

THE WITHIN-GENERATION MORTALITY,  
WITHIN-TREE DISTRIBUTION, AND  
DAMAGE OF THE JACK PINE TIP BEETLE,  
*CONOPHTHORUS BANKSIANAE* MCPHERSON

Thesis for the Degree of Ph. D.  
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DAVID JAMES HALL  
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This is to certify that the

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THE WITHIN-GENERATION MORTALITY, WITHIN-TREE  
DISTRIBUTION, AND DAMAGE OF THE JACK PINE  
TIP BEETLE, *Conophthorus banksianae* McPherson

presented by

David James Hall

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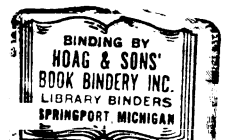
Ph.D degree in Forestry

Louis F. Wilson

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## ABSTRACT

### THE WITHIN-GENERATION MORTALITY, WITHIN-TREE DISTRIBUTION, AND DAMAGE OF THE JACK PINE TIP BEETLE, CONOPHTHORUS BANKSIANAE MCPHERSON

By

David James Hall

To determine age-specific density estimates, a more accurate method was devised to replace the total incidence method. It uses the numbers of dead plus living insects to arrive at age-specific density estimates. The major mortality factor was parasitism in the second instar by Cecidostiba dendroctoni Ashmead (Hymenoptera: Pteromalidae), and accounted for 15 to 40 per cent of the second instar. It was the only factor that contributed significantly to total generation mortality. Other mortality factors included: desiccation; engulfing by resin; being chewed upon by Pityophthorus sp., an unidentified lepidopterous larvae, and other tip beetles. These factors, individually, caused an average of less than 3 per cent of age-specific mortality. Density-dependent mortality was not observed, but the range of densities studied was so narrow that density-dependence may have been unobservable.

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Adult jack pine tip beetles preferred the upper crown where the most highly exposed tips occur. Forty-seven per cent of the attacks were in the top 10 inches and 88 per cent were in the top 25 inches of the crown. They avoided tips smaller than 3 mm. in diameter.

The tip beetle was responsible for the culling of 2-12 per cent of the jack pine stems. Trees on poorer sites sustained more damage than trees on more productive sites.

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DISTRIBUTION, AND DAMAGE OF THE JACK PINE  
TIP BEETLE, CONOPHTHORUS  
BANKSIANAE MCPHERSON

By

David James Hall

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## TABLE OF CONTENTS

	Page
INTRODUCTION . . . . .	1
Objectives. . . . .	3
WITHIN-GENERATION MORTALITY . . . . .	4
Study Areas . . . . .	4
Sampling System . . . . .	4
Methods. . . . .	7
Sample Unit Size and Sample Size . .	7
Sampling Universe . . . . .	10
Field Procedures. . . . .	10
Lab Techniques . . . . .	11
Results. . . . .	12
Age-Specific Developmental Rates . . . . .	14
Methods. . . . .	14
Results. . . . .	15
Age-Specific Density Estimates . . . . .	15
Methods. . . . .	16
Results. . . . .	16
Mortality Analysis . . . . .	25
Methods. . . . .	26
Results. . . . .	27
WITHIN-TREE DISTRIBUTION . . . . .	34
Methods . . . . .	34
Results . . . . .	35

	Page
DAMAGE . . . . .	42
Methods. . . . .	42
Results. . . . .	43
DISCUSSION AND CONCLUSIONS . . . . .	46
LITERATURE CITED . . . . .	52
APPENDICES	
Appendix	
A. Tables. . . . .	54
B. Tables. . . . .	55

## LIST OF TABLES

Table	Page
1. Age-Specific Density Estimates Represented as Insects/ft <sup>2</sup> Based on the Total Incidence Method for 1970, 1971 Data . . . . .	17
2. Age-Specific Density Estimates Represented as Insects/ft <sup>2</sup> Based on the Accumulation Method. . . . .	22
3. Egg Intensities, Egg Density Estimates, and Reproductive Attack Densities of the JPTB in 1970, 1971 . . . . .	24
4. Age-Specific and Total Generation Mortality (Per Cent) for All Stages and Generation of JPTB in 1970, 1971. . . . .	28
5. Factors Causing Mortality (Per Cent) of the Various Stages of the Jack Pine Tip Beetle for 1970, 1971 . . . . .	30
6. The Vertical Distribution of JPTB Attacks in Jack Pine in 1971 . . . . .	37
7. The Damage to Young Jack Pines Caused by the Jack Pine Tip Beetle . . . . .	45
A-1. Age-Specific Developmental Rates--Cage Study .	54
B-1. Sampling Data . . . . .	55
B-2. Sampling Data . . . . .	56
B-3. Sampling Data . . . . .	57
B-4. Sampling Data . . . . .	58
B-5. Sampling Data . . . . .	59
B-6. Sampling Data . . . . .	60

Table		Page
B-7.	Sampling Data . . . . .	61
B-8.	Sampling Data . . . . .	62



Figure

1.

2.

3.

4.

5.

6.

7.

8.

9.

10.

## LIST OF FIGURES

Figure	Page
1. Standard Error of Mean Number of Attacks per 1 ft <sup>2</sup> Over Number of Sample Units Per Sample. Cut-off Level refers to Distance from the Ground below which Attacks Were Discounted . . . . .	9
2. Standard Error Over Mean Density of Reproduc- tive Attacks. White Discs are for 1970 and Black Discs are for 1971 . . . . .	13
3. Total Incidence Curves for the Eggs, Larvae, and Pupae of the JPTB for Plantation 1 in 1971 . . . . .	18
4. Accumulation Curves for All Stages of the JPTB and Reproductive Attacks for Plantation 3 in 1971 . . . . .	20
5. The Contribution of Age-Specific Mortality to Total Generation Mortality for Eggs, Larvae, and Pupae of the JPTB . . . . .	32
6. The Vertical Distribution of Attacks of the JPTB Through the Oviposition Period. Numbers Refer to Inches Below Top of Tree . . . . .	36
7. Attacks of JPTB Over Jack Pine Height . . . . .	38
8. Frequency Distributions of Attacked and Unattacked Tips in Relation to Per Cent of Exposure to Sky . . . . .	39
9. Frequency Distributions of Diameters of Attacked and Unattacked Tips . . . . .	41
10. JPTB Damage to Jack Pine: A, Typical Appearance of Terminal Two Years After Attack; B, Typi- cal Appearance of Main Stem 6 Years After Attack; C, Probable Cull Caused by JPTB; D, Cull Caused by JPTB 15 Years Earlier . . . . .	44

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## INTRODUCTION

Shoot infesting insects seldom kill the trees but nearly always deform them. Relatively low insect populations can do serious damage to a stand because a single insect is enough to cause damage to a single tree. Shoot infesting insects are difficult to kill because they spend a considerable part of their life cycle within the plant material. Spraying programs often require a heavy dosage of a persistent insecticide which is detrimental to the environment and sometimes more costly than the economic loss from the insect.

Shoot damage on jack pine (Pinus banksiana Lamb.) is a case in point. The per-acre value of jack pine is low because it is used almost exclusively for pulpwood. Pre-harvest treatments including chemical spraying are uneconomical. On the other hand, jack pine is an important tree in the environment and economy of Michigan. After the great fires that swept through the lower peninsula near the turn of the century, jack pine seeded in over large areas. In addition, the species has been planted extensively on much of the abandoned

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farm land of the state, and it is now a major pulp species in Michigan. In 1970, jack pine accounted for 56 per cent of the coniferous pulpwood harvested (Blyth, 1971). The jack pine standing crop in Michigan is a resource that warrants protection.

The jack pine tip beetle (Conophthorus banksianae McPherson) is a shoot-infesting insect of jack pine in Michigan. It was previously believed to be a variant of C. resinosae Hopkins which attacks red pine cones and shoot tips. McPherson separated the two species by their behavior and life cycles (McPherson et al., 1970a, 1970b). Efforts to separate them based on morphology have been unsuccessful (Herdy, 1963).

The life cycle in brief is as follows: the adult jack pine tip beetle (herein after referred to as JPTB) attacks the apical one inch of the new shoot shortly after the new flush of growth is completed. According to McPherson et al. (1970a) and my observations, the beetle bores into the side of the shoot just below the bud and excavates an enlarged nuptial chamber immediately inside the entrance. An egg gallery is excavated apically from the nuptial chamber. From 1-5 eggs (rarely more) are laid in niches along the gallery. These attacks are called reproductive attacks. Attacks that are without eggs are called feeding attacks. Oviposition extends from early July to early August.

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The larvae pass through two instars during the summer and begin to pupate in early August. Adults appear in mid August. The adults overwinter within the dead tips which fall to the ground in late fall.

### Objectives

In the future, it may be necessary to evaluate the applicability of potential biological control measures upon the JPTB. Necessary information for this evaluation is knowledge of the population biology of the insect, its distribution within the tree, and the damaging effects of its attack. Thus, the objectives of this study were:

- (1) To determine the influence of natural mortality factors upon the total within-generation mortality of the JPTB;
- (2) To determine the within-tree distribution of reproductive attacks;
- (3) To characterize the damage of the JPTB to heavily infested jack pine stands.



## WITHIN-GENERATION MORTALITY

The purpose of the within-generation mortality study was to evaluate the amount and causes of mortality of the immature stages of the JPTB. This necessitated studying a range of population densities at several locations.

### Study Areas

Four young jack pine plantations, planted between 1954 and 1962, were selected in Northern Lower Michigan. Average tree height within each plantation ranged from 12 to 15.5 feet. The crowns were closed. The locations of the plantations were:

<u>Plantation Number</u>	<u>Location</u>	<u>County</u>
1	T24N, R9W, S16, NE1/4	Wexford
2	T23N, R13W, S23, SW1/4	Manistee
3	T27N, R9W, S11, SW1/4	Grand Traverse
4	T27N, R9W, S15, NE1/4	Grand Traverse

### Sampling System

A sampling system for the study of insect populations must provide reasonably precise estimates of the mean absolute insect density. (The absolute density is

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the number of insects per unit area.) But insect populations are usually aggregated making precision difficult to achieve, and complications of habitat or life cycle often make the sampling job difficult. As a result, a sampling system that can provide adequate precision is often time consuming and expensive.

It is not surprising, then, that the literature contains many papers dealing with the problem of accomplishing reasonable precision at reasonable expense. Some of these including Foltz et al. (1968), Lyons (1964), and Morris (1955) designed sampling systems for the study of forest insect populations, and Morris (1960) reviewed the subject in depth.

The problem encompasses determination of the sampling universe, sample unit, sample size, and timing of sampling. Morris (1955) restricted the sampling universe to 25-acre plots within "homogenous" balsam fir stands for the study of the spruce budworm. He later discussed restricting the sampling universe in order to reduce sample variance and to increase the correlation between successive samples (Morris, 1960).

According to Morris (1955):

- (1) Each sample unit in the sampling universe should have an equal chance of selection;
- (2) The number of units available to the insects must not be affected by changes in the plant;

- (3) The proportion of the insect population using the sample unit as a habitat must remain constant;
- (4) The sample unit should be small enough so that enough units can be taken to calculate the variance;
- (5) The sample unit should lend itself to conversion to a per-acre basis; and
- (6) The sample unit should be easily delineated in the field and collected without wiping out or disturbing the population.

The degree of precision generally considered desirable is attained by keeping the standard error within 10 per cent of the sample mean (Southwood, 1966; Morris, 1955). However, this level of precision has not always been realized (Morris, 1963; Embree, 1965). Foltz et al. (1968) did not attempt to achieve this level of precision because the sample size required to bring the standard error below 10 per cent of the mean would have been so large that it would have made the sampling system impractical. Several authors have discussed methods of calculating the optimum combination of sample unit and sample size using precision and cost per sampling unit as a basis (Southwood, 1966; Morris, 1955; Lyons, 1964). The timing of sampling depends

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upon the life cycle of the insect, the rate of development, and the method used to analyze the data.

### Methods

Because the developmental stages of the JPTB occur exclusively in the shoot tip, it might seem reasonable to use one or a number of tips as a sample unit. After determining the number of tips per acre, the number of insects per tip could then be converted to a per-acre value for the estimate of absolute population density.

The difficulty herein lies in the fact that not all the tips on the crown surface are equally susceptible to attack by the adult. And it is not easily determined which tips are preferred. Furthermore, estimating the number of tips per unit area (available or otherwise) would be an extremely laborious process and the accuracy would be doubtful. It was decided to use a unit area within the crown as a sample unit. Specifically, the sample unit was the crown surface over a unit area of ground surface. One advantage of this sample unit is that it requires no conversion to achieve an estimate of absolute density.

