

SEX-SPECIFIC RESPONSES TO AGGREGATION
PHEROMONE:
Regulation of Colonization Density in the Bark Beetle
Ips paraconfusus

JOHN A. BYERS¹

Department of Entomological Sciences, University of California
Berkeley, California 94720

(Received November 18, 1981; revised May 10, 1982)

Abstract—About equal numbers of each sex of flying *Ips paraconfusus* Lanier (Coleoptera: Scolytidae) were caught on traps several meters downwind from a male-infested ponderosa pine log releasing pheromone while a significantly different ratio of over four times more females than males were caught at the pheromone source. Females oriented directly to higher concentrations of colonizing males in a felled tree while males tended to land on the host in adjacent uncolonized areas. The attraction response of walking males to a 1:1:1 mixture of the synthetic pheromone components ispenol-ipsdienol-*cis*-verbenol was reduced progressively at higher concentrations while female response continued to increase. These responses may function to regulate density of colonization and limit intraspecific competition.

Key Words—Coleoptera, Scolytidae, *Ips paraconfusus*, bark beetle, *Pinus ponderosa*, ispenol, ipsdienol, *cis*-verbenol, pheromone, attractant, intraspecific competition.

INTRODUCTION

Most bark beetle species studied, including *Ips paraconfusus* Lanier (Coleoptera: Scolytidae), use pheromones to attract individuals of both sexes to a suitable host tree for breeding (Borden, 1977). Each species probably has evolved behavioral and physiological mechanisms which attenuate aggregation that would otherwise result in overcolonization and severe competition

¹Present address: Department of Animal Ecology, University of Lund, S-22362 Lund, Sweden.

for food and space. In the bark beetle, *Dendroctonus brevicomis* (Renwick and Vité, 1970; Bedard et al., 1980a), *D. pseudotsugae* (Rudinsky et al., 1972, 1974), and *Trypodendron lineatum* (Nijholt, 1973) inhibitory pheromones may assist in regulating the density of colonization and/or termination of aggregation on host materials. The reduction or inhibition of attraction response in these beetles either affects both sexes or may be limited to one, such as *T. lineatum* in which effects on females have not been determined. One of the intraspecific inhibitors of attraction response in *D. brevicomis*, verbenone, also decreases response of its competitor, *I. paraconfusus*, to its conspecific pheromone (Byers and Wood, 1980). Attractive pheromone components of certain *Ips* species may, in addition, function to inhibit response of competing bark beetle species to their conspecific pheromone (Birch and Wood, 1975; Birch et al., 1980; Byers and Wood, 1981).

Male *I. paraconfusus* begin colonizing ponderosa pine, *Pinus ponderosa* Laws., by excavating a "nuptial chamber" under the bark cortex primarily in the phloem layer. Two attractive pheromone components, ipsenol and ipsdienol (Silverstein et al., 1966), are synthesized only in males from the host terpene, myrcene (Hughes, 1974; Byers et al., 1979; Hendry et al., 1980). A third pheromone component, *cis*-verbenol, is synthesized from another host compound, α -pinene, in both sexes (Renwick et al., 1976; Byers, 1981a). The three components together are attractive to both males and females in the field (Wood et al., 1968). *I. paraconfusus* males appear to regulate their attack density since Struble and Hall (1955) reported a maximum of 374 attacks/m² with the majority of samples ranging from 121 to 186/m². The density of females infesting pine is proportional to the density of males which allow entry of up to five females (usually three) into the nuptial chamber. Subsequently, others seeking entry are forcefully rejected (Barr, 1969). A recent study has indicated that the attraction of male *I. paraconfusus* to logs infested with males was inhibited by volatiles from an additional log infested with mated males and females (Byers, 1981b). This study implicated an olfactory mechanism that may regulate the attack density. The present study reports differences between the sexes in their upwind flight to a male-infested log and in their attraction to a concentration series of pheromone components. In addition, differences between the sexes in landing patterns on a felled tree under colonization reveal a mechanism of male inhibition by high levels of pheromone, which appears to regulate colonization density and intraspecific competition.

METHODS AND MATERIALS

Upwind Flight Response to Pheromone. The pattern of flying beetles of each sex orienting to pheromone released by 50 males boring in a ponderosa

pine log was determined by intercepting their flight with a grid of sticky-traps placed downwind from the infested log (September 20–28, 1975). The grid of traps (Figure 1) was located in a narrow valley in the Sierra National Forest (Miami Creek drainage at 1200 m elevation, Mariposa County, California). Observations of a wind-vane placed in various positions in the grid indicated a consistent wind direction perpendicular to the trap rows throughout the flight period (time of catch from about 0800 to 2000) probably due to solar heating at lower elevations forcing air upslope in a laminar flow.

