POPULATION STUDIES OF THE MOUNTAIN PINE BEETLE

by

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INTRODUCTION

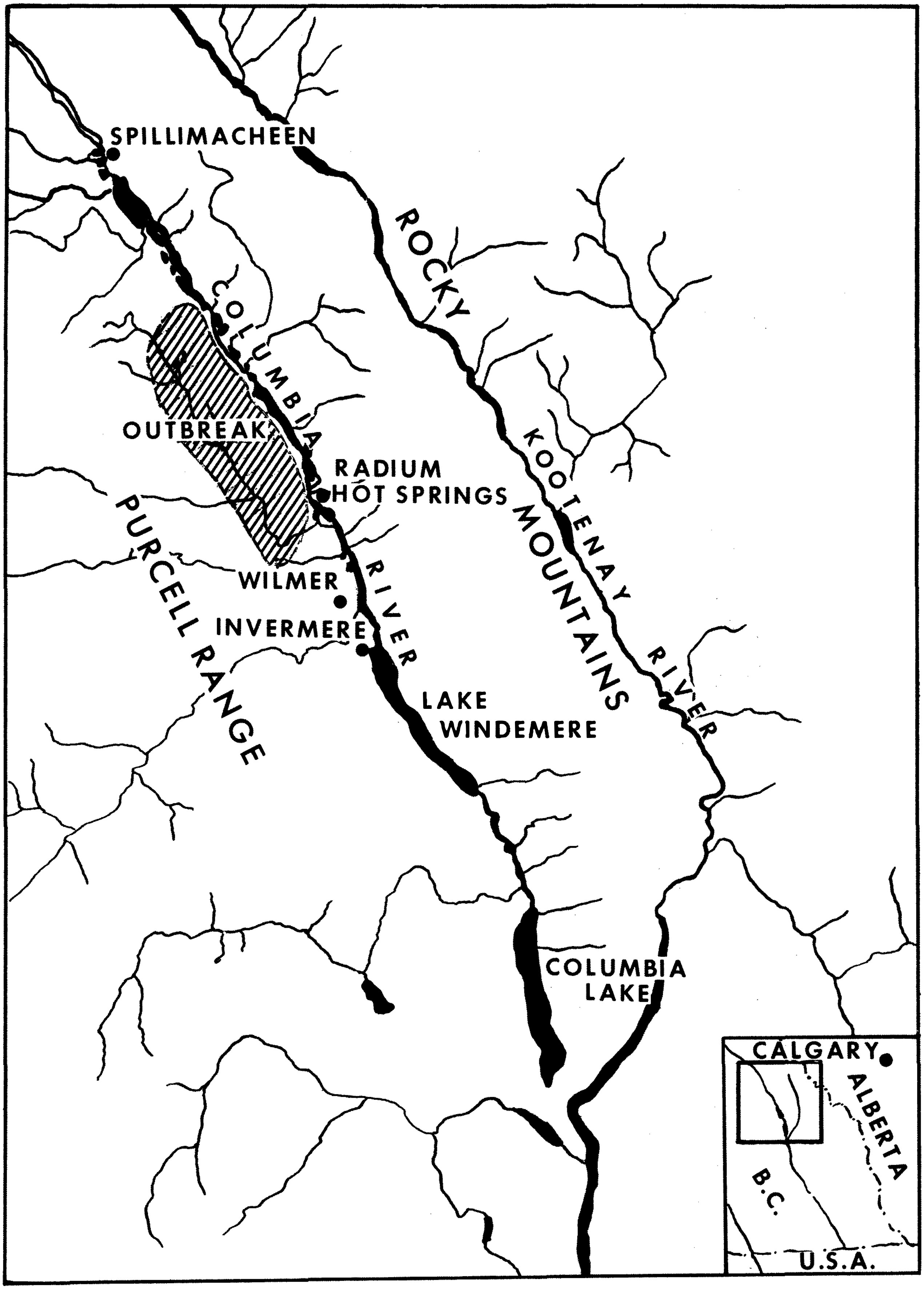
Three integrated phases of research are being carried out simultaneously in this study: Population sampling and evaluation of population trends, tree susceptibility and attraction, and reactions of adult beetles to various environmental factors. These studies are also coordinated with those of R. W. Reid on the biology and moisture relationships between the beetle, and environment and with studies by J. A. Cook on the influence of drought on the susceptibility of trees to beetle attack. These investigations are on a continuing basis and results of previous studies are given in earlier reports (Shepherd 1956, 1958, Reid 1956, 1957, 1958).

