone, *trans*-verbenol, attractants, inhibition, pheromones.

[1]Coleoptera: Scolytidae. This paper is based in part upon a dissertation submitted by J.A.B. to the University of California, Berkeley, in partial fulfillment of the requirements for the PhD in entomology. These studies were supported in part by the Rockefeller Foundation; U.S. Forest Service; Regional research Project W-110, S.E.A./U.S.D.A.; and the National Science Foundation and Environmental Protection Agency through a grant (NSF GB-34719/BMS 75-04223) to the University of California.

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INTRODUCTION

The western pine beetle, *Dendroctonus brevicomis* LeConte, and the California 5-spined ips, *Ips paraconfusus* Lanier, colonize the phloem and cambium tissues of ponderosa pine, *Pinus ponderosa* Laws., during the same time periods in California. Once the beetles begin feeding, pheromones and other volatile compounds accumulate in their hindguts and are excreted with fecal material in the frass (Wood and Bushing, 1963; Pitman and Vité, 1963; Pitman et al., 1965; Wood et al., 1966; Renwick, 1967; Silverstein et al., 1966a, 1968). The pheromone components of *D. brevicomis* are *exo*-brevicomin (E) (female produced), frontalin (F) (male produced), and myrcene (M) (released by wounding of the host resin system) (Silverstein et al., 1968; Kinzer et al., 1969, Pitman et al., 1969). The attractive pheromone components of *I. paraconfusus* are ipsenol (male produced), *cis*-verbenol (produced by both sexes), and ipsdienol (male produced) (Silverstein and Rodin, 1965; Silverstein et al., 1966a,b; Wood et al., 1966; Renwick et al., 1976). The three pheromone components of each species must be released simultaneously for maximum activity in attracting both sexes in laboratory and field bioassays (Wood et al., 1976, 1967, 1968; Bedard et al., 1969, 1970, 1980a; Silverstein et al., 1968; Vité and Pitman, 1969a,b; Wood, 1970).

The female *D. brevicomis* initiates the entrance tunnel and is joined by a male, usually within a day or two (Miller and Keen, 1960). The males of emerged *D. brevicomis* are reported to contain verbenone in their hindguts (Renwick, 1967; Vité and Renwick, 1970; Renwick and Vité, 1970) which is released (Libbey et al., 1974; Browne et al., 1979) and inhibits the beetles' response to pheromones (Renwick and Vité, 1970; Hughes and Pitman, 1970; Wood, 1972; Bedard et al., 1980b). Verbenone has been proposed to cause beetles to terminate aggregation when the tree is fully colonized (Renwick and Vité, 1970; McNew, 1970). By contrast, in *I. paraconfusus* the male initiates the attack and is then joined usually by 3 females. Intraspecific compounds that inhibit the attractive response of *I. paraconfusus* have not been reported, and the cessation of the aggregation phase may simply result from a reduction in pheromone production (Pitman et al., 1966).

Both species frequently inhabit the same ponderosa pine. However, *D. brevicomis* usually begins colonization in the lower trunk and lower level of the crown while *I. paraconfusus* usually initiates attacks in upper areas of the crown (Struble and Hall, 1955; Miller and Keen, 1960). The proportion of the tree occupied by either species varies considerably, but the area of their overlap is usually quite limited. The mechanism of segregation may include the production and release of interspecific inhibitory compounds as shown by Birch and Wood (1975) for *I. paraconfusus* and *I. pini* (Say). The primary objective of this study was to determine if similar interspecific inhibition could

be demonstrated for *I. paraconfusus* and *D. brevicomis* (i.e., the lowering of the catch at traps baited with pheromones of both species).

METHODS AND MATERIALS

I. paraconfusus beetles were collected from the Sierra National Forest near Bass Lake, Madera Co., California, at an approximate elevation of 1000 m. Logging slash containing late larval stages and callow adults was placed in emergence cages for the rearing and collecting of adult beetles (Browne, 1972).

