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EMERGENCE AND ATTACK BEHAVIOR
OF THE MOUNTAIN PINE BEETLE IN LODGEPOLE PINE

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ABSTRACT

Factors influencing the behavior of mountain pine beetles infesting lodgepole pine were studied during 1974 and 1975. More and larger beetles emerged from trees having thickest phloem, with the largest beetles usually emerging first. Beetles emerging in 1974 constructed more gallery and laid more eggs than did beetles emerging in 1975, probably due to the late beetle flight in 1975 and larger size of the females. Trees that were successfully mass attacked had lower inner bark temperatures than trees unsuccessfully attacked. The sex ratio of emerging beetles was 1.52:1, females to males; for attacking beetles it was about the same, 1.50:1, but for the boring beetles it was 2.34:1.

KEYWORDS: mountain pine beetle, temperature, behavior

The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) is the most destructive insect infesting lodgepole pine (*Pinus contorta* Dougl.) forests throughout most of its range. Each year this bark beetle kills large numbers of trees over vast areas. Although beetle behavior has been the subject of many studies, much still remains to be learned. In an effort to better understand the mountain pine beetle, factors that influence and regulate its attack, and emergence behavior were studied in 1974 and 1975. Temperature is one of the most apparent influences (see Safranyik [1978] for an excellent review of climatic effects on beetle biology); however, aspect of attack, beetle size, and sex ratios also influence behavior.

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METHODS

The study area was located in the Wasatch Mountains of northern Utah at an elevation of 2 248 m (7,600 ft). The area consists of a rather isolated stand of lodgepole pine of about 64.7 ha (160 acres), with an active, although somewhat static mountain pine beetle infestation. Data were recorded and beetles were collected daily throughout the length of the emergence and attack period, which lasted from July 24 to August 8, 1974, and July 30 to August 25, 1975. During each study year emerging beetles were caught in two 15.2 x 30.4 cm (6 x 12 inch) cages stapled to 20 trees infested the previous year. Twenty attacking beetles were collected at random from each of a total of 12 trees. Boring beetles were excised and collected at random from 10 galleries from each of 37 freshly attacked trees. Beetles were labeled, preserved in 70 percent alcohol, and taken to the laboratory where they were sexed according to the method described by Lyon (1958) and measured. In the fall, two 15.2 x 15.2 cm (6 x 6 inch) bark samples from each of 20 trees were removed to determine brood (egg), attack, and gallery densities.

RESULTS AND DISCUSSION

Influence of Temperature on Emergence, Attacks, and Egg Laying

Beetle emergence and flight usually occur in late July and early August after a period of warm weather (Reid 1962a; Rasmussen 1974). In the study area, this is consistently the warmest period of the summer. Peak emergence dates for the years of this study occurred July 31, 1974, and August 17, 1975. The peak emergence date in 1975 was later than usual, probably because frequent storms and cool temperatures delayed larval development in the spring, and delayed adult emergence in late July and August.

In 1974, air and inner bark temperatures were measured at breast height when the initial attack on a tree was observed. The average air temperature at the time of initial attack for trees successfully mass attacked was 22.9° C (73° F). For trees unsuccessfully attacked the average air temperature was 23.1° C (74° F)--not significantly different. However, the average inner bark temperatures were significantly different between successfully and unsuccessfully attacked trees (table 1).

