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Jack E. Coster

W.D. Bunt

P.C. Johnson

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W. D. BUNT,[3] J. E. COSTER,[4] AND P. C. JOHNSON[5]

School of Forestry, Stephen F. Austin State University, Nacogdoches, Texas 75962

ABSTRACT

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Twenty-two percent of the southern pine beetles, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), that landed on the bark during the 1st 4 days of mass attack in east Texas, eventually entered the tree. Other beetles either flew away (43%), dropped off the host (32%), or were eaten (2%). No significant difference in searching time or distance traveled was found for day of attack or beetle sex. Males spent significantly less total time on the bark than females.

The population aggregation pheromones of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (SPB), mediate behavior that, eventually, results in colonization and death of host trees (Renwick and Vité 1969). The colonization process occurs in 3 phases: 1) dispersal and selection, 2) concentration, and 3) establishment (Wood 1972). The concentration phase is characterized by a mass attack of thousands of SPB on a living tree over a period of 2–4 days (Coster et al. 1977). This mass attack is caused by a secondary attractant consisting of pheromones produced by female beetles in combination with host odors (Renwick and Vité 1969). The termination of the concentration phase may be influenced by pheromones also (Renwick and Vité 1970, Rudinsky et al. 1974).

Two main sequences of events occur with responding scolytids during the concentration phase. First, they orient toward, and fly to, the tree under mass attack. Second, they cease flight, land on the bark, and search for a suitable place to bore into the host (if they are female *Dendroctonus*) or locate and enter a gallery with an available female inside (if they are males) (Borden 1974). Most information on landing and searching have been incidental observations during other studies or from laboratory studies on the olfactory response of walking beetles. This study describes the sequence of behavior displayed by SPB after landing on host trees, and examines the influence of beetle sex and day of attack within the mass attack period on the behavior of beetles that have landed on a tree under mass attack.

Procedures

The study was conducted during July and August, 1978 at a SPB infestation within an uneven-aged pine-hardwood forest in Montgomery County, Texas. Host trees were loblolly pine (*Pinus taeda* L.), 20–30 m tall and ranging 25–50 cm DBH. Total basal area of the infested stand was 36.9 m^2/ha with a 30.8 m^2/ha of loblolly pine.

Several uninfested trees adjacent to the infestation were selected as likely to come under attack during the normal sequence of tree infestation within stands (Gara and Coster 1968). They were prepared for study by lightly scraping away outer bark scales within an observation area approximately 70 × 40 cm. This method was used by Dix and Franklin (1974, 1977) to study behavior of SPB parasites and the clerid beetle, *Thanasimus dubius* F. The top of the study area was at the 3 m level on the bole, corresponding to the zone of greatest attack by SPB during days 2–4 of mass attack (Coster et al. 1977). A rectangular grid consisting of cells 4 cm on a side was lightly etched onto the bark surface within the observation area to assist in tracking and measuring the path of the walking SPB.

Plastic landing traps (Hynum 1978) were placed on each tree just above the study area at 3.5 m and the trapped SPB were removed daily. SPB sex was determined by the presence of a pronounced frontal suture (male) or a mycangium (female) (Osgood and Clark 1963). When more than 5 beetles were captured in the landing trap on a given tree, behavioral observations began the next day.

Observations were made intermittently between 0800 and 2000 hr on 6 loblolly pines for the 1st 4 days of mass attack (the 4th day for tree 1 and the 1st day for tree 2 were not observed). Observations on the 1st day and on the 5th day of mass attack were unsuccessful because very few beetles were landing. The observer used a 3 m tree climbing ladder and a climber's harness to allow freedom of both hands. On 3 occasions, the study trees were checked at night (2200 hrs) to see if SPB were walking on the bark.

Each beetle was observed from landing to successful entrance into the host tree or until it departed from the tree. Females that bored into the tree were considered successful if they disappeared from the bark surface; males were considered successful if they entered a gallery and did not emerge within 15 min. Successful beetles, along with others in the gallery, were excised from the tree and sexed in the laboratory. Beetles that disappeared under bark scales for extended periods of time or that left the study area were given a null termination code.