Sample Unit Size and Sample Size.--To determine the desired size of sample unit and sample size, preliminary data were collected in April of 1970 and

analyzed. An area 12 ft. x 12 ft. in a heavily attacked jack pine plantation was laid out and each square foot of area was marked off to form a grid with 144 squares. Then the number of beetle attacks from the previous year was counted and the vertical distance of each attack from the tree top was measured.

I then sampled these data by simulation. The sample size was varied from 20-50 sample units. Sample unit sizes of 1, 2, and 4 ft<sup>2</sup> were used. The 2 ft<sup>2</sup> and 4 ft<sup>2</sup> sample units were formed by combining 2 or 4 adjacent 1 ft<sup>2</sup> sample units. The cut-off level (the distance from the ground below which attacks were discounted) was varied from 60-95 inches. The variance and standard error of the means of each simulated sample were computed.

The 1 ft<sup>2</sup> samples gave the lowest standard errors. The relationship between standard error and sample size for 1 ft<sup>2</sup> sample is presented in Figure 1. Standard error was high when all tips were considered. That is, this occurred when the cut-off level was 60 inches. There were no attacked tips below 60 inches so the true mean of the 144 ft<sup>2</sup> sample area was obtained. The standard error was somewhat lower when the cut-off level was 70 or more inches (Figure 1), so some of the attacks in the lower part of the crown can be eliminated from sampling. In order to stay within 10 per cent of the mean a sample size of about 34 sample units is needed.

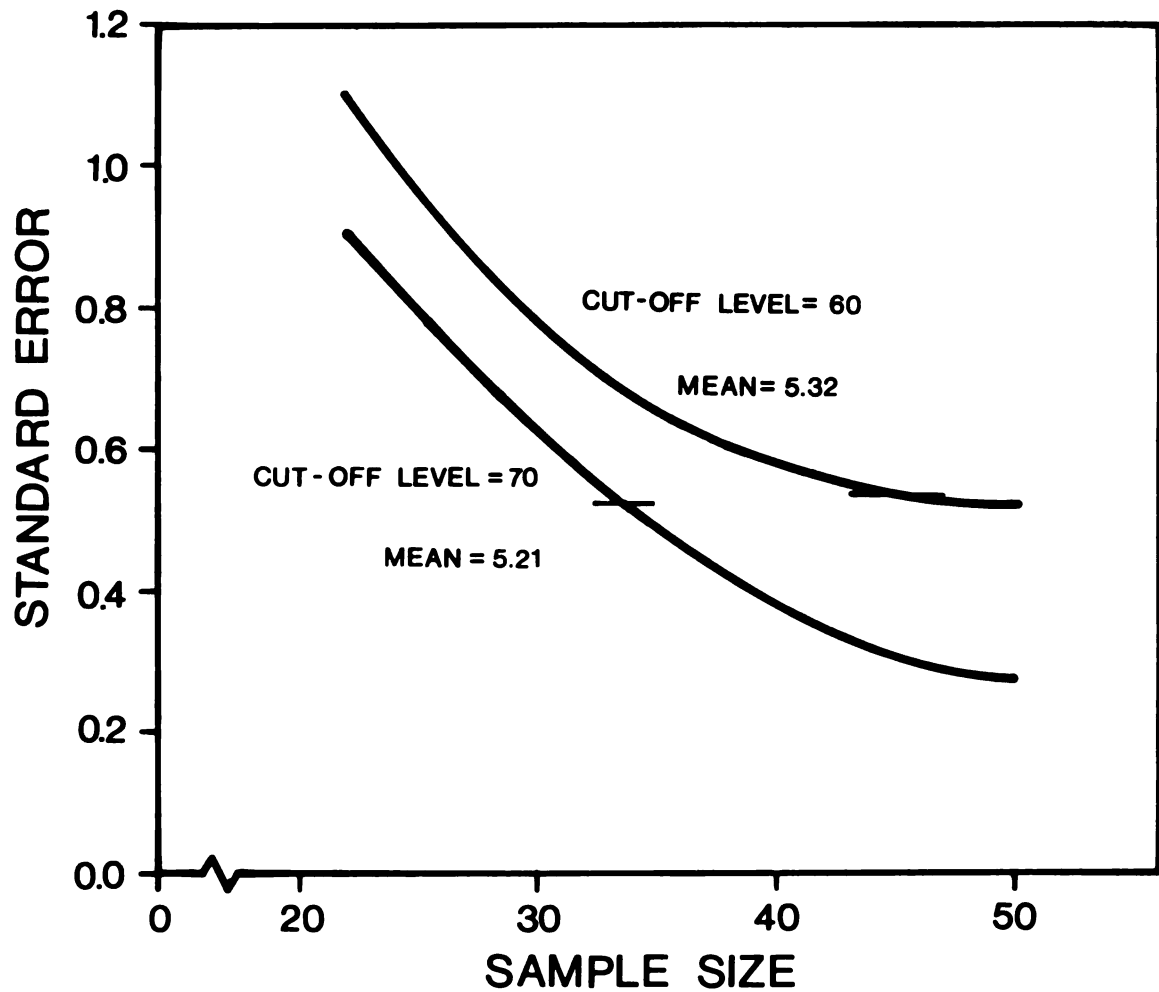


Figure 1.--Standard error of mean number of attacks per 1 ft<sup>2</sup> over number of sample units per sample. Cut-off level refers to distance from the ground below which attacks were discounted.



In 1970, I felt that sampling a low density population with a 1 ft<sup>2</sup> sample unit would result in excessive numbers of zeros in the samples, so I used a 2 ft<sup>2</sup> sample unit size. I used the 1 ft<sup>2</sup> sample unit size in 1971.

A sample size of 30 sample units in the three high-density populations and 45 sample units in the one low-density population were used both years.

In order to physically move about and conduct the sampling program, I pruned the lower limbs within the sampling plots approximately to the 70-inch cut-off level. At most this eliminated a few tips susceptible to beetle attacks.

Sampling Universe.--Within each plantation, the 30 (or 45) sample units were divided evenly among 3 plots. The plots were located so that they were easily accessible and representative of the plantation. Each plot was nearly 60 ft x 60 ft and included about 100 trees.

Field Procedures.--In 1970 the sample units were located by throwing a marker into the plot. In 1971, a grid was marked off on the ground, each square was numbered, and numbers for each sampling date were drawn from a random number table. The marker in 1970 and a stake in the ground in 1971 located the center of a sample unit. A 12-foot aluminum pole was held vertically in the center of the sample unit so that it projected

7

through the crown surface. A length of heavy aluminum wire was bent around the pole so that it could slide up and down the pole and maintain a right angle to the pole. Its length was such that when revolved around the pole, it circumscribed a circle with an area of the desired sample unit size. The wire was moved up or down the pole in the area of the crown surface, so that attacked tips inside a cylinder described by the device were collected. An eight-foot aluminum step ladder was used to collect the samples.

Samples were taken every six days while eggs were present from about 1 July to 10 August and every 7 or 8 days thereafter until virtually all the insects reached the adult stage. The attacked tips from each sample unit were placed in a plastic bag with a label and sealed. They were held in a freezer at 5° F until they could be dissected in the lab.

Lab Techniques.--Each tip was sliced in half length-wise and then classified as either a feeding attack or a reproductive attack. The number of each stage of the insect present was recorded. The number of insects that died prior to being placed in the freezer were recorded and the cause of death diagnosed when possible. These could be distinguished from normal healthy larvae by color and physical appearance. The presence of parasites, an unidentified lepidopterous

larva, and Pityophthorus sp. were recorded. These insects had previously been observed within JPTB galleries and were suspected of causing some mortality.

### Results

Periodic samples of the JPTB were taken in four jack pine plantations during the summers of 1970 and 1971. The mean and standard error of the reproductive attacks and each insect stage present in each sample were calculated. The relationship between standard error and density of reproductive attacks is presented in Figure 2.

The graph shows that the standard error of the reproductive attacks increased proportionally with the mean and the standard error was higher for the 1971 data than in 1970. However, the 1970 data were based on a sample unit of  $2 \text{ ft}^2$ ; the means and standard errors were halved before plotting. In addition the system of sampling was different during the two years.

The densities of the insects were lower than the densities of the reproductive attacks in most of the samples. Consequently the standard errors of the mean numbers of insects were relatively higher (in terms of per cent of the means). The complete results including reproductive attack and insect densities are in Appendix B.

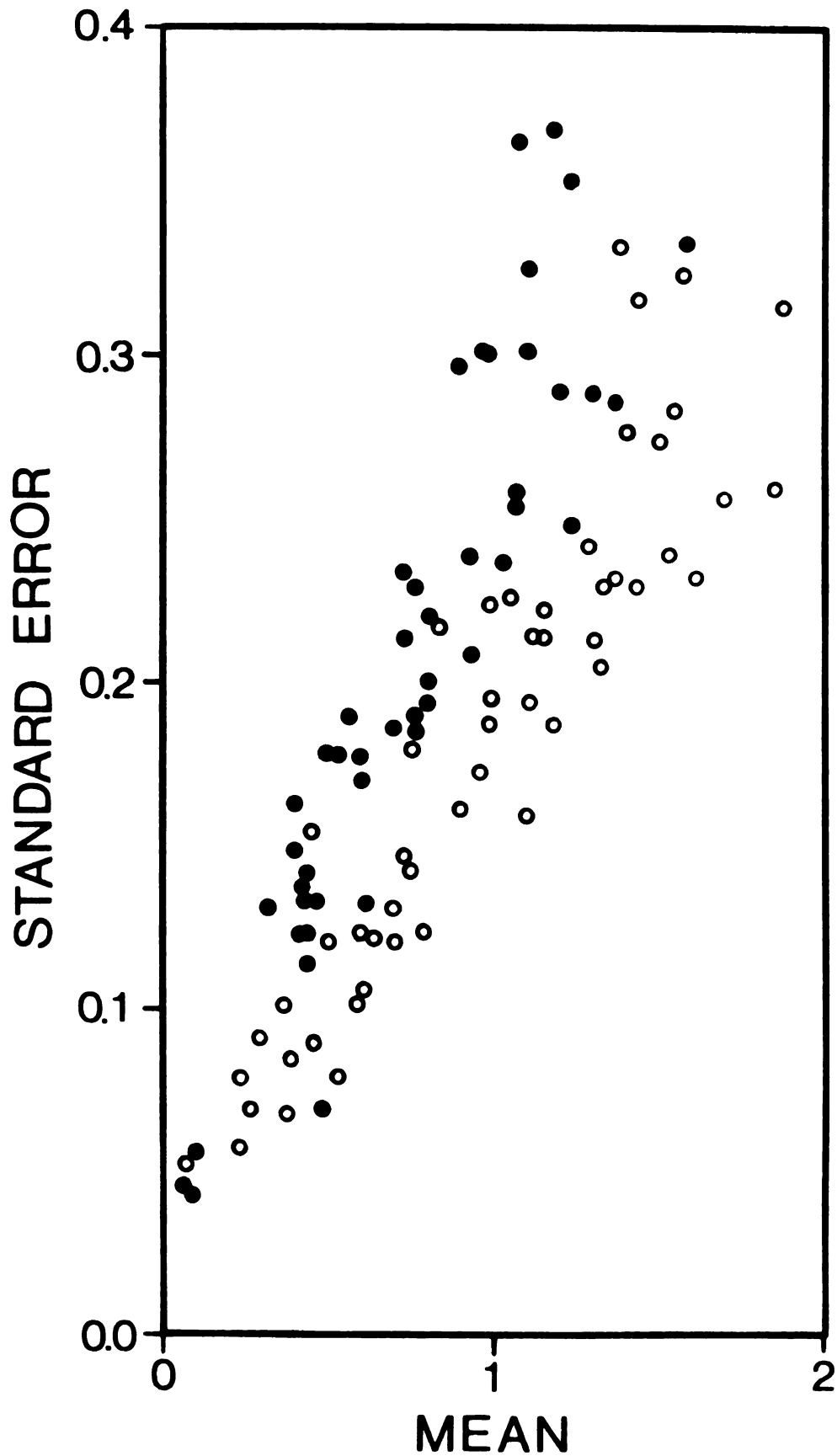


Figure 2.--Standard error over mean density of reproductive attacks. White discs are for 1970 and black discs are for 1971.

