

POPULATION STUDIES OF THE
MOUNTAIN PINE BEETLE

by

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INTRODUCTION

In 1956 a project was started with the objective of determining relative values of the natality and mortality factors which influence populations of the mountain pine beetle, Dendroctonus monticolae Hopk. It is the intention to formulate life tables for populations which are increasing to outbreak status, decreasing following an attack, and endemic.

An adequate sampling technique is essential to life table studies. Therefore the first stage of this study was to learn something of the distribution of the beetles in the trees and the variability of that distribution. Data was collected only on the location of 'strikes' on the tree trunk, no attempt was made at this time to determine the success of the attacks. The investigations were also concerned with factors which may influence the distribution of beetle attacks within the individual tree.

METHODS

The study area was located on Steamboat Mountain, on the west side of the Columbia River, near Edgewater, B.C. The area had been heavily logged during the past decade, principally for Douglas fir. Much of the lodgepole pine from the original stand was left and subsequently was attacked by the mountain pine beetle. It was obvious that the peak of the outbreak occurred before the present investigation began as only scattered groups of trees were attacked in 1956.

The sample unit chosen was one square foot of bark surface. The linear dimensions were varied, depending on diameter. Before felling, cardinal directions were marked on the trunk. After felling, square-foot

samples were taken from each quadrant thus formed for the entire length of the tree. As the width of the quadrant decreased, the length of the sample was increased to maintain the area of one-square foot. At least eight of the basal sample units were marked, peeled, and recorded before each tree was felled in order to prevent disruption by the felling cuts.

The information was tabulated for Remington Rand punch cards. The data from each sample were placed on a separate card. Table I shows the information recorded on the cards and the card column number. Cards

TABLE I
REMINGTON-RAND PUNCH CARD CODE FOR BARK-BEETLE
DISTRIBUTION DATA

| | Column Number |
|--|------------------|
| Laboratory Number (08) | 1-2 |
| Project Number (3019--) | 3-8 |
| Area Number | 9-10 |
| Date | 11-16 |
| Tree Number | 17-19 |
| Diameter breast-high (nearest tenth inch) | 20-22 |
| Height to bottom of crown (nearest foot) | 23-24 |
| Examiner (Shepherd - 01, Hatkoski 02) | 25-26 |
| Height to top of sample (nearest inch) | 27-29 |
| Diameter at top of sample (nearest 1/10 inch) | 30-32 |
| Direction (N-1, E-2, S-3, W-4) | 33 |
| Number of branches (per sample) | 34-35 |
| Number of strikes per sample visible from outside | 36-37 |
| Number of strikes per level (4 samples) visible from outside | 38-39 |
| Number of strikes per sample (inside counts) | 40-41 |
| Number of strikes per level (4 samples) (inside counts) | 42-43 |

were prepared only for samples up to the height of the last strike on the tree, although in the field three levels (4 samples per level) were examined and recorded above the last strike to insure a complete tally of all strikes in the tree. This system provided a means for rapid sorting and also allowed an easy integration of subsequent data.

In 1956, three groups of attacked trees were sampled. All attacked trees in each area were felled and sampled. This provided data on varying intensities of attack and eliminated the possibility of personal bias in the selection of trees.

Thirty attacked trees were felled, yielding a total of 1,325 square-foot samples. The number of strikes varied from 1 to 897 per tree and a total of 6,841 strikes were found.

Various hypotheses were tested, some of which have been postulated by many men over a period of years, but seldom supported by adequate quantitative data. A synthesis of theory and supposition yielded the following questions which are tested and discussed.

1. Are beetle attacks distributed randomly over the tree trunk or is there a tendency towards 'clumping'?
2. Is there a different distribution under different intensities of attack? That is, is the distribution random at low intensities but 'contagious' at high attack intensities?
3. What is the variability in the number of strikes per tree within one group of attacked trees.
4. Is there any difference in intensity of attack in trees of different diameters?
5. Does cardinal direction affect intensity of attack?

6. Does the presence of branches affect the intensity of attack?
7. Is there a change in attack intensity with height?
8. Can populations be accurately estimated by counts of entrance holes, thus avoiding the additional labour of peeling off the bark?
9. Assuming the above questions can be answered, can a partial sampling system accurate enough for life tables, be developed?

TYPE OF FREQUENCY DISTRIBUTION

Most standard statistical techniques are based on the normal distribution. For the use of these techniques therefore, it is necessary to determine the frequency distribution of the bark beetle strikes.

A knowledge of the frequency distribution also provides indications of the behaviour of the attacking beetles, for example, if the beetles attack randomly the distribution is Poisson, but if they aggregate together the distribution is contagious.

The samples were divided into four classes, depending upon the intensity of attack, the means of which appear in the caption facing Fig. 1. Fig. 1 illustrates the frequency distribution of each intensity of attack with smoothed, free-hand curves.

In the class of lowest attack intensity (1.93 strikes per square foot), there is an extremely high number of zero values, that is no strikes. There is a second, much lower peak at three strikes per sample,

and then the frequency decreases asymptotically in the samples with a high number of strikes.

This distribution would indicate that at this intensity of attack the strikes tend to be aggregated, resulting in nil attack or a preponderance of groups of three or more.

At the highest attack intensity (6.81 strikes per square foot) the number of nil attacks is greatly reduced, the peak of the frequency curve shifts to a larger number of strikes per sample and the frequency distribution approaches normality. The other intensity classes are intermediate and shift regularly from the form of the lowest to that of the highest.

All the data were combined to form a single frequency distribution and the averages used to formulate theoretical distributions. Three non-normal distributions were tested: Poisson, negative binomial, and Neyman's contagious. None of these types gave a fit within acceptable probability limits although Neyman's contagious did show some promise. These frequency distributions appear in Table II and are illustrated by curves in Fig. 2.

A further test of the two distributions, Neyman's and negative binomial was made to determine the influence of attack intensity upon the distribution. A different break down of intensity was used than that for the general curves of Fig. 1. An intensity classification based upon the total population per tree was devised, as it eliminates the variable of the number of samples per tree. Two intensity classes were tested, 0 to 105 strikes per tree and 306 to 405 strikes per tree. The theoretical distributions were calculated from the parameters of the observed data

and compared by Chi-Square tests. The results appear in Table III.

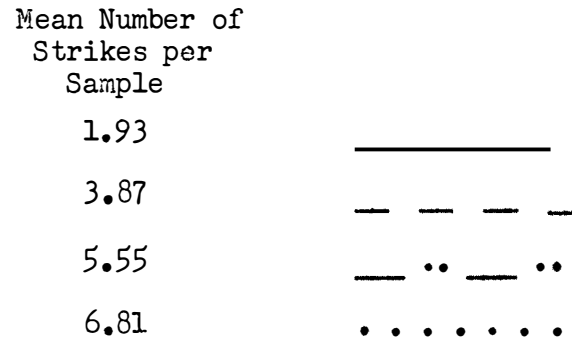
TABLE II
OBSERVED AND THEORETICAL FREQUENCY DISTRIBUTIONS

| No. of strikes per sample | Frequency of Samples | | | |
|------------------------------|----------------------|---------|-----------|------------|
| | Observed | Poisson | Neg. Bin. | Ney. Cont. |
| 0 | 206 | 10 | 106 | 207 |
| 1 | 121 | 47 | 152 | 89 |
| 2 | 114 | 115 | 162 | 128 |
| 3 | 119 | 189 | 155 | 138 |
| 4 | 107 | 233 | 145 | 131 |
| 5 | 117 | 230 | 123 | 118 |
| 6 | 132 | 188 | 102 | 103 |
| 7 | 81 | 132 | 83 | 87 |
| 8 | 70 | 81 | 67 | 72 |
| 9 | 62 | 45 | 52 | 58 |
| 10 | 47 | 22 | 41 | 46 |
| 11 | 32 | 10 | 31 | 35 |
| 12 | 33 | 7 | 24 | 27 |
| 13 | 22 | | 19 | 17 |
| 14 | 14 | | 14 | 15 |
| 15 | 10 | | 11 | 10 |
| 16 | 6 | | 8 | 29 |
| 17 | 4 | | 6 | |
| 18 | 4 | | 8 | |
| 19 | 5 | | | |
| 20 | 0 | | | |
| 21 | 0 | | | |
| 22 | 2 | | | |
| 23 | 1 | | | |
| $P\chi^2$ | | <.001 | <.001 | .005 |