The field experiments were conducted in the same areas where the beetles were collected at elevations from 900 to 1200 m. Logs with 50 male *I. paraconfusus*, logs from trees naturally infested with *D. brevicomis*, and synthetic pheromones of *D. brevicomis* were used in various tests. Logs (approximately 14 cm diam. by 28 cm long) were cut from ponderosa pine trees and stored less than one month at 4°C before male beetles were introduced head-first into drilled holes (Wood et al., 1968; Lanier et al., 1972). Each log then was wrapped with aluminum window screen to prevent attack by attracted beetles. Control logs were drilled and screened in the same way but without beetles. Beetles were introduced 48 hr before each test to allow maximum pheromone production (Wood et al., 1966). The log then was placed in a "small" sticky-trap (19 cm diam. × 30.5 cm high) supported on a pipe standard 1.2 m above the ground (Bedard and Browne, 1969).

Synthetic pheromones were used in some of the tests to provide a source of attraction or inhibition. *Exo*-brevicomin (>95%), frontalin (>95%), and myrcene (>97%) (E,F,M) (Chem. Samples Co., Cleveland, Ohio) were released in the field from a releasing device (developed by Rodin for U.S. Forest Service). The device consisted of an inverted 7.6-cm salt shaker covered with aluminum foil which contained each compound in separate glass tubes sealed at one end. *Exo*-brevicomin and myrcene were in 5- × 55-mm tubes filled to a level 30 mm below the opening, while frontalin was in a 4- × 65-mm tube filled to a level 40 mm from the top. Weight losses for each of these compounds averaged 2 mg/day under field conditions (Browne, 1978). Verbenone (GLC purified, >99.8%, $[\alpha]_{25}^{D} = +90°$, Chem. Samples Co.) was released at about 4 mg/day from a glass container (1 cm diam. × 0.5 cm high) half filled and placed inside the salt shaker (Bedard et al., 1980b).

Natural *D. brevicomis* pheromone substrates were obtained by placing several E, F, M release devices on a ponderosa pine tree so that beetles would initiate the mass-attack (Bedard et al., 1980b; Wood and Bedard, 1977). After about 2 days, the tree was felled and sectioned into 0.5- or 0.6-m logs and 2 logs were placed on pipe standards inside sticky-traps. These large sticky-traps were built by criss-crossing two (76 × 203 cm) vinyl-coated fiberglass

screens (Browne, 1978) coated with Stikem Special® (Mickel and Pelton, Emeryville, California) over 4 (1.54 m long) stakes driven vertically into the ground in such a way as to form a box 76 cm wide × 67 cm high.

Inhibition of Response of D. brevicomis. The inhibition of the response of *D. brevicomis* to either E, F, M or its naturally produced pheromone by *I. paraconfusus* was tested by comparing the number of *D. brevicomis* caught daily at two sticky-traps. In the first test, two small sticky-traps placed 11–12 m apart each contained an E, F, M release device while one trap also contained a log infested with 50 male *I. paraconfusus* and the other trap contained an uninfested log. These 2 logs were interchanged each day of the test period while the E, F, M release devices and sticky-traps remained stationary (August–September, 1975). A test of the inhibition of *D. brevicomis* by synthetic pheromones of *I. paraconfusus* was not attempted because sufficient quantities of the compounds were not available.

In the second test, inhibition of the response of *D. brevicomis* to naturally produced pheromone by logs infested with *I. paraconfusus* was tested by comparing the catch of *D. brevicomis* at two large sticky-traps. The large sticky-traps, placed 11–12 m apart, each contained two logs (0.5 m long) from a tree naturally-infested with *D. brevicomis*. One trap also contained a log with 50 male *I. paraconfusus* and the other trap contained an uninfested log. The *I. paraconfusus* log and uninfested log were interchanged each day while the traps and *D. brevicomis* logs remained in place (September, 1975). The naturally infested *D. brevicomis* logs were obtained by sectioning a 32-cm-DBH (diameter of breast height) ponderosa pine tree 2 days after inducing an attack of *D. brevicomis* by placing E, F, M release devices at heights of 3, 6, and 12 m.