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## Age-Specific Developmental Rates

### Methods

The developmental period of a stage of an insect is used to calculate age-specific density estimates by the total incidence method (Southwood, 1966).

In order to determine the developmental period, I collected attacked tips with adults still in them. These tips can be identified by the appearance of a fresh pitch tube with frass piled loosely inside and hanging from the entrance.

Sixty tips about 4 inches long were collected on each of two consecutive days. The tips collected on the first day were labeled "A" and those collected on the second day labeled "B." The tips were placed upright in a cage. Every other day, 3 tips were taken from each of the two groups of tips and dissected immediately or placed in the freezer for dissection later. This, in effect, accomplished two days of sampling in one day. For example, the tips taken from the cage on 15 July were dissected 5 and 6 days after the original collection. This method is valid if the tips collected on the second day were attacked on the average of one day later than the first group collected, but this is difficult to prove.

## Results

The developmental periods were 7 days for the eggs, 6 days for the first instar, 12 days for the second instar, and 9 days for the pupae (see Appendix A).

### Age-Specific Density Estimates

In order to estimate the mortality of the JPTB it was necessary to estimate absolute density of the insects in each stage. However, no one sample mean will accurately estimate the density of any stage because the eggs are laid over a period of about 40 days and there is no one time when all the immature insects are present in one stage.

Several methods of analyzing data of this sort are discussed by Southwood (1966). The most straight forward of these methods is the total incidence method which has been used successfully on the cereal leaf beetle (Helgesen and Haynes, 1972). In this method, successive sample means are plotted on graph paper over sampling day. When all the means for one stage (say the eggs) are plotted, a curve is drawn through the points. The total area under the curve (the total incidence) represents the total number of egg-days. The area can be determined by counting squares under the curve or by using a planimeter. This area, then, divided by the mean developmental time gives an estimate of the average egg density throughout the generation.



Mortality does not occur just at the end of each stage, so this method gives an underestimate of age-specific density. When a mortality factor kills uniformly over a stage or only late in a stage, the density estimate is more accurate.

### Methods

Total incidence curves were constructed for the egg, larval, and pupal stages of the JPTB using the mean density estimates provided by periodic sampling. The total incidence was calculated by counting squares of known area under the curves and dividing by the appropriate developmental time obtained from the cage study. Callow adult densities were estimated by plotting the successive sample means over sampling date and reading the density directly off this curve. This method also produces an underestimate because some callows die within the tip and a few others vacate the tip in early September.

### Results

The density estimates calculated by this method for all study areas are shown in Table 1. The density estimate of the first instar was greater than the egg density in two cases (see Table 1). This could be due to underestimation of the egg total incidence, overestimation of the larval total incidence, underestimation

of the first instar developmental time, or overestimation of the egg developmental time. Since the errors were both in the first instar, underestimation of developmental time was the probable cause.

TABLE 1.--Age-specific density estimates represented as insects/ft<sup>2</sup> based on the total incidence method for 1970, 1971 data.

Stage	Plantation No.				Plantation No.			
	1	2	3	4	1	2	3	4
	1970				1971			
Egg	2.27	1.31	2.06	2.70	1.70	2.01	2.21	1.97
Larva I	1.69	1.19	1.72	1.77	1.98 <sup>a</sup>	1.27	1.78	2.17 <sup>a</sup>
Larva II	1.46	0.87	1.55	1.42	0.92	1.06	1.24	1.32
Pupa	1.15	0.66	1.08	0.94	0.24	0.40	0.74	0.64
C. adult	0.55	0.35	0.80	0.85	0.15	0.30	0.30	0.25

<sup>a</sup>Estimates greater than egg density estimates.

A typical set of total incidence curves for the JPTB is presented in Figure 3.

The incidence of the eggs and first instar increased and decreased rapidly indicating that the six-day interval between samples may have been slightly too long to accurately describe the true total incidence. The interval should be shorter than the shortest developmental period expected, which was between 6 and 7 days.

In order to arrive at improved age-specific density estimates another method of estimation was used which I call the "accumulation method." The densities

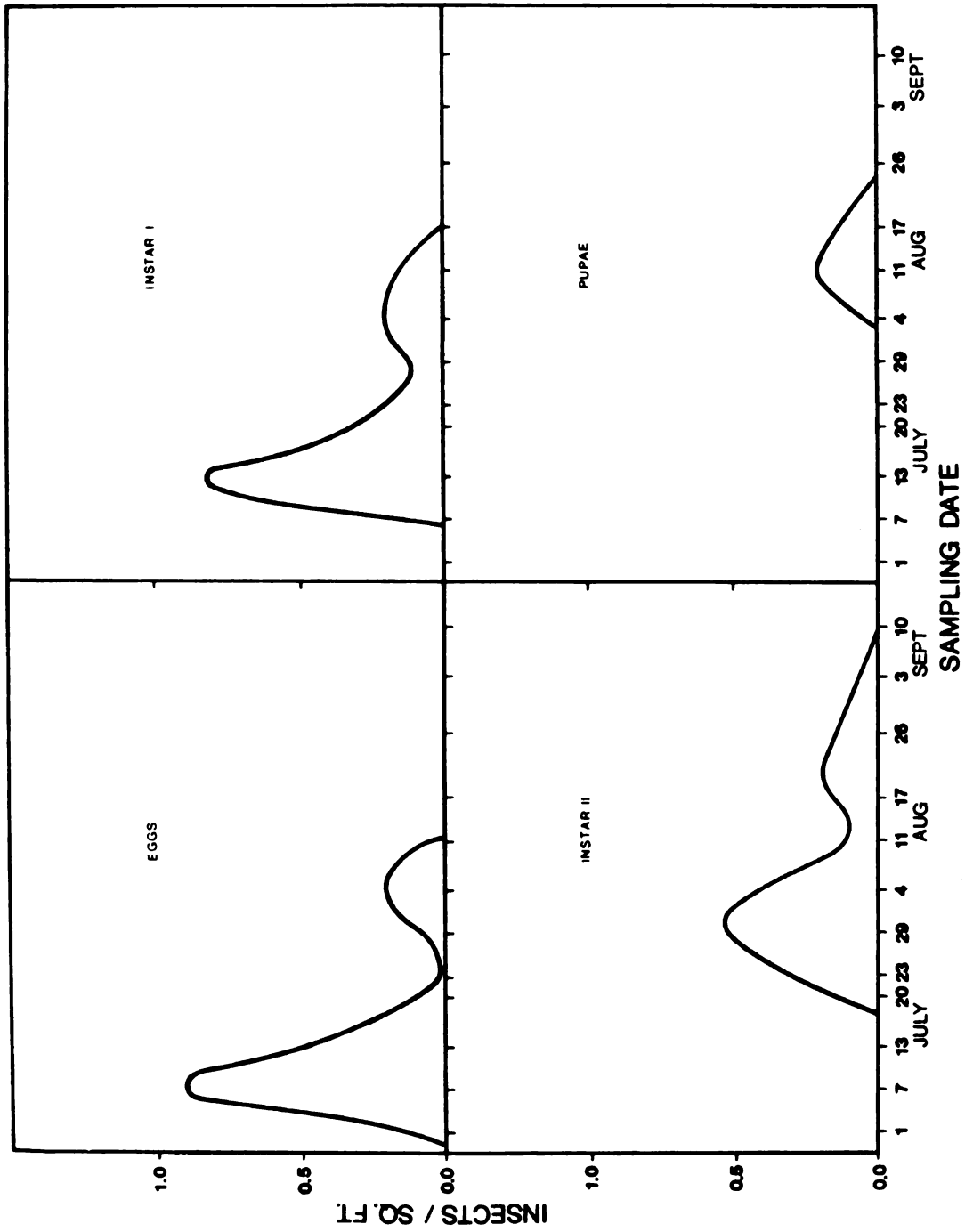


Figure 3.--Total incidence curves for the eggs, larvae, and pupae of the JPTB for plantation 1 in 1971.

are calculated in the following way: First the numbers of dead plus living callow adults in the sample were plotted over sampling date. Then, the numbers of dead plus living pupae in the sample were added to the previously calculated callow adult densities and these numbers were plotted. In like manner the numbers of second instar, first instar, and egg numbers were calculated and plotted for each sampling date. The number of reproductive attacks in each sample was also plotted.

A curve was first drawn through the points (r) representing the sample means of the reproductive attacks. Because the number of reproductive attacks remains constant after oviposition has ceased, a horizontal line was drawn through the points from early August to the end of the season. Deviations from this line were considered sampling error. Curves were then drawn through points for the various stages of the insect. The deviation of a point (r) above or below the curve for reproductive attacks was taken into account when deciding where to draw the curves for the individual stages. If the r-point was considerably above the reproductive attack curve, the r-point was considered to be an overestimate and the curve for the egg density was placed below the point e. Where the points leveled off and began to decrease the curve was drawn horizontally from there to the end of the sampling season. The density estimate for each stage was read off the end of its curve.

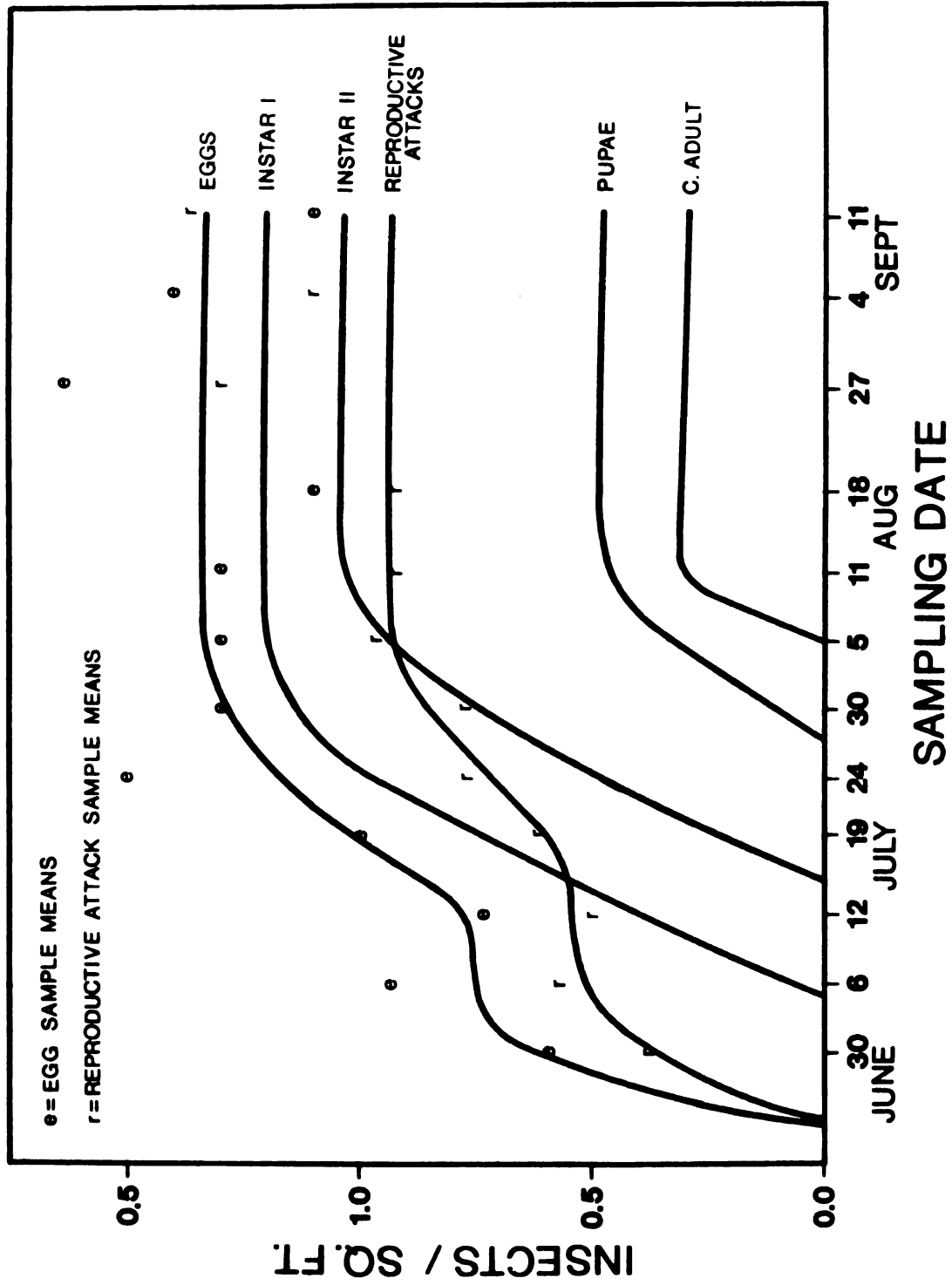


Figure 4.--Accumulation curves for all stages of the JPTB and reproductive attacks for plantation 3 in 1971.

