

PRELIMINARY STUDIES ON THE ESTIMATION
OF LARVAL POPULATIONS
OF THE LARCH SAWFLY, PRISTIPHORA ERICHSONII (HTG.)

by

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A B S T R A C T

The seasonal development of eggs and larvae of the larch sawfly are shown for 1957 and 1958. The general trends were similar for both years although the position of a minor peak differed between the two years.

A comparison of cumulative adjusted oviposition curves with numbers of egg scars suggests that rate of development in the insectary was comparable to that under field conditions.

The percentages of mortality estimated from cumulative adjusted population figures were: egg to first instar - 27.0 per cent; first to second instar - 1.3 per cent; second to fourth instar - 32.0 per cent; fourth to fifth instar - 37.0 per cent. These estimates compared favourably to figures derived from alternative methods of estimating mortality.

The magnitude and nature of the variation in insect numbers is discussed briefly.

1. INTRODUCTION

Sampling techniques have been developed for estimating larch sawfly populations at various stages in the insect's life cycle, but not for estimating feeding larval populations. Most of the mortality during the insect's life cycle occurs in the interval between the oviposition of eggs and the completion of larval feeding (Graham, 1956; Ives, 1954; Turnock, 1956). An attempt is therefore being made to develop a sampling method for estimating mortality during this period.

The most obvious approach to the problem of evaluating mortality is to tag a series of shoots containing eggs of the larch sawfly, then make periodic examinations and record the numbers and stages of larvae present. In practice, however, this is impractical. It is virtually impossible to obtain accurate counts of the early-instar larvae on the foliage, since they are gregarious feeders. Furthermore, colonies of larvae tend to split up and wander, especially during the fifth instar, so that a decrease in numbers may be due to wandering of some individuals. Confinement of the larvae by tanglefoot bands or other means might prevent insect predators from reaching them. The first of these difficulties could be circumvented by tagging a large number of shoots and estimating the number of insects present by sampling a number of the tagged shoots at each examination. However, this would not overcome the problem of larval wandering.

Assessment of mortality by observing tagged colonies was abandoned in favor of periodic sampling of whole branches. A number of difficulties are encountered in this approach also, as will be seen in this preliminary report covering work done in 1957 and 1958. The abundance of the various stages in the field at any given point in time is **relatively** easy to determine, since no particular mechanical difficulties were encountered. However, such figures do not give a true picture of the total number in each stage throughout the season. Eggs and fifth-instar larvae remain in their respective stages for a considerable period of time. Samples taken every four days will, in effect, sample a portion of these populations at least twice. The

other four larval instars may or may not last less than four days, depending upon temperature, so that some of these may not have been sampled at all. For example, larvae in the first instar at one sampling period may be in the third instar when the next sample is taken four days later. These larvae will have formed part of the second-instar population for the period under consideration but will not be included in estimates based on field collections only. For this reason it was considered necessary to conduct a rearing program in conjunction with the sampling program, to provide estimates of the number of insects missed or sampled twice. In the present study it has been assumed that the rate of development under insectary conditions is the same as under field conditions, although the validity of this assumption will have to be tested.

Several approaches are available for estimating mortality. These are: (1) cumulative population totals; (2) hatch records; (3) association of larval colonies with shoots containing oviposition scars; and (4) comparison of field collections with insectary rearings of previous collections. None of these methods is completely satisfactory, as will be noted in the following discussion.