Each trap held the treatment and check an equal number of days to minimize variation due to trap position and to E, F, M or natural pheromone release rates. *D. brevicomis* were picked from the traps each day and placed in mineral spirit solvent to remove the stikem. The sex of the beetles was determined, and the sex ratios with binomial confidence limits (95%) were determined by the following formulas adapted for use with the quadratic formulas of Spiegel (1961) for determining binomial confidence limits for proportions:

$$\text{Sex ratio} = \text{number of males}/\text{number of females} = P/1 - P$$
$$\text{Upper confidence limit} = P_u/1 - P_u$$
$$\text{Lower confidence limit} = P_l/1 - P_l$$

The nonparametric Wilcoxon test for two paired samples (McCall, 1970) was employed for the comparison of the number and sex caught on the treatment and check traps the same day. Also, the Wilcoxon test was used to compare the treatment and check catches on successive days in the same trap

position, i.e., compare position a, day 1, containing the *I. paraconfusus* log to position a, day 2 without the *I. paraconfusus* log. However, only day 1 with 2, day 3 with 4, and day 5 with 6 were compared. Finally, the Wilcoxon test was used to determine if one sex was inhibited more than the other. The ratio of the number of male *D. brevicomis* caught on the treatment traps to the number caught on the check traps was compared to a similar ratio of catch for females.

Inhibition of Response of I. paraconfusus. The possibility that the attraction of *I. paraconfusus* to male pheromone substrates could be inhibited by the presence of natural *D. brevicomis* pheromone substrates was investigated. The naturally infested *D. brevicomis* substrates were obtained as described above by placing two E, F, M elution devices on a 39-cm-DBH ponderosa pine tree at heights of 1.5 and 6.8 m at 8 AM, on August 24, 1976. At 8 AM, August 27, the tree was sectioned into 0.6-m logs, numbered 1–9, with the first log beginning at the 1.2-m height. Each of three replicates consisted of two large sticky-traps 11–12 m apart both containing a log with 50 male *I. paraconfusus* and one trap also contained two of the *D. brevicomis* logs (#1 + 6, 2 + 5, or 3 + 8). On each day of the test (August 27–30, 1976) the *D. brevicomis* logs were alternated between paired traps while the *I. paraconfusus* logs and traps remained stationary. The bark beetle predator, *Enoclerus lecontei* Wolc. (Coleoptera: Cleridae) also was collected each day from the traps.

Finally, the possibility that E, F, M could inhibit the attraction of *I. paraconfusus* to naturally produced pheromone was tested by placing two small sticky-traps 11–12 m apart, each containing a log infested with 50 male *I. paraconfusus*. One of the traps also contained an E, F, M release device. The E, F, M release device was alternately placed on one trap of the pair each day during the test (August 30–September 4, 1976). The possibility that verbenone could inhibit the response of *I. paraconfusus* to naturally produced pheromones was tested in a similar way (June 25–28, 1976).

Identification and Quantification of Pheromones in Hindgut of D. brevicomis *Removed from a Naturally Infested Tree.* The sex ratio within the galleries and the production of pheromones compounds by *D. brevicomis* were monitored near the start and at the end of the inhibition of *I. paraconfusus* test period. Log 4 was dissected at 4 PM on August 27 by carefully peeling the bark off with a draw knife, collecting the beetles from the galleries, and recording the number of excavations. Log 5 (used in the test) was dissected similarly at 10 PM on August 31.

The identification and quantities of pheromones found in the hindguts of *D. brevicomis* feeding in ponderosa pine for approximately 3 days and 8 days (tree parts used in the test of inhibition of *I. paraconfusus*) were determined by extraction and gas-liquid chromatography (GLC). The last abdominal segment was grasped with fine forceps and pulled away from the beetle to

remove the hindgut and a portion of the midgut from 50 males and 50 females collected on the two dates from the dissected logs. The guts were placed in 1-ml Mini-Vials (Applied Science Lab., Inc.) containing 0.1 ml ground glass and 0.35 ml diethyl ether, and crushed with a small glass rod. The extracts were injected onto two GLC (1.8 m × 2 mm ID) glass columns (10% FFAP on 80/100 Gas Chrom Q with the N_2 carrier gas at 30 ml/min at 100°C and 3% Apiezon L on 100/120 Gas Chrom Q with the N_2 flow at 12 ml/min at 100°C. Standards of *exo*-brevicomin, frontalin, *trans*-verbenol (GLC purified, >99%) (Glidden Organics, Jacksonville, Florida), and verbenone were compared quantitatively to the peaks from the hindgut extracts. The pheromones and some of the associated compounds in the hindgut extracts also were identified by coinjecting on both columns a portion of each hindgut extract with comparable quantities of *exo*-brevicomin (2.5×10^{-8} g/μl), frontalin (2.5×10^{-8} g/μl), *trans*-verbenol (10^{-8} g/μl), and verbenone (6×10^{-9} g/μl).