The rationale behind the method is that at any one time during the period when immatures are present, the number of insects that entered the egg stage is equal to the sum of the living and dead insects in all the stages following the egg stage.

This method is roughly equal to removing the bark covering a bark beetle gallery after the brood has matured. One can count the egg niches, the number of exit holes of the new adults, and determine the age at death of the remainder of the brood.

The method requires that the individual insect remain within the original host during its entire immature life, and the remains of the dead insects must not be lost or destroyed. The first requirement is fully met by the tip beetle, but the second requirement is not entirely met for the following reasons. Infertile or nonviable eggs are impossible to recognize when present with other eggs, and later they may be consumed by larvae. Thus some eggs were lost. Also, a few of the dead first instar may be lost but usually the head capsule can be detected and recorded. A few dead pupae and some callow adults may be destroyed by other callow adults. All of these losses cause an underestimate of densities of the immature stages when using the accumulation method. The method is fairly accurate in

estimating second instar through callow adults but the underestimate of the egg and first instar densities is quite large.

The age-specific density estimates calculated by this method are shown in Table 2. By definition the method postulates that the density of any stage must be equal or greater than that of any succeeding stage.

TABLE 2.--Age-specific density estimates represented as insects/ft<sup>2</sup> based on the accumulation method.

Stage	Plantation No.				Plantation No.			
	1	2	3	4	1	2	3	4
	1970				1971			
Egg	2.20	1.21	2.26	2.02	1.08	1.12	1.33	1.71
Larva I	1.92	1.07	2.11	1.81	0.92	1.05	1.20	1.49
Larva II	1.72	0.93	1.86	1.68	0.67	0.83	1.03	1.04
Pupa	0.82	0.52	1.16	1.17	0.25	0.37	0.47	0.45
C. adult	0.67	0.36	0.84	0.96	0.15	0.32	0.31	0.31

The egg and first instar density estimates from the accumulation method are generally lower than those calculated by the total incidence method. This bears out the expectation of the method. The second instar estimates are higher in 1970 and lower in 1971 than the total incidence estimates. This may be due to temperature, which may have affected developmental time differently in the two years. On the other hand the mortality may have occurred earlier in 1970 causing a

relative underestimate by the total incidence method in that year. The fault here does not lie with the total incidence method, but rather with the lack of information available.

The accumulation method is more reliable than the total incidence method in this study because it is not affected by temperature differences between years or between populations, nor is it affected by differential timing of mortality. However, it underestimates the stages where the dead insects are difficult to recover, especially the egg and first instar. Egg intensities were determined to improve upon the egg density estimates. This method uses the estimated number of eggs per reproductive attack (egg intensity) and the density of reproductive attacks. The raw data from each population were scanned for reproductive attacks which contained eggs. Then, the mean number of eggs per reproductive attack (egg intensity) and the standard error were computed. The egg intensity for each population was multiplied by that population's reproductive attack density to arrive at the egg density estimate. Thus, the formula used was:

$$\text{Eggs/ft}^2 = \text{Eggs/Repro. attack} \times \text{Repro. attacks/ft}^2$$

or

$$\text{Egg density} = \text{Egg intensity} \times \text{Repro. attack density}$$



The egg intensities and egg density estimates are shown in Table 3. The egg intensities show little variation within years as well as between years. Most of the differences in egg densities are accounted for by density of reproductive attacks.

TABLE 3.--Egg intensities, egg density estimates, and reproductive attack densities of the JPTB in 1970, 1971.

Parameter	Plantation No.				Plantation No.			
	1	2	3	4	1	2	3	4
	1970				1971			
Egg								
Intensity	1.89	2.00	1.77	1.97	2.15	1.83	1.88	1.85
SE	0.09	0.13	0.12	0.11	0.23	0.15	0.13	0.17
Repro.								
Attack								
Density	1.41	0.70	1.51	1.33	0.78	0.80	0.93	1.04
Egg								
Density	2.66	1.40	2.67	2.62	1.68	1.46	1.76	1.92

These egg density estimates are higher than those calculated by the accumulation method as expected. Comparison with the egg density estimates calculated by the total incidence method shows the egg intensity estimates to be higher in 1970 and lower in 1971. The most obvious reason for this would again be a differential temperature effect upon the density estimates by the total incidence method. The egg intensity method is not affected by temperature.

For mortality analysis, egg densities were used from Table 3 and densities for remaining stages of the insect were used from Table 2. Inspection reveals that the density estimates were higher in 1970 than in 1971 with the exception of plantation 2. However, the densities in plantation 4 as well as 2 increased in 1971, as was evident from field observation. The density estimates do not reflect these increases.

This is probably due to different sampling systems used each year. In 1970, a marker was thrown into the plots to locate each sample unit, which probably biased the sample because the marker frequently landed in the tree tops where the population density is greater. In 1971, a grid was used and the numbered sample units were chosen from a random number table.

Because the 1970 and 1971 density estimates were not comparable, the figures from the two years were kept separate when examining the relationships between mortality and density.

#### Mortality Analysis

In the previous section, the absolute density of each stage of the JPTB was calculated for eight populations. These figures represent the numbers of insects that entered each stage. The difference between densities of two successive stages (say the egg and first instar) represents the absolute density of the dead

eggs. Likewise, the difference between the densities of the first and second instars represents the absolute density of dead first instars.

Southwood (1966) defines apparent mortality as "the numbers dying as a percentage of the numbers entering that stage" and real mortality as "the numbers of a stage dying as a percentage of the numbers entering the generation." The apparent mortality is normally used in analysis of mortality data.

Apparent mortality is normally plotted over various parameters to look for relationships. The effect of population density upon apparent mortality is an important concept in population biology. Basically, density-dependent mortality occurs when a particular mortality factor takes an increasing proportion of the population as the population density increases. Density-dependent mortality may be manifested in a variety of factors; often it results from competition for food or from the activity of a predator.

### Methods

The apparent mortality was calculated using the age-specific density estimates from the previous section. Thus:

$$M_n = \frac{D_n - D_{n+1}}{D_n}$$

where  $M_n$  is the apparent mortality of stage  $n$  and  $D_n$  and  $D_{n+1}$  are the absolute densities of stage  $n$  and the succeeding stage  $(n+1)$ , respectively. Total generation mortality was calculated by dividing the difference between the egg and callow adult density by the egg density.

The mortality due to each factor was first calculated as a proportion of the number of dead insects recorded in each stage. Each of these proportions was multiplied by the apparent mortality of the stage to arrive at the estimated apparent mortality due to each factor.

### Results

The age-specific and total generation mortalities are shown in Table 4. The apparent mortality figures are useful for comparing the per cent dead larvae with the per cent dead eggs or pupae; they show the relative "killing power" of age-specific mortality or actual mortality factors. The greatest apparent mortality occurred in the second instar with an overall mean of 49.2 per cent. Egg mortality was slightly lower with a mean of 31.0.

Recall that the first instar densities used in calculating the mortalities were underestimates. Thus, this would cause an overestimation of egg mortality and

TABLE 4.--Age-specific and total generation mortality (per cent) for all stages and generation of JPTB in 1970, 1971.

Stage	Plantation No.				Plantation No.				Mean
	1	2	3	4	1	2	3	4	
	1970				1971				
Egg	27.8	23.6	21.0	30.9	45.2	28.1	31.8	22.4	31.0
Larva I	10.4	13.1	11.8	7.2	27.2	20.9	14.2	30.2	16.9
Larva II	52.4	44.1	37.6	30.2	62.7	55.4	54.3	56.7	49.2
Pupa	18.3	30.8	27.6	17.9	40.0	13.5	34.0	31.1	26.6
Total Generation Mortality	74.8	74.3	68.5	63.3	91.1	78.1	82.4	83.9	77.0

also an underestimation of first instar mortality. Therefore, the egg mortality is smaller than it appears in the table and the first instar mortality is larger.

The mortalities attributable to various factors are shown in Table 5. Most of the known factors had little apparent effect upon the populations. Those that appeared important were parasitism in the second instar and pupa, accounting for a mean of 27.0 and 13.8 per cent respectively.

Two parasitoid species (both Hymenoptera) were encountered. Over 95 per cent of the parasitism was by Cecidostiba dendroctoni Ashmead (Pteromalidae).<sup>\*</sup> The other parasitoid was not reared to adulthood and, therefore, not identified. The numbers of dead insects due to the two parasitoids were combined for calculation of apparent mortality.

C. dendroctoni was easily recognized by its distinctive egg chorion which is quite durable. The adult parasitoid, apparently works from outside the attacked tip, paralyzes the host and deposits the egg next to the host within the tip. The parasitoid larva feeds externally on the host. When it matures, it chews an exit hole through the side of the tip. Since adults have been collected in early June, there must be at

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<sup>\*</sup> Determined by B. D. Burks of the Systematic Entomology Laboratory, USDA, U.S. National Museum.

TABLE 5.--Factors causing mortality (per cent) of the various stages of the jack pine tip beetle for 1970, 1971.

	Plantation No.				Plantation No.				Mean	Range
	1970				1971					
	1	2	3	4	1	2	3	4		
Egg										
Dessication	3.1	4.3	0.0	0.0	0.0	0.0	5.3	2.6	1.9	0.0- 5.3
Pityophthorus	0.0	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.5	0.0- 3.8
Misc. and unknown	24.7	19.3	17.2	30.9	45.2	28.1	26.5	19.8	25.8	17.2-45.2
Total egg	27.8	23.6	21.0	30.9	45.2	28.1	31.8	22.4	31.0	21.0-45.2
L1										
Dessication	0.3	0.0	0.0	0.3	1.5	3.5	0.0	0.6	0.8	0.0- 3.5
Pitched	0.9	0.6	0.2	0.2	0.8	0.0	0.0	0.6	0.4	0.0- 0.9
Chewed	0.8	0.9	0.6	0.2	2.3	0.0	3.4	1.1	1.2	0.0- 3.4
Pityophthorus	0.4	0.0	0.2	0.2	0.8	0.0	0.0	0.0	0.2	0.0- 0.8
Parasitism	0.4	2.7	0.4	0.5	3.0	3.5	1.3	6.3	2.7	0.4- 6.3
Misc. and unknown	7.6	8.9	10.3	5.8	18.9	13.9	9.5	21.6	12.1	5.8-21.6
Total L1	10.4	13.1	11.8	7.2	27.2	20.9	14.2	30.2	16.9	10.4-30.2
L2										
Pitched	4.2	2.6	1.8	0.6	3.0	0.0	0.6	0.7	1.7	0.0- 4.2
Chewed	4.9	2.9	2.0	3.1	0.0	5.0	2.5	2.0	2.8	0.0- 5.0
Pityophthorus	0.6	0.0	0.0	0.4	0.0	0.6	0.0	0.0	0.2	0.0- 0.6
Lep. larvae	0.0	0.0	0.0	0.4	0.0	0.0	0.6	0.7	0.2	0.0- 0.7
Parasitism	24.6	18.3	15.9	15.0	39.8	36.1	32.8	33.6	27.0	15.0-39.8
Misc. and unknown	18.0	20.3	17.9	10.6	19.9	13.7	17.7	19.8	17.2	10.6-20.3
Total L2	52.4	44.1	37.6	30.2	62.7	55.4	54.3	56.7	49.2	30.2-62.7
Pupae										
Pitched	4.3	2.6	5.3	3.3	5.0	0.0	0.0	0.0	2.6	0.0- 5.3
Chewed	2.1	5.1	3.2	2.7	10.0	0.0	0.0	0.0	2.9	0.0-10.0
Pityophthorus	3.2	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.7	0.0- 3.2
Lep. larvae	0.0	0.0	1.1	0.7	0.0	0.0	2.8	0.0	0.6	0.0- 2.8
Parasitism	2.1	12.8	6.4	6.6	25.0	13.5	25.5	18.7	13.8	2.1-25.5
Misc. and unknown	6.5	10.3	9.5	4.6	0.0	0.0	5.7	12.4	6.1	0.0-12.4
Total pupae	18.3	30.8	27.6	17.9	40.0	13.5	34.0	31.1	26.6	13.5-40.0

least one more generation per year on an alternate host. The known hosts are nearly all in the family Scolytidae (Muesebeck et al., 1951; Peck, 1963). This is the first record of the parasitoid upon the JPTB.