TABLE III
PROBABILITY OF THE OBSERVED DATA BEING SIMILAR TO A THEORETICAL TYPE

| Total Population per tree | $P\chi^2$ | |
|------------------------------|-------------------|---------------------|
| | Negative Binomial | Neyman's Contagious |
| 0 - 105 | <.001 | .054 |
| 306 - 405 | <.001 | .473 |

Fig. 1 Frequency distribution of strikes
of the mountain pine bark beetle
per square-foot of bark for four
attack intensities.



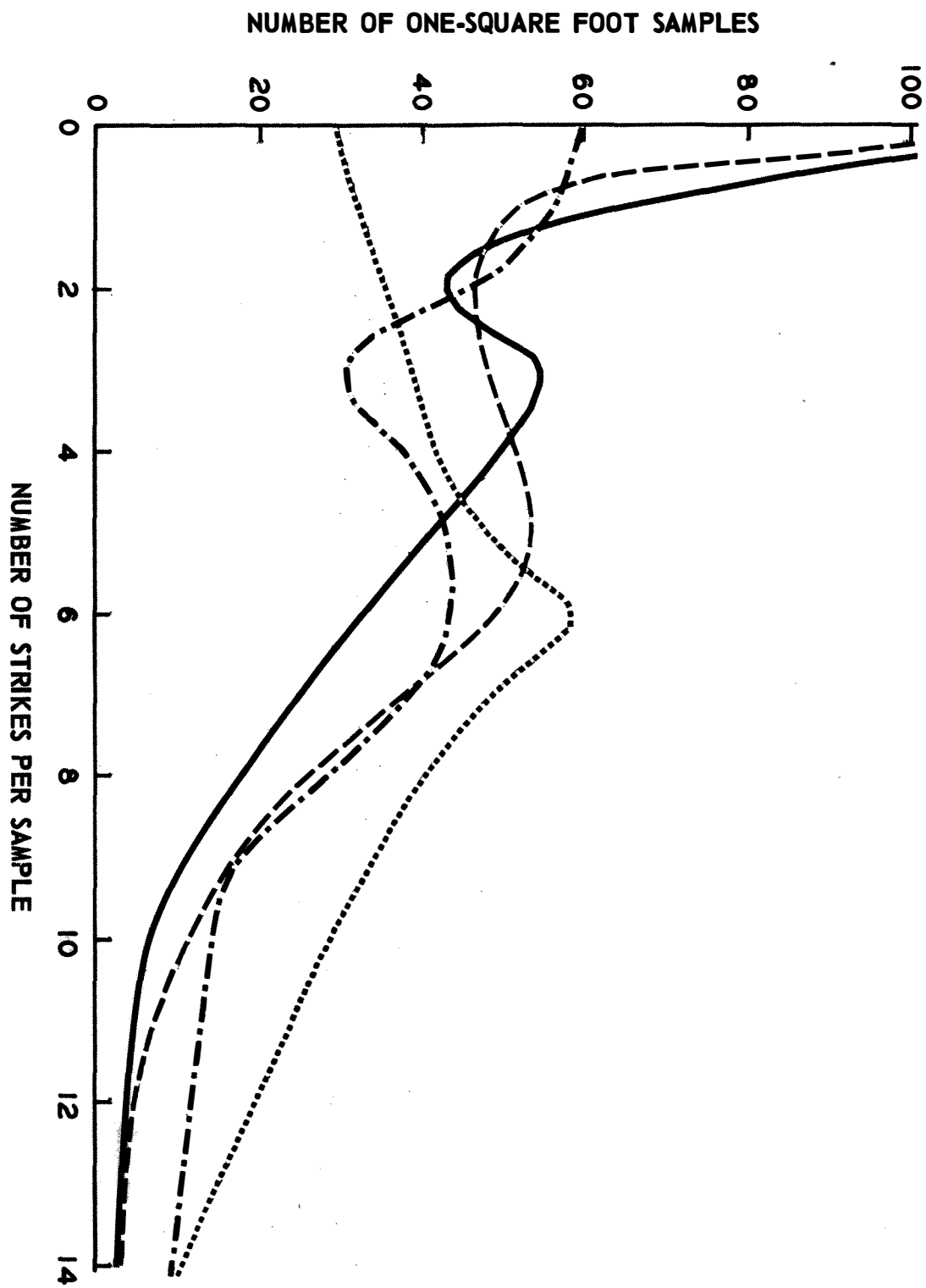
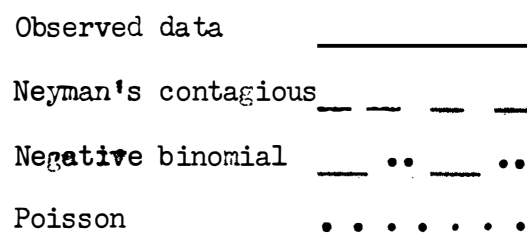
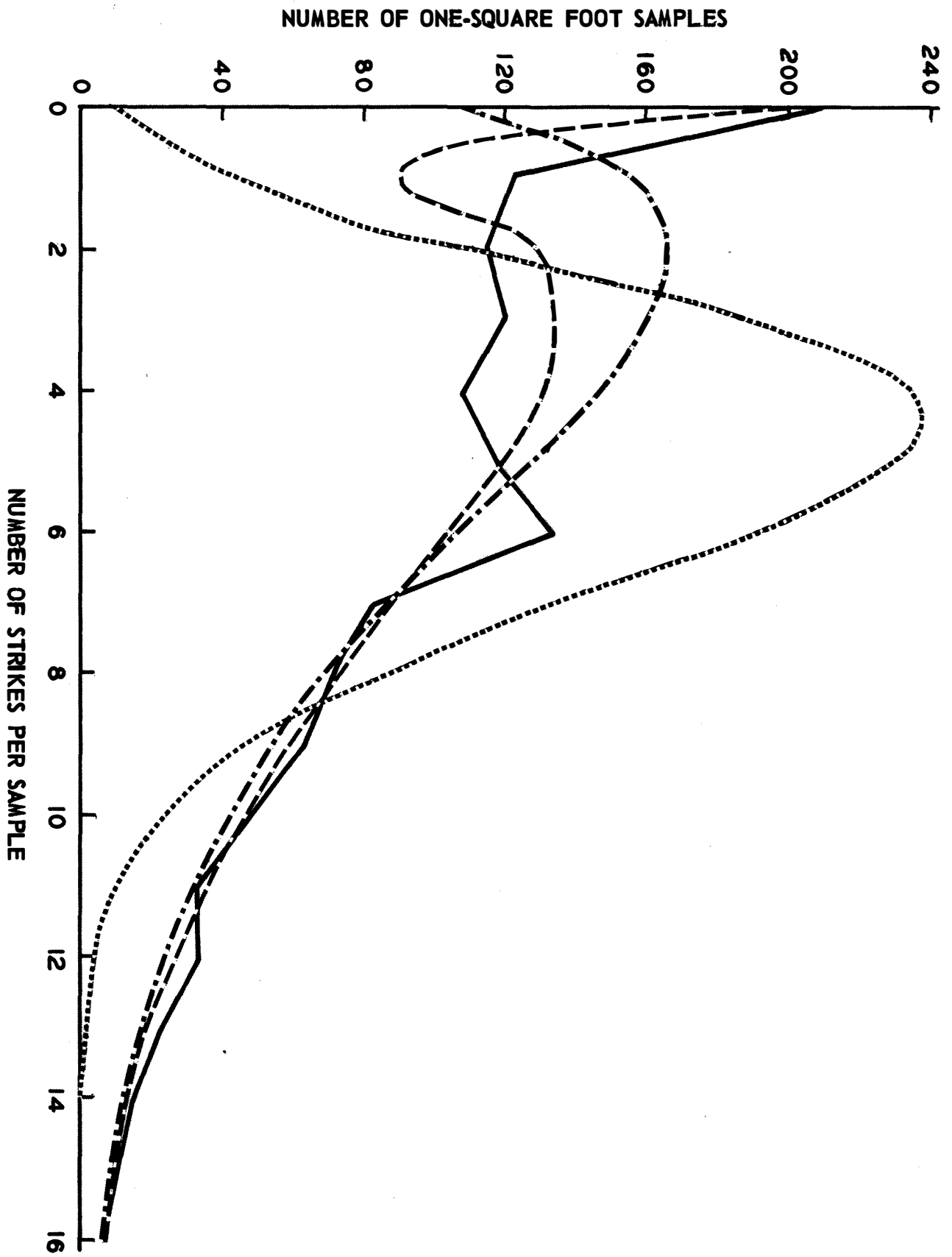


