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Aggregation of the Southern Pine Beetle¹ in Response to Attractive Host Trees²

J. E. COSTER,³ T. L. PAYNE,⁴ E. R. HART,⁵ AND L. J. EDSON⁴

ABSTRACT

Dendroctonus frontalis Zimmerman were attracted to shortleaf pines, *Pinus echinata* Mill., using infested shortleaf pine bolts. Response was monitored during the ensuing mass attack period by the use of sticky traps suspended along the tree boles. Uninfested host materials or host materials containing only male beetles did not elicit mass attack of trees. Female beetles either alone or in combination with males, usually stimulated mass attack within 24 h. Traps at 3–4 m above the ground caught the greatest number (26.7%) of beetles. Trap catches peaked on the 3rd day of attack and declined rapidly thereafter. Daily flight activity was greatest at ca. 1700 h during the summer. Male beetles outnumbered females by a ratio of 1:0.86. The sex ratio of trapped beetles varied consistently both diurnally and over the mass attack period.

Pheromones are used by bark beetles to cause aggregations of the beetles on host trees. The literature pertaining to population aggregation pheromones in scolytids recently has been reviewed by Borden (1974). Such pheromones have been demonstrated to be important regulators of flight and attack behavior of the southern pine beetle, *Dendroctonus frontalis* Zimm. (Vité et al. 1964). Beetles rapidly aggregated on, "mass attacked," individual pine trees. When population levels in an area were high and the rate of attack on a tree was rapid, mass attack by the responding beetles soon became concentrated upon an adjacent tree (Gara and Coster 1968). As the process was repeated the infestation became larger, and as long as pheromone sources were present in an infestation, it continued to enlarge (Gara 1967). Beetle populations were experimentally manipulated in the forest with natural sources of attractant (Gara et al. 1965).

The relative density of flying beetles increased with proximity to freshly attacked trees (Coster and Gara 1968, Reeve 1975⁶). Where population levels

were high and the rate of attack was rapid, southern pine beetles landed on adjacent host trees over a radius of ca. 9 m from attractive host materials. In areas with a low population and a slow rate of attack on a central pine, landing on surrounding trees was limited to a radius of ca. 1.5 m from the attractive materials (Coster and Gara 1968).

The insect-produced compound, frontalin (Kinzer et al. 1969), and a compound from the host, alpha-pinene, constitute the aggregation pheromone known as frontalure (Vité 1970). The roles of these compounds, as well as trans-verbenol and verbenone in regulating the attack behavior of southern pine beetle have been suggested by Renwick and Vité (1969, 1970) and Coster (1970⁷). However, in order to accurately understand the roles of any behavioral chemicals that may be involved in regulating response and attack by the beetle, it is necessary to know, first of all, the natural patterns of response to pheromones that occur during attack of pine trees. Then, with that knowledge and a knowledge of the behavior of the beetle in response to the compounds, the roles of individual behavioral chemicals may be postulated. This paper describes field studies conducted during 1973–74 to describe the arrival patterns of southern pine beetles at naturally attacked trees.

Methods and Materials

Arrival patterns were studied on individual shortleaf pine (*Pinus echinata* Mill.) trees that occupied dominant or co-dominant positions in the forest canopy. The study trees were between 21.3–38.1 cm

¹ Coleoptera: Scolytidae.

² The work was funded in part by U.S. Forest Service (Southern Forest Exp. Stn.) Coop. Agreement #USDA-SFES 19-145 to SFASU and TAES, McIntire-Stennis projects 1525 (TAES) and TEXY-00011 (SFASU), and the USDA program entitled "The Expanded Southern Pine Beetle Research and Applications Program" through TAES-CSRS grant #680-15-10 and SFASU-CSRS grant #680-15-13. The findings, opinions, and recommendations reported here are those of the authors and not necessarily those of the USDA. Texas Agric. Exp. Stn. Paper 13216. Submitted for publication Mar. 14, 1977.

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⁶ R. J. Reeve. 1975. Temporal and spatial distribution of flying *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae) and the predator *Thanosimus dubius* F. (Coleoptera: Cleridae) in and near small infestations. M.S. Thesis. Stephen F. Austin State University.