RESULTS AND DISCUSSION

Inhibition of Response of D. brevicomis. The attraction of *D. brevicomis* to E, F, M or to naturally infested *D. brevicomis* logs was inhibited by logs infested with *I. paraconfusus* males (Figures 1 and 2; Table 1). In both cases, *D. brevicomis* males and females were inhibited to about the same degree (Table 1). The pheromone-producing substrates used in the tests had only one species present in each log, so the observed inhibition probably was due to responses of flying beetles to the pheromones and/or other compounds released by the two species. If both species had been placed in the same log (Birch and Wood, 1975), there could have been interactions between feeding beetles which might have inhibited production and release of compounds in one or both species. Furthermore, by separating the two species in different logs and by interchanging the *I. paraconfusus* infested log and the uninfested log each day, the variation due to day, position, trap, and unequal pheromone release could be equally distributed between treatment and check. In the tests for inhibition of *D. brevicomis* response to E, F, M or to natural pheromone, an average of 17 and 142 *I. paraconfusus* were caught per day, respectively, showing that pheromone was released during each test period.

The *I. paraconfusus* infested logs had an immediate effect on the response of *D. brevicomis* because traps containing the same *D. brevicomis* logs caught significantly different numbers of beetles on successive days (Figure 1; Table 1). This effect was terminated as soon as the *I. paraconfusus* log was replaced with a check log. The inhibition of *D. brevicomis* response to E, F, M by an *I. paraconfusus* log proved that the reduced catch was caused by compounds released by *I. paraconfusus* rather than possible effects of species interaction

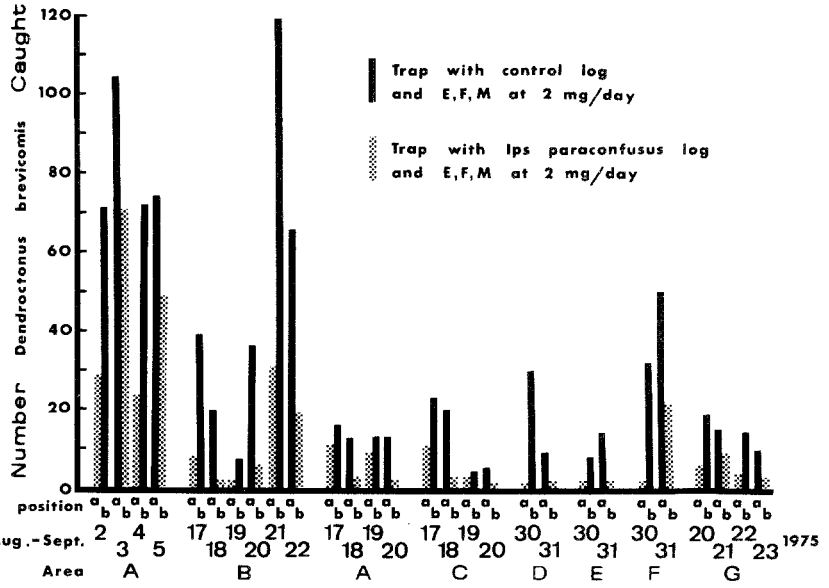

FIG. 1. Inhibition of the response of *Dendroctonus brevicomis* to E, F, M by volatiles released by *Ips paraconfusus* males boring in ponderosa pine. Treatment and check were alternated each day between positions a and b.