Fig. 2 Comparison of the observed and theoretical distributions.





From Table III it can be seen that the probability of the number of strikes per sample approaching Neyman's contagious distribution is greatest at the highest attack intensities. This is illustrated in Figs. 3 and 4.

Further tests were made by comparing other distributions of the Neyman contagious series. The one used in the previous calculations was his type A, or $n = 1$ as called by Beal (1953). As the series progresses from $n = 1$ to $n = 2$, $n = 3$ etc. to $n = \infty$ the number of zero's is reduced and one's increased. Some of these types were calculated and compared with the observed data, but none gave as good a fit as the original type where $n = 1$.

Although the distribution of the bark beetle attacks approaches Neyman's type A distribution, there is little biological basis for expecting a good fit. His models were based on larval dispersion from large egg masses, i.e. a centre of 'contagion'. He assumed that the egg masses were distributed randomly and therefore if there was only 1 egg per mass, a Poisson (random) distribution would result. The bark beetle strikes, upon which our distribution is based did not originate from a centre of contagion, but rather from a centre of attraction in the attacked area. This attraction may possibly be an original single strike. Furthermore, as will be shown in a later section, the original attractants, if they are strikes, are not themselves randomly distributed.

From these analyses therefore, we are able to answer the first question proposed. There is a definite tendency toward contagion of bark beetles attacking a single tree but this distribution does not give a close fit into any of the known contagious distributions.

Fig. 3 Comparison of the observed data and the theoretical contagious and negative binomial distributions for the trees which had a total of 0 - 105 strikes.

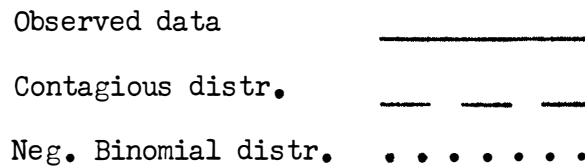
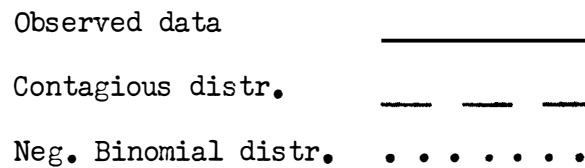
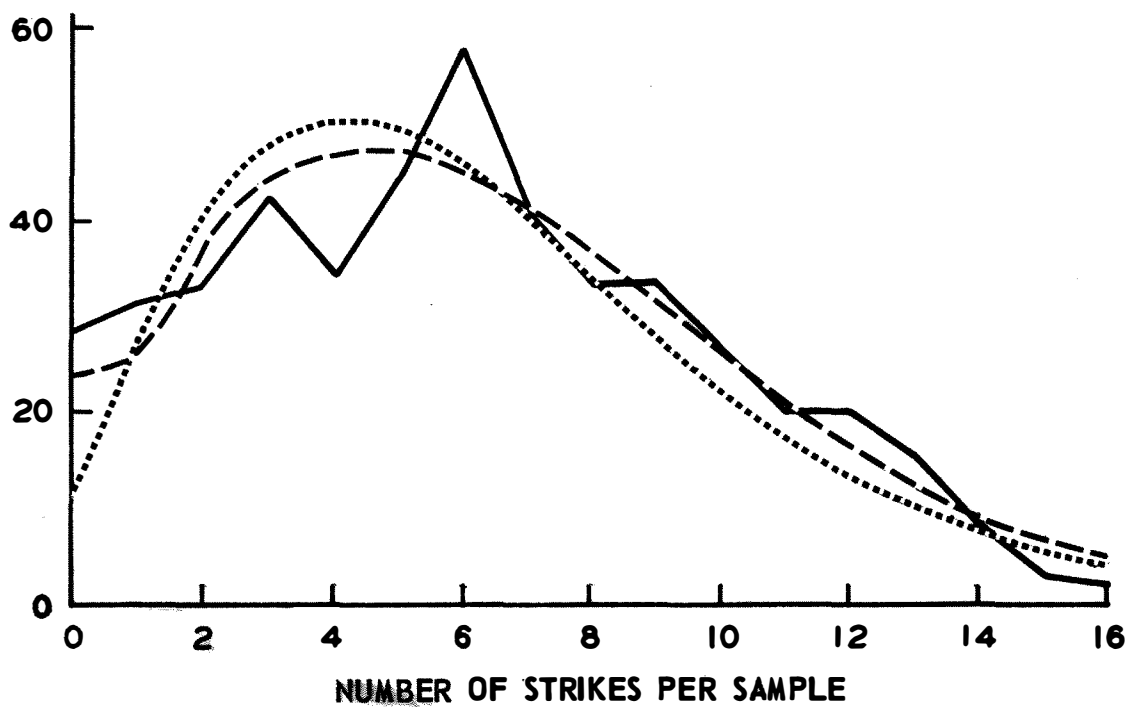
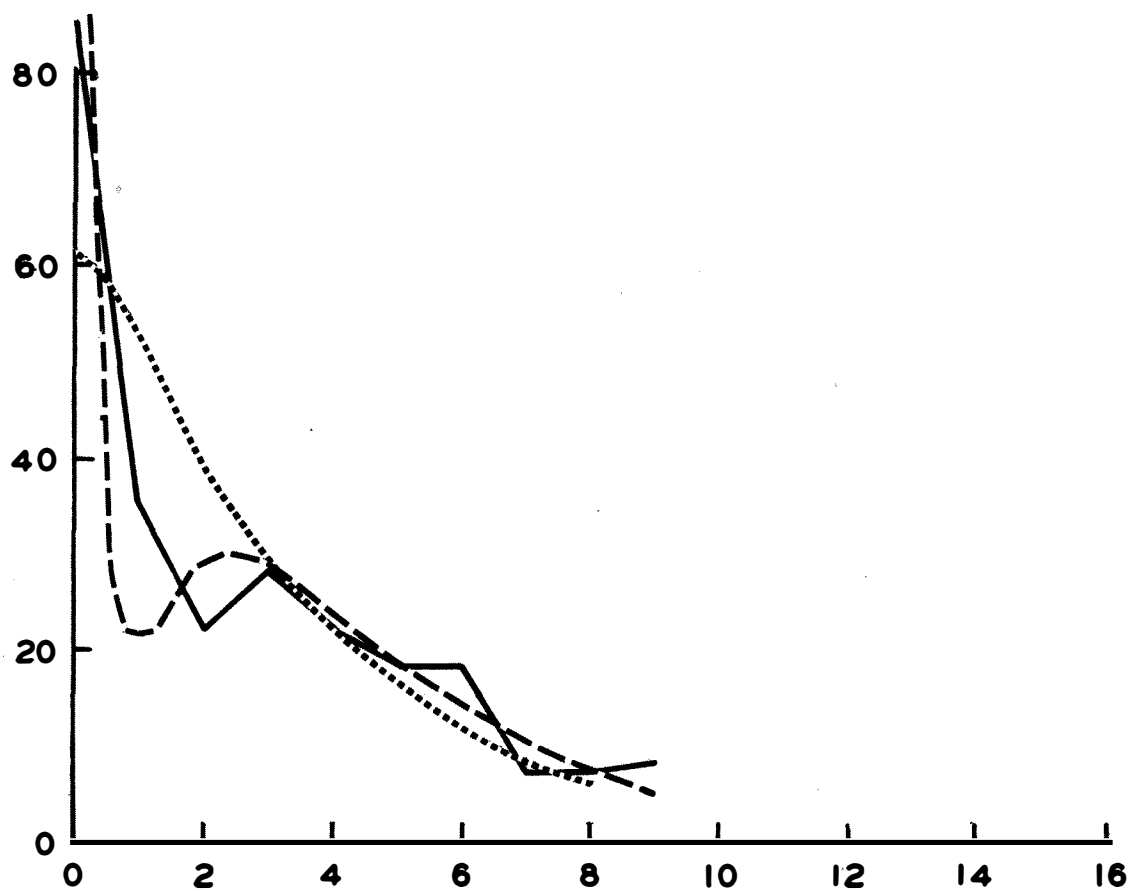