⁷ Jack E. Coster. 1970. Certain aspects of pheromone release and aggregation behavior in the southern pine beetle. Ph.D. dissertation. Texas A&M University.

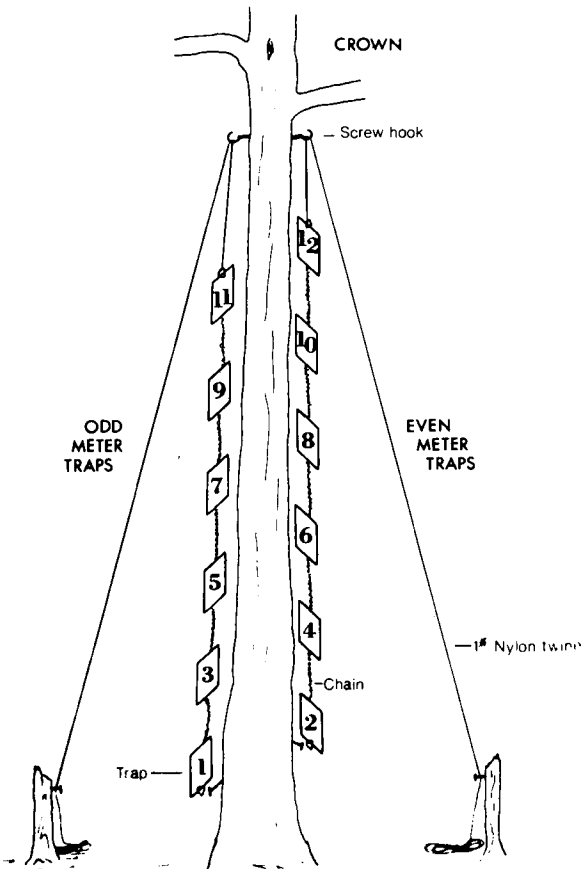


FIG. 1.—Installation of sticky traps on host trees for study of aggregation behavior.

DBH and from 13.7–24.4 m in total height. All trees chosen for study were adjacent to natural infestations of the southern pine beetle in order to insure high beetle populations and ready attack of the trees.

Each study tree was equipped with 2 traplines, each of which consisted of 6 hardware cloth traps (15.2×30.5 cm; 0.32-cm mesh) separated by 1.7 m lengths of light-weight chain (Fig. 1). The traps were coated with Stickem Special[®]. The traplines were situated on opposite sides of the tree without regard to aspect. Traps on one side of the tree were situated at odd-meter heights starting at 1 m from the ground and ending at 11 m. Traps on the other line were at even-meter heights ending at 12 m. In order to facilitate inspection, each trapline was suspended from nylon cord which extended from ground level through a screw-hook at 15 m on the tree. The traps were not in contact with the tree trunk. The total trap surface area was 55.63 dm²/tree.

Beetles were attracted to the study trees by the use of artificially-infested pine bolts (20 cm diam × 45

cm long). The bolts were infested as follows: beetles which had emerged from naturally-infested host material were collected and sexed, the presence of the transverse pronotal ridge identifying females (Fronk 1947, Osgood and Clark 1963). Before introduction of beetles, the bolts were kept at ca. 20°C for 12–24 h, and their cut ends coated with melted paraffin to retard moisture loss. A hand drill was used to drill holes (ca. 2 mm diam) at a 45° angle into the phloem. After one female beetle was placed in each hole and covered with small squares of aluminum insect screening, the bolts were placed in a chamber at ca. 5°C for 12–24 h. The bolts were then taken to the field. In cases where attraction from both sexes was desired, a male beetle was similarly confined with each female before transport to the field. When only male beetles were to be placed in the bolts, they were introduced to the unoccupied holes, covered with screen squares, and the bolts were held 12–24 h before being taken to the field. The infestation treatments used for the bolts were: male beetles only (MAB), 75 beetles/bolt; female beetles only (FEB), 75 beetles/bolt; male and female beetles (MFB), 75 beetles of each sex.

