

INFLUENCE OF OPPOSITE SEX ON ATTRACTION PRODUCED BY PIONEER SEX OF FOUR BARK BEETLE SPECIES COHABITING PINE IN THE SOUTHERN UNITED STATES

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Abstract—Catches of *Dendroctonus frontalis* and *Ips avulsus* on traps surrounding bolts infested with both sexes of each species in the gallery were not significantly different from catches at bolts infested only with the sex which normally pioneers the host colonization process. In contrast, the presence of the second sex in the gallery significantly reduced catches of *I. grandicollis* and *I. calligraphus* and, additionally, the presence of females in the male galleries of *I. calligraphus* significantly reduced the catch of *I. avulsus* females as compared with their response to bolts infested with the male *I. calligraphus* only.

Key Words—*Dendroctonus frontalis*, *Ips calligraphus*, *I. grandicollis*, *I. avulsus*, Coleoptera, Scolytidae, mating, attraction.

INTRODUCTION

The chemically mediated behavior of four cohabiting bark beetle species, *Dendroctonus frontalis* Zimmerman, *Ips avulsus* (Eichhoff), *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff), which colonize loblolly pines, *Pinus taeda* L., was described by Birch et al. (1980). These four species often colonize the same tree in characteristic temporal and spatial patterns (Birch and Švihra, 1979; Švihra et al., 1980; Paine et al., 1981). However, little is known about the role of the sexes of each of these four species in the patterns of colonization. Coulson (1979) delineated five phases in host-tree colonization by *Dendroctonus* species: (1) host selection and gallery initiation by pioneer beetles, (2) concentration of responding sex (females), (3) production of additional pheromones and response of both sexes, (4) mating and oviposi-

tion, and (5) reemergence of parent adults. This chronology does not explain whether or not the arrival of the second sex and subsequent mating in galleries influence the attraction or termination of host colonization by that or other species. The presence of males (the second sex) in the galleries of some species of *Dendroctonus* may enhance attractiveness (Coster and Vité, 1972), or may cause an abrupt decline in attractiveness of flying beetles (McMullen and Atkins, 1962; Rudinsky, 1969). However, in *Ips*, where males are the pioneer sex, male attractiveness progressively declines as the male mates with more females (Borden, 1967; Werner, 1972).

Preliminary observations in previous work by Švihra et al. (1980) indicated that interactions between males and females may influence not only the behavior of the same species, but also the in-flight and landing behavior of other sympatric species which colonize the same pine tree. These experiments were conducted to demonstrate whether or not the presence of the second sex affected the inter- and intraspecific attraction generated by the pioneering sex.

METHODS AND MATERIALS

All tests were conducted between May and June 1977 in pine forests near Nacogdoches, in east Texas. Their basic design was similar to that described by Birch et al. (1980). In each test, three bolts (30 cm long and 10–15 cm diameter) were cut from apparently healthy loblolly pine, *P. taeda*, and allowed to age in the laboratory for two days after felling. Twenty-five holes were drilled through the bark of each bolt at an angle of about 30° to the long axis. Twenty-five males of either one of the three *Ips* species or 25 females of *D. frontalis* were introduced (head first) into the preformed holes in two bolts, and the holes were covered with fine mesh metal screening to prevent escape. The third bolt was left empty as a control. All three bolts were left for 24 hr in the laboratory, then the mesh screenings were removed from the holes on one bolt and beetles of the second (or opposite) sex were introduced into each hole (two females for *Ips* species; one male for *D. frontalis*). Thus each experiment tested three treatments: (1) the bolt with the pioneering sex alone, (2) the bolt with males and females together in each hole, and (3) the control bolt with drilled holes but no beetles. The mesh was again stapled over each hole, and the bolts were entirely wrapped in fine mesh screening to prevent additional colonization by responding beetles during the field tests.

Attractiveness of the bolts was tested in the field by placing them in sticky traps (Bedard and Browne, 1969; Birch et al., 1980). Traps were placed 15 meters apart in a line and their positions rotated systematically as described by Birch et al. (1980). The duration of each experiment and the number of replications in each are indicated in the tables. After the experiment was terminated, the bark was peeled from each bolt to confirm the sex and

mortality of introduced beetles and to establish that no attack by other species had occurred.

Differences in the response of *D. frontalis*, *I. calligraphus*, *I. grandicollis*, and *I. avulsus* to the attractive sources were analyzed by the nonparametric Friedman test for multiple comparisons. The sex-specific responses were measured by comparing the sex ratio of each treatment by the chi-square goodness-of-fit test, with an expected response sex ratio 1:1.