Fig. 4 Comparison of the observed data and the theoretical contagious and negative binomial distributions for the trees which had a total of 306 - 405 strikes.



NUMBER OF ONE-SQUARE FOOT SAMPLES



VARIANCE AND TRANSFORMATION

The use of the analysis of variance, in addition to assuming normality, also assumes that the variances of the samples are homogenous. That is, the variance of the dependent variable is similar at all levels of the independent variable.

The mean and variance of the number of strikes per tree was calculated and are illustrated in Fig. 5. From this graph it was obvious that there was a relationship between variance and mean and that it was probably logarithmic. Various logarithmic transformations were applied to the raw data ($\log x + \frac{k}{2}$, $\log x + 2$ etc.) and it was found that the transformation $\log (x + 1)$ largely removed the relationship (Fig. 6). There still remained a tendency for the variances to be smaller at the extremes than at mid-values.

Bartlett's test of homogeneity of variance (Walker and Lev, 1953) was applied to the transformed data. The test indicated a probability of .90 that the differences were due to random sampling and therefore the transformation was accepted as a means of removing the variance-mean relationship.

The use of transformation to modify the variance also had an effect on the distribution. The data for the curves presented in Figures 3 and 4 were transformed and are presented in Figures 7 and 8. Although both curves are still slightly skewed to the right it is believed that they approximate mortality and an analysis of variance is now possible.

ANALYSIS OF VARIANCE

The transformed data were tested by the analysis of variance.

Considerable restrictions in the number of sub-classes and interactions had to be imposed to keep the analysis manageable. Only enough interactions were determined to provide proper denominators for the 'F' test. These interactions were selected as the ones which would probably have the largest variance. The results of the analysis of variance are summarized in Table IV.

As all interaction terms were found to be significant, the single factors were compared with their respective interactions. All factors except diameters were significant at the one per cent probability level.

The significance of the variance between trees is self explanatory but that of the non significance between diameters requires some explanation.

Hopping and Beal (1948) found a definite preference by the mountain pine beetle for larger trees within a stand. This study did not contradict their findings as no comparison was made between attacked and non-attacked trees. It simply showed that within the trees attacked, there was no difference in the number of attacks per square foot owing to diameter. This would indicate that the beetle shows a preference for larger trees, but after the initial attack has been made, the number attacking the tree is relatively constant for that beetle population, irrespective of tree diameter. This implies an attraction of the larger diameters and also of established galleries of the mountain pine beetle. The latter attraction is much greater, so that with beetles making later attacks, the attraction of the larger diameters is masked or replaced by the attraction of previously established galleries.

Fig. 5 Relationship of variance to the
 mean of the untransformed data.

Fig. 6 Relationship of variance to the
 mean after the application of a
 $\log (x + 1)$ transformation.