The bolts were taken to the field and tied to the study trees at a height of 5 m above the ground. Each study tree was baited with 3 bolts, all containing the same infestation treatment. The FEB and MFB bolts remained on the trees until the 1st sign of mass attack, boring dust and beetles on sticky traps which usually occurred within 24 h. MAB bolts were left on the trees for no longer than 5 days, since mortality of the males in the bolts increased after longer periods.

After the trees were baited with the bolts, the sticky traps were inspected every 2 h from 0900–1900 h (6 inspections daily) for 11 days. Trees were not monitored longer to avoid possible recapture of reemerging parent adults. The southern pine beetles caught on the sticky traps were placed in 2-dr vials containing hexane and appropriate identification labels. The beetles were counted and sexed in the laboratory.

In addition to the FEB, MFB, and MAB bolts, sticky traps were installed on trees with uninfested bolts (UNB) and on unbaited trees immediately adjacent (3–5 m) to FEB trees. Known as "adjacent" (ADJ) trees, these latter study trees reveal the beetles' response patterns on naturally attacked pines. A total of 18 trees were used in the study: MFB, 5; FEB, 4; ADJ, 2; UNB, 5; and MAB, 2.

Significance of statistical tests was assessed at the 0.05 probability level unless otherwise indicated.

Results and Discussion

Effect of Beetle Sex on Initial Aggregation

The use of various sex combinations in the artificially-infested bolts was an attempt to determine their influence on the numbers and sex ratio of beetles trapped during the earliest stages of aggregation. Colonization of hosts by the southern pine

[®] Michel and Pelton Co., Emeryville, Calif.

beetle has been shown to involve behavioral chemicals from both male and female beetles (Renwick and Vité 1969, Coster 1970⁷).

Landing activity of beetles on trees with MAB and UNB bolts was very low and these trees were not attacked by southern pine beetles. The low rates of landing (0.05 and 0.79 beetles/dm²/day, respectively) probably reflect the rates of landing of southern pine beetles on uninfested host trees near infestations. The lack of attraction by male beetles, in comparison to females, was in agreement with other field and laboratory studies (Renwick and Vité 1969, Coster 1970⁷).

ADJ, FEB, and MFB trees were all successfully attacked by southern pine beetles. A 1-way analysis of variance was used to test the hypothesis that there were no significant differences in total number of beetles trapped at the ADJ, FEB, and MFB trees. The total mean catches/tree and standard errors (SE) for the 11 trees are:

Study tree type	Mean±SE
ADJ	2719.0±1396.0
FEB	2386.5± 468.6
MFB	3418.8± 701.3

The means did not differ significantly ($F_{2,8} = 0.61$).

If, in fact, the number and sex ratio of beetles responding to the FEB, MFB, and ADJ trees differed, the differences would likely be most apparent during the early hours of attack before volatiles from the comparatively few attacks on the bolt were overwhelmed by those of the subsequent mass attack period. A 1-way analysis of variance tested the mean numbers of southern pine beetles trapped at the 3 types of study trees during the 1st 24 h after installation; a χ^2 test for differences among proportions was used to examine whether the proportion of females trapped during this period differed significantly among the 3 bait types. The % of females and mean catch/tree during the initial 24-h period were:

Study tree type	% females	Mean±SE
ADJ	51.1	66.6±29.5
FEB	50.8	44.2±20.5
MFB	56.9	14.4± 7.0

The mean catches/tree during the initial period were not significantly different ($F_{2,8} = 2.28$). The proportion of females did not vary significantly ($\chi^2 = 0.84, 2 \text{ df}$).

Since there were no differences between the study tree types for either total (11 day) mean catches or for mean catches during the initial 24-h period and, further, since sex ratios of trapped beetles did not differ significantly among study trees, the 3 types of successfully attacked trees were combined for all subsequent analysis.