To examine the relative contribution of age-specific mortality to variance of total generation mortality, the apparent mortality of each of the immature stages plus the apparent mortality due to parasitism in the second instar were plotted over total generation mortality. Also the coefficient of determination ( $r^2$ ) of each relationship was calculated. The results are shown in Figure 5. Mortality in the second instar was the largest contributor to variance in the total generation mortality with an  $r^2$  of 0.90. Most of this variation is contributed by parasitism with an  $r^2$  of 0.83.

Relative mortality can be assessed by comparison of the positions of the points on the graph as well as by examining Table 5. Because greater mortality in any one stage necessarily increases total generation mortality, it would seem that higher mean age-specific mortality would force higher correlation between age-specific and total generation mortality. Such is not necessarily the case. The egg stage has the second highest mean mortality rate but the lowest  $r^2$ . The first instar and pupal stages showed lower mean mortality rates but had higher correlations than the egg mortality.



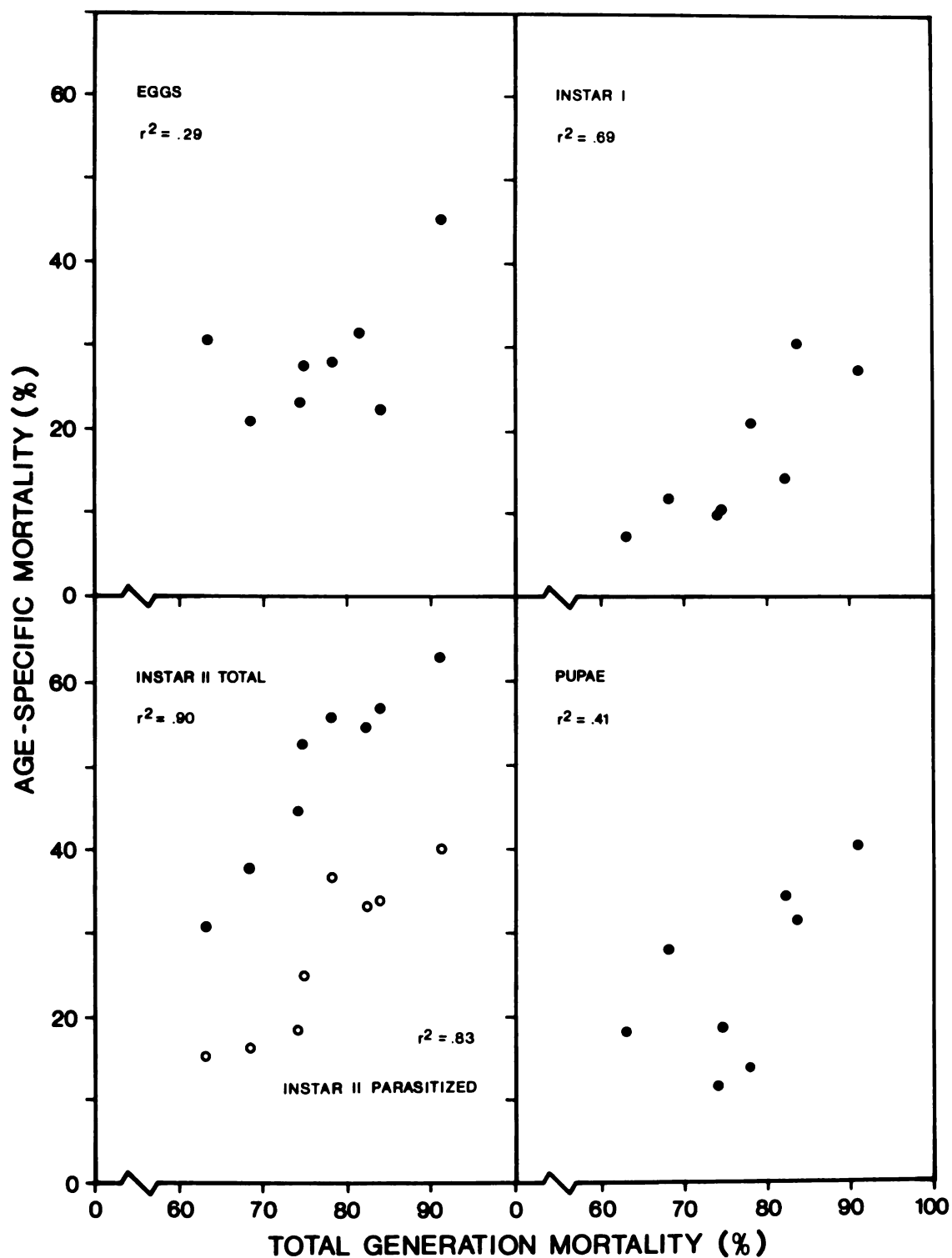


Figure 5.--The contribution of age-specific mortality to total generation mortality for eggs, larvae, and pupae of the JPTB.

High apparent mortality in the second instar means high generation mortality; the same cannot be said of mortality in the remaining stages.

The apparent mortality was examined to determine if there was a density-dependent relationship. The egg, larval, and pupal mortalities plus the mortality of the second instar due to parasitism, plus the total generation mortalities were plotted over egg density. Density-dependence was not observed.

## WITHIN-TREE DISTRIBUTION

Casual observation indicated that the reproductive attacks were aggregated in the tops of the crowns, and the tall trees appeared to be the most heavily attacked. It was not known, however, if the beetles attacked in response to light, tip size, or if they were attracted to the highest tree in sight.

The purpose of this aspect of the study was to determine the distribution of the reproductive attacks in relation to:

- (1) Distance from the top of the tree;
- (2) Tree height;
- (3) Degree of exposure to the sky; and
- (4) Tip diameter.

### Methods

Measurements were taken on four occasions during the summer of 1971 on nine jack pines in a young plantation adjacent to plantation 1 of the mortality study.

Tree height, attacked tips, and nearest unattacked tips were measured. Measurements taken were:

- (1) Distance of tip from the top of the tree (in inches);
- (2) Diameter of the tip (in millimeters) about 3/8 inch below the base of the bud; and
- (3) The per cent of open sky to which the tip was exposed, estimated visually.

The measurements were taken on 2 July, 9 July, 27 July, and 10 August.

### Results

Figure 6 depicts the change in the numbers of attacks in the various levels within the crown during the oviposition period. The figures are accumulated on the measuring dates after 2 July.

During the first two weeks of the reproductive attack, the top 5 inches of the crown received the heaviest number of attacks even though it contained far fewer tips than the lower crown levels. Later on the 6-10 inch class surpassed the top 5 inches. The rate of attack slowed after 27 July and ceased by 10 August.

Table 6 shows the final number of attacks in successive classes and the respective percentages of the total number of attacks. The percentages are relatively high in the upper levels and decrease through the lower

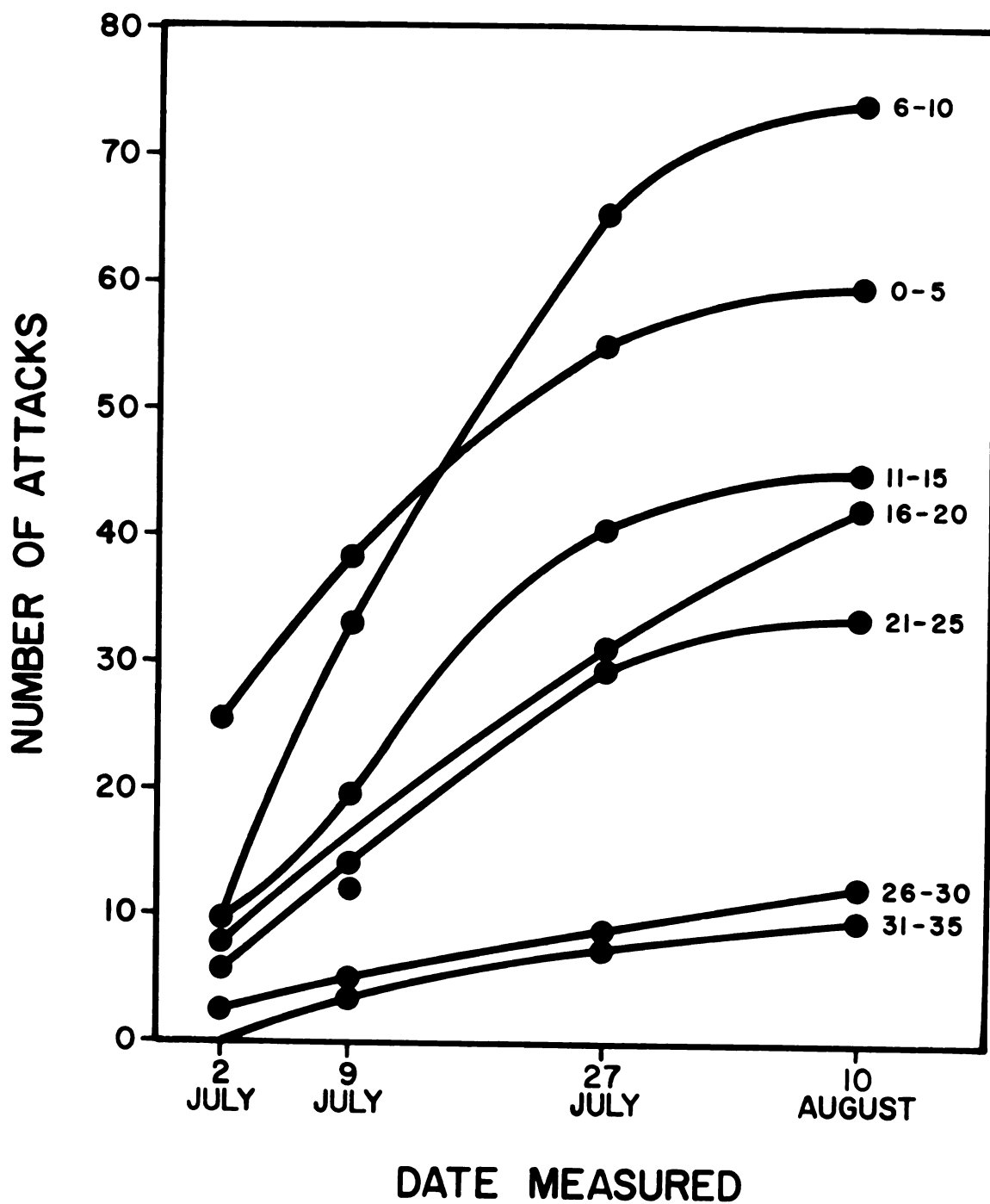


Figure 6.--The vertical distribution of attacks of the JPTB through the oviposition period. Numbers refer to inches below top of tree.

levels. Nearly 50 per cent of the attacks are in the top 10 inches of the crown and nearly 90 per cent in the top 25 inches.

TABLE 6.--The vertical distribution of JPTB attacks in jack pine in 1971.

Crown Height Class  Inches Below Top of Tree	Attacks in Each Crown Level		Accumulated Attacks	
	Number	Percentage	Number	Percentage
0-5	59	21	59	21
6-10	76	26	135	47
11-15	44	15	179	62
16-20	42	15	221	76
21-25	33	12	254	88
26-30	12	4	266	93
31-35	9	3	275	96
36-	12	4	287	100
Totals	287	100		

Figure 7 shows the relationship between incidence of attack and tree height. The relationship is weak ( $r^2 = .32$ , not significant at .05 level) but a trend is evident. This is not particularly surprising because a taller tree has proportionally more susceptible tips to attack than a shorter one.