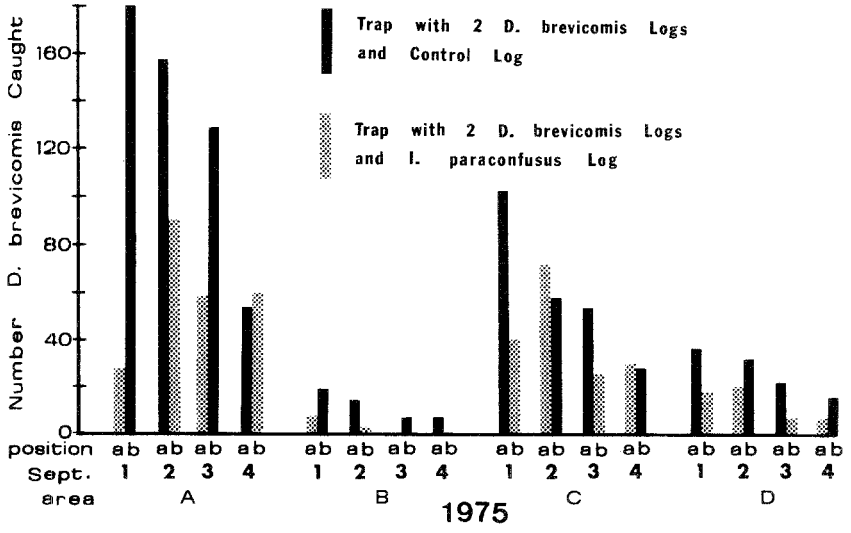

FIG. 2. Inhibition of the response of *Dendroctonus brevicomis* to natural pheromones by volatiles release by *Ips paraconfusus* males boring in ponderosa pine. Treatment and check were alternated each day between positions a and b.

TABLE 1. INHIBITION OF RESPONSE OF *D. brevicomis* and *I. paraconfusus* TO NATURAL AND SYNTHETIC PHEROMONE BY VERBENONE OR VOLATILES FROM INFESTED LOGS

Treatment vs. control	No. caught (♂:♀)	Sex ratio (♂:♀)	Inhibition *P* value[b] (total) Sex: Male	Female	Same day	Successive day	♀ > ♂[c]
Inhibition of *D. brevicomis*							
D. brevicomis,	463	0.84					
I. paraconfusus,	212:251	(0.70–1.00)[a]	0.007		0.002		0.31
vs.							
D. brevicomis	896	0.93	0.010		0.001		
	432:464	(0.82–1.06)					
EFM,	329	1.02					
I. paraconfusus	166:163	(0.82–1.26)	<0.001		<0.001		0.13
vs.							
EFM	928	0.87	<0.001		<0.001		
	433:495	(0.77–0.96)					
Inhibition of *I. paraconfusus*							
I. paraconfusus,	899	0.51					
D. brevicomis	305:595	(0.45–0.59)	0.010		0.004		0.008
vs.							
I. paraconfusus	2,622	0.33	0.003		0.015		
	651:1,971	(0.30–0.36)					
I. paraconfusus,	1,156	0.20					
EFM	194:962		0.960		0.390		
vs.							
I. paraconfusus	1,283	0.20	0.290		0.750		
	214:1,069						
I. paraconfusus,	67	0.34					
verbenone	17:50	(0.20–0.59)	0.036		0.012		0.036
vs.							
I. paraconfusus	798	0.13	0.012		0.012		
	91:707	(0.10–0.16)					

[a] Binomial confidence limits (95%) in parentheses.
[b] *P* values obtained with the Wilcoxon signed-rank test from comparisons of catch on the same day except as indicated.
[c] A small *P* value (<0.05) indicates that female beetles were inhibited more strongly than males.

on release of E, F, M by *D. brevicomis* in logs. Although E, F, M might effect *I. paraconfusus* pheromone production, nevertheless, *I. paraconfusus* inhibited the *D. brevicomis* response to E, F, M. The number of *D. brevicomis* caught on traps with E, F, M was relatively constant each day (Figure 1) while the number caught on traps with natural pheromone decreased each day ($r = -0.39$; $S_{yx} = 53.1$) (Figure 2).