Table 1.--Comparison of average inner bark temperatures (centigrade), of seven successfully and four unsuccessfully attacked lodgepole pines

Aspect	n	Successfully attacked		Unsuccessfully attacked		Difference in average temperature	t-test probability	
		Average temperature	Temperature range	Average temperature	Temperature range			
North	7	23.5	21.5 - 25.0	4	25.9	25.5 - 26.0	2.4	<0.005
East	7	23.8	21.0 - 26.0	4	26.0	26.0 - 26.0	2.2	< .010
South	7	24.2	21.0 - 27.0	4	26.4	26.0 - 27.0	2.2	< .025
West	7	24.0	21.0 - 26.5	4	27.0	26.0 - 28.0	3.0	< .005

In addition, the initial attack on successfully attacked trees was either on the north or east aspect where the lowest inner bark temperatures occurred. Initial attacks on unsuccessfully attacked trees were not consistently related to any aspect. The reasons for these differences are unclear. Solar radiation heats the south and west aspects of trees to higher temperatures than north and east aspects (Powell 1967). Therefore, the higher temperatures recorded on unsuccessfully attacked trees may have deterred the beetles. It appears that high inner bark temperatures of about 26° C (79° F) limit successful colonization of lodgepole pine by the mountain pine beetle.

North and east aspects of successfully colonized trees had the highest attack densities. Average attack densities per 30.4 x 30.4 cm (12 x 12 inch) for each aspect were: north = 10.0; east = 12.5; south = 8.4; and west = 7.1. The cooler inner bark temperatures of the north and east aspects seemed more conducive to beetle attack. Reid (1963) and Shepherd (1965) also observed highest attack densities on north aspects for mountain pine beetles infesting lodge-pole pine in British Columbia and Alberta.

Prewinter (mid-October 1974 and early November 1975) samples of mountain pine beetle populations show that shorter galleries were constructed and fewer eggs were laid in 1975 than 1974, even though attack densities were nearly equal for the 2 years (table 2).

Table 2.--Comparison of average mountain pine beetle attack, gallery and egg densities per 15.2 x 15.2 cm (6 x 6 inch) sample in 1974 and 1975

Year	Peak emergence date	Average female length	Average attack density	Average gallery density	Average gallery/attack	Average egg density	Average number eggs/cm gallery
		<i>mm</i>		<i>cm</i>	<i>cm</i>		
1974	July 31	5.1	2.4	73.2	31.1	90.5	1.2
1975	August 17	4.9	2.6	52.6	20.6	44.8	0.8

Because the beetles flew later in 1975 they had fewer days (before the onset of cold weather) to construct gallery and lay eggs. An adverse effect on the beetle population could occur when proportionately more eggs and fewer larvae enter winter because all eggs are killed by cold temperatures. In addition, the 1975 parent females were, on the average, smaller than in 1974; this also probably contributed to fewer eggs being laid that year. Reid (1962b) found large mountain pine beetles generally laid more eggs than did small beetles. McGhehey (1971) and Amman (1972a) in laboratory studies found that larger females generally laid more eggs per inch of gallery and that they also laid more eggs per day.