RESULTS AND DISCUSSION

The response of *D. frontalis* was not significantly reduced, nor was the sex ratio changed in either of the two experiments when males were present with females in the galleries (Table 1). Insufficient numbers of *Ips* species were attracted to either of the *Dendroctonus* treatments to assess the effects of the presence of *D. frontalis* males on the cross-attraction of *Ips* species. Similar results were found after *I. avulsus* females were introduced to the males in the gallery (Table 2). Their presence apparently had no significant effect on the number of either sex of *I. avulsus* trapped.

In contrast, the presence of *I. calligraphus* females with male *I. calligraphus*, and *I. grandicollis* females with male *I. grandicollis*, significantly decreased the catch of conspecifics without any change in sex ratios (Tables 3 and 4). In addition, male *I. calligraphus* attracted large numbers of both *I. grandicollis* and *I. avulsus*. However, with the addition of female *I. calligraphus* to the gallery, the response of *I. avulsus* females was significantly reduced.

TABLE 1. RESPONSE (TRAP CATCH) TO BOLTS CONTAINING 25 FEMALE *D. frontalis*; 25 FEMALE *D. frontalis* PLUS 25 MALE *D. frontalis* (IN THE SAME HOLES); AND TO A CONTROL BOLT CONTAINING NO BEETLES^a

Test	Treatment (bolt)	Response ^b			
		<i>D. frontalis</i>	<i>I. avulsus</i>	<i>I. calligraphus</i>	<i>I. grandicollis</i>
A	<i>D. frontalis</i> (♀♀)	23 ^a (1:0.9)	5 (1:0.25)	0	4 (1:0)
	<i>D. frontalis</i> (♀♀ & ♂♂)	17 ^a (1:0.7)	4 (1:0.3)	3 (0:1)	5 (1:0.7)
	Control	2 ^b (0:2)	2 (1:1.0)	0	0
B	<i>D. frontalis</i> (♀♀)	27 ^a (1:0.5)	3 (1:0)	0	6 (0:1)
	<i>D. frontalis</i> (♀♀ & ♂♂)	16 ^a (1:0.8)	2 (0:1)	0	6 (1:5)
	Control	2 ^b (1:1.0)	2 (1:0)	0	0

^aEast Texas. Test A: April 29-30, 1977, 16 × 0.75-hr replications of all treatments. Test B: May 18-20, 1977, 30 × 0.75-hr replications of all treatments. Numbers are the sum caught in each test and sex ratio (m:f).

^bLetters within columns in a test denote homogeneous subsets, Friedman's tests, $P \leq 0.05$.

TABLE 2. RESPONSE (TRAP CATCH) TO BOLTS CONTAINING 25 MALE *I. avulsus*; 25 MALE *I. avulsus* AND 48 FEMALE *I. avulsus* (IN THE SAME HOLES); AND TO A CONTROL BOLT CONTAINING NO BEETLES^a

Treatment (bolt)	Response ^b			
	<i>D. frontalis</i>	<i>I. avulsus</i>	<i>I. calligraphus</i>	<i>I. grandicollis</i>
<i>I. avulsus</i> (♂♂)	0	123 ^a (1:0.9)	9 (1:0.5)	6 (1:0.5)
<i>I. avulsus</i> (♂♂ & ♀♀)	0	109 ^a (1:1.1)	1 (1:1)	5 (1:0.2)
Control	0	1 ^b (1:0)	1 (0:1)	0

^aEast Texas, June 9–11, 1977. Numbers are sum of 24 1.5-hr replications of all treatments and sex ratio (m:f).

^bLetters with columns in a test denote homogeneous subsets, Friedman's tests, $P \leq 0.05$.

By trapping beetles as they arrived, these experiments excluded subsequent natural activity of responding beetles on the host, and the manner in which the second sex was added to the pioneering sex in the laboratory may not occur as quickly under natural conditions. However, under these experimental conditions, the effects of the second sex were: (1) the intraspecific responses of *D. frontalis* and *I. avulsus* were not significantly affected, (2) intraspecific attraction of *I. calligraphus* and *I. grandicollis* was apparently reduced, and (3) the cross-attraction of *I. avulsus* females to *I. calligraphus* was reduced.