The male-infested log was screened and prepared as described earlier (Byers and Wood, 1980). It was placed inside a tubular sticky-trap (19 cm diam × 30.5 cm high) made of 6.3-mm mesh screen coated with Stickem Special® and 1.2 m above the ground (Bedard and Browne, 1969). Each row of traps had a nylon line perpendicular to the wind direction which suspended 15 flat sticky-trap screens (each 30.5 × 61 cm high) coated with Stickem Special and spaced at 1.5 m intervals 1.2 m above ground. The sticky-traps were

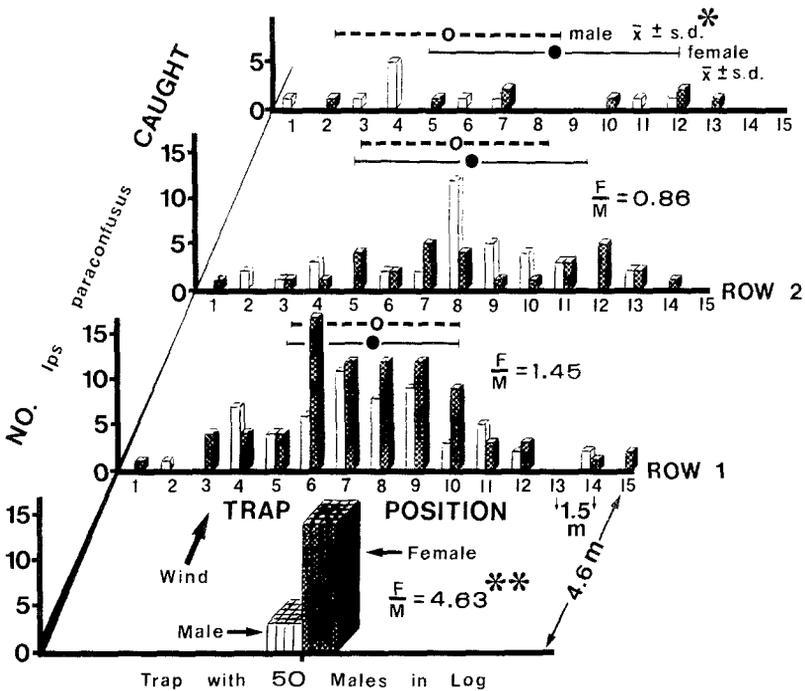


FIG. 1. Distribution of male and female *Ips paraconfusus* caught on sticky-traps spaced in a grid downwind from a log infested with 50 males in the Sierra National Forest, California (September 20–28, 1975). *Mean of distribution of catch \pm standard deviation. **Female/male sex ratio was significantly different from sex ratios in either row 1 or 2 ($P < 0.001$, chi-square).

monitored for beetles two days prior to introducing the infested log and six days after its removal. The "weighted" mean distances of catch from the pheromone source for each row and sex were calculated from numbers caught on traps 3-13 (and their respective distances) in each row.

Walking Response to Synthetic Pheromone Components. Beetles used for tests in a laboratory olfactometer (Byers et al., 1979, modified from Browne et al., 1974) were collected from naturally infested pine logs obtained from the same area described above. Walking beetles of each sex were tested for their attraction response to a series of increasing concentrations of a 1:1:1 mixture of ipsenol-ipsdienol-*cis*-verbenol (racemic chemicals >97% pure, Chemical Samples Co.). Concentrations of each compound ranged in decimal steps from 10^{-11} to 10^{-6} g/ μ l diethyl ether.

Landing on Trunk of Felled Pine during Colonization. Numbers of male and female *I. paraconfusus* caught on sticky-traps along the trunk of a felled pine were analyzed to determine whether behavioral differences between the sexes existed under conditions of actual colonization. An apparently healthy ponderosa pine tree (0.36 m diam at 1.5 m height) was felled at 08:00 on October 1, 1978, and all branches were removed except those above the 16.3 m height (trap 1). Eighteen sticky-trap screens, 21 \times 21 cm, were placed horizontally on the upper side of the felled tree at intervals of 0.76 m beginning 3.6 m from the "top" (0.1 m diam) and extending along the trunk to 3.3 m from the base. An aggregation of *I. paraconfusus* near the top of the tree was induced by baiting with a log that had been infested two days earlier with 50 males. The male-infested log was removed 24 hr later. The portion of the tree that was under attack, as indicated by boring dust piles, was noted each day.

The slopes of linear regression of male versus female catch on the 18 traps for successive two-day periods (October 1-8, 1978) were compared to corresponding 95% lower binomial confidence limits (LBCL) of sex ratios of catch (Byers and Wood, 1980) with a *t* test method (Mendenhall, 1967). The total male and female catch and the percentage of males in the catch per day during the mass aggregation period were summarized.

RESULTS

Upwind Flight Response to Pheromone. The distribution of catch of *I. paraconfusus* on the grid of traps appeared as a narrowing pattern focusing to the pheromone source (Figure 1). This pattern is to be expected if beetles are flying upwind toward the source of pheromone. The broad overlaps of the standard deviations of the sexes caught within each row of traps (Figure 1) indicated that both sexes initially directed their flight upwind toward the pheromone source. The increase in catch on trap rows closer to the source was probably a function of an increase in the proportion of the cross-sectional area

of the pheromone "odor plume" that was intercepted by trap area. About equal numbers of male and female beetles appeared to enter the grid area since catches of each sex on rows 3 and 2 were almost identical. However, proportionately fewer males than females were attracted upwind to the source, as the sex ratio caught there was significantly less than on row 1 (Figures 1 and 2), and row 1 was significantly less than rows 2 and 3 ($P < 0.05$). No beetles were caught after removing the infested log.