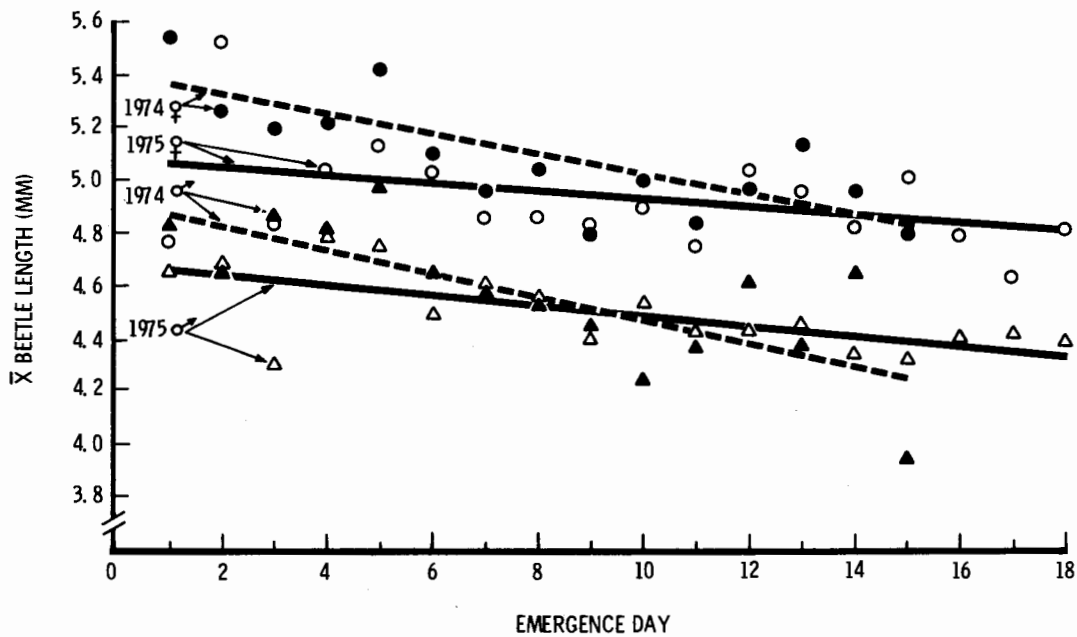
Beetle Size

The average sizes (beetle length) of both females and males that emerged early were generally larger than those that emerged later (fig. 1). Similar observations were made by Safranyik and Jahren (1970). In addition, both the number of emerging beetles and beetle size were directly related to phloem thickness, relationships noted by Amman (1972b) and Amman and Pace (1976) (table 3).

Both female and male beetle lengths appear to increase with an increase in phloem thickness. Differences between mean lengths in the thin and medium thickness groups, and between those of the medium and thick phloem thickness groups are significant at $P < 0.05$ for both sexes. Further, the variances about the means for both females and males are relatively small, ranging from only 6-11 percent of the means.

Sex Ratios

The sex ratio of the emerging, attacking, and boring beetles was determined for both years. The attacking beetles were those that had just landed on a tree or were walking about, making no attempt to bore in. The boring beetles were those actively engaged in gallery construction (table 4).



Females 1974: $\hat{Y} = (X) - 0.0371 + 5.3821$; $r^2 = 0.59$; ($P < 0.005$)

1975: $\hat{Y} = (X) - 0.0162 + 5.0790$; $r^2 = 0.20$; ($P < 0.100$)

Males 1974: $\hat{Y} = (X) - 0.0448 + 4.9255$; $r^2 = 0.54$; ($P < 0.005$)

1975: $\hat{Y} = (X) - 0.0193 + 4.6755$; $r^2 = 0.46$; ($P < 0.005$)

Figure 1.--Comparison of female and male mountain pine beetle size in relation to emergence day for 1974 and 1975.

Table 3.--Comparison of the density and average size of emerging female and male mountain pine beetles per 30.4 x 30.4 cm (12 x 12 inch) cage

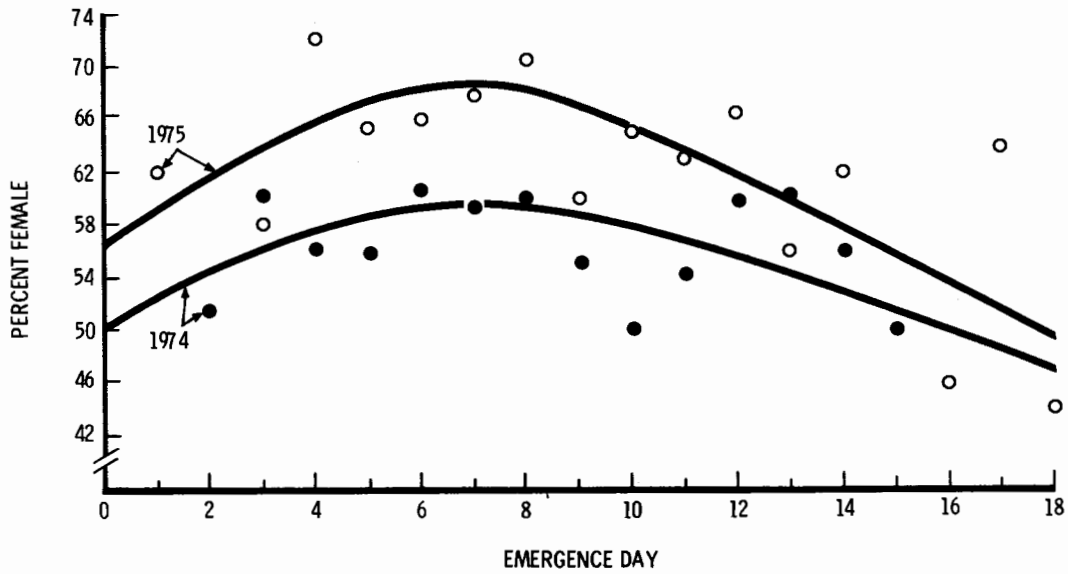
Phloem thickness	Females				Males			
	Total number	Average number per cage	Average size	Standard deviation	Total number	Average number per cage	Average size	Standard deviation
<i>mm</i>			<i>mm</i>				<i>mm</i>	
1.1 - 1.6	142	14.2	4.77	0.364	82	8.2	4.36	0.326
1.7 - 2.1	161	10.1	4.87	.469	97	6.1	4.45	.372
2.2 - 3.2	281	20.1	5.01	.437	186	13.3	4.52	.375