Figure 8 shows the relationship between exposure to sky and attack. The degree of exposure is expressed as per cent of the hemisphere of sky visible at the tip. The distribution of attacked tips is clearly shifted to

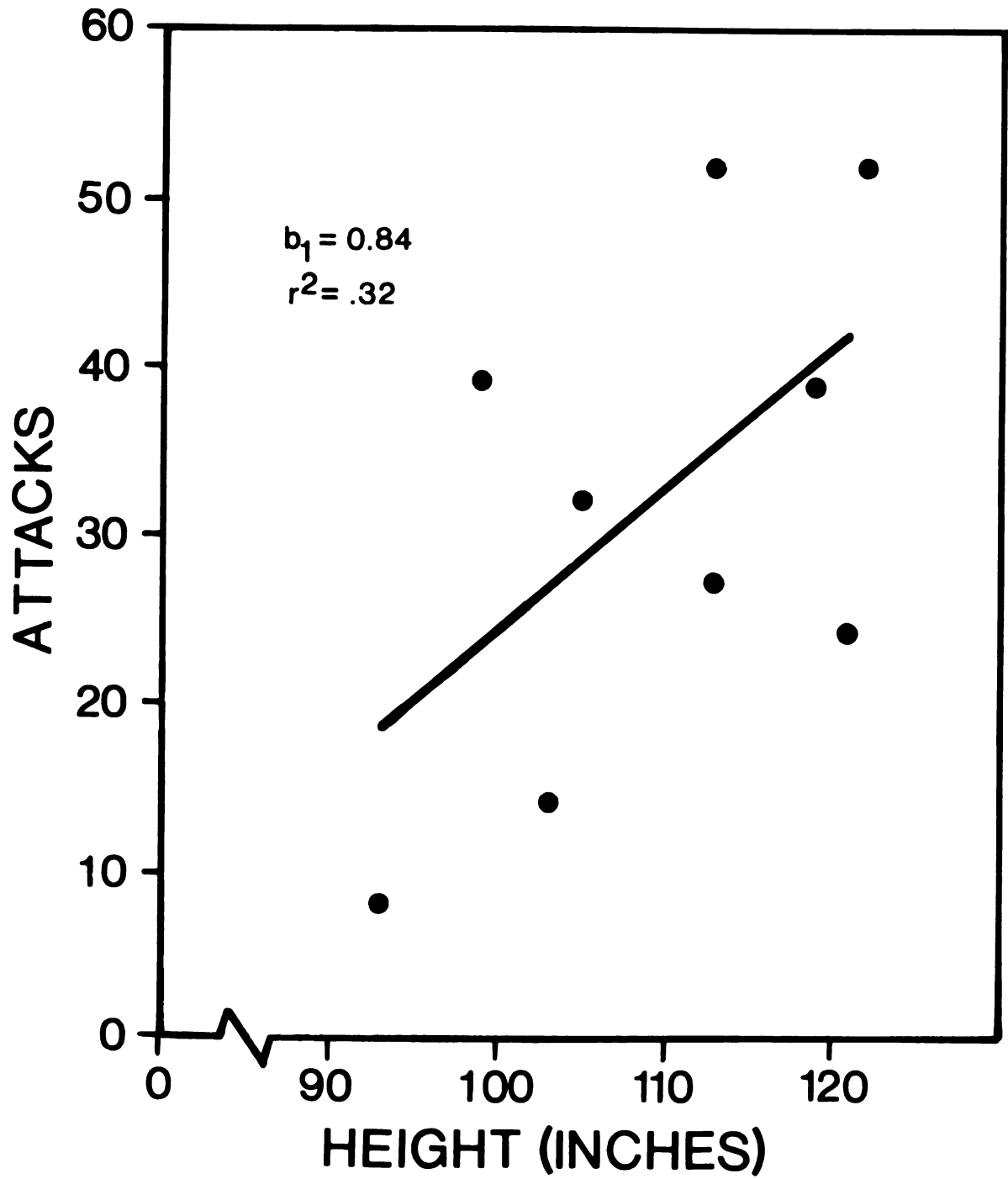


Figure 7.--Attacks of JPTB over jack pine height.

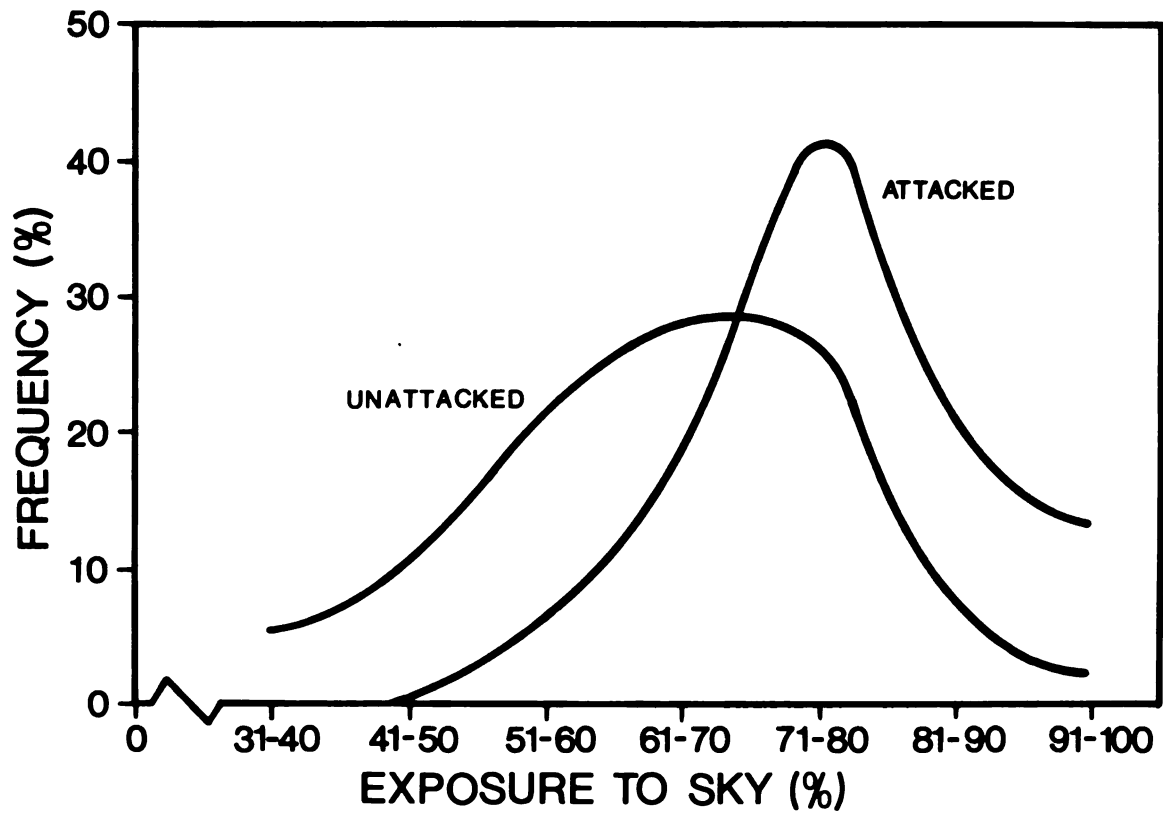


Figure 8.--Frequency distributions of attacked and unattacked tips in relation to per cent of exposure to sky.



the higher classes indicating that the most exposed tips are most likely to be attacked. A few tips in the classes below 61 per cent were attacked indicating that the adult is not limited to highly exposed tips. Also there were many unattacked tips in the classes above 70 per cent indicating that the adults were not driven to the shaded tips due to lack of exposed tips. On the last measurement date, more than half the unattacked tips were exposed to 61 per cent sky or more.

Figure 9 compares the diameter classes of attacked tips and the nearest unattacked tips. The two curves are very similar in shape. However, there were only 10 attacked tips with diameters less than 3.0 mm while there were over 100 available unattacked tips in this category. Of these 10, six were 2.9 mm in diameter. Also, there were very few tips in the two largest diameter classes left unattacked.

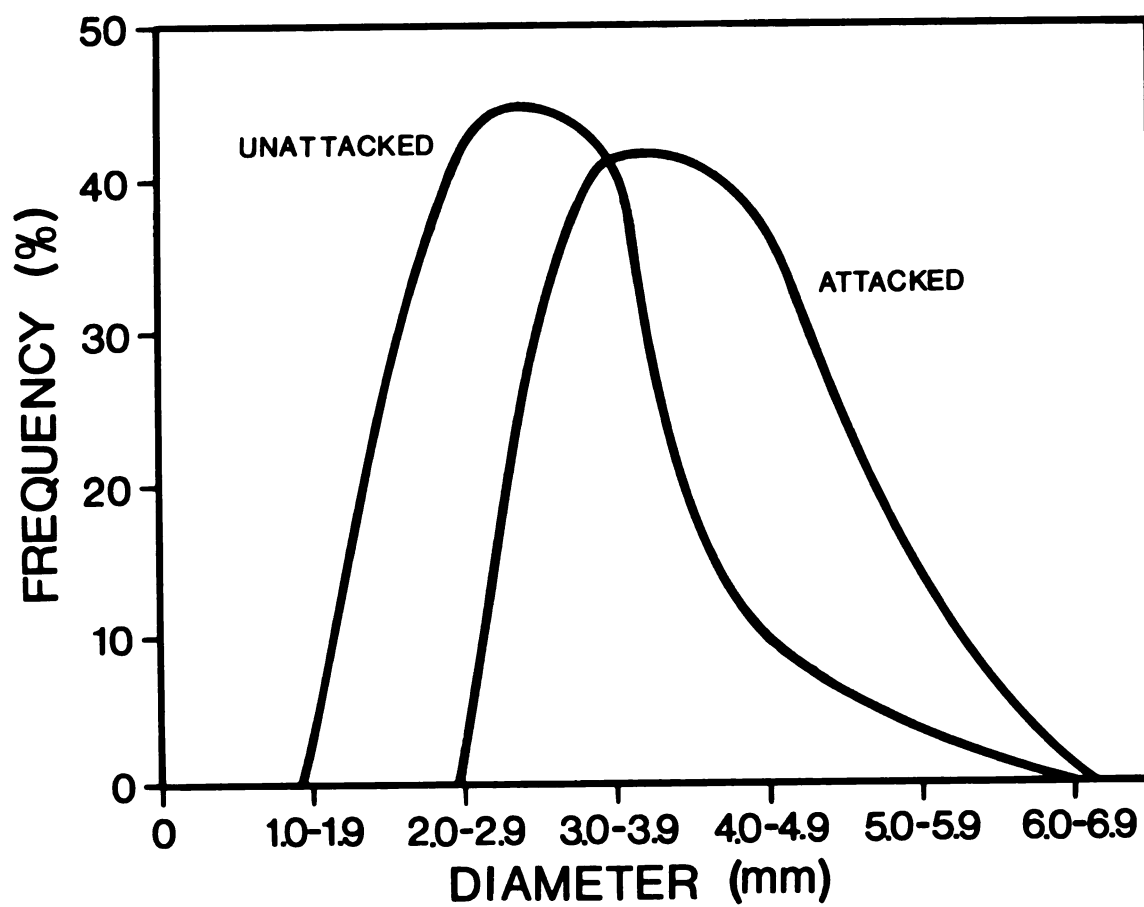


Figure 9.--Frequency distributions of diameters of attacked and unattached tips.

## DAMAGE

The damage caused by the JPTB occurs during the reproductive attack. Every terminal is attacked nearly every year at all but the lowest insect densities. Immediately below the attack, several buds form at the bases of needles. During the following year the shoots from these buds compete for dominance. Occasionally no one shoot expresses clear dominance and a fork results. The purpose of the damage study was to characterize the damage done by the JPTB to heavily attacked jack pine stands. This was done by determining the percentage of stems culled due to deformation by the insects.

## Methods

Since the major use for jack pine in Michigan is pulpwood, a method was used that would measure the loss of pulpwood. Young jack pines ranging from 10-19 feet tall were rated as pulp quality or cull in the lower eight feet of stem. Any crook severe enough to put the stem in the cull category was called "tip beetle cull" if it was caused by the tip beetle and "cull" if it was not.

The decision as to whether a cull stem was caused by the JPTB was not considered 100 per cent accurate. It was necessary to examine the results of recent attacks and follow the attacks down the stem in order to characterize the appearance of old attacks.

Figure 10 shows some typical results of attack by the JPTB. Figure 10A shows a terminal two years after attack. Figure 10B shows the most common result of attack--a slight crook not severe enough to cause a cull. Figures 10C and D illustrate the most commonly occurring cause of cull, namely forking. Occasionally, one of the branches of a fork will become suppressed, thereby removing the stem from the cull category.

Three of the four plantations used in the mortality study were used for damage observations. Sixty-five trees within each of the three plots were rated, yielding a total of 195 trees per plantation. The 50-year site index (S.I.) was calculated for each plantation.

### Results

Table 7 shows there were large between-plantation differences in both number of total culls and in number of tip beetle culls. The site index varied inversely to both total cull and tip beetle cull.