Inhibition of Response of I. paraconfusus. The response of *I. paraconfusus* to pheromones produced by males was inhibited by volatiles released from naturally infested *D. brevicomis* logs (Figure 4; Table 1). However, the response of *I. paraconfusus* was not inhibited by the synthetic pheromones, E, F, M, of *D. brevicomis* (Table 1). Instead verbenone, which is produced by male *D. brevicomis*, inhibited the attraction of *I. paraconfusus* to logs infested with males (Figure 3; Table 1). Although both sexes were inhibited by verbenone, females appeared to be more strongly affected than males (Table 1). Female *I. paraconfusus* are reported to be more responsive to synthetic pheromones and to naturally produced frass than male beetles (Wood and Bushing, 1963; Pitman et al., 1965; Borden, 1967) so that verbenone might disproportionately inhibit females. The structural similarity of verbenone to *cis*-verbenol indicates that verbenone may competitively inhibit the acceptor site for *cis*-verbenol in *I. paraconfusus*. The other pheromones of *I. paraconfusus*, ipsenol and ipsdienol, have been shown to be essentially unattractive in the field without the addition of *cis*-verbenol (Wood et al., 1967; 1968). The enantiomeric composition of verbenone was approximately 68% (+) and 32% (−). The possible role of specific enantiomers, as demonstrated already for *D. brevicomis* (Wood et al., 1976) and *Gnathotrichus sulcatus* (Borden et al., 1976), remain to be examined.

Young et al. (1973) isolated ipsenol, *cis*-verbenol, ipsdienol, and verbenone from both the male frass and headspace volatiles of *I. confusus*

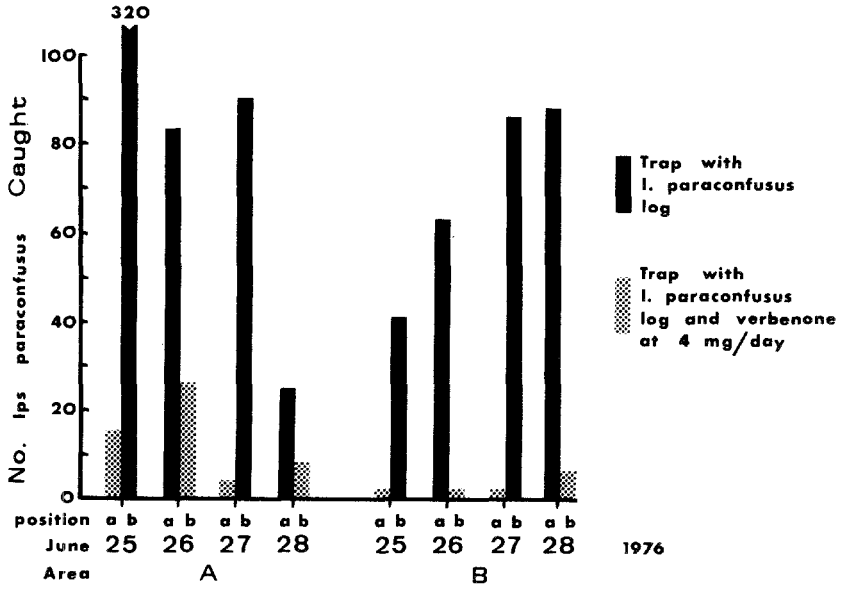

FIG. 3. Inhibition of the response of *Ips paraconfusus* to natural pheromone by verbenone.

LeC., a sibling species of *I. paraconfusus*, that feeds in pinyon pine, *Pinus monophylla* Torr. and Frem. Lanier and Wood (1975) found that *I. paraconfusus* and *I. confusus* infested logs were interspecifically attractive in areas where only one of the species occurred. However, *I. paraconfusus* preferred its own frass when samples of each species were presented simultaneously in the laboratory. In another experiment, significantly more *I. paraconfusus* females entered male nuptial chambers of their own species than those of *I. confusus* when logs containing each species alone were placed together in the field. Finally, in that experiment there were 107 volunteer attacks by *I. paraconfusus* on the logs containing *I. paraconfusus* while only three occurred on the *I. confusus* logs. Therefore, the preference of *I. paraconfusus* for its own species may be due, in part, to the release of verbenone from male *I. confusus* infested logs.