When a beetle landed on the tree a stop watch was started, the time of day was recorded, and the initial grid location was noted. Behavioral observations were

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[3] Current address: U.S. Forest Service, P.O. Box 20, Escalante, UT 84726. Send reprint requests to Coster.

[4] Current address: Division of Forestry, West Virginia Univ., Morgantown, WV, 26506.

[5] Current address: Dept. of Entomology, Univ. of New Hampshire, Durham, NH 03824.

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taken for each beetle during its stay on the bark. If a beetle successfully entered the tree, the total time was separated into searching time and gallery construction time (time it took to enter the host once a suitable boring site or entrance hole was found). Each pathway, from landing grid cell to termination grid cell, was recorded and measured with a circular map-measurer using the cumulative distance between the center of each grid cell visited during the beetle's walk. The general direction of each path, whether up or down, was noted.

The observations were used to divide behavior into categories, and these were used to construct an on-bark behavior flow-chart. Chi-square tests of independence were performed on contingency tables of behavioral categories and day of mass attack to detect shifts in behavior through time.

Mean search time, gallery construction time, total on-bark time, and distance traveled were used to compare behavior of SPB by sex and day of attack. Prior to analyses, tests of normality (Kolmogorov-Smirnov tests) and homogeneity of variances (Bartlett's F-test) were performed and ANOVA or Kruskal-Wallis tests applied as appropriate. Statistical analyses were performed using the Statistical Package for the Social Sciences (Nie et al. 1975). Significance on statistical tests was assessed at the 0.05 probability level.

Results and Discussion

General response pattern.—A total of 154 SPB were observed landing on the 6 study trees. Distribution over the 6 trees was fairly uniform and ranged 22–29 beetles observed per tree. The number of beetles observed reflected an increasing and then decreasing attack activity with peak activity on day 2 as follows:

Day of attack	*No. SPB observed*
1	28
2	55
3	41
4	30
Total	154

Of the 154 beetles, 28 could not be observed completely because they were lost, usually in bark crevices. One hundred twenty-six SPB were observed from landing until they terminated their behavior on the bark. Twenty-eight of these beetles (15 attacking females and 13 males) eventually entered the tree.

The daily pattern of arrival at the landing traps (Table 1), resembled that reported by Coster et al. (1977), except that heaviest attack occurred on the 2nd day of attack instead of the 3rd day. Since beetles usually appeared in the window trap the day before observation began, mass attack probably began on that day, but behavioral observations were not possible due to the low number of landing SPB. Females were proportionally higher on the 1st day, while males exceeded females from the 2nd day, increasing in proportion through day 4 (Table 1). Females have been reported to outnumber males in the early stages of mass attack (Coster et al. 1977).

Landing beetles were observed only from 0900 to 2000 and the diurnal behavior was similar to that reported by Coster et al. (1977). Although a few beetles were observed walking on the bark before 0900 and for a short time after 2000, arrival was too slow for direct observation of landing. A little flight activity was reported during the evening and early morning by Vité et al. (1964) and Coster et al. (1977), and in our studies only a few SPB were caught between 2000 and 0800 the next morning. Checks at 2200 did not reveal any walking activity, but beetles were observed working in pitch tubes.

Table 1.—Number and sex-ratio of SPB catch in landing traps by day of attack.

Day of attack	Mean no. beetles/trap (± SD)	No. trees	Sex-ratio (M:F)	No. trees
1	55.2 ± 35.0	5	0.78 : 1.00	4[a]
2	116.8 + 71.6	6	1.08 : 1.00	5
3	57.7 ± 18.1	6	1.34 : 1.00	5
4	20.2 ± 11.3	5	1.30 : 1.00	5

[a] SPB trapped on tree 1 were not sexed.

Behavior sequence.—Activities were arranged into 12 descriptive categories. These were grouped into 2 classes: on-bark behavior, including activities of the beetles on the bark surface; and termination behavior, including activities that resulted either in the beetle leaving the tree, being killed by a predator, or entering a gallery. The categories of on-bark behavior are Landing (LAND), Walking (WALK), Searching (SEARCH), Investigating an entrance hole (PITCH), Encountering another SPB (SPB), Encountering a predator (PRED), and Fighting with another SPB (FIGHT). Termination behavior is divided into Flew from the tree (FLY), Dropped from the tree (DROP), Captured by a predator (EATEN), Bored a gallery (BORE), and Entered entrance hole (ENTER).