General Response Patterns

A total of 32,077 southern pine beetles were trapped on all trees. The mean total density of beetles trapped per tree during 11 days was 52.4±7.4

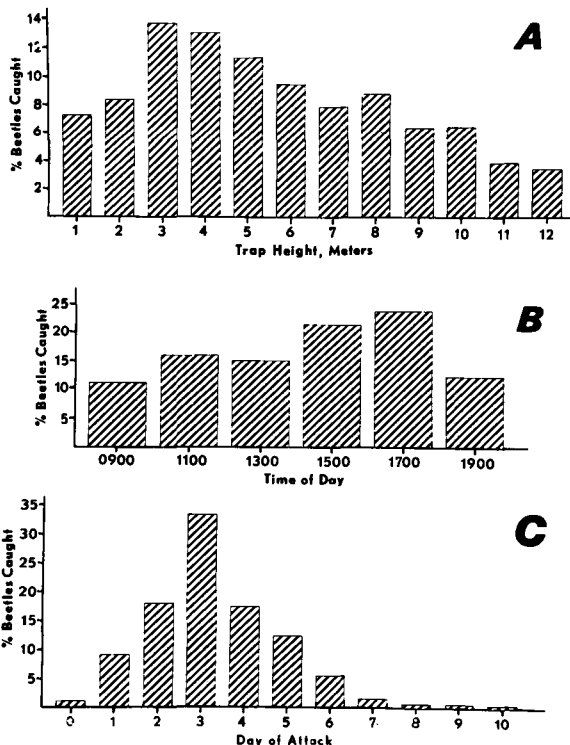


FIG. 2.—Distribution of southern pine beetles trapped at pine trees during 11 days of mass attack. A, by height of trap; B, by time of day; C, by day of attack. Based on 11 trees. $n = 32,077$ beetles.

(SE)/dm². This density is considerably higher than the attacking adult densities of 2–6/dm² reported by Coulson et al. (1976) and Stephen and Taha (1976). Our numbers must not be interpreted as representing attacking densities of southern pine beetle but rather as reflecting capture of beetles on trees under attack. The mean total density is an accumulative density since beetles on the traps were prevented from departing and were generally unavailable to mortality factors on the bark surface such as predators and parasites. General response patterns are shown in Fig. 2.

Height Distribution.—The height of maximum trap catch was at 3 m where 13.7% of the beetles were taken (Fig. 2A). 53.7% of the total beetles were taken on the 5 lowest traps. It is unlikely that the location of the artificially-infested bolts at 5 m appreciably altered the height distribution of trapped beetles on the FEB and MFB trees. On the non-baited ADJ trees, landings were also most frequent at the 3–4 m levels. Similarly, Gara et al. (1965), with bolts attached at 1.2 m, found maximum beetle response at 3 m.

At each of the 6 daily check periods, traps at 3–4 m caught more beetles than those at other heights (Fig. 3). A χ^2 test was used to determine whether proportional response at each of the trap heights was constant throughout the day. Significant

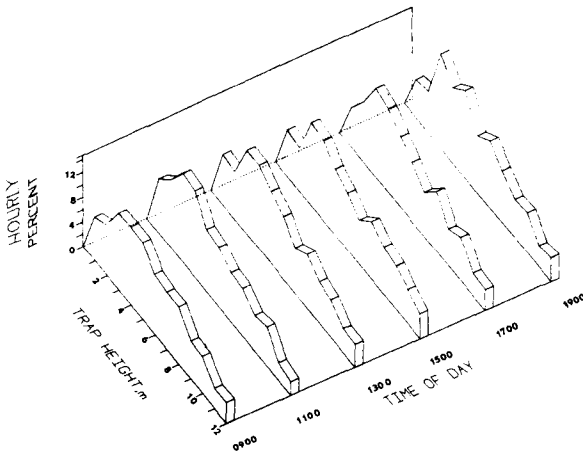


FIG. 3.—Distribution, by trap heights, of bihourly catch of southern pine beetles at pines undergoing mass attack.

variations in proportional response were found for all trap heights except 3, 4, and 6 m. Traps at these 3 heights captured a constant % of total beetles at each of the check periods. Three and 4 m were also the heights of greatest landing frequency throughout the day (Fig. 3).