Walking Response to Synthetic Pheromone Components. Male and female response was similar at lower release rates (10^{-11} – 10^{-9} g/ μ l) of ipsenol-*cis*-verbenol-ipsdienol. However, attraction of males, but not females, was inhibited at higher release rates (10^{-8} – 10^{-6} g/ μ l, Figure 3). The actual release rate (g/min) was estimated to be about 2.2 times the g/ μ l concentration, which assumes that the compounds were released in proportion to the volume reduction of solvent (Byers and Wood, 1981). These results indicated that response of males increased with an increase in pheromone concentration to a threshold above which a reduction in attraction occurred. On the other hand,

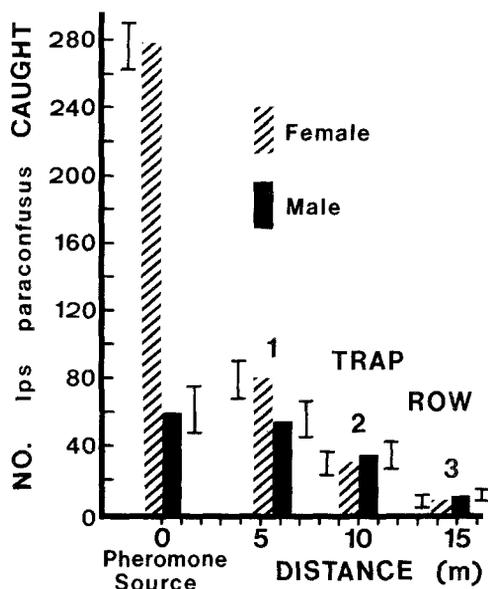


FIG. 2. Total number of male and female *Ips paraconfusus* caught at the log infested with 50 males and on sticky-traps (nos. 3–13) in rows of increasing distance downwind from the pheromone source, Sierra National Forest, California (September 20–28, 1975). The distance from the pheromone source for each row is based on the average trap distance weighted by the catch. Brackets represent 95% asymmetric binomial confidence limits.

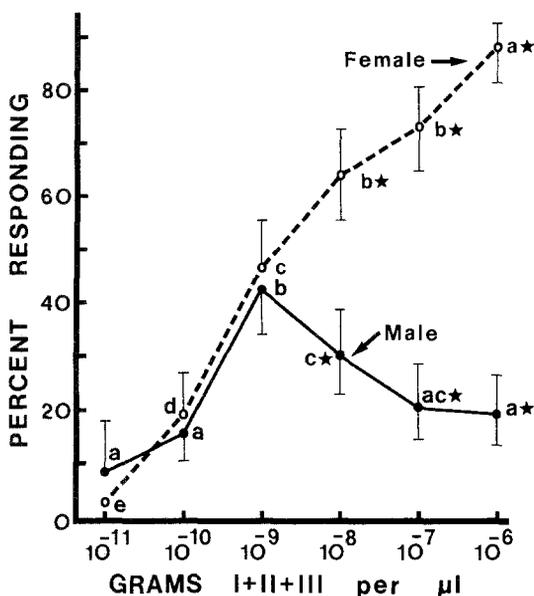


FIG. 3. Response of male and female *Ips paraconfusus* to a 1:1:1 mixture (separate weights) of the pheromone components ipsenol (I), *cis*-verbenol (II), and ipsdienol (III) in the laboratory olfactometer. Means compared within each sex between concentrations followed by the same letter were not significantly different at $\alpha = 0.05$, and means compared at the same concentration between sexes followed by star symbols were significantly different at $\alpha = 0.01$ (chi-square). Brackets represent 95% binomial confidence limits, $N = 90-120$.

the attraction of females continued to increase in proportion to the logarithm of the concentration of pheromone components.

Landing on Trunk of Felled Pine during Colonization. Traps progressively further from the origin of colonization at the "top" of the felled tree caught increasingly higher proportions of males on the first, second, and third days of aggregation (Figure 4). In order to observe these trends in sex ratio it was necessary to combine the catches of each three successive traps for a total of six groups. Numerous piles of boring dust were observed only at the "top" of the tree beginning on the second day. On the third day piles appeared further along the tree corresponding to the highest catches. By the fourth day, the entire surface that was covered with traps appeared to be relatively uniformly attacked (about 110-150 attacks/ m^2) and no trends in sex ratio then were observed (Figure 4).