The behavioral sequence observed for each SPB was used to construct a behavioral sequence flow diagram for SPB on the bark. The diagram (Fig. 1) shows the percentage of instances in which one kind of behavior was followed by a SPB performing another kind of behavior (e.g., walking was followed by flying 47% of the time, by dropping 21% of the time and by encountering a predator 32% of the time). A beetle might cycle through a behavioral sequence several times before ter-

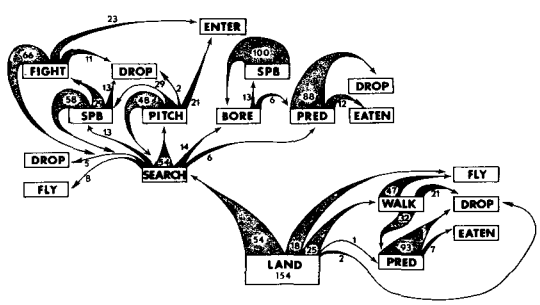

FIG. 1.—Behavioral sequence flow diagram for SPB behavior on the bark of host trees. Percentage of beetles within a behavior category that proceed to another are indicated (n = 154).

minating its behavior on the bark (e.g., SEARCH—PITCH—SEARCH—PITCH—ENTER).

Beetles were observed landing on nearby non-host trees and often landed on the observer. Their landing posture was similar to that observed for *Dendroctonus pseudotsugae* Hopkins by Bennett and Borden (1971). Wings were usually folded down at each side and held back while the elytra remained slightly open. Then the elytra were closed and the wings were slowly pulled beneath them. Following landing, the beetles would often raise up on the meso- and metathoracic legs and pivot, sometimes in a complete circle. Pivoting was accompanied by movement of antennae. Beetles did not immediately begin walking or searching, but remained in the same place for at least 30 sec.

Landing was followed by walking in 25% of the observations. Walking beetles displayed no obvious searching behavior such as crevice exploration or investigation of pitch tubes. Beetles stayed exposed on bark scales, frequently stopping, pivoting, and then walking again until they left the tree or encountered predators.

Fifty-four percent of the landed beetles immediately began searching behavior, characterized by beetles poking their head and body into crevices and cracks in the bark and by the investigation of entrance holes and pitch tubes. Sometimes a beetle crawled under bark scales and then reappeared in a few seconds. Beetles occasionally stopped and sometimes reared up and pivoted, usually changing direction. This behavior seemed to correspond to behavior in the laboratory described as chemoklinotaxis for *Ips paraconfusus* (Wood et al. 1966) and for *Trypodendron lineatum* (Francia and Graham 1967). Flying and dropping from the tree were greatly reduced during searching behavior. Perhaps these beetles detected high concentrations of pheromones and/or host odors and were inhibited from flying, as Borden (1967) reported for *I. paraconfusus* in the laboratory. Another possibility is that these beetles were physiologically conditioned to search the bark instead of continuing to disperse as discussed by Borden (1977). Seventy-seven beetles (63%) walked or searched in an upward direction from where they landed and 46 (37%) walked or searched in a downward direction.

Investigation of fresh entrance holes and pitch tubes followed searching behavior in 54% of the observations. Pitch tube investigation consisted of circling the hole, poking the head and thorax in and out of the hole, clearing frass away from the hole, or some combination of these behaviors. Occasionally, beetles became gummed up with pitch and appeared to swim back and forth in the pitch flow coming from the fresh entrance hole. Both sexes were observed investigating pitch tubes. Some beetles appeared to walk directly toward fresh entrance holes, whereas others seemed to encounter entrance holes randomly during their search. Frequently, a beetle would pass over or within 1 cm of a pitch tube without stopping or noticing the hole. Investigation of pitch tubes may stimulate females to bore since in 8 cases females began boring within 1 or 2 cm of a fresh attack that had just been investigated. Their galleries went in a different direction from those of the adjacent attacks.