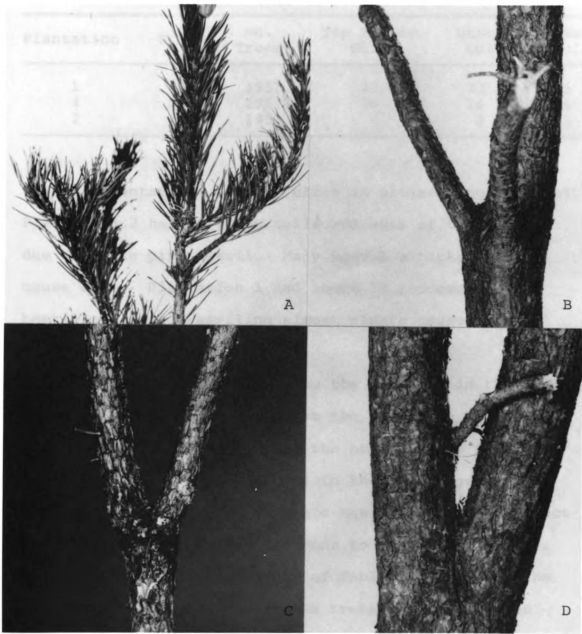


Figure 10.--JPTB damage to jack pine: A, typical appearance of terminal two years after attack; B, typical appearance of main stem 6 years after attack; C, probable cull caused by JPTB; D, cull caused by JPTB 15 years earlier.

TABLE 7.--The damage to young jack pines caused by the jack pine tip beetle.

Plantation	S.I.	No. Trees	Tip Beetle Cull	Other Cull	Total Cull
1	45	195	22	23	45
4	59	195	20	16	36
2	71	195	4	8	12

Plantations 1 and 2 offer an interesting contrast. Plantation 2 had very few culls and most of these were due to white pine weevil. Many weevil attacks did not cause cull. Plantation 1 had about 12 per cent tip beetle culls and weeviling almost always caused the tree to be culled.

Most of the cull due to the JPTB was in the form of a fork. The fork was due to the inability of any one bud to express dominance over the others. The fact that relatively more forks occurred in the slower growing trees indicates that growth rate has a significant effect upon the ability of terminal buds to express dominance.

The important feature of Table 7 is that on the poorest site 12 per cent of the trees were culled due to the tip beetle and on the best site 2 per cent were culled.

## DISCUSSION AND CONCLUSIONS

Parasitism, which was the most important mortality factor in this study, accounted for 15 to 40 per cent of the second instar mortality and up to 25 per cent of the pupal mortality. It was the only mortality factor observed which contributed strongly to total generation mortality and the only factor which appeared to affect it. The parasitoid, Cecidostiba dendroctoni, exerted the most influence on the within-generation mortality but did not exhibit density-dependence. This parasitoid has more than one generation per year and necessarily depends upon other scolytids besides the JPTB, and thus should not be expected to respond to densities of the JPTB alone. Density-dependence was not observed in the within-generation mortality for any other factor affecting the JPTB either, but that does not mean that the JPTB is free of density-dependent influences altogether. For instance, mortality from adult dispersal might increase as population density rises. Density-dependence probably was not observed because the insect densities studied were within a range so narrow that density-dependence was not discernible.

Other mortality factors contributed very little to total generation mortality in any stage of the insect, but contributed up to 45 per cent mortality within any one stage. In some instances the actual mortality factors were not determined. Desiccation, indicated by a shriveled appearance of the insect and a dried appearance within the tip, was noted in the egg and first instar stages. Some of the heavy undetermined mortality in these stages may also have been due to desiccation. The significance of desiccation is not certain. Perhaps the size of the shoot tips or stresses in the tree may contribute to water losses and premature wilting of the tissues.

Sometimes the larvae and pupae were engulfed in resin ("pitched") within the shoots. This was encountered most often after a period of rainy weather. Apparently the resin within the dead tip absorbs water and expands or increased turgor pressure enhances pitch flow. Whatever the cause, the insect is unable to cope with the excess resin.

Occasionally larvae and pupae were disfigured ("chewed") by some other inhabitant of the shoot. The majority of mortality in this category was probably accomplished by sibling cannibalism. The larvae particularly exhibit aggressive and antagonistic behavior to siblings. Dead insects were frequently encountered



when larval feeding galleries intersected. Callow adults may also have killed some of the lesser developed insects in the shoots as well. Adult bark beetles, Pityophthorus sp., and an unidentified larval lepidopteran may also have killed some larvae as they were present with disfigured larvae or pupae.

Mites, which were occasionally observed in the galleries, may have caused a small amount of mortality. Their size made them difficult to spot among the debris.

Precision was considered in sampling the JPTB and was sacrificed at low densities if sample size requirements were too difficult to adhere to. For the most part, standard errors of the sample means were above 10 per cent of the means. However, because the age-specific density estimates calculated from the sample means reflected density differences from field observations, the precision appeared to be adequate for the objective.

The within-tree distribution study has some interesting points with regard to sampling. Recall that the attacks are strongly aggregated in the top few inches of the tree early in the oviposition period and less strongly aggregated later. This would cause the standard error to be a high percentage of the mean early in the oviposition period because there would be a large number of zero sample units.

The distribution of the eggs would be similar to that of the reproductive attacks early in the attack period but it would be different later on. When the attacks are concentrated lower in the tree, the first laid eggs would then be in the larval stage. This would cause an actual "hole" in the aggregation of eggs. The same thing would occur in the aggregation of each of the stages of the insect at some time during the season. What this might mean to the standard error of the number of each insect stage is unknown.

The precision of the sample means could have been improved by restricting the sampling universe to the higher portions of the crown. This would be difficult to achieve with the sampling system used. One sample unit may include tips two feet apart on a vertical axis. A sample unit that was a wedge-shaped section of the crown would allow easy restriction to the upper portion of the crown. However, this restriction would ignore the mortality which takes place in the lower parts. It is not known if this mortality is an important part of the overall mortality.

The within-tree distribution of tip beetle attacks can be explained largely by adult preference for highly exposed shoots, regardless of the location on the tree. However, because most highly exposed shoots occur on the top of the crown, attacks there are more

prevalent. The adults further descriminate shoots by their size. Shoots smaller than 3 mm. in diameter at the normal attack site are rejected regardless of exposure. When growing side by side, taller trees are attacked more than shorter trees within the range of trees studied (93-122 inches). A tall tree, however, has more shoots and more exposed shoots, hence the heavier attack. Attack variation will occur, however, when short trees have more open crowns or tall trees have especially closed crowns.

In Northern Lower Michigan, jack pine has traditionally been planted upon poor growing sites such as eroded, abandoned farmland. Often it has been planted with the intent of stabilizing sand blows.

It is on these poor sites that the most severe insect-caused deformation occurs. Insects were not the cause of all the cull stems in the three plantations studied, but they accounted for considerably more than half of it. The JPTB caused roughly half the cull stems counted in the two plantations on the poorer sites and one-third of the cull stems on the best site. The white pine weevil caused most of the remaining cull on the best site which accounted for more than that by the JPTB. Cull from JPTB, however, accounted for only 12 per cent on the sites examined.

In conclusion, the JPTB is limited by several mortality factors of which parasitism is the most important. The adult beetle prefers to attack the tops of jack pine primarily due to exposure of the shoots and abundance of shoots of preferred size. Trees repeatedly attacked became crooked and forked, sometimes resulting as cull from a pulpwood standpoint.

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## LITERATURE CITED

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## APPENDICES



**APPENDIX A**

**TABLES**

# APPENDIX A

TABLE A-1.--Age-specific developmental rates--cage study.

<u>Days</u>	<u>Eggs</u>	<u>Eggs and L1</u>	<u>L1</u>	<u>L1 and L2</u>	<u>L2</u>	<u>L2 and Pup</u>	<u>Pup</u>	<u>Pup and C.ad</u>	<u>C.ad</u>
0									
1									
2									
3	2								
4	3								
5	3								
6	3								
7	3								
8	1	1	1						
9	1		1						
10			2						
11	2		1						
12			2						
13									
14				1	2				
15			1		1				
16									
17			1		1				
18			1		1				
19									
20					2				
21					2				
22					2				
23					1				
24						1			
25						1			
26					1				
27					1	1			
28							2		
29							1		
30						1			
31							2		
32									
33							1	1	
34							2		
35							1		1
36							1		
37							1		1
38							2		
39								1	2
40							1		
41									2
42									2
43									2
44									1
45									1

**APPENDIX B**

**TABLES**

# APPENDIX B

Table B1. Sampling data.

## PLANTATION 1 1970

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
28 June	$\bar{X}$	.095	.024	.095	—	—	—	—
	SE	.056	.024	.056	—	—	—	—
5 July	$\bar{X}$	.367	.250	.317	.067	—	—	—
	SE	.067	.071	.091	.039	—	—	—
11 July	$\bar{X}$	.700	.233	.617	.250	.050	—	—
	SE	.130	.085	.156	.092	.050	—	—
17 July	$\bar{X}$	.983	.100	.733	.350	.233	—	—
	SE	.195	.050	.190	.173	.137	—	—
23 July	$\bar{X}$	.833	.050	.233	.200	.767	.067	—
	SE	.216	.037	.095	.126	.283	.039	—
29 July	$\bar{X}$	1.050	.033	.233	.450	.350	.200	.017
	SE	.226	.023	.104	.130	.099	.106	.017
3 Aug.	$\bar{X}$	1.567	.016	.300	.217	.767	.383	.067
	SE	.325	.016	.097	.085	.188	.156	.031
9 Aug.	$\bar{X}$	1.400	.050	.117	.117	.550	.450	.367
	SE	.277	.028	.082	.074	.111	.127	.137
15 Aug.	$\bar{X}$	1.100	.050	.033	.050	.183	.233	.383
	SE	.159	.028	.033	.037	.051	.075	.078
20 Aug.	$\bar{X}$	1.433	—	.017	.087	.183	.050	.633
	SE	.317	—	.017	.048	.077	.028	.185
26 Aug.	$\bar{X}$	1.333	—	—	.017	.150	.250	.483
	SE	.205	—	—	.017	.068	.078	.130
1 Sept.	$\bar{X}$	1.533	—	—	—	.033	.033	.566
	SE	.238	—	—	—	.023	.023	.126
8 Sept.	$\bar{X}$	1.367	—	—	—	.050	.067	.267
	SE	.232	—	—	—	.028	.031	.066
17 Sept.	$\bar{X}$	1.283	—	—	—	—	—	.167
	SE	.241	—	—	—	—	—	.050

Table B2. Sampling data.

## PLANTATION 2 1970

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
26 June	$\bar{X}$	.071	.166	.024	—	—	—	—
	SE	.052	.216	.024	—	—	—	—
2 July	$\bar{X}$	.233	.100	.250	.133	—	—	—
	SE	.078	.050	.135	.053	—	—	—
8 July	$\bar{X}$	.233	.083	.233	.200	—	—	—
	SE	.057	.048	.075	.103	—	—	—
14 July	$\bar{X}$	.378	.044	.189	.178	.178	—	—
	SE	.084	.021	.070	.083	.071	—	—
20 July	$\bar{X}$	.589	.033	.322	.278	.355	—	—
	SE	.123	.019	.102	.090	.101	—	—
26 July	$\bar{X}$	.455	.011	.211	.044	.267	.078	—
	SE	.089	.011	.086	.035	.105	.039	—
1 Aug.	$\bar{X}$	.611	.011	.133	.122	.244	.200	.022
	SE	.106	.011	.056	.042	.070	.075	.015
7 Aug.	$\bar{X}$	.789	.022	.233	.100	.544	.289	.067
	SE	.123	.015	.085	.049	.163	.093	.025
13 Aug.	$\bar{X}$	.644	.022	.044	.033	.222	.211	.289
	SE	.122	.015	.026	.024	.068	.066	.094
19 Aug.	$\bar{X}$	.700	.011	—	.067	.100	.067	.355
	SE	.120	.011	—	.034	.037	.034	.119
25 Aug.	$\bar{X}$	.522	—	—	.011	.089	.078	.322
	SE	.078	—	—	.011	.033	.042	.081
31 Aug.	$\bar{X}$	.744	—	—	—	.022	.055	.233
	SE	.142	—	—	—	.015	.028	.060
7 Sept.	$\bar{X}$	.722	—	—	—	.033	.033	.233
	SE	.146	—	—	—	.041	.019	.079
16 Sept.	$\bar{X}$	.578	—	—	—	.011	—	.244
	SE	.101	—	—	—	.011	—	.054

Table B3. Sampling data.