Males responded differently from females to areas of colonization corresponding to the 18 trap locations on all four two-day periods since the slopes of the regression lines of male against female catch were significantly

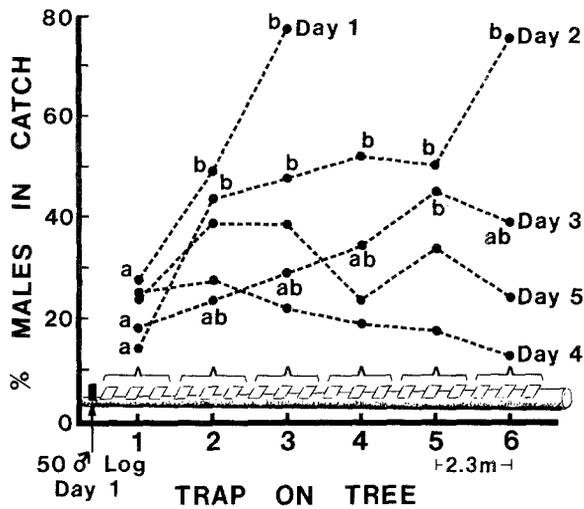


FIG. 4. Trends in the proportion of male *Ips paraconfusus* caught on sticky-traps distributed distally from the origin of colonization on the trunk of a felled ponderosa pine in the Sierra National Forest, California (October 1-5, 1978). An aggregation of *I. paraconfusus* near the top of the tree was induced by placing a 50-male-infested log there for one day only. Proportions within each day followed by the same letter were not significantly different at $\alpha = 0.05$ (chi-square).

TABLE 1. COMPARISON OF SEX RATIO OF TOTAL CATCH OF *Ips paraconfusus* AND LINEAR REGRESSION OF MALE AND FEMALE CATCH ON 18 STICKY-TRAPS ALONG TRUNK OF FELLED PONDEROSA PINE TREE, SIERRA NATIONAL FOREST, CALIFORNIA (OCTOBER 1-8, 1978)

| Date | Sex ratio ($\sigma / \text{♀}$) | LBCL (95%) ^a sex ratio | Regression slope ($x = \text{♀}$ vs. $y = \sigma$) | Difference between LBCL and regression slope (P value) ^b |
|----------|-----------------------------------|-----------------------------------|--|---|
| Oct. 1-2 | 0.660 | 0.511 | 0.107 | <0.001 |
| Oct. 3-4 | 0.346 | 0.274 | 0.093 | 0.034 |
| Oct. 5-6 | 0.418 | 0.297 | 0.141 | 0.030 |
| Oct. 7-8 | 0.300 | 0.185 | -0.078 | 0.027 |

^a Lower binomial confidence limit (95%) of the sex ratio of total catch.

^b A P value less than 0.05 indicates the regression slope was significantly less than the LBCL of the sex ratio.

less than the corresponding LBCL (95%) sex ratios of catch on all traps (Table 1). Similarly, compared to the first and second days of attack, the proportion of males that landed on the fourth day significantly decreased (each $P < 0.001$, chi-square) when female aggregation was the most intense (Figure 5).

DISCUSSION

Previous reports indicated that males were less responsive to pheromone than females based on their attraction in the laboratory to naturally produced pheromone (Wood, 1962) or to gut extracts of fed males (Pitman et al., 1965). The attraction of walking males to pheromone has been described as an "area orientation" (higher number of turns per unit distance traveled) compared to the female's "straight-line orientation" (Wood and Bushing, 1963). It was further speculated that males would be attracted to host substrates under colonization but that after landing thigmotactic or gustatory stimulants might induce attacks on the bark before the source of pheromone, a male entrance tunnel, was reached. The present study indicates that these earlier observations were the result of an inhibition of male response to higher concentrations of ipsenol, *cis*-verbenol, and ipsdienol. Furthermore, my laboratory bioassays indicate that the differences in sex ratio of catch in the grid trap experiment

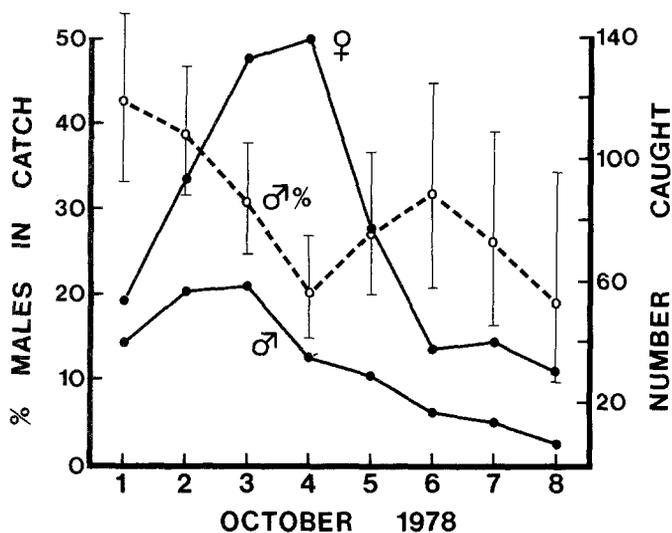


FIG. 5. Relationship between proportion of male *Ips paraconfusus* caught and the number of each sex caught daily on sticky-traps on the trunk of a felled ponderosa pine during colonization in the Sierra National Forest, California (October 1-8, 1978).

were probably due to inhibition of male response by higher concentrations of these pheromone components encountered when the male-infested log was approached. Colonizing males produce the highest amounts of ipsenol and ipsdienol during the first eight days of an attack (Byers, 1981b), so these levels of pheromone were available to inhibit the response of males. In the first experiment, females were not allowed to join males at the pheromone source so the possibility of release of inhibitors by females, or female-induced release of inhibitors by males, cannot account for the sex-specific differences in attraction.