The field studies are conducted in the Francis Creek Valley 10 miles north-west of Invermere, B.C. where lodgepole pine has been attacked in small groups for at least ten years (Fig. 1.).

SELECTION TESTS

When beetles attack a tree they usually do so in large numbers. That is, a tree is usually heavily attacked or not attacked at all. This has led to the theory that certain trees are more susceptible to beetle attack and presumably the beetles can sense this type of tree and are attracted to it. The following tests were designed to determine the attractiveness of the various tree characters and to help explain the behavior patterns of attacking beetles.

Fig. 1. Map of the Invermere area of the East Kootenay Region showing the infested area used in the field studies.



SPILLIMACHEEN
COLUMBIA
ROCKY
OUTBREAK
RADIUM HOT SPRINGS
KOOTENAY
MOUNTAINS
PURCELL RANGE
WILMER
RIVER
INVERMERE
RIVER
LAKE WINDEMERE
COLUMBIA LAKE
CALGARY
ALBERTA
B.C.
U.S.A.

Bark Roughness

Bottom logs were taken from four trees to give as wide differences in bark roughness as possible but with the diameter outside bark approximately the same. The four logs were arranged randomly in a row three or four feet apart. They were held vertical by a cross brace nailed across the tops. This arrangement was replicated in four separate areas where beetles were active. After exposure to attack the bark was removed from the logs and the galleries counted. A higher intensity of attack on one log was interpreted as a preference of the beetles for that log. This study was run in 1957 and 1958. The data for the two years were combined together and are presented in Table I. The analysis of variance and Q test of the means of this data appear in Tables II and III. The difference between areas was significant at the one percent level but the difference between years was not significant. There was a significant difference between bark types at the five percent level. An extension of this analysis utilizing the Q test of the separate means at the five percent level showed that the difference was significant only between the smoothest and roughest barks.

Table I. Relation between bark roughness and intensity of attack.

Bark Character

Area		1 (Smooth)	2	3	4 (Rough)
		Intensity of Attack (Strikes/sq.ft.)			
1956	I	0	50	103	89
	II	2	8	0	9
	III	2	8	0	9
	IV	0	4	0	0
1957	V	0	0	13	19
	VI	0	5	14	0
	VII	3	6	22	32
	VIII	3	26	15	25
	Average	1.25	13.38	20.75	22.88

Table II. Three way analysis of variance to test the difference between intensity of attack and bark characteristics.

Source of Variation	Sum of Squares	d.f.	Mean Square	Variance Ratio
Years	312.50	1	312.50	1.26
Areas within Years	10134.88	5	2026.98	8.17**
Bark	2288.13	3	762.71	3.08*
Error	5456.37	22	248.02	
Total	18191.88	31		

Table III. A test of means of intensity of attack upon logs of different bark characteristics.

Bark Type	$\bar{X}$	$\bar{X}$-1.25	$\bar{X}$-13.38	$\bar{X}$-20.75
4 (Rough)	22.88	21.63	9.50	2.13
3	20.75	19.50	7.37	
2	13.38	12.13		
1 (Smooth)	1.25			

$Q_{s_{\bar{x}}}$ .05 = 21.55

Bark and Height Interaction

A study on the distribution of attacks over the surface of the tree indicated that there was a decrease in intensity of attack vertically up the tree. Associated with this vertical gradient was a decrease in bark roughness up the tree. An attempt was made to separate those two factors by exposing logs in different positions to beetle attack. Logs were selected which were rough at the butt end and smooth at the top end. These were placed in a row; two logs with the rough end down and two with the rough end up. This was replicated in four areas in 1957 and four more areas in 1958.