Investigation of pitch tubes resulted in encounters with other SPB in 29% of the cases, while 12% of the searching beetles encountered other SPB. Encounters were defined as 2 beetles touching each other during their stay on the bark surface. Females initiating galleries were occasionally bumped in the posterior by other beetles. The female continued boring, while the beetle that made the contact left after a few minutes. Fifty-eight percent of the encounters resulted in a return to searching without any obvious change in behavior. Thirteen percent of the SPB dropped from the host after encountering another SPB and 29% of the encounters resulted in fighting. Fighting usually occurred outside entrance holes and consisted of 2 beetles butting their heads together and pushing, with the larger one pushing the smaller one out of the way. Two males actually drove other beetles away from an entrance hole and successfully entered. Two females, before moving on and boring into the tree, fought with other SPB near entrance holes. Fighting was followed by a return to searching 66% of the time. One SPB was dislodged from the tree during a fight. Fighting has also been described by Yu and Tsao (1967).

Twenty-one beetles encountered the clerid beetle, *Thanasimus dubius* F., and one encountered the trogositid beetle, *Temnochila virescens* F. Ten of these encounters resulted in the predator making an unsuccessful effort to capture the SPB; 10 encounters resulted in no contact, with the predator showing no interest in the SPB; and only 2 encounters resulted in the SPB being eaten, both by *T. dubius*. One was captured as it walked exposed on the bark surface, and the other was a female pulled from a crevice as she was boring into the tree. The frequency of predation in these studies may have been reduced by the removal of outer bark scales since both *T. dubius and T. virescens* were observed searching and hiding in bark crevices and under scales, and most observed predation by the 2 predators occurred as they attempted to pull SPB from crevices. In addition, escape by dropping may have been made easier for SPB because of the reduction of crevices and large scales in the observation area, although these same scales and crevices may help SPB hide from their enemies. Finally, the observers' presence may have been a disturbing influence leading to a reduced predation rate. Both predators avoided the area in front of the observer, unless he was very still. In any case, predators did disrupt walking and searching SPB and cause them to leave the tree.

Fifty-four SPB flew from the host, and 18% of all landing beetles flew away without moving from their landing place (Fig. 1). Walking was followed by flying 47% of the time. Although these beetles did not remain on the tree, they may have returned after another brief flight. Twenty-eight SPB dropped from the tree. Dropping seemed to be an escape, or alarm behavior, occurring when they encountered predators or other SPB. Eighteen fell from the host for no apparent reason.

Fifteen females (12%) successfully bored into the host, with all attacks occurring in bark crevices or underneath scales, possibly providing support and concealment during boring. Thirteen males (10%) success-

fully found and entered entrance holes during the study, with 6 males successfully entering the 1st hole that they found. Males usually circled around the hole before entering, and manipulated frass and pitch outside the hole while moving their antennae up and down. Observed behavior was similar to arrestment behavior described by Wood et al. (1966). Time required for entrance into the gallery depended on how much pitch and frass were present.

Behavior changes in progression of mass attack.— The release of inhibitor pheromones such as verbenone (Renwick and Vité 1970) and endo-brevicomin (Payne et al. 1978) and the effects of crowding during mass attack, have been implicated in the "switching phenomenon" by which landing and boring activity is shifted to an adjacent unattacked tree (Gara and Coster 1968). Under this hypothesis, several changes in beetle behavior might be expected as the attack progresses: 1) a greater percentage of landing SPB could depart the tree by flying or dropping; 2) more beetles could walk without searching due to increasing concentrations of inhibitors; and 3) searching SPB could spend more time and cover more distance due to a lack of suitable boring sites or available galleries. Contingency tables were developed from behavioral sequence data to examine the dependence of initial behavior (i.e., the behavioral category entered after landing) and termination behavior by day of attack. Numbers of SPB cross-tabulated by initial behavior and day of attack (Table 2) showed no significant dependence (χ^2 test of independence) and a similar independence was found for termination behavior and day of attack (Table 3).