## PLANTATION 3 1970

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
25 June	$\bar{X}$	.262	.452	.190	—	—	—	—
	SE	.074	.137	.073	—	—	—	—
30 June	$\bar{X}$	.283	.183	.233	.087	—	—	—
	SE	.092	.097	.092	.048	—	—	—
6 July	$\bar{X}$	.500	.266	.633	.100	—	—	—
	SE	.120	.104	.185	.044	—	—	—
12 July	$\bar{X}$	.783	.100	.400	.350	.100	—	—
	SE	.201	.044	.167	.090	.055	—	—
18 July	$\bar{X}$	.750	.050	.300	.333	.233	—	—
	SE	.169	.028	.097	.123	.098	—	—
24 July	$\bar{X}$	1.333	.116	.483	.400	.400	.133	—
	SE	.229	.057	.147	.103	.125	.053	—
30 July	$\bar{X}$	1.433	.050	.267	.467	.583	.633	.050
	SE	.229	.028	.088	.131	.115	.190	.037
4 Aug.	$\bar{X}$	.966	.016	.050	.033	.583	.317	.150
	SE	.162	.016	.037	.023	.152	.130	.049
10 Aug.	$\bar{X}$	1.500	—	.033	.117	.550	.617	.517
	SE	.273	—	.033	.057	.136	.172	.173
16 Aug.	$\bar{X}$	1.117	.016	—	.050	.283	.250	.650
	SE	.194	.016	—	.028	.092	.082	.303
21 Aug.	$\bar{X}$	1.150	—	—	—	.100	.133	.800
	SE	.214	—	—	—	.037	.058	.198
27 Aug.	$\bar{X}$	.983	—	—	—	.050	.117	.483
	SE	.223	—	—	—	.037	.046	.156
4 Sept.	$\bar{X}$	1.850	—	—	—	—	.017	.550
	SE	.260	—	—	—	—	.017	.120
9 Sept.	$\bar{X}$	1.700	—	—	—	—	.033	.350
	SE	.256	—	—	—	—	.033	.080

Table B4. Sampling data.

## PLANTATION 4 1970

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
30 June	$\bar{X}$	.367	.183	.133	.083	—	—	—
	SE	.101	.106	.071	.048	—	—	—
6 July	$\bar{X}$	.450	.233	.867	.133	—	—	—
	SE	.154	.078	.319	.093	—	—	—
12 July	$\bar{X}$	.900	.133	.900	.483	.217	—	—
	SE	.161	.041	.236	.152	.101	—	—
18 July	$\bar{X}$	.983	.133	.667	.333	.333	—	—
	SE	.186	.041	.136	.116	.108	—	—
24 July	$\bar{X}$	1.050	.083	.567	.267	.767	.150	—
	SE	.140	.042	.147	.082	.185	.072	—
30 July	$\bar{X}$	1.616	.016	.233	.133	.917	.400	.167
	SE	.232	.016	.092	.053	.227	.103	.077
4 Aug.	$\bar{X}$	1.183	.050	.200	.217	.450	.233	.233
	SE	.186	.037	.085	.082	.100	.075	.106
10 Aug.	$\bar{X}$	1.133	—	.017	.050	.300	.267	.350
	SE	.215	—	.017	.037	.074	.078	.107
16 Aug.	$\bar{X}$	1.383	—	—	.017	.333	.183	.800
	SE	.338	—	—	.017	.094	.077	.305
21 Aug.	$\bar{X}$	1.550	—	—	—	.067	.200	.867
	SE	.283	—	—	—	.031	.061	.204
27 Aug.	$\bar{X}$	1.150	—	—	—	.050	.033	.700
	SE	.222	—	—	—	.028	.023	.180
2 Sept.	$\bar{X}$	1.316	—	—	—	.017	.033	.467
	SE	.212	—	—	—	.017	.033	.117
9 Sept.	$\bar{X}$	1.767	—	—	—	—	.017	.300
	SE	.315	—	—	—	—	.017	.066

Table B5. Sampling data.

## PLANTATION 1 1971

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
1 July	$\bar{X}$	.100	.167	.100	—	—	—	—
	SE	.056	.067	.073	—	—	—	—
7 July	$\bar{X}$	.400	.067	.900	.033	—	—	—
	SE	.163	.046	.422	.033	—	—	—
13 July	$\bar{X}$	.533	.033	.433	.833	—	—	—
	SE	.177	.033	.157	.307	—	—	—
20 July	$\bar{X}$	.433	—	.100	.333	.133	—	—
	SE	.124	—	.056	.154	.079	—	—
23 July	$\bar{X}$	.733	.100	—	.200	.500	.067	—
	SE	.214	.073	—	.139	.178	.046	—
29 July	$\bar{X}$	.400	—	.033	.033	.367	—	—
	SE	.148	—	.033	.033	.162	—	—
4 Aug.	$\bar{X}$	.433	—	.133	.233	.300	—	—
	SE	.133	—	.079	.124	.160	—	—
11 Aug.	$\bar{X}$	1.067	—	.067	.233	.100	.200	.100
	SE	.258	—	.046	.103	.056	.100	.056
17 Aug.	$\bar{X}$	1.200	—	—	.167	.233	.100	.133
	SE	.289	—	—	.096	.103	.056	.079
26 Aug.	$\bar{X}$	.600	—	—	—	.133	—	.133
	SE	.177	—	—	—	.062	—	.079
3 Sept.	$\bar{X}$	.900	—	—	—	.067	—	.100
	SE	.297	—	—	—	.066	—	.056
10 Sept.	$\bar{X}$	.767	—	—	—	.033	—	.100
	SE	.228	—	—	—	.033	—	.056



Table B5. Sampling data.

## PLANTATION 1 1971

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
1 July	$\bar{X}$	.100	.167	.100	—	—	—	—
	SE	.056	.067	.073	—	—	—	—
7 July	$\bar{X}$	.400	.067	.900	.033	—	—	—
	SE	.163	.046	.422	.033	—	—	—
13 July	$\bar{X}$	.533	.033	.433	.833	—	—	—
	SE	.177	.033	.157	.307	—	—	—
20 July	$\bar{X}$	.433	—	.100	.333	.133	—	—
	SE	.124	—	.056	.154	.079	—	—
23 July	$\bar{X}$	.733	.100	—	.200	.500	.067	—
	SE	.214	.073	—	.139	.178	.046	—
29 July	$\bar{X}$	.400	—	.033	.033	.367	—	—
	SE	.148	—	.033	.033	.162	—	—
4 Aug.	$\bar{X}$	.433	—	.133	.233	.300	—	—
	SE	.133	—	.079	.124	.160	—	—
11 Aug.	$\bar{X}$	1.067	—	.067	.233	.100	.200	.100
	SE	.258	—	.046	.103	.056	.100	.056
17 Aug.	$\bar{X}$	1.200	—	—	.167	.233	.100	.133
	SE	.289	—	—	.096	.103	.056	.079
26 Aug.	$\bar{X}$	.600	—	—	—	.133	—	.133
	SE	.177	—	—	—	.062	—	.079
3 Sept.	$\bar{X}$	.900	—	—	—	.067	—	.100
	SE	.297	—	—	—	.066	—	.056
10 Sept.	$\bar{X}$	.767	—	—	—	.033	—	.100
	SE	.228	—	—	—	.033	—	.056

Table B6. Sampling data.

## PLANTATION 2 1971

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
29 June	$\bar{X}$	.089	.067	.044	—	—	—	—
	SE	.043	.038	.031	—	—	—	—
5 July	$\bar{X}$	.489	.200	.578	.133	—	—	—
	SE	.170	.113	.207	.068	—	—	—
11 July	$\bar{X}$	.355	.067	.555	.178	.044	—	—
	SE	.124	.049	.306	.091	.044	—	—
18 July	$\bar{X}$	.422	.089	.178	.089	.267	—	—
	SE	.137	.043	.086	.053	.136	—	—
23 July	$\bar{X}$	.467	.222	.178	.222	.133	—	—
	SE	.133	.222	.091	.105	.068	—	—
29 July	$\bar{X}$	.711	.111	.422	.155	.333	.111	—
	SE	.158	.065	.183	.084	.135	.111	—
4 Aug.	$\bar{X}$	.822	.133	.267	.267	.800	.111	.022
	SE	.220	.068	.147	.163	.362	.073	.022
10 Aug.	$\bar{X}$	.622	.022	—	.044	.133	.089	.111
	SE	.132	.022	—	.044	.060	.070	.057
17 Aug.	$\bar{X}$	1.067	—	—	.033	.100	.066	.233
	SE	.253	—	—	.033	.056	.045	.124
26 Aug.	$\bar{X}$	.700	—	—	—	.166	—	.333
	SE	.186	—	—	—	.096	—	.161
3 Sept.	$\bar{X}$	.800	—	—	—	.033	.100	.066
	SE	.200	—	—	—	.033	.056	.045
10 Sept.	$\bar{X}$	.800	—	—	—	—	—	.233
	SE	.194	—	—	—	—	—	.092

Table B7. Sampling data.

## PLANTATION 3 1971

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
30 June	$\bar{X}$	.367	.267	.467	—	—	—	—
	SE	.131	.126	.298	—	—	—	—
6 July	$\bar{X}$	.567	.233	.800	.033	—	—	—
	SE	.190	.171	.305	.033	—	—	—
12 July	$\bar{X}$	.500	.133	.267	.300	.067	—	—
	SE	.178	.079	.151	.153	.067	—	—
19 July	$\bar{X}$	.600	.033	.266	.533	.133	—	—
	SE	.170	.033	.126	.233	.079	—	—
24 July	$\bar{X}$	.767	—	.433	.333	.433	—	—
	SE	.190	—	.207	.168	.141	—	—
30 July	$\bar{X}$	.767	.033	.100	.167	.533	.100	—
	SE	.184	.033	.056	.118	.177	.056	—
5 Aug.	$\bar{X}$	.967	.033	.167	.267	.433	.300	—
	SE	.301	.033	.167	.158	.157	.145	—
11 Aug.	$\bar{X}$	.933	—	.100	.100	.167	.200	.300
	SE	.239	—	.100	.100	.069	.100	.128
18 Aug.	$\bar{X}$	.933	—	—	.033	.100	.133	.300
	SE	.209	—	—	.033	.056	.063	.137
27 Aug.	$\bar{X}$	1.300	—	—	.067	.300	.100	.267
	SE	.288	—	—	.046	.109	.073	.143
4 Sept.	$\bar{X}$	1.100	—	—	—	.133	.133	.133
	SE	.326	—	—	—	.079	.079	.079
11 Sept.	$\bar{X}$	1.367	—	—	—	—	.033	.300
	SE	.286	—	—	—	—	.033	.098

Table B8. Sampling data.

## PLANTATION 4 1971

Date	Stat.	Reprod. attack	Adult	Egg	Larva I	Larva II	Pupae	Callow adult
30 June	$\bar{X}$	.067	.267	.100	—	—	—	—
	SE	.046	.106	.073	—	—	—	—
6 July	$\bar{X}$	.433	.300	.500	.033	—	—	—
	SE	.124	.119	.196	.033	—	—	—
12 July	$\bar{X}$	.433	.067	.567	.133	.100	—	—
	SE	.141	.046	.248	.079	.073	—	—
20 July	$\bar{X}$	.967	.133	.400	.633	.267	—	—
	SE	.301	.079	.212	.330	.106	—	—
24 July	$\bar{X}$	1.167	.066	.367	.333	1.000	.033	—
	SE	.368	.046	.162	.146	.386	.033	—
30 July	$\bar{X}$	1.067	.067	.133	.433	.367	.033	.067
	SE	.365	.067	.079	.228	.140	.033	.067
5 Aug.	$\bar{X}$	1.100	—	.033	.300	.367	.167	.267
	SE	.301	—	.033	.137	.140	.118	.203
11 Aug.	$\bar{X}$	1.233	—	.033	.333	.400	.200	.166
	SE	.248	—	.033	.111	.132	.074	.084
18 Aug.	$\bar{X}$	1.567	.033	.067	.267	.200	.100	.233
	SE	.334	.033	.067	.143	.100	.056	.124
27 Aug.	$\bar{X}$	.733	—	—	—	.067	.200	.200
	SE	.234	—	—	—	.067	.121	.121
4 Sept.	$\bar{X}$	1.233	—	—	—	.067	.100	.100
	SE	.354	—	—	—	.067	.056	.056
11 Sept.	$\bar{X}$	1.033	—	—	—	—	.067	.100
	SE	.237	—	—	—	—	.046	.056

1

10

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