The data was tallied by the upper or lower halves of the logs. The results are given in Table IV and the analysis of variance is given in Table V. There is a significant difference between plots and also between log ends. When a Q analysis of means was made (Table VI) it was found that there was no difference between the rough ends or the smooth ends in the two positions but there was between the rough ends of the logs in the usual position and the smooth ends of the logs in both positions. This indicates that the beetles prefer the rough end of the log irrespective of its position.

Table IV. Relation between intensity of attack and the end of the log selected when half the logs are reversed.

	Usual Position		Reversed Position	
Area	Upper Half	Lower Half (Butt)	Upper Half (Butt)	Lower Half
1	2	1	0	0
	0	1	0	0
2	0	5	0	0
	1	14	14	1
3	5	21	21	5
	4	35	6	5
4	0	0	0	0
	0	0	0	0
5	1	1	14	9
	20	24	22	20
6	0	1	1	0
	0	0	0	0
7	0	0	0	0
	1	1	2	0
8	1	5	3	4
	0	1	0	0
Average	2.19	6.88	5.19	2.75

Table V. Two-way analysis of variance with replicates to test the difference in the intensity of attack between the upper and lower halves of logs when half the logs were placed with butt end up.

Source of Variation	Sum of Square	d.f.	Mean Square	Variance Ratio
Log Ends	228.4	3	76.12	3.41*
Plots	1866.7	7	266.67	11.94**
LEXP	692.0	12	57.66	2.58
Error	915.0	41	22.32	
Total	3702.1			

Table VI. Q test of means of intensity of attack upon upper and lower halves of logs when half the logs are placed with the butt end up.

Log End	$\bar{X}$	$\bar{X}$-2.188	$\bar{X}$-2.750	$\bar{X}$-5.188
Butt end, log in usual position	6.875	4.687*	4.125*	1.687
Butt end, log reversed	5.188	3.000	2.438	
Upper end, log reversed	2.750	0.562		
Upper end, log in usual position	2.188			

$$Q_{s_{\bar{x}}}\ .05 = 3.53$$

Bark Moisture Content

A theory that trees which are suffering from drought are the most susceptible and attractive to the beetle was partially tested by determining the preference of the beetles for bark of different moisture contents.

The bark material used was taken from a log which was cut from a healthy green tree and placed in a high humidity chamber within 30 minutes after felling. The chamber was a small corner of the laboratory enclosed by polyethylene sheeting. Wet towels were hung up inside and the room and walls were frequently sprayed with a mist to keep the humidity as high as possible during the experiment. Sixteen strips of bark (including outer and inner bark) 3" x 9" were cut from the log and each divided into three equal pieces. The bark roughness was similar throughout the length of each strip. The allocation of the pieces of each strip to a wet or dry or medium moisture content was done on a random basis. One of these pieces was immediately weighed and was assumed to approximate the moisture content of the bark in that tree while standing. This was approximately 76 per cent. One piece of each strip was placed on a laboratory table and allowed to dry at room temperature until about 20 per cent of the moisture had been lost. The other piece of each strip was placed in cold water for six seconds and then blotted and the surface moisture allowed to evaporate. At the completion of the drying or wetting procedures each group was placed in the high humidity chamber to prevent further evaporation. The three pieces of each strip were then weighed and tacked to a shingle in the same order as they occurred in the original strip.

Fiberglas screening was stapled on top of each of the strips to make sixteen cages. Ten beetles were introduced into each cage. The cages were left for three days and then the pieces were taken off the shingles, weighed, and the number boring into each piece recorded. The pieces of bark were then dried to a constant weight at 105°C. and weighed again.

The beetles were collected in cages as they emerged from naturally infested logs. They were stored in a refrigerator in aluminium boxes with moist, fresh bark, for about a week before the experiment. The mortality during the experiment was about 40 per cent.