The response of *I. paraconfusus* to its naturally produced pheromone was inhibited by volatiles released from *D. brevicomis* logs in the field (Figure 4; Table 1), and as with verbenone, both sexes were inhibited but females to a greater extent (Table 1). The ponderosa pine logs infested with *D. brevicomis* obtained by baiting a tree with E, F, M appeared to be comparable to naturally infested trees. The attack density (166/m^2) and sex ratio (1 m: 1.16 f; no more than 1 m/f) were within the limits observed for a tree under colonization for less than 3.5 days (Miller and Keen, 1960; Bedard et al., 1980b). The logs infested with *D. brevicomis* appeared to be releasing E, F, M since *D. brevicomis* were attracted each day of the 4-day inhibition test (Figure 5). However, the number of *D. brevicomis* caught declined each day during the trapping period which was from 3 to 7 days after baiting

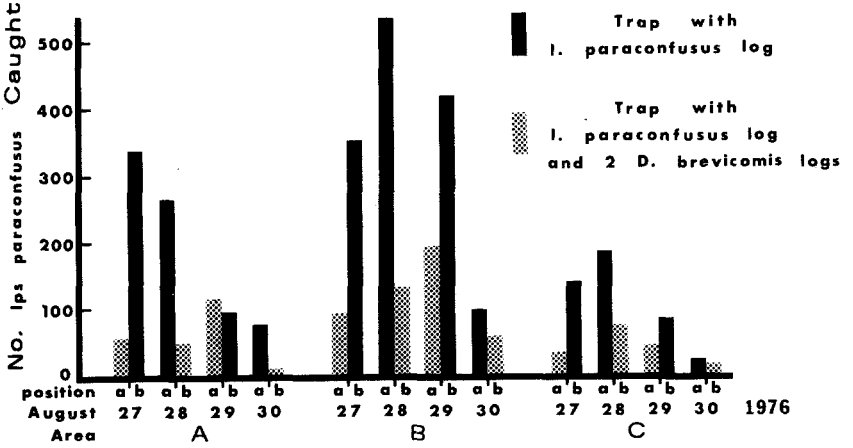

FIG. 4. Inhibition of the response of *Ips paraconfusus* to natural pheromone by volatiles released by *Dendroctonus brevicomis* boring in ponderosa pine logs removed from trees under attack.

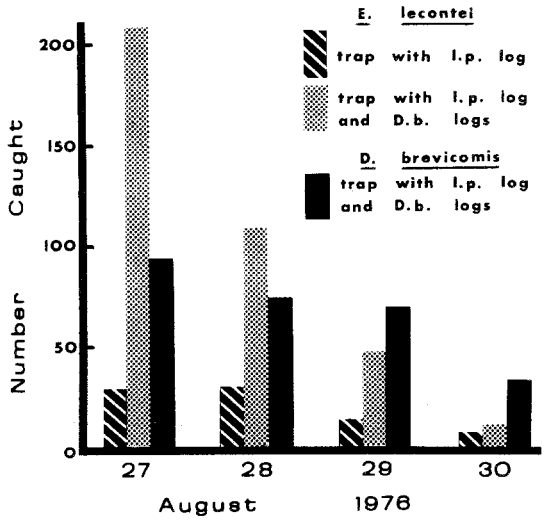

FIG. 5. Attraction of *Enoclerus lecontei* and *Dendroctonus brevicomis* to traps containing logs infested with *Ips paraconfusus* and to traps containing logs with both *Ips paraconfusus* and *Dendroctonus brevicomis*.

($r = -0.44$; $S_{yx} = 15.6$). This reduction in attraction to naturally infested logs was probably due to a reduction in pheromone production and release (Figure 6). Similarly, a decline in number caught also was observed during the study of *D. brevicomis* inhibition (Figure 2) as well as in other studies observing infested logs or trees (Miller and Keen, 1960; Vité and Pitman, 1968; Stephen and Dahlsten, 1976). However, our findings do not support the statement by Vité and Pitman (1968) that "production of pheromone continues only as long as the host resists extensive feeding and gallery construction." Browne et al. (1979) have quantified these pheromonal components released into the air around infested logs in the laboratory and trees under attack in the field but the relationship of these estimates to production of these compounds in the beetle is not known.

Interspecific inhibition of the response to pheromones may function to segregate the two bark beetle species in distinct areas of the tree and to reduce areas of competition for food and space. Verbenone and compounds isolated from *I. paraconfusus* that inhibit response of *D. brevicomis* to its pheromones may prove useful as behavior modifying chemicals that would inhibit the aggregation phase of host colonization and perhaps reduce tree mortality.