These experiments failed to demonstrate that the addition of the male to the female increased attraction of *D. frontalis* as Coster and Vité (1972)

TABLE 3. RESPONSE (TRAP CATCH) TO BOLTS CONTAINING 25 MALE *I. calligraphus*, 25 MALE PLUS 50 FEMALE *I. calligraphus* (IN THE SAME HOLES); AND A CONTROL BOLT WITH NO BEETLES^a

Treatment (bolt)	Response ^b			
	<i>D. frontalis</i>	<i>I. avulsus</i>	<i>I. calligraphus</i>	<i>I. grandicollis</i>
<i>I. calligraphus</i> (♂♂)	0	207 ^a (1:1.6)*	471 ^a (1:3.0)	47 ^a (1:1.4)
<i>I. calligraphus</i> (♂♂ & ♀♀)	0	79 ^b (1:0.7)*	128 ^b (1:2.9)	33 ^a (1:1.2)
Control	0	0	0	0

^aEast Texas, June 7–9, 1977. Numbers are sum of 24 1.5-hr replications of all treatments and sex ratio (m:f).

^bLetters within columns in a test denote homogeneous subsets, Friedman's tests, $P \leq 0.05$. Asterisks denote significant ($P \leq 0.05$) deviation from 1:1 sex ratio response; χ^2 goodness-of-fit-test.

TABLE 4. RESPONSE (TRAP CATCH) TO BOLTS CONTAINING 25 MALE *I. grandicollis*, 25 MALE PLUS 50 FEMALE *I. grandicollis* (IN THE SAME HOLES), AND TO A CONTROL BOLT CONTAINING NO BEETLES^a

Test	Treatment (bolt)	Response ^b			
		<i>D. frontalis</i>	<i>I. avulsus</i>	<i>I. calligraphus</i>	<i>I. grandicollis</i>
A	<i>I. grandicollis</i> (♂♂)	0	2 (0:1)	0	143 ^a (1:2.7)
	<i>I. grandicollis</i> (♂♂ & ♀♀)	2 (1:1)	7 (1:0.4)	5 (1:4)	78 ^b (1:2.2)
	Control	0	0	0	7 ^c (1:2.5)
B	<i>I. grandicollis</i> (♂♂)	1 (1:0)	2 (1:1)	1 (1:0)	147 ^a (1:1.5)
	<i>I. grandicollis</i> (♂♂ & ♀♀)	0	2 (1:0)	1 (0:1)	86 ^b (1:1.1)
	Control	0	0	0	0

^aEast Texas. Test A: May 9–11, 1977. Test B: May 13–15, 1977. Numbers in both tests are sum of 30 0.75-hr replications of all treatments and sex ratio (m:f).

^bLetters within columns in a test denote homogeneous subsets, Friedman's tests, $P \leq 0.05$.

reported. Also, these data indicate that the interpretation of host colonization by *D. frontalis* proposed by Vité and Francke (1976) is perhaps oversimplified. They suggested that females release the attractant and males carry inhibitors which terminate the colonization process. The results presented here imply that there may be factors other than the presence of males that influence colonization in this species.

When *D. frontalis* attacks apparently healthy pines, a copious resin flow is usually triggered, which may influence aggregation. While it was not possible in these experiments to simulate host conditions of standing trees under attack, it appears that, at least for three days, the colonization process of *D. frontalis* and *I. avulsus* is not curtailed by the presence of both sexes and their subsequent mating in the galleries. After the bark was peeled off those logs, the 2- to 4-cm-long egg galleries were found to contain eggs, which is sufficient evidence that mating took place.

Mason (1970) considered *I. avulsus* an aggressive species able to attack healthy pines. Vité et al. (1972) stated that some aggressive bark beetle species, such as *D. frontalis* and *I. avulsus*, aggregate on the host using "contact pheromones," which are produced after arrival but before the pioneering species begin to feed in the host. The secondary species, such as *I. calligraphus* and *I. grandicollis*, tend to produce "frass pheromones" only after feeding and gallery construction have been initiated. The response of the less aggressive species, *I. calligraphus* and *I. grandicollis*, was significantly reduced after the second sex had been added to the pioneering one. Nevertheless, in these significantly reduced beetle responses, the responding males could enter the bark and initiate new sources of attraction.

The reduced cross-attraction of *I. avulsus* to the bolt with both sexes of *I. calligraphus* in the gallery is of particular interest since Birch et al. (1980) found that the presence of *I. avulsus* males in the same bolt with *I. calligraphus* males significantly reduced the responses of *I. calligraphus*. Similar interspecific relationships did not appear in other species as may have been expected. Thus, oversimplified models of colonization by these four sympatric species may be misleading if they imply that the pioneering sex carried the attractants and that the mates or the mating process inhibits this phenomenon.

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