Although significant differences in initial and terminal behavior were not detected due to day of attack, some interesting behavior trends should be noted. The percentage of SPB that flew immediately without walking or searching (FLY, Table 2) was relatively constant for days 1 through 3, but increased markedly on day 4 to 33%. The percentage of beetles departing the trees by flying showed a similar pattern, being relatively constant over days 1 through 3 with an increase to 50% on the 4th (FLY, Table 3). The percentage of SPB that began their behavior by walking or searching remained relatively constant over the 4 days (Table 2). Dropping caused by *T. dubius* was slightly higher on day 2 (23%, Table 3), and activity by *T. dubius* was observed to be heaviest on this day for all study trees. No females were observed attacking the host on day 4. This corresponded with the change in sex ratio in landing trap catch to an increase of males on day 3 and 4 (Table 1).

There is a lag between the daily proportion of females starting new galleries (BORE) and the proportion of males entering new galleries (ENTER). This may result in part from the lower proportion (44%) of males arriving on the 1st day (Table 1). But males outnumber females on subsequent days and it is not until the 3rd day that the rate of entry by males becomes equal to the rate of new gallery boring. Since no new galleries were started on the 4th day, males were then entering galleries begun on previous days and by the end of that day almost all of females (87%) were attended by males. On the 4th day there was also a marked increase in the rate of flight from the trees by the landed beetles. Their activities may result from the interplay of chemical and auditory stimuli from males as they search on the bark surface galleries (Rudinsky 1973).

Landing trap catches do not truly measure the change in overall attractiveness of the tree since landed beetles are prevented from departing. Since rate of beetle departure by flight increases on the 4th day, the decline

Table 2.—Distribution of initial behavior of SPB after landing on tree by day of attack.

Initial behavior	% of beetles at day of attack[a]				Total
	1	2	3	4	
WALK	22 (6)	29 (16)	29 (12)	17 (5)	25 (39)
SEARCH	61 (17)	53 (29)	56 (23)	47 (14)	54 (83)
PRED	3 (1)	2 (1)	0 (0)	0 (0)	1 (2)
DROP	3 (1)	0 (0)	3 (1)	3 (1)	2 (3)
FLY	11 (3)	16 (9)	12 (5)	33 (10)	18 (27)
Total	100 (28)	100 (55)	100 (41)	100 (30)	100 (154)

[a] Figures in parentheses are daily numbers for each behavior category.

Table 3.—Distribution of terminal behavior of SPB on host trees by day of attack.

Terminal behavior	% of beetles at day of attack[a]				Total
	1	2	3	4	
FLY	37 (7)	43 (20)	41 (13)	50 (14)	42 (54)
DROP					
SPB	0 (0)	4 (2)	6 (2)	0 (0)	3 (4)
PRED	16 (3)	23 (11)	9 (3)	11 (3)	15 (20)
UNKNOWN	26 (5)	9 (4)	12 (4)	18 (5)	14 (18)
EATEN	5 (1)	0 (0)	0 (0)	3 (1)	2 (2)
BORE	11 (2)	17 (8)	16 (5)	0 (0)	12 (15)
ENTER	5 (1)	4 (2)	16 (5)	18 (5)	10 (13)
Total	100 (19)	100 (47)	100 (32)	100 (28)	100 (126)

[a] Figures in parentheses are daily numbers for each behavior category.

in tree attractiveness indicated by studies using sticky traps to measure response (e.g., Coster et al. 1977) may be even more rapid than the trap catches suggest.

Mean distance walked and search times by day of attack are shown in Table 4 for all SPB that did not terminate their behavior sequence immediately upon landing (i.e., those which entered a walk or search category). No significant differences were found for search time or distance traveled between days of attack (Kruskal-Wallis test). The observations indicate that SPB do not travel long distances or spend long periods of time on the bark surface. Mean distance traveled was 0.21 m and mean searching time was 0.04 hr. And of the 28 SPB lost by the observer, only 10 left the observation area. Therefore, SPB appear to enter or leave the host rather than spend long periods of time on the bark surface.