Sex-specific responses were clearly shown in the experiment that monitored beetles landing on the felled ponderosa pine tree being colonized. The highest proportion of males in the trap catches occurred farthest from the origin of attack during the first three days. By the fourth day male attacks had occurred throughout the trunk, and there were no significant trends in sex ratio along the trunk, probably because pheromone was being released at all trap locations. The regression slope of male to female catch was significantly less than the 95% lower binomial confidence limit of the overall sex ratio of the catch, a fact which may be explained by inhibition of male response, while female response increased at those areas of high colonization density and pheromone concentration. As the colonization of the tree progressed during the week, the proportion of males in the catch significantly decreased, and it was lowest at the peak of the aggregation when pheromone release was presumably the highest (Byers, 1981b). The responding population would probably arise from several brood locations not necessarily of the same age that each contributed a sex ratio of approximately 1:1 over the period (Struble and Hall, 1955). Furthermore, based on the beetle's longevity in the laboratory, it appears that the absolute sex ratio of the population in nature would be composed of several days' emergence as well as reemerged parent adults (Struble and Hall, 1955). Thus, the significant change in the sex ratio of catch observed during the first four days of colonization is probably a result of differential response of the sexes to varying pheromone release rates rather than a significant change in the sex ratio of the available adults.

Many investigators of bark beetle biology have wondered about the discrepancy between the approximate male-female ratio of emerging beetles (1:1) to the sex ratio caught on traps with male-infested logs (1:3) or the sex ratio in nuptial chambers (1:3) (Struble and Hall, 1955; Wood, 1962; Gara, 1963; Cameron and Borden, 1967). One previous hypothesis suggested that *I. paraconfusus* males sustain higher levels of mortality than females because of greater exposure to predation and host tree resin during the initial attack (Gara, 1963). The higher male mortality might result in absolute numbers of males of about 1/3 those of females in the responding population. However, the 1:0.86 male-female sex ratio of beetles believed to be entering the grid

area, and the 1:1.35 male-female ratio landing during the first day on the felled tree, suggests that differences in mortality between the sexes because of such differences in predation and death during initial burrowing does not appear to significantly change the sex ratio of flying beetles from that at emergence.

In this study, males and females appeared to be equally responsive to low concentrations of pheromone, but many of the males deviated from the path taken by females when flying to infested hosts to land on areas adjacent to those with higher densities of males which are releasing higher amounts of pheromone. This behavioral mechanism would function to regulate density of colonization and intraspecific competition for food and space. The sexual difference in response was shown to occur even before beetles landed, and it is probable that the effect intensifies after landing. Once males are on the host, other factors may contribute to density regulation and prevent new attacks in fully infested substrates. If no new attacks occur, the colonized areas would become nonattractive since ipsenol and ipsdienol quantities in mated males decrease to negligible levels after 7-10 days (Byers, 1981b).

In contrast to *I. paraconfusus*, both sexes of the bark beetle *Scolytus multistriatus* have been shown to respond in about equal numbers to sources of natural attraction (Peacock et al., 1971). Tilden et al. (1979) reported that more males than females of the monogamous bark beetle, *D. brevicomis*, were trapped close to the source of synthetic pheromones than on surrounding unbaited traps further away. However, the sex ratio was different only between the source and two comparisons on outlying traps while six other comparisons at similar distances were not significantly different. In other studies, the sex ratio of *D. brevicomis* was found not to be significantly different from unity during attraction to a trap releasing synthetic pheromones (Vité and Pitman, 1969; Wood, 1972; Wood et al., 1976; Byers and Wood, 1980; Bedard et al., 1980b) or, more importantly, to traps containing naturally infested host logs (Byers and Wood, 1980). Neither sex of *D. brevicomis* appeared to be inhibited by increasing the concentrations of its synthetic pheromone components in the same laboratory walking bioassay (Byers and Wood, 1981) that demonstrated inhibition of male *I. paraconfusus* in the present study. The responses of the sexes of *D. brevicomis* to individual components of its pheromone (*exo*-brevicommin and frontalin) were shown to be different (Vité and Pitman, 1969), but this may be an artifact since these compounds are never released alone during mass colonization, except by the first female (Byers and Wood, 1980). However, certain ratios of these pheromone components might function to regulate "close-range" behavior after landing such as mating and avoidance of competition. Verbenone, produced by male *D. brevicomis* (Renwick, 1967), inhibits the response of both sexes to their attractants in the laboratory (Hughes and Pitman, 1971) or

field (Bedard et al., 1980a) and may function to regulate attack density (Byers and Wood, 1980) or terminate aggregation (Renwick and Vité, 1970). *D. frontalis* males also release verbenone which inhibits male response (females were not tested; Rudinsky, 1973), and synthetic verbenone released at "higher concentrations" inhibited both sexes (Vité and Renwick, 1970; Payne et al., 1978).