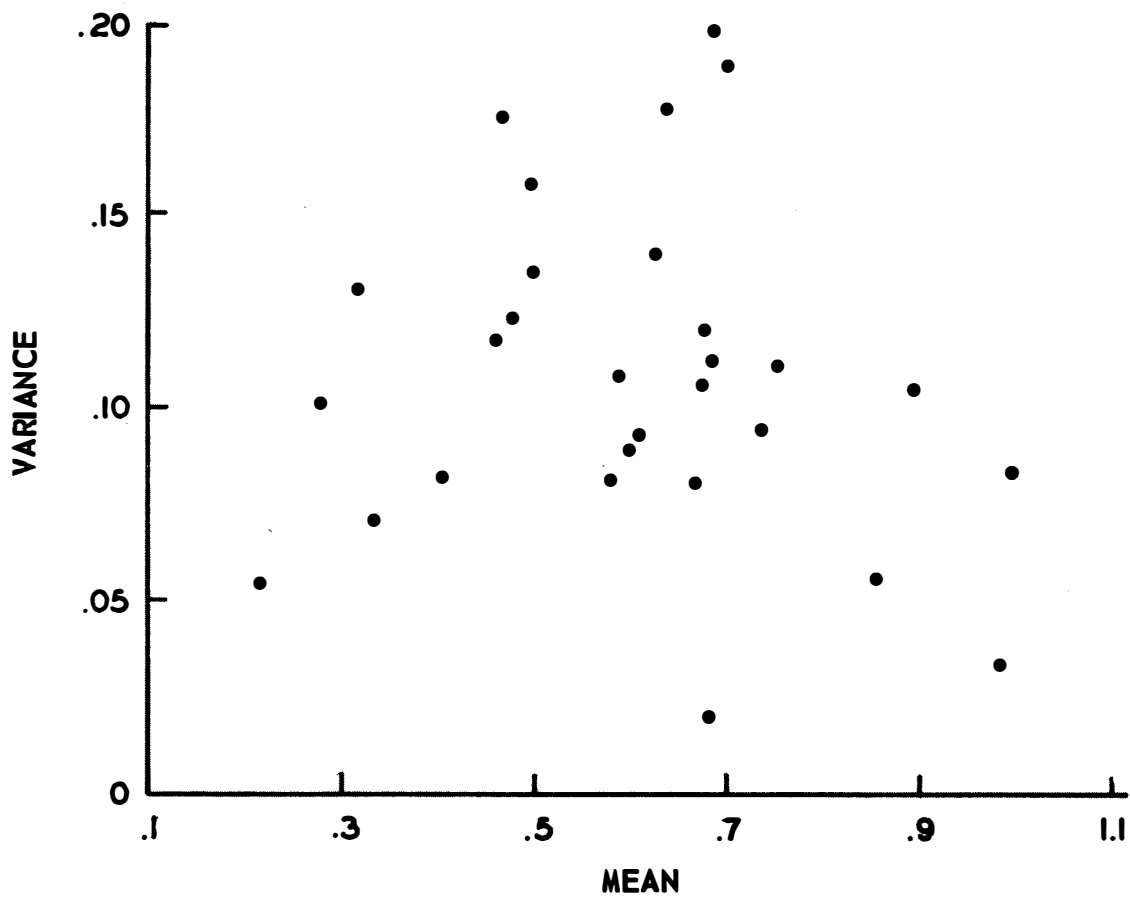
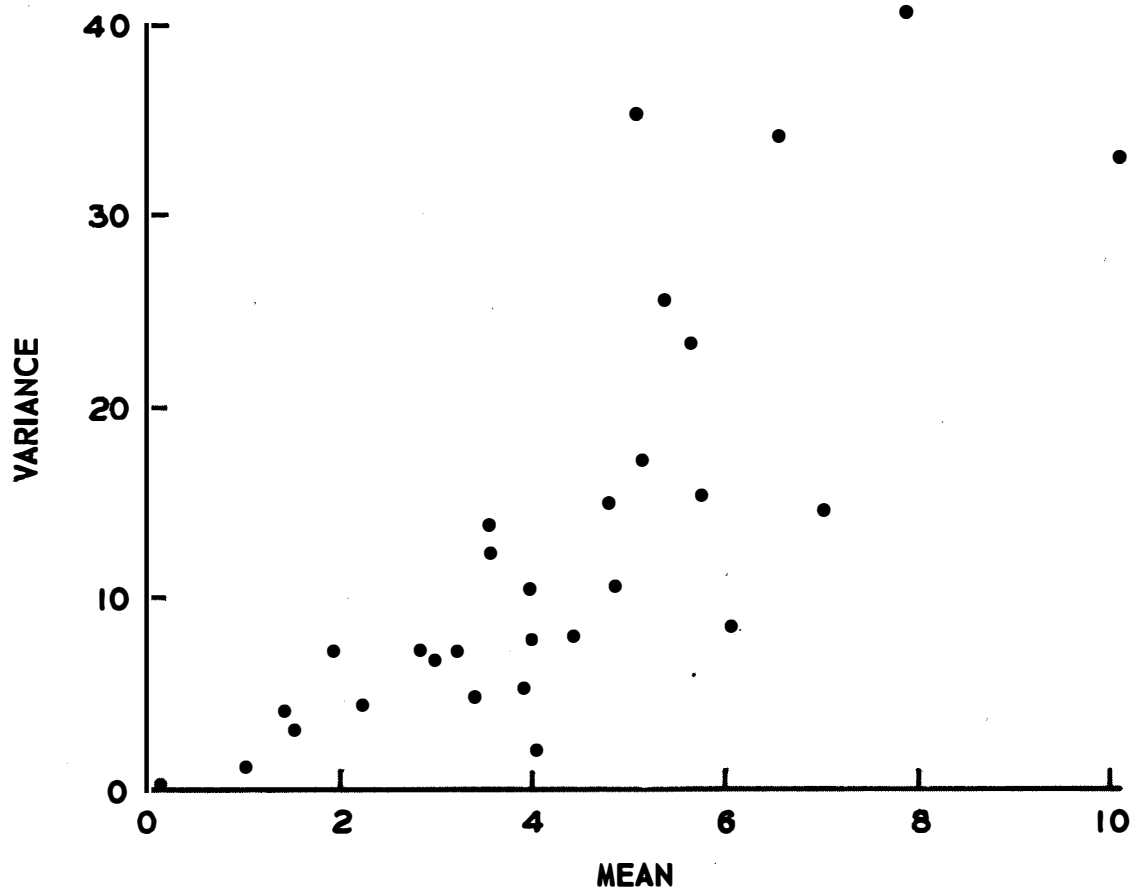


Fig. 7 Frequency curves to show the distribution of transformed and untransformed samples taken from trees with a total population of 305 - 405 strikes.

Fig. 8 Frequency curves to show the distribution of transformed and untransformed samples taken from trees with a total population of 0 - 105 strikes.

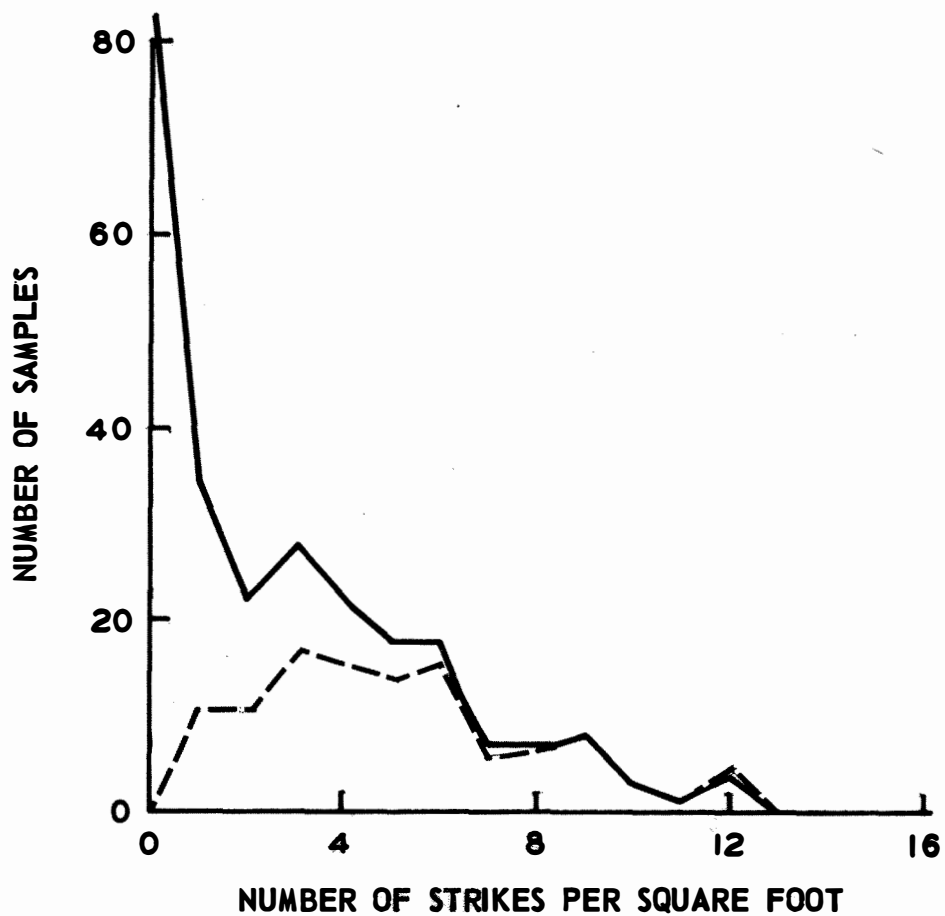
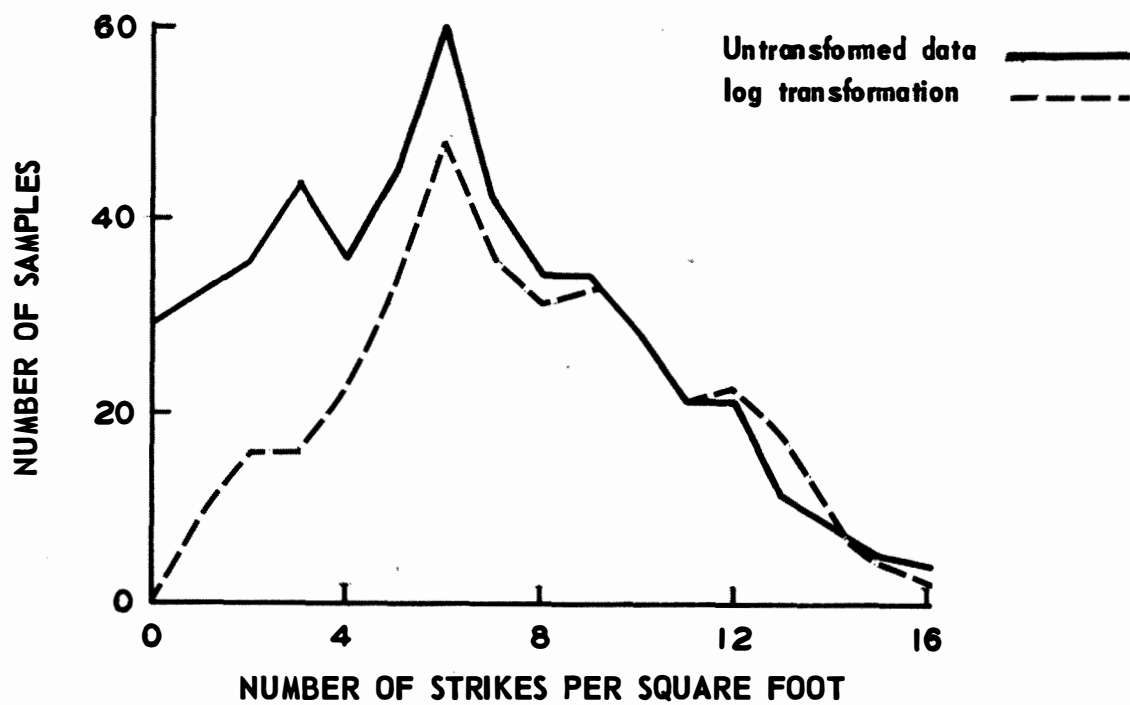