Behavioral differences between sexes.—Twenty-eight beetles that entered the tree successfully were subsequently removed and sexed (13 males, 15 females). These were used to examine the influence of sex on distance traveled, searching time, gallery construction time, and total time on the bark (Table 5).

Both total time and gallery construction time were found to be significantly affected by sex and day of attack for successful SPB. Searching time and distance traveled were not affected by either factor. (Kruskal-Wallis tests for search time and 2-way ANOVA for the others). Since searching time was not significantly different between the sexes, females appeared to have as much difficulty finding suitable places to bore into the host as males did finding available females inside galleries. Since males had only to move some frass and/or pitch out of the entrance hole before entering, gallery construction time, and hence total on-bark time was significantly less for them. Females took a mean of 1.41 hr to search and bore into the host, whereas males took a mean of 0.55 hr to search for and enter a female gallery. One male on day 1 took 2.49 hr to enter a gallery due to a strong flow of pitch from the entrance hole. He joined a female in her effort to clear pitch from the hole, with both SPB walking in and out of the hole and pushing pitch with their bodies and legs, forming a characteristic pitch tube. The beetles finally entered the host tree, although one periodically appeared at the entrance, usually backing out and pushing pitch with its back legs and body.

Since landing trap catch indicated a change in sex ratio over the 4 days (Table 1), gallery construction time was examined separately for each sex to see if the significant day-of-attack effect observed for the combined sexes might be due only to a change in the sex of SPB observed constructing galleries. No significant day-of-attack effect was found for either sex. Therefore, the significant effect of day-of-attack on gallery construction time in the combined sex analysis would appear to be due to the difference in gallery construction time between sexes coupled with the shift in sex ratio during mass attack.

The results are in general agreement with others that show peak attractiveness of beetles occurs at 48 hrs after they had begun boring (Coster and Vité 1972); and peak responses of field populations to mass attacked pines occurs about 3 days after initial attacks (Gara and Coster 1968, Coster et al. 1977). The decline in number of new attacks beginning on the 3rd day would correlate with a decline of attractants produced (Coster and Vité 1972). And the increase in flight activity from the tree on the 4th day could result from increasing concentrations of repellents or inhibitors (Rudinsky 1973). The net result is that the focus of new attacks shifts to an adjacent tree (Gara and Coster 1968), but response to the initial tree continues at a low level for several days (Coster et al. 1977) because the balance of the attraction:inhibition stimuli is probably not uniform along the infested bole of the tree.

Table 4.—Mean distance traveled and search time ($\bar{x}$ ± SE) for walking and searching SPB by day of attack.

Day of attack	Distance (m)	Search time (hr)
1	0.18 ± 0.04	0.04 ± 0.02
2	0.18 ± 0.03	0.06 ± 0.02
3	0.23 ± 0.03	0.04 ± 0.02
4	0.26 ± 0.05	0.02 ± 0.01
Total	0.21 ± 0.02	0.04 ± 0.01

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Table 5.—Mean distance traveled, search time, gallery construction time and total time ($\bar{x}$ ± SE) for successful SPB by day of attack and sex.

Day of attack	Sex	n	Distance traveled (m)[a]	Search time (hr)[a]	Gallery time (hr)[b]	Total time (hr)[b]
1	M	1	0.02	0.01	2.49	2.50
	F	2	0.37±0.06	0.12±0.01	2.13±0.76	2.25±0.75
2	M	2	0.15±0.05	0.09±0.06	0.09±0.05	0.18±0.11
	F	8	0.15±0.04	0.21±0.09	1.28±0.12	1.50±0.18
3	M	5	0.30±0.12	0.18±0.07	0.14±0.12	0.30±0.13
	F	5	0.20±0.07	0.10±0.04	0.94±0.36	1.04±0.35
4	M	5	0.29±0.12	0.07±0.02	0.45±0.21	0.53±0.20
	F	0	—	—	—	—
Totals	M	13	0.25±0.07	0.11±0.03	0.43±0.20	0.55±0.19
	F	15	0.22±0.04	0.17±0.05	1.24±0.17	1.41±0.18

[a] No significant DAY or SEX effect.
[b] Significant DAY and SEX effects.

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