The drier pieces of bark gained moisture, and the wetter pieces lost moisture during the three days, but in no case were the relative positions of dry, medium, and wet changed. The average moisture content based on the mean of the beginning and ending weights was 51.6 per cent for the dry bark, 69.7 per cent for the medium bark, and 90.4 per cent for the wet bark. These are the moisture contents as a percentage of oven dry weights.

In one case there were more beetles boring into the dry bark, two cases where there were more boring into the medium-wet bark, and in the remaining 13 cases the beetles preferred the wet bark. The average number of beetles per section was 0.75 for the dry bark, 1.75 for the medium bark, and 3.63 for the wet bark. These differences as indicated by a "t" test are significant with a probability of .05 or less.

Within the ranges studied the beetles preferred the relatively wetter bark. The actual percentage moisture content of the bark is not too meaningful as it depends upon the relative amounts of inner and outer bark. The level of the moisture percentages may be important. In this test the beetles preferred the highest moisture content, but they may have preferred even a higher moisture level if it had been available.

The condition of the beetles before they make their selection may also be important. In this test the beetles had been stored for a week in a refrigerator before they were used and their water balance may have been different from that of attacking beetles in a stand of trees.

Observations along the edges of the bark pieces indicated that where possible the beetles would go directly to the inner bark and would only mine through the outer bark if they could find no other way of getting through it.

Contagious Tests

A field experiment was set up to test the attraction of beetles to other beetles already attacking a tree. Trees were picked in pairs close to groups of trees containing developing broods so there would be a reasonably good attacking population at flight time, and there were sufficient unattacked "susceptible" trees in the vicinity. The members of each pair were as close in bark, size, and crown characteristics as could be found. Care was taken to pick trees that were not close together. Four such pairs were chosen in each of four different areas and each tree tagged. One member of each pair was selected at random and beetles were caged upon the bark of the tree by stapling fiberglas screening to the bark. Care had to be taken that the screening fitted tightly into all cracks and crevices. Where branches would interfere with the caging, comparable branches were cut off both members of the pair. Four, eight, sixteen, and twenty-four pairs of beetles were placed on the four trees of each plot. After the flight period the trees were cut and the location and length of each gallery inside and outside the screen noted. Galleries which were one inch or less in length and full of pitch were classified as unsuccessful; the others which were usually five to ten inches long without abundant pitch and frequently containing adults and eggs, were called successful. There was rarely any doubt as to which category they belonged.

In case of the trees with caged beetles, fourteen out of sixteen were attacked by two or more of the wild population. The probability that the ratio of subsequent attacks is different on trees with and without caged beetles is .001. This would indicate that beetles are attracted to trees on which an attack is already initiated.

A further important observation is possible from the data (Table VII). When the caged population was unsuccessful in establishing galleries the subsequent attack by the wild population was small, thirteen or less. When most of the caged population was successful in establishing galleries the subsequent attack was large, 178 or larger. This would indicate that the degree of attraction depends upon the success of the initial attacks on a tree. No relation could be found between trees from which the branches had been cut and the resin was oozing out, and subsequent attack by the beetles.

Table VII. The number of subsequent attacks by the wild population on trees successfully and unsuccessfully attacked by caged beetles.

	Number of attacks per tree			
Tree No.	Forced attacks under screens		Subsequent attack by wild population	
	Successful	Unsuccessful	Successful	Unsuccessful
1	0	1	0	2
2	0	2	1	2
3	0	3	0	0
4	0	4	0	0
5	0	5	2	11
6	0	6	1	3
7	0	7	0	2
8	2	8	1	1
9	9	3	344	0
10	11	0	178	0
11	14	0	334	0
12	17	1	727	0
13	20	2	281	0
14	26	2	220	0
15	28	3	365	0
16	40	2	289	0

Growth, and Number and Size of Resin Ducts

To determine if there was a relationship between either the abundance and size of resin ducts, or of the rate of growth and the success of the beetles, in the previous study, sections were taken from the tree at breast height. The diameter growth rate for each tree was determined for the last five years on four radii. Four blocks were then cut out for microtome sectioning purposes. The sections which were cut at 30 - 40 microns with a sliding microtome were soaked in acetone to remove the resin, stained in a 0.5 aqueous solution of chlorazol black, and mounted with a water - mounting medium. A cover slip was etched with hydrogen fluoride to produce a square 135 mm^2 in size with four horizontal sections marked off just the width of the field of a stereoscopic microscope at x35. This was laid over the microscope slide and was used as a guide in counting the number of resin ducts.