The % catch varied through the day at each of the other 9 trap heights. The lowest traps (1, 2 m) caught their highest % in mid-morning (1100 h) while the mid-height traps (5, 7 m) caught their highest % late in the day (1900 h). The highest proportion of catch for the 8–12 m traps occurred at the 1500 or 1700 h check period. A χ^2 analysis showed that there was no daily check period when landing activity was equally distributed among all heights.

The proportionally higher landing activity on the upper bole during the afternoon may be due to upward movement of pheromones by convection currents caused by heating of the bole of the tree ("chimney effect") (Fritschen et al. 1970). The increased landing (relative to other heights) on the mid-bole about 1900 h may have resulted from cooling of the tree trunk and cessation of convection.

Height distribution patterns of daily catch vary as attack progresses (Fig. 4). On days 0 and 1, highest proportions were caught at 4 m; on days 2–4, peak catch was at 3 m. During days 0–4, beetles were landing, proportionately, in greater numbers at the higher levels so that, by day 5, traps at 8–12 m caught 48% of the total days' catch. On the 6th and 7th days, the 8–12 m traps caught 53.4% and 37.2%, respectively, of the total days' catch. Thereafter, highest landing activity returned to the 3–4 m level.

The response patterns were examined by halves of installed height, 1–6 m and 7–12 m. Beetles caught on traps on the lower half of the bole declined from an initial level of ca. 84.5% of daily activity to 38.9% on day 6. Activity on the lower

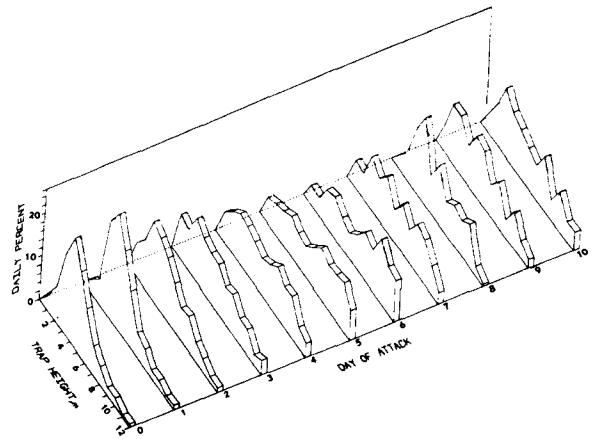


FIG. 4.—Distribution, by trap heights, of daily catch of southern pine beetles after beginning of mass attack.

bole then began to increase and for the last 4 days reached about $\frac{2}{3}$ of the total daily activity. On the 5th day of attack the trap catches were about equally distributed by halves.

Diurnal Response.—The diurnal response pattern showed peak flight activity at 1700 h when 23.8% of the beetles were caught (Fig. 2B). Flight activity generally increased until 1700 h with a leveling off during mid-day (1100–1300). After 1700, flight activity decreased until darkness arrived. The total response from check period to check period varied significantly ($\chi^2 = 2504.9$, 5 df). The diurnal response was similar to the summer pattern reported by Vité et al. (1964) but did not exhibit the bimodality of their spring pattern. About 11% of the beetles were removed from traps at 0900. This reflects both some flight after 1900 h the previous evening and some flight between sunrise and 0900. Flight during these evening and early morning periods was observed by Vité et al. (1964).

Bait bolts were placed on tree on day 0. Attack was not evident during that initial period. Maximum

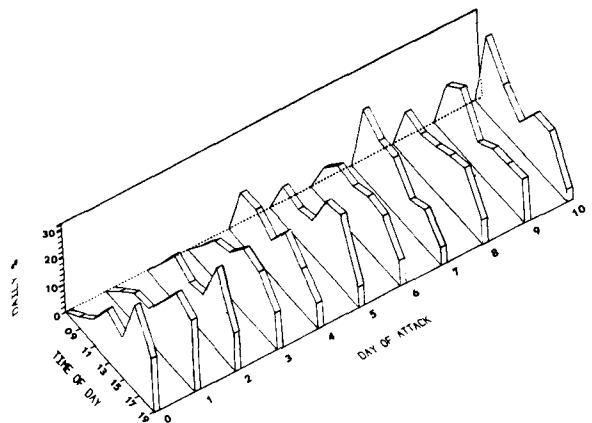


FIG. 5.—Distribution, by time of day, of daily catch of southern pine beetles after beginning of mass attack.