E. lecontei, a predator of both bark beetle species, has been reported to be attracted to *D. brevicomis* infested trees (Berryman, 1966; Vité and Gara, 1962) as well as to *I. paraconfusus* synthetic pheromones (Wood et al., 1968) and to several ponderosa pine monoterpenes such as M (Pitman and Vité,

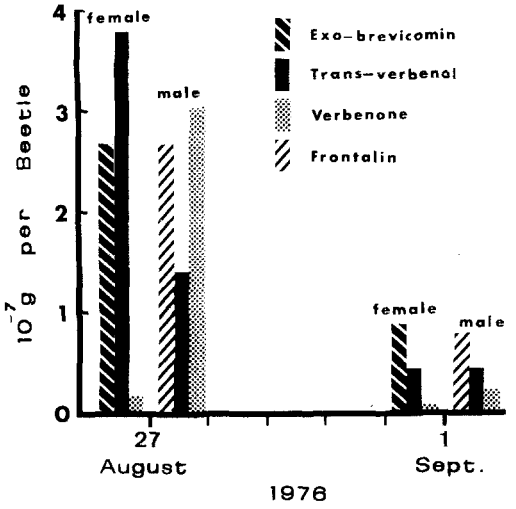

FIG. 6. Quantities of pheromonal compounds (E,F), verbenone, and *trans*-verbenol found in hindguts of male and female *Dendroctonus brevicomis* feeding in ponderosa pine logs cut from a tree under colonization.

1970). *E. lecontei* was attracted in higher numbers to traps containing logs infested with both bark beetle species than to logs with *I. paraconfusus* only ($P = 0.006$). Because logs infested with *D. brevicomis* were not tested alone, we could not determine if this increased response was due to synergism among compounds produced by both species or simply due to the attraction produced by *D. brevicomis* alone.

Identification and Quantification of Pheromones in Hindguts of D. brevicomis *Removed from a Naturally Infested Tree.* The quantities of F and E found in male and female *D. brevicomis*, respectively (Figure 6), following dissection from the logs used in the test demonstrating inhibition of the *I. paraconfusus* response, indicates that these pheromones were present in the greatest amounts at the beginning of the trapping period when the catch of *D. brevicomis* also was highest (Figure 5).

Previous studies have shown that hindguts of emerged *D. brevicomis* males that have not fed on the new host had verbenone and trace amounts of *trans*-verbenol while the females contained *trans*-verbenol and either undetectable or trace amounts of verbenone (Renwick, 1967; Renwick and Vité, 1968, 1970; Vité and Renwick, 1970; Pitman et al., 1969). In those studies, the amounts of *trans*-verbenol and verbenone present in these beetles were not quantified. The presence of verbenone in feeding males has been reported (Hughes, 1973), and this compound was recently found in air surrounding either female or female/male infested logs (Browne et al., 1979). In our

studies, verbenone occurred in the largest amounts in male *D. brevicomis* at the same time that the greatest inhibition of the response of *I. paraconfusus* occurred (Figure 4). For example, on the first day of the test, the traps containing both *D. brevicomis* infested logs and a log infested with *I. paraconfusus* caught only 23% as many *I. paraconfusus* as did traps containing logs infested with *I. paraconfusus* alone. On succeeding days, traps with both species caught 27%, 60% and 39% as many. The quantities of verbenone found in male *D. brevicomis* were similar to the amounts of F and E in these beetles. Furthermore, *I. paraconfusus* response was inhibited by quantities of verbenone which were similar to release rates of E and F necessary to attract *D. brevicomis*. Therefore, verbenone was probably released in sufficient quantities to account, at least in part, for the observed inhibition of the response of *I. paraconfusus* to its pheromone.

E and F as well as verbenone occurred in the largest concentrations in the hindguts of *D. brevicomis* near the beginning of the aggregation period (3 days after baiting), and these compounds had decreased at a similar rate 5 days later (Figure 6). It has been postulated that termination of the aggregation phase of host colonization may be caused by the release of verbenone in large enough quantities to inhibit the attraction to pheromones (Renwick and Vité, 1970; McNew, 1970; Bedard et al., 1980b). Our results, on the other hand, suggest that the observed reduction in attraction (Figures 5 and 6) was caused by a reduction in the quantities of E and F produced and not by an increase in verbenone production. Nevertheless, verbenone may play a role in regulation of the attack density and thus would influence the termination of the aggregation phase. However, the eventual decrease in attraction is probably caused by a reduction in E, F release.

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