The attack density and termination of mass attack in *D. pseudotsugae* may be controlled in part by release of 3-methyl-2-cyclohexene-1-one (MCH) from females when a male arrives and stridulates at the entrance hole (Rudinsky and Michael, 1972). On the other hand, Pitman and Vité (1974) found that males contain considerably more MCH than females, and they believe males are primarily responsible for release of the inhibitor. The responses to pheromone in both sexes are inhibited (Rudinsky et al., 1974), but males appear to be more strongly affected (Rudinsky et al., 1972). The density of *D. pseudotsugae* attack on a tree under colonization has been reduced by MCH released at multiple sources, and the distance of nearest attack from MCH elution points increased with the concentration of MCH (Furniss et al., 1974). Surprisingly, at the highest concentrations of MCH release, the attack density increased (Hedden and Pitman, 1978). Nijholt (1973) reported that males of *Trypodendron lineatum* released an unidentified inhibitory pheromone after joining the female. Unfortunately, the possibility of changes in the sex ratio of the responding beetles after inhibitors were released was not investigated. However, a recent study has shown that female *T. lineatum* decrease their release of the attractive pheromone, lineatin, after the male arrives (Klimetzek et al., 1981). Klimetzek et al. found evidence of a male-induced inhibition of response which appeared to operate only at close range and may "involve a communication system other than olfaction" (possibly acoustic).

The theory that sex-specific differences in response to intraspecific semiochemicals can function to regulate density of colonization has not been suggested elsewhere for *Ips* species. However, Lanier et al. (1972) found sex-specific differences in *I. pini* in which females, but not males, from Idaho could discriminate between New York and Idaho male-infested logs, while both sexes of New York beetles could differentiate Idaho and New York pheromone. These differences appear to be the result of differential response of the geographical populations to enantiomers of ipsdienol (Lanier et al., 1980). Mustaparta et al. (1980) showed that both Idaho and New York females (males not tested) had two receptor cells each specialized for a specific enantiomer of ipsdienol. Since the receptor systems for ipsdienol of the two populations are virtually identical, the response differences appear to be governed by the central nervous system rather than the peripheral receptors (Lanier et al., 1980). Indicative of the present study, Lanier et al. (1980) found

in the laboratory that the responses of male *I. pini* from New York or Idaho to odor from male-infested logs were always less than those for the same type of female. Electrophysiological studies may reveal whether receptors on the antenna of a male *I. paraconfusus* (and *I. pini*) adapt at lower concentrations of pheromone than the receptors of females, or whether the sexual difference in response is a consequence of the central nervous system.

In all *Ips* species distributed throughout the northern hemisphere, the males initiate the attack, are polygamous, and in many species studied, the males produce various ratios and amounts of ipsenol, *cis*-verbenol, and ipsdienol (Vité et al., 1972). Therefore, olfactory mechanisms similar to that described here may operate in reducing intraspecific competition in other species of the genus *Ips*.

Acknowledgments—I thank D.L. Wood, Department of Entomological Sciences, University of California at Berkeley, for support and use of his research facilities; I also thank W.D. Bedard and P.E. Tilden of the USDA Forest Service for use of their research facilities at Oakhurst, California. I am grateful to R.P. Akers, A.M. Liebhold, D.R. Owen, and D.L. Wood, Department of Entomological Sciences, University of California at Berkeley, and J.S. Elkinton, Department of Entomology, University of Massachusetts, for helpful reviews of the manuscript. The work was supported in part by grants from the Rockefeller Foundation, USDA Forest Service, and Regional Research Project W-110, SEA/USDA (to D.L.W.)