TABLE IV

TABLE OF ANALYSIS OF VARIANCE

| Source | D of f. | SS | MS | F |
|----------------------|---------|----------|---------|----------|
| Between Trees | 28 | 31.65818 | 1.13065 | 2.82 ** |
| Between Diameters | 3 | 6.38209 | 2.12736 | 1.83 |
| Between Directions | 3 | 3.00060 | 1.00020 | 14.13 ** |
| Between Levels | 4 | 36.42952 | 9.10738 | 7.85 ** |
| Between Branches | 4 | 14.42375 | 3.60593 | 50.95 ** |
| Trees x Levels | 116 | 46.40494 | .40004 | 17.21 ** |
| Diameters x Levels | 12 | 13.91635 | 1.15970 | 49.86 ** |
| Direction x Branches | 12 | .84934 | .07077 | 3.04 ** |
| Error | 1142 | 26.57201 | .02326 | |

The significant difference in bark beetle attack between directions was unexpected, no report of it having been found in the literature for any of the Scolytidae. The average number of strikes for each cardinal directions is given in Table V.

TABLE V

AVERAGE NUMBER OF STRIKES PER SQUARE FOOT BY CARDINAL DIRECTION

| Direction | N | E | S | W |
|---------------------------------|------|------|------|------|
| Average no. strikes per sq. ft. | 5.62 | 5.00 | 4.35 | 4.66 |

The most logical explanation for the differences found is based on bark surface temperature. The mountain pine beetle flies only when air temperatures are fairly high and skies are clear. Under such

conditions bark surface temperature would be highest where direct radiation fell upon it. These temperatures may be too extreme for establishment of galleries or for successful attack and the beetles would move around to a more suitable (cooler) location. From this, we would expect the greatest number of strikes to occur on the north side, second greatest on the east, third on the west and the south should have the least number. This was the distribution found in the study (Table V).

The results of this analysis was further checked with a Chi-square test of the distribution of strikes in the four directions. This indicated a probability of only .002 that the differences as large as this could occur solely through the errors of random sampling.

Observations on the amount of protection from trees, shrubs, etc. were also made on each attacked tree and related to cardinal direction. Four arbitrary classes of protection were established and the quadrants of the trees grouped in them to give four distributions. A chi-square test of these distributions gave a probability of .72 that the differences could have been due to errors of random sampling. It was concluded that the amount of protection around a tree did not influence the distribution of bark-beetle attack.

The average number of strikes per sample compared to the presence of branches are shown in Table VI. No allowance was made for the reduction in clear surface area in the bark samples owing to the presence of branches. Most of the branches were small however, and this bias would be negligible. Previously it had been suggested that beetles may prefer the rough bark around the base of the branch but the significant differences found in

TABLE VI

RELATION BETWEEN THE NUMBER OF STRIKES AND THE NUMBER OF BRANCHES
PER SQUARE-FOOT SAMPLE

| No. of branches per sample | 0 | 1 | 2 | 3 | 4 |
|--------------------------------|------|------|------|------|------|
| Mean no. strikes per sample | 6.46 | 4.54 | 4.04 | 3.14 | 2.97 |

this study would suggest a definite aversion of the beetles to the presence of branches, or a preference for clear bark surfaces.

VERTICAL REGRESSION

The distribution of the bark beetle strikes was found to be related to height. The number of attacks in each 30 vertical inches of trunk was recorded and the cumulative per cent of the total number of attacks per tree calculated. The average of thirty trees showed that 50 per cent of population occurred below 5.5 feet and ninety per cent below 19.6 feet. The vertical distribution was regular and followed a logarithmic curve of the form.

$$\log y = a + bx$$

The curves for four intensities of attack are illustrated in Figure 9.

The curve to fit the combined data is described by:

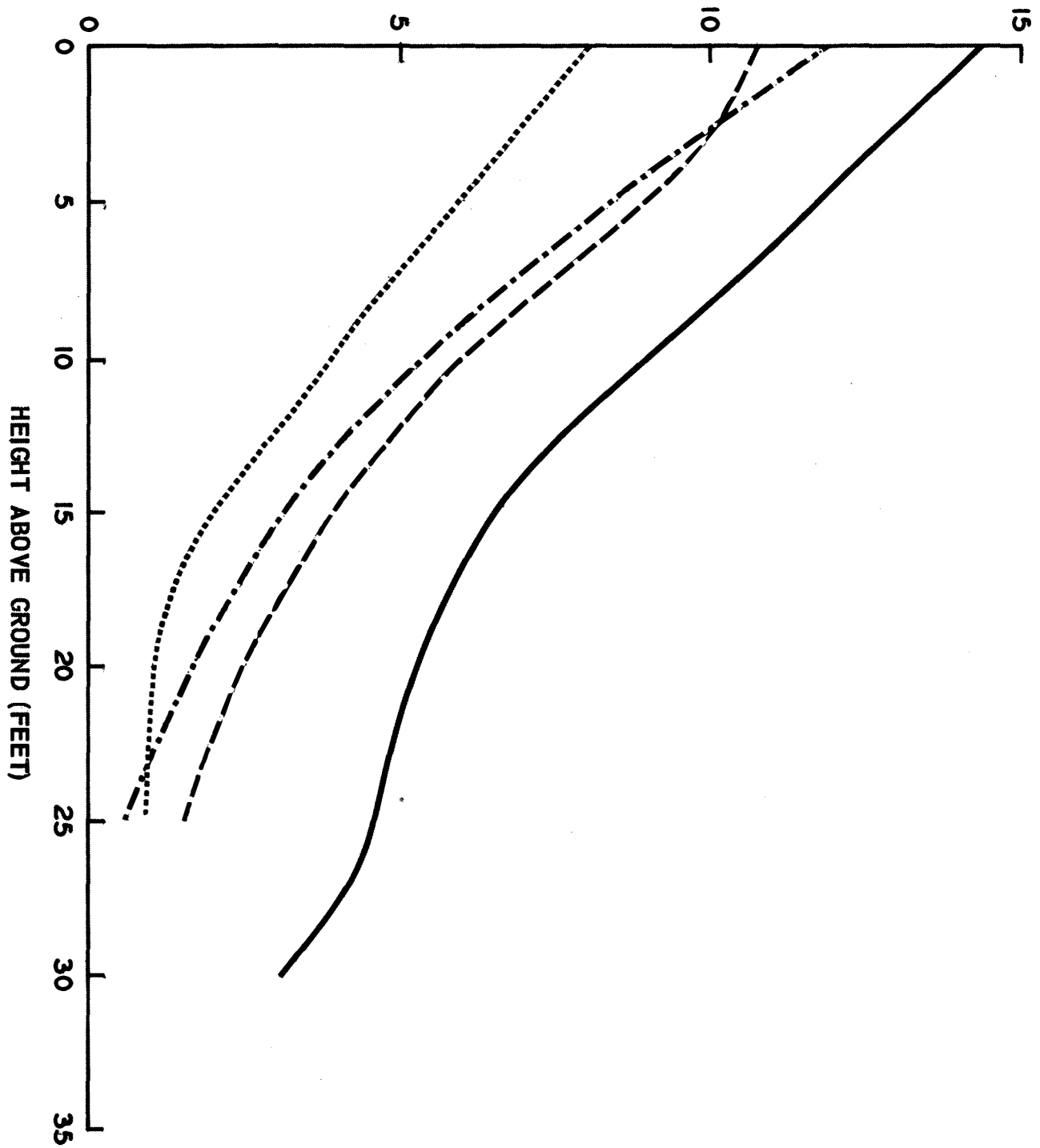
$$\log y + 1 = .90406 - .00204x$$

Readings cannot be made directly from this graph, as curves of transformed data are based on geometric rather than arithmetic means. The former are considerably smaller than the latter, the difference depending to some extent on the skewness of the distribution. Also the curves are based upon $y + 1$ rather than y because of the large number of

Fig. 9 Free-hand curves of the distribution of strikes up the tree at four intensities of attack.

| Number of Trees | Total number of strikes per tree | Average number strikes per tree | |
|--------------------|-------------------------------------|------------------------------------|-----------|
| 8 | 106 - 205 | 170 | |
| 5 | 206 - 305 | 246 | — . . — |
| 3 | 306 - 405 | 356 | — — — — |
| 2 | 406 - 605 | 576 | ———— |

AVERAGE NUMBER OF STRIKES PER SQUARE FOOT



zeros present. However, comparisons can be made for different intensities of attack as they are treated by identical procedures.

Two classes of attack intensity were compared: 106-205 strikes per tree and 306 - 405 strikes per tree. The regression equations derived were:

$$\log y + 1 = .99365 - .00326 x$$

$$\log y + 1 = 1.13275 - .00268 x$$

The value of 'a', or the point at which the curves meet the ordinate were obviously related to the intensity of attack. The slope values, 'b', were similar and a 't' test was applied to test for a difference. The test statistic was 20.4 based upon a standard error of .00032 for 'b' while the t.01 value was 2.5. This test is approximate as the assumption of normal distribution was not met. However, the value of the statistic was large enough to justify the assumption of a real difference between the slopes.

In terms of biology or behaviour, this means that where small populations are present, the beetles tend to concentrate at lower levels on the trunk. As the population increases the proportion of attacks at higher levels increases.

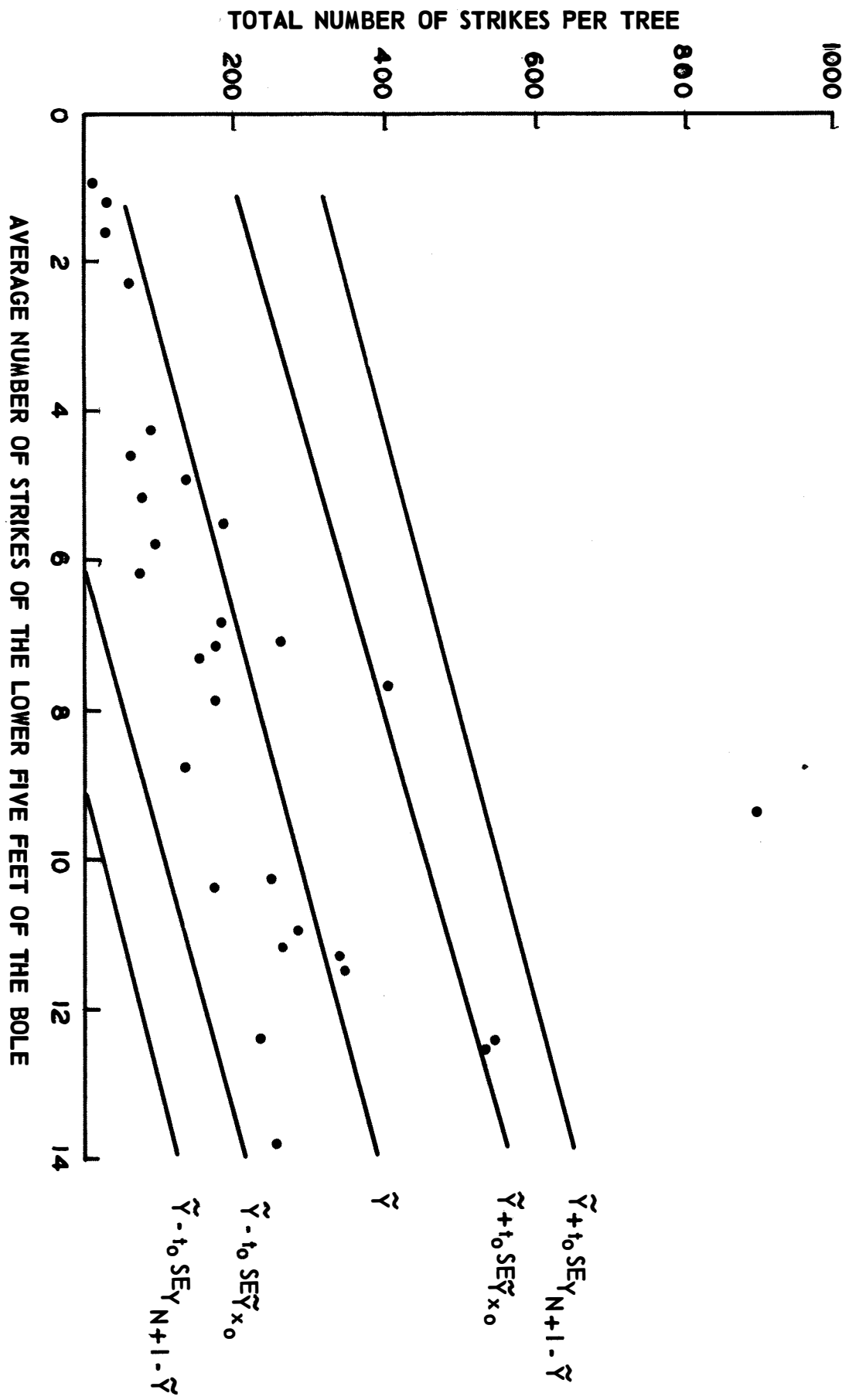
The sampling method used was tedious and time-consuming, particularly when felling of each tree was required. An attempt was made to develop a technique of estimating total population on standing trees.