trap catches occurred on the 3rd day of attack when 33.4% of the total beetles were caught (Fig. 2C). By the end of the 3rd day, ca. 61% of the total catch had been accumulated. Response at the trees declined rapidly after the 3rd day until on day 10 only 0.2% of the total beetles were caught. Similar results were reported by Gara and Coster (1968).

The general response pattern by time of day was arrayed so that the diurnal response pattern for each day of attack could be examined (Fig. 5). A χ^2 test indicated that in all cases the daily response pattern differed significantly from the overall response pattern ($\chi^2 = 39076.3$, 11 df) (Fig. 2B). The time of peak response was 1500 or 1700 h on each of the 1st 6 days of attack. However, after day 1 there was a trend for more of each day's catch to occur in the AM. This shift towards more AM activity with progress of mass attack may result from declining attractiveness of the tree and its inability to compete with more recently attacked trees for the major PM flight of beetles. Coster (1967)⁹ observed that new attacks on neighboring trees caused a marked depression of flight to adjacent study trees. On days 7-10, AM catch was greater than that during the mid-day or PM period, except for day 8 when AM and PM flight were ca. equal. Mid-day activity remained more or less constant, proportionally, throughout the attack period.

Sex Ratios of Responding Beetles

Females were 46.1% of the total number of beetles trapped (sex ratio = 1:0.86, male:female). The ratio was significantly different from a postulated 1:1 ratio ($\chi^2 = 190.97$, 1 df). Sex ratios of 1:0.72 (Gara et al. 1964), 1:1 (Vité and Crozier 1968), and 1:0.90 (Reeve 1975¹⁰) have been reported for responding field populations. Sex ratios of 1:0.95 (Stein 1975¹⁰) and 1:1 (Osgood and Clark 1963) have been observed from emerging brood and 1:1 for attacking adults (Coulson et al. 1976).

Based on total data from all 11 trees, the % females observed at each daily check period were:

Time of day	% females trapped
0900	36.9
1100	47.6
1300	50.9
1500	48.7
1700	45.5
1900	43.6

A χ^2 test rejected the hypothesis that the % females trapped remained constant throughout the day ($\chi^2 = 199.7$, 5 df).

To determine the nature of sex ratio variation by time of day, the means for % females trapped for each tree and for each daily check period were fitted to linear ($Y = a + bx$), exponential ($Y = ae^{bx}$), power

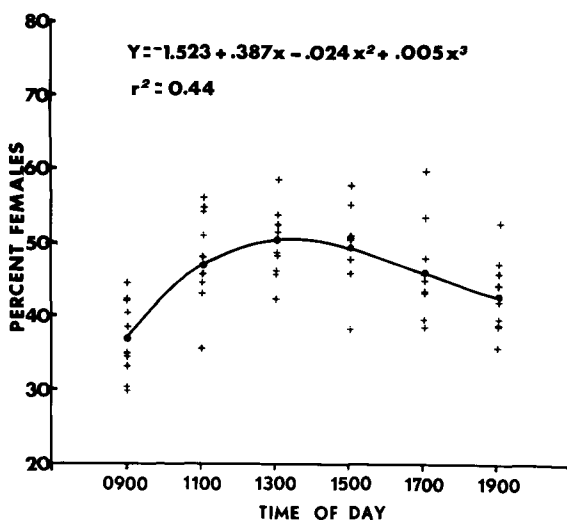


FIG. 6.—Diurnal change in sex ratio of southern pine beetles trapped at trees undergoing mass attack.

($Y = ax^b$), 2nd-order polynomial ($Y = a + bx + cx^2$) and 3rd-order polynomial ($Y = a + bx + cx^2 + dx^3$) regression models. The best fit was the highly significant ($F_{3,62} = 16.43$) 3rd-order polynomial (Fig. 6). Females were fewer in number in the mornings and during the late afternoons and were ca. equal to males during mid-day. Vité and Crozier (1968) report that "females arrive earlier in the afternoon than males."