Ten of the resin ducts were selected at random across the section and the vertical and horizontal axis of each of these ducts were measured using a micrometer eyepiece and a magnification x450. The measurements were made to the outside of the epithelial cells. These were converted to cross section areas of the ducts and averaged for each tree.

Analysis showed that there was a significant difference (P = .003 by a "t" test) growth between the successfully attacked and the unsuccessfully attacked trees (Table VIII). The former had an average annual growth rate of 0.543 mm and the latter 1.110 mm over the past five years. No relationships could be found between the number or the size of the resin ducts and the success of the attack. No relationship could be found between the number or size of resin ducts and either diameter or rate of growth. Schopmeyer and Larson (1955) found with trees used for the naval stores industry that resin yield was correlated not only with growth of the last inch of radial growth, but also with diameter and crown - length ratio.

Table VIII. The average annual growth rate of the last five years of successfully and unsuccessfully attacked trees. Each figure is the average of four radii.

Tree No.	Successful Growth rate mm./year	Tree No.	Unsuccessful Growth rate mm./year
1	0.579	9	1.121
2	0.400	10	1.586
3	0.450	11	1.400
4	0.300	12	0.821
5	0.843	134	1.428
6	0.314	14	0.850
7	0.514	15	0.564
8	0.943		
Average	0.543	Average	1.110