REFERENCES

- BARR, B.A. 1969. Sound production in Scolytidae (Coleoptera) with emphasis on the genus *Ips*. *Can. Entomol.* 101:636-672.
- BEDARD, W.D., and BROWNE, L.E. 1969. A delivery-trapping system for evaluating insect chemical attractants in nature. *J. Econ. Entomol.* 62:1202-1203.
- BEDARD, W.D., TILDEN, P.E., WOOD, D.L., LINDAHL, K.Q., and RAUCH, P.A. 1980a. Effects of verbenone and *trans*-verbenol on the response of *Dendroctonus brevicomis* to natural and synthetic attractant in the field. *J. Chem. Ecol.* 6:997-1014.
- BEDARD, W.D., WOOD, D.L., TILDEN, P.E., LINDAHL, K.Q. JR., SILVERSTEIN, R.M., and RODIN, J.O. 1980b. Field response of the western pine beetle and one of its predators to host and beetle produced compounds. *J. Chem. Ecol.* 6:625-641.
- BIRCH, M.C., and WOOD, D.L. 1975. Mutual inhibition of the attractant pheromone response by two species of *Ips* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 1:101-113.
- BIRCH, M.C., LIGHT, D.M., WOOD, D.L., BROWNE, L.E., SILVERSTEIN, R.M., BERGOT, B.J., OHLOFF, G., WEST, J.R., and YOUNG, J.C. 1980. Pheromonal attraction and allomonal interruption of *Ips pini* in California by the two enantiomers of ipsdienol. *J. Chem. Ecol.* 6:703-717.
- BORDEN, J.H. 1977. Behavioral responses of Coleoptera to pheromones, allomones, and kairomones, pp. 169-198, in H.H. Shorey, and J.J. McKelvy, Jr. (eds.). *Chemical Control of Insect Behavior*. John Wiley, New York.
- BROWNE, L.E., BIRCH, M.C., and WOOD, D.L. 1974. Novel trapping and delivery systems for airborne insect pheromones. *J. Insect Physiol.* 20:183-193.
- BYERS, J.A. 1981a. Pheromone biosynthesis in the bark beetle, *Ips paraconfusus*, during feeding or exposure to vapours of host plant precursors. *Insect Biochem.* 11:563-569.

- BYERS, J.A. 1981b. Effect of mating on terminating aggregation during host colonization in the bark beetle, *Ips paraconfusus*. *J. Chem. Ecol.* 7:1135-1147.
- BYERS, J.A., and WOOD, D.L. 1980. Interspecific inhibition of the response of the bark beetles *Dendroctonus brevicornis* and *Ips paraconfusus* to their pheromones in the field. *J. Chem. Ecol.* 6:149-164.
- BYERS, J.A., and WOOD, D.L. 1981. Interspecific effects of pheromones on the attraction of the bark beetles, *Dendroctonus brevicornis* and *Ips paraconfusus* in the laboratory. *J. Chem. Ecol.* 7:9-18.
- BYERS, J.A., WOOD, D.L., BROWNE, L.E., FISH, R.H., PIATEK, B., and HENDRY, L.B. 1979. Relationship between a host plant compound, myrcene and pheromone production in the bark beetle *Ips paraconfusus*. *J. Insect Physiol.* 25:477-482.
- CAMERON, E.A., and BORDEN, J.A. 1967. Emergence patterns of *Ips confusus* (Coleoptera: Scolytidae) from ponderosa pine. *Can. Entomol.* 99:236-244.
- FURNISS, M.M., DATERMAN, G.E., KLINE, L.F., and RUDINSKY, J.A. 1974. Effectiveness of the Douglas-fir beetle antiaggregative pheromone methycyclohexenone at three concentrations and spacings around felled host trees. *Can. Entomol.* 106:381-392.
- GARA, R.I. 1963. Studies on the flight behavior of *Ips confusus* (LeC.) (Coleoptera: Scolytidae) in response to attractive material. *Contrib. Boyce Thompson Inst.* 22:51-66.
- HEDDEN, R.L., and PITMAN, G.B. 1978. Attack density regulation: a new approach to the use of pheromones in Douglas-fir beetle population management. *J. Econ. Entomol.* 71:633-637.
- HENDRY, L.B., PIATEK, B., BROWNE, L.E., WOOD, D.L., BYERS, J.A., FISH, R.H., and HICKS, R.A. 1980. In vivo conversion of a labelled host plant chemical to pheromones of the bark beetle *Ips paraconfusus*. *Nature* 284:485.
- HUGHES, P.R. 1974. Myrcene: A precursor of pheromones in *Ips* beetles. *J. Insect Physiol.* 20:1271-1275.
- HUGHES, P.R., and PITMAN, G.B. 1971. A method for observing and recording the flight behavior of tethered bark beetles in response to chemical messengers. *Contrib. Boyce Thompson Inst.* 24:329-336.
- KLIMETZEK, D., KIESEL, K., and MOHRING, C. 1981. *Trypodendron lineatum*: reduction of pheromone response by male beetles. *Naturwissenschaften* 68:148-150.
- LANIER, G.N., BIRCH, M.C., SCHMITZ, R.F., and FURNISS, M.M. 1972. Pheromones of *Ips pini* (Coleoptera: Scolytidae): Variation in response among three populations. *Can. Entomol.* 104:1917-1923.
- LANIER, G.N., CLASSON, A., STEWART, T., PISTON, J.J., and SILVERSTEIN, R.M. 1980. *Ips pini*: The basis for interpopulational differences in pheromone biology. *J. Chem. Ecol.* 6:677-687.
- MENDENHALL, W. 1967. Introduction to Probability and Statistics. Wadsworth, Belmont, California.
- MUSTAPARTA, H., ANGST, M.E., and LANIER, G.N. 1980. Receptor discrimination of enantiomers of the aggregation pheromone ipsdienol, in two species of *Ips*. *J. Chem. Ecol.* 6:689-701.
- NIJHOLT, W.W. 1973. The effect of male *Trypodendron lineatum* (Coleoptera: Scolytidae) on the response of field populations to secondary attraction. *Can. Entomol.* 105:583-590.
- PAYNE, T.L., COSTER, J.E., RICHESON, J.V., EDSON, L.J., and HART, E.R. 1978. Field response of the southern pine beetle to behavioral chemicals. *Environ. Entomol.* 7:578-582.
- PEACOCK, J.W., LINCOLN, A.C., SIMEONE, J.B., and SILVERSTEIN, R.M. 1971. Attraction of *Scolytus multistriatus* (Coleoptera: Scolytidae) to a virgin-female-produced pheromone in the field. *Ann. Entomol. Soc. Am.* 64:1143-1149.
- PITMAN, G.B., and VITÉ, J.P. 1974. Biosynthesis of methycyclohexenone by male Douglas-fir beetle. *Environ. Entomol.* 3:886-887.
- PITMAN, G.B., KLIEFOTH, R.A., and VITÉ, J.P. 1965. Studies on the pheromone of *Ips confusus* (LeConte). II. Further observations on the site of production. *Contrib. Boyce Thompson Inst.* 23:13-17.