Table 4.--Sex ratios of the emerging, attacking, and boring mountain pine beetles

Year	Emerging beetles		Attacking beetles		Boring beetles	
	Female:Male	Percent female	Female:Male	Percent female	Female:Male	Percent female
1974	1.48 : 1	59.7	1.58 : 1	61.3	2.11 : 1	67.8
1975	1.53 : 1	60.4	1.22 : 1	55.0	2.47 : 1	71.2
Both years	1.52 : 1	60.1	1.50 : 1	60.1	2.34 : 1	70.1

Sex ratios of the emerging and attacking beetles are similar; however, the sex ratio of the boring beetles favors the females a great deal more. The reason for this discrepancy probably is related to the polygamous nature of the males. Many leave galleries after mating and search for other unmated females. This could have resulted in a number of males being outside when galleries were opened for observation and in addition the number of males probably would be reduced during increased exposure to predation by clerid beetles and birds.

The percentage of emerging beetles that was female first increased and then decreased over the emergence time period. This difference was more pronounced in 1975 than in 1974 (fig. 2). From curves fitted to the data, using the method of Jensen and Homeyer (1971), it was estimated that the percentage of females rose from about 50 percent to a maximum of about 59 percent, then declined to about 47 percent in 1974. A similar response was noted in 1975 when the percent female rose from 56 to 68 percent, then declined to 49 percent at the end of the emergence period. Although the correlation coefficient for 1974 data is low, it is evident that the same general trend exists in 1974 and 1975.



	Limits→	r ²	Pr.
1974: $\hat{Y} = 59.3 - 0.375 (7 - X)^{1.65}$	0 ≤ X ≤ 7	0.042	N.S.
$\hat{Y} = 59.3 - 0.439 (X - 7)^{1.4}$			
1975: $\hat{Y} = 68.4 - 0.480 (7 - X)^{1.65}$	0 ≤ X ≤ 7	0.518	<0.005
$\hat{Y} = 68.4 - 0.669 (X - 7)^{1.4}$			

Figure 2.--Percentage of the emerging mountain pine beetles that was female in relation to emergence day for 1974 and 1975.

CONCLUSIONS

The three most important results found in this study are:

1. Lodgepole pine trees successfully attacked by mountain pine beetles had significantly lower inner bark temperatures than trees unsuccessfully attacked.
2. Cooler inner bark temperatures on north and east aspects seemed more conducive to beetle attack where higher attack densities were found and where the initial attack occurred on successfully attacked trees.
3. Beetles emerged earlier, constructed more gallery, and laid more eggs in 1974 than in 1975, probably due to warmer, drier weather.

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