Reactions of Beetles to Environmental Factors

Temperature

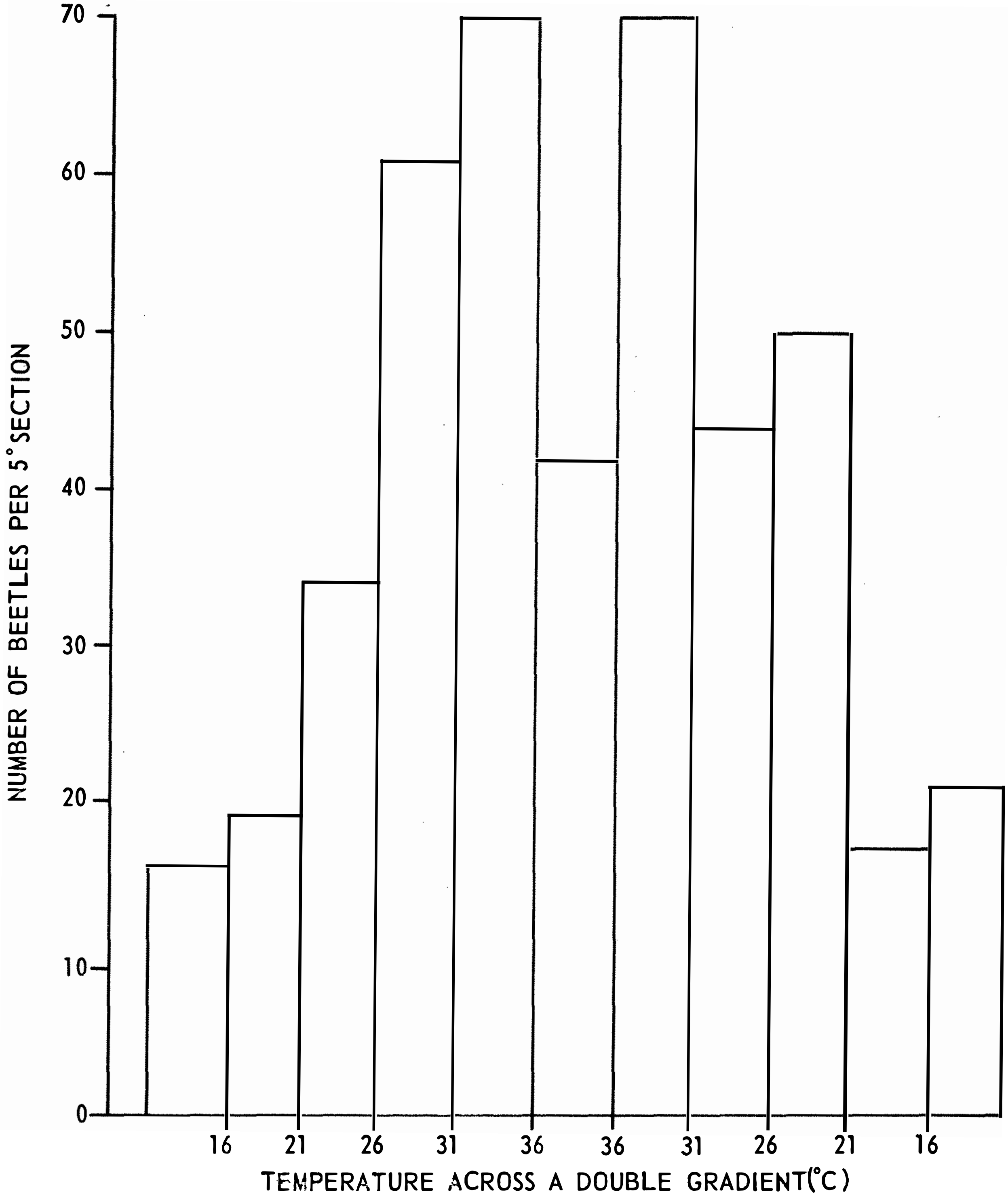
A double temperature gradient was established on a copper plate. Under the center, two flanges hung down which were spread wide enough to cover a 60 watt light bulb. The bulb was connected to a rheostat to control the intensity of heating at the center. The ends of the plate were bent down and immersed in ice baths. Cardboard insulation underneath the plate prevented temperature changes due to air currents in the room. An even gradient of 11 to 41°C. from each end to the center could be maintained for considerable time with this apparatus. On top of the copper plate was laid a copper screen to give the beetles better footing, and on top of this was placed a lucite box 3.5 x 21 x 1 inches. The top had holes cut through at 5 - inch intervals to allow for the entrance of beetles. The holes were covered with microscope slides to prevent any air currents from cooling or heating the surface. Thermocouples were woven through the screen on the floor and connected to a multiple switch and potentiometer.

After collecting beetles daily from emergent cages they were sexed and placed in seamless aluminium cans containing moist filter-paper and fresh inner bark and stored in a refrigerator. Before use the beetles were acclimatized for at least one hour in moist dark containers at 22°C.

Twenty beetles were distributed evenly through the top holes except the outside two. Under the latter the temperature was so cold (11°C.) that if beetles were placed in this region they were immobilized. The box was divided into sections by placing lines across the lucite lid corresponding to five degree changes along the gradient. After twenty minutes the number of beetles in each section was counted. Two desk-type fluorescent lamps were placed above the gradient giving an even light intensity of 200 foot candles the length of the test chamber.

The results of the tests of females are illustrated in Fig. 2. The males showed a similar response. The avoidance of high temperatures (above 36°C.) was probably not due to a definite choice by the beetles but

Fig. 2. Frequency Distribution of beetles in a double temperature gradient.


70
60
50
40
30
20
10
0
NUMBER OF BEETLES PER 5° SECTION
16
21
26
31
36
36
31
26
21
16
TEMPERATURE ACROSS A DOUBLE GRADIENT(°C)

due to the relative rates of activity. Beetles in this region flew more and crawled faster and therefore the spread and number leaving the hottest part of the gradient was greater than the number entering. The lower temperatures seemed to be avoided in preference for the 31 to 36°C. region.

This type of chamber is not completely satisfactory. The positive thigmotactic and negative geotactic responses of the beetles are so strong that the beetles spend a good deal of time against the walls. For this reason no definite preferendum can be established, only the fewer number in areas of the extremes seems obvious.