- RENWICK, J.A.A. 1967. Identification of two oxygenated terpenes from the bark beetles *Dendroctonus frontalis* and *Dendroctonus brevicomis*. *Contrib. Boyce Thompson Inst.* 23:355-360.
- RENWICK, J.A.A., and VITÉ, J.P. 1970. Systems of chemical communication in *Dendroctonus*. *Contrib. Boyce Thompson Inst.* 24:283-292.
- RENWICK, J.A.A., HUGHES, P.R., and KRULL, I.S. 1976. Selective production of *cis*- and *trans*-verbenol from (-) and (+) alpha-pinene by a bark beetle. *Science* 191:199-201.
- RUDINSKY, J.A. 1973. Multiple functions of the southern pine beetle pheromone verbenone. *Environ. Entomol.* 2:511-514.
- RUDINSKY, J.A., and MICHAEL, R.R. 1972. Sound production in Scolytidae: Chemostimulus of sonic signal by the Douglas-fir beetle. *Science* 175:1386-1390.
- RUDINSKY, J.A., FURNISS, M.M., KLINE, L.N., and SCHMITZ, R.F. 1972. Attraction and repression of *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae) by three synthetic pheromones in traps in Oregon and Idaho. *Can. Entomol.* 104:815-822.
- RUDINSKY, J.A., MORGAN, M.E., LIBBEY, L.M., and PUTMAN, T.B. 1974. Additional components of the Douglas-fir beetle (Col., Scolytidae) aggregative pheromone and their possible utility in pest control. *Z. Angew. Entomol.* 76:65-77.
- SILVERSTEIN, R.M., RODIN, J.O., and WOOD, D.L. 1966. Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science* 154:509-510.
- STRUBLE, G.R., and HALL, R.C. 1955. The California five-spined engraver its biology and control. USDA Circular No. 964.
- TILDEN, P.E., BEDARD, W.D., WOOD, D.L., LINDAHL, K.Q., and RAUCH, P.A. 1979. Trapping the western pine beetle at and near a source of synthetic attractive pheromone: Effects of trap size and position. *J. Chem. Ecol.* 5:519-531.
- VITÉ, J.P., and PITMAN, G.B. 1969. Aggregation behaviour of *Dendroctonus brevicomis* in response to synthetic pheromones. *J. Insect Physiol.* 15:1617-1622.
- VITÉ, J.P., BAKKE, A., and RENWICK, J.A.A. 1972. Pheromones in *Ips* (Coleoptera: Scolytidae): occurrence and production. *Can. Entomol.* 104:1967-1975.
- WOOD, D.L. 1962. The attraction created by males of a bark beetle *Ips confusus* (LeConte) attacking ponderosa pine. *Pan-Pac. Entomol.* 38:141-145.
- WOOD, D.L. 1972. Selection and colonization of ponderosa pine by bark beetles, pp. 101-117, in H.F. van Emden (ed.). *Insect/Plant Relationships*. Blackwell Sci. Publ., Oxford.
- WOOD, D.L., and BUSHING, R.W. 1963. The olfactory response of *Ips confusus* (LeConte) (Coleoptera: Scolytidae) to the secondary attraction in the laboratory. *Can. Entomol.* 95:1066-1078.
- WOOD, D.L., BROWNE, L.E., BEDARD, W.D., TILDEN, P.E., SILVERSTEIN, R.M., and RODIN, J.O. 1968. Response of *Ips confusus* to synthetic sex pheromones in nature. *Science* 159:1373-1374.
- WOOD, D.L., BROWNE, L.E., EWING, B., LINDAHL, K., BEDARD, W.D., TILDEN, P.E., MORI, K., PITMAN, G.B., and HUGHES, P.R. 1976. Western pine beetle: specificity among enantiomers of male and female components of an attractant pheromone. *Science* 192:896-898.