The regression line was calculated for the relation between the mean of all the samples in the lower five feet and the total population in the tree. The formula was

$$y = 26.82407 + 25.82425 x$$

Fig. 10 Relationship between the average number of strikes per square foot in the lower five feet of the tree and the total population in the tree. Two 90% confidence intervals are also shown: one of the regression line itself $(\bar{y} \pm t_c SE_{\bar{y}_{x_0}})$ and one of any single subsequent observation

$$(\bar{y} \pm t_c SE_{y_{N+1} - \bar{y}}).$$



where y was the total population in the tree and x the average number of strikes per square foot in the lower five feet. The correlation coefficient of the relationship was 0.68. The 90 per cent confidence interval of the regression line at any fixed value of x was as follows:

$$x = 4 \quad 286.24057 \quad < \hat{y} < 0$$

$$x = 12 \quad 510.38027 \quad < \overline{y} < 163.04987$$

The 90 per cent confidence interval of a subsequent single observation was

$$x = 4 \quad 393.31130 > y_{n+1} > 0$$

$$x = 12 \quad 600.02637 > y_{n+1} > 0$$

The confidence intervals are presented diagrammatically in Figure 10. It is obvious from these that samples as taken were not adequate for estimation of populations from the standing trees. The question then arises as to how many observations would be required to obtain a confidence interval within ten per cent. The following formula was used to determine the required N for two levels of x (average number of strikes per square foot):

$$S.E. \ y_{x_0} = \frac{S_y \cdot x}{\sqrt{N}} \cdot \sqrt{1 + \left(\frac{x_0 - \bar{x}}{S_x} \right)^2}$$

From which: if $x = 4$ $N = 268$

" $x = 12$ $N = 334$

It must be noted that two assumptions necessary to the application of the regression line are not met. These are homogeneity of variance, and normality. Therefore, the above calculations are approximate

and not conclusive. As noted above there is an indication of greater proportion of attacks at higher levels with larger populations. This would probably result in a curvilinear rather than straight line relationship. As additional data is collected this curve can be calculated with a probable reduction of the confidence interval. The situation is further complicated by an increase of variance at higher attack intensities.

POSSIBLE USE OF COUNTS ON THE OUTSIDE OF THE BARK

Determining strikes by bark removal is time consuming. It was therefore attempted to relate the number of strikes visible on the outside to the actual number of galleries counted after bark removal. The analysis was made with an objective of determining an average difference between outside and inside counts, which could be used as a conversion figure. The average difference was 2.29 with a standard deviation of 2.16. At the 95 per cent level, the confidence interval of difference was 0 to 6.51. As the mean number of strikes per square foot was only about six, the variance of the difference between the outside and inside counts was too high to allow any confidence in a system based on outside counts.

REQUIRED NUMBER OF OBSERVATIONS

If extensive population work is to be considered, sampling must be done on a statistically sound basis with an adequate number of samples for any condition. To determine the latter, and its practicability, the techniques of Morris (1955) were followed.

Two variables require consideration; variability within the tree, and between trees. These allow some latitude in choice of sample.

For example, if inter-tree variability is greater than intra-tree variability, the most practical sample would consist of few samples from many trees. If the variability were reversed, the best sample would consist of many observations from few trees. The formula used to determine the various combinations is:

$$N_T = \frac{S_T^2 N_W + S_W^2}{S_{\bar{x}}^2 N_W}$$

where N_T = number of trees
 N_W = number of observations per tree
 S_T^2 = variance between trees
 S_W^2 = variance within trees
 $S_{\bar{x}}^2$ = allowable variance of the mean
 (set by the worker)

To determine S_T^2 the analysis of variance table was recalculated by combining the degrees of freedom and the sum of squares of all factors except between trees. This gave a new mean square value which represents the variance within the trees. (Table VII).

TABLE VII
 RECALCULATED ANALYSIS OF VARIANCE TO DETERMINE THE VARIANCE WITHIN TREES

| Source | d.f. | S.S. | M.S. | E.M.S. |
|---------------|------|-----------|---------|-----------------|
| Between Trees | 28 | 31.65818 | 1.13065 | $S_T^2 + S_W^2$ |
| Within Trees | 1298 | 147.97860 | .11401 | S_W^2 |

The mean square value for between trees also included the variance within trees, therefore the

$$S_T^2 = MS_{\text{Bet trees}} - MS_{\text{With trees}} \quad \text{or in this study}$$

1.01164.

The allowable error of the mean was taken as ten per cent. The determination of the allowable variance of the mean was complicated by the log (x + 1) transformation of the original data.

The mean is 4.92 and 10% of this is .49, so the allowable range of the mean is 4.92 + .49 or 4.41 to 5.41 in original scale values. Log (x + 1) of 4.92 is .77232, of 4.41 is .73320, and of 5.41 is .80686. If we subtract the transformed range values from the transformed mean we obtain two different values for $S_{\bar{x}}$ (.03454 and .03912). The average might be used but for this analysis the smallest of the two was used, thus leaving some margin of safety.

Substitution in the above formula yields:

$$N_T = \frac{1.01664 (N_w) + .11401}{.01193 N_w}$$

from which the required number of trees can be found for any number of samples per tree. The results of this calculation appear in part 1 (whole tree) of Table VIII. This gives the required number of samples when considering the variability of the whole tree under the assumption that future samples would be taken at random throughout the tree.

The smallest number of required samples is when one sample per tree is taken. If two samples per tree are taken the number of samples increases considerably but the number of trees is reduced. In the final

TABLE VIII

REQUIRED NUMBER OF SAMPLES

| Whole tree Number of Samples per tree | Number of trees | Total number of samples requ'd. |
|---|-----------------|------------------------------------|
| 1 | 948 | 948 |
| 2 | 900 | 1800 |
| 3 | 884 | 2652 |
| 4 | 876 | 3504 |

0 - 5 foot level, east side, no branches

| | | |
|------------------|-----|--------------|
| .25 (36 sq. in.) | 439 | (110 sq.ft.) |
| .50 (72 sq. in.) | 274 | (137 sq.ft.) |
| 1 (144 sq. in.) | 191 | 191 |
| 2 | 150 | 300 |
| 3 | 136 | 408 |
| 4 | 130 | 520 |

analysis the most economical sample would have to consider the time necessary in making population counts, vs. the time of moving to and cutting additional trees. The number of trees available would also have to be considered.

The number of samples necessary to obtain population estimates on an absolute basis is beyond the range of practicability, as the manpower is not available and only in extreme outbreaks are there enough trees to fulfill such a sample. Therefore the approach to the life table will have to be changed from absolute to relative population estimates. In

this manner estimates of the various mortality and natality factors could be compared by small sample techniques for populations under different epidemic stages.

Following this, the variance was determined for the samples which contained no branches and which came from the east side of the trees in the 0 to 5 foot level. The required number of samples necessary to sample this part of the trees alone appears in the last part of Table VIII. Even in such a restricted sampling universe the required samples at the 90 per cent level of confidence is still high, although enough data may be collected over a period of years to fulfill the requirements.

SUMMARY

A whole tree analysis was made of thirty lodgepole pine which had been attacked by the mountain pine beetle in varying intensities. Each tree was divided into one-foot square samples and the number of strikes per sample recorded. The analysis was facilitated by a punch card sorting system.

The beetle attacks tend to be aggregated together, although their distribution does not follow closely any of the common contagious distributions. The probability of the observed data being similar to Neyman's contagious distribution is greater at the higher intensities of attack.

The variance of the number of attacks per sample seems to be logarithmically related to the mean number of attacks. A $\log (x + 1)$ transformation made the variance independent of the mean and at the same time changed the contagious distribution to one which approached normal

in the intensity of attack.

There was a significant difference between cardinal directions with the north side receiving the greatest number of attacks and the south side the least.

The beetles seem to prefer clear bark areas as the intensity of attack was significantly reduced with the presence of branches.

No difference in intensity could be attributed to diameter, or to the amount of protection the sample received from shrubs or surrounding trees.

The intensity of attack decreased regularly towards the upper levels of the tree and a logarithmic curve was calculated of this relationship between the intensity of attack and the vertical level of the tree. The distribution up the tree varied under different intensities of attack.

Making gallery counts without removing the bark proved too erroneous to be of use in population work.

The variability of the number of attacks per tree is high, so that an extremely large sample would be required to place population estimates on an area basis.

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