The % females observed for each day of attack using the overall totals for all trees were:

Day of attack	% females
0	52.1
1	46.1
2	48.9
3	47.1
4	44.6
5	44.4
6	39.7
7	40.6
8	43.2
9	51.5
10	44.1

Chi-square evaluation was used to test whether the observed frequency of females trapped for each individual day differed from a frequency expected on the basis of the % females (46.1) in the general responding population. For example, on day 0 the observed frequency of females was 199 and the expected frequency was 176.

Significant variations in the observed frequency of females existed on day 2 ($\chi^2 = 10.28$, 1 df) and day 6 ($\chi^2 = 15.36$, 1 df), the deviations on the 2 days being in opposite directions, however. On day 2, more females were trapped than expected; on day 6, the proportion of females was less than expected. Although deviations on other days were not signifi-

⁹Jack E. Coster. 1967. Studies of the attack behavior of the southern pine beetle, *Dendroctonus frontalis* Zimmerman. M.S. Thesis. Texas A&M University.

¹⁰C. R. Stein. 1975. Seasonal and height distribution of predators and parasites of the southern pine beetle (Coleoptera: Scolytidae) in two species of pine in East Texas. M.S. Thesis. Stephen F. Austin State University.

cant, there was a trend for females to arrive in greater than expected proportion during the 1st 3 days of attack and in lesser proportion thereafter. The increase in the female sex ratio beginning on day 7 may be due to capture of emerging parent beetles which, in laboratory broods, occurs 10–14 days after 1st attack (Thatcher and Pickard 1964). Females outnumber males during this re-emergence, especially during the 1st 2 days (Coster 1970').

The mean % females for each trap height using the overall totals for all 11 trees were:

Trap ht (m)	% females
1	47.6
2	47.8
3	46.4
4	44.3
5	44.4
6	44.9
7	45.8
8	46.2
9	47.7
10	46.7
11	48.8
12	47.5

It was found that the proportion of females varied significantly by trap height ($\chi^2 = 23.1$, 11 df). The means suggest a higher than expected proportion of females on the lower and upper 3 m of the tree boles and lower proportions of females in the 4–7 m sections.

Conclusions

1. Beetle aggregation during the 1st 4 days of attack on pine trees was concentrated at 3–4 m above the ground. Subsequently, trap catches became proportionally greater on the upper bole of the trees.
2. Mass attack of the trees occurred rapidly. Over 60% of beetles caught in an 11 day period were taken during the 1st 3 days. The highest daily catch was on the 3rd day of attack.
3. Flight aggregation at trees under attack generally increased throughout the day becoming greatest in late afternoon (1500–1700 h) and then declined as sunset approached. With succeeding days of attack, more of the total daily flight activity occurred in the morning hours.
4. Males outnumbered females in the total population captured. There was a trend, however, for female numbers to be proportionally highest during the 1st 3 days of attack and proportionally lower thereafter.
5. Sex ratio of the beetles varied within days. Female response was lowest in the AM, became greatest during mid-day, and then declined for the remaining portion of the daily flight period.
6. Over the entire mass attack period, the proportion of females was lower at the mid-bole region of the tree than at either the lower or upper regions of the bole.

Acknowledgment

We thank Temple-Eastex, Inc., Owens-Illinois Co., Southland Paper Co., and the National Forests of Texas (Raven Ranger District) for allowing the use of forest lands. Assisting in the studies were P. Billings, W. Dixon, W. H. Hoffard, F. McCarty, L. McWorter, I. R. Ragenovich, R. J. Reeve, D. Stallings, and C. R. Stein. R. N. Coulson, J. Foltz, E. Nebekker, and G. K. Stephenson provided helpful reviews of the manuscript. W. Dixon kindly drew Fig. 1, S. Gray drafted Fig. 2–6, and J. P. Kole assisted in computer summarization of the data.

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