Rudinsky and Vité (1956) completed similar studies with D. pseudotsugae in which a u shaped channel was used with a water bath in each end to establish a single gradient. The tests were made in the dark and the beetles were allowed one hour to choose before counts were made. They found a preference for the region of 21°C. with a noticeable decrease above and below this temperature.

Humidity

Attempts were made to test the reactions of beetles when given a choice of humidities. A lucite box was made with a screen bottom which was placed over another open box containing petri dishes of sulphuric acid solutions. The screen was about one quarter of an inch above the surface of the solutions. The relative humidities obtained were fairly close to those desired with relatively narrow boundary zones between adjacent humidities. The humidities were measured with cobalt thiocyanate paper.

The types of tests used were: gradients, a choice between two extremes both in a linear and concentric circles arrangement, and a choice of alternating extremes. These tests were attempted with both wet and dry adapted beetles.

No consistent results were obtained with any of these tests. The thigmotactic and negative geotactic responses were so great that the beetles never seemed to respond to the humidity gradients.

Sampling System

A sampling model was devised where the bottom twenty feet of the tree was divided into two strata, 0 - 5' and 5' - 15'. All the attacked trees within a sample area were tagged and one square foot samples were selected at random within the strata. Height and direction were used to designate the quadrats. The quadrats were cut from the standing trees using a beaver-tail chain saw. An aluminium extension ladder was used above 5 ft. An optimum sample distribution was calculated based on previous estimates of variance and sample size of the number of attacks within each strata. Two sampling periods were selected, one in the fall after the attack was well established, and one in spring just before the flight period.

To test this model two sample areas were selected, one with a large number of successfully attacked trees and another with a small number of unsuccessfully attacked trees. A sample was taken in the Fall of 1958 and analysed; the brood was mostly in the larval stage at the time. Tentative life tables of this first sample are set up and appear in Tables IX and X. The data on parasitism, predation and competition were recorded separately for each species but are lumped here for convenience. The percentage error of the different stages alive at the time of sampling is given in Table XI. Definite conclusions of success of this model can not be determined until after the second sample is taken.

Table IX. Interim life table of the first sample taken early in the development of the mountain pine beetle in a successfully attacked group of trees based on the average number per square foot.

x	lx	dxF	dx	100 qx
Female Adult	5.44	Fecundity 45.59 eggs/female		
Eggs	248.00	Viable unhatched	22.65	9.13
		Unhatched	14.63	5.90
			37.28	15.03
Larvae	210.72			
		Living	110.16	52.28
		Died while hatching	6.12	2.90
		Mortality from parasitism, predation, and competition other than intergallery	11.44	5.43
		Competition between galleries	39.09	18.55
		Mortality from unknown causes	17.79	8.44
		Missing	23.56	11.18
			208.16	98.78
Pupae	2.56	Living	1.67	65.23
Tenerals	.89	Living	.89	100.00

Table X. Interim life table of the first sample taken early in the development of the mountain pine beetle in an unsuccessfully attacked group of trees based on the average number per square foot.

x	lx	dxF	dx	100 qx
Female Adult	3.25	Fecundity 22.62 eggs/female		
Eggs	73.50	Viable unhatched	0.58	0.79
		Unhatched	1.25	1.70
			1.83	2.49
Larvae	71.67			
		Living	12.17	16.98
		Died while hatching	0.67	0.88
		Mortality from parasitism, predation, and competition other than intergallery	6.08	8.48
		Competition between galleries	5.83	8.13
		Mortality from unknown causes	21.58	30.11
		Missing	24.75	34.53
			71.08	99.11
Pupae	0.58	Living	0.50	86.21
Tenerals	0.08	Living	0.08	100.00

Table XI. Percentage errors of the different stages sampled in the two areas based upon the ratio of two standard errors over the mean times 100. Forty-two samples were taken in the successful area, twelve were taken in the unsuccessful area.

	Successful area	Unsuccessful area
Number of attacking females	19.4	58.2
Total number of eggs laid	35.8	18.8
Number of larvae living	33.2	22.4

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