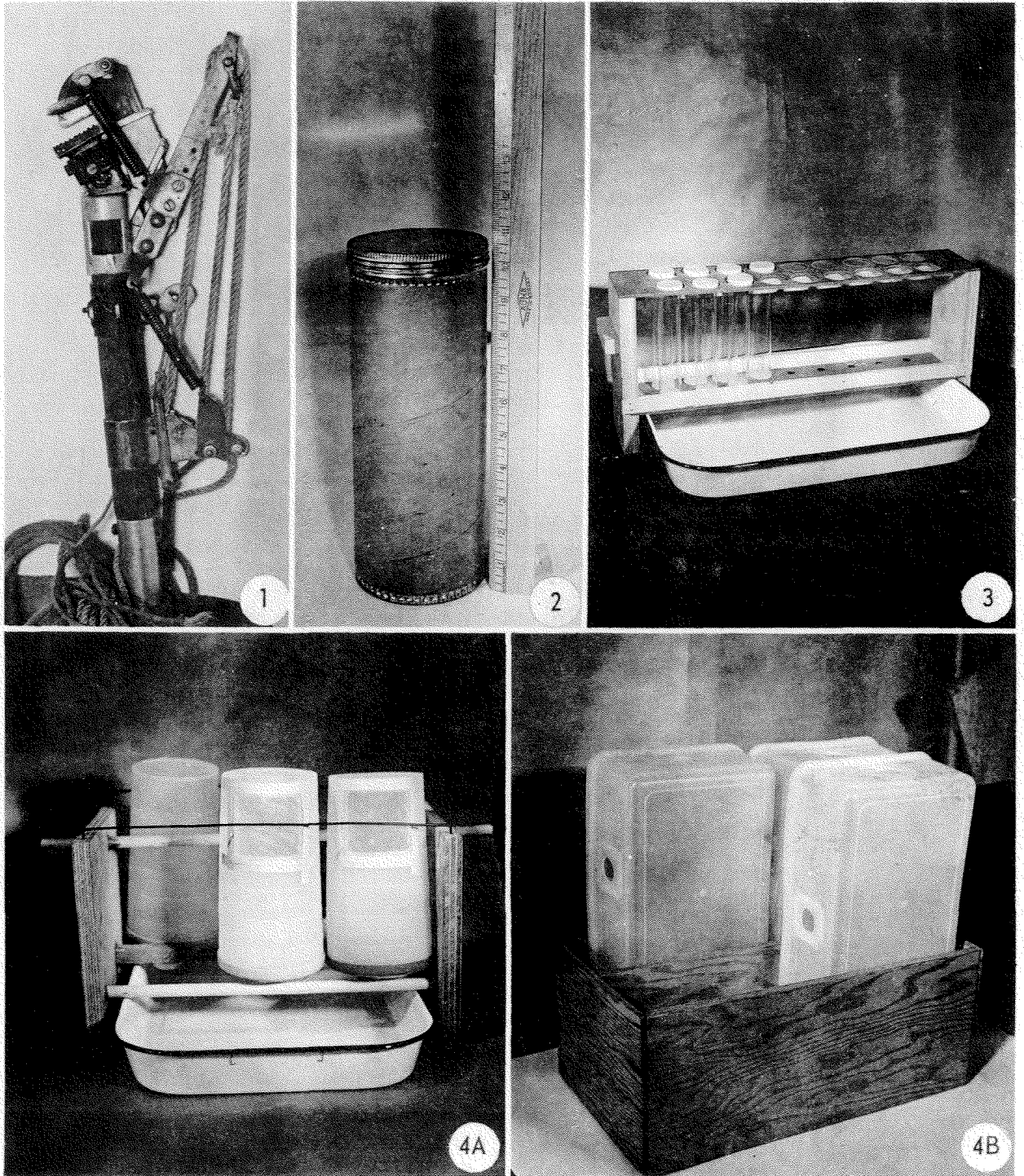
2. METHODS

The basic method used in randomizing the selection of branches was the same as in egg sampling (Ives, 1955). The 1957 sample consisted of two whole branches selected at random from below 30 feet on each of five trees. The branches were removed with pole pruners fitted with a clamp held by a locking device permitting the branches to be lowered gently (Fig. 1). Samples were taken every four days from a different random group of five trees. Sampling commenced June 10 and ended August 9. Only large branches were sampled and completely defoliated branches were rejected. A large net was periodically attached to the pole pruners to determine if larvae were being lost. Total shoots, scarred shoots, foliated length

and foliated width were recorded for each branch. Separate containers were used for packaging shoots containing eggs, shoots with egg scars not associated with larvae and larvae not associated with shoots. Each colony of larvae that was associated with a shoot was placed in a container with the respective shoot.

Upon return to the laboratory the shoots containing eggs were placed in water in small vials which in turn were placed in 4-inch shell vials stoppered with a cotton plug. The shoots were examined in four days and the number of larvae for each shoot recorded. Eggs that had not hatched in this period of time were reared until hatching occurred or until mortality could be assumed. After hatching was complete, the scars in each shoot were counted and recorded. All larvae were killed and counted by instar upon return to the laboratory, and records kept of the numbers of scars in associated shoots. Larvae or scarred shoots that could not be associated with one another were recorded separately, as were shoots containing scars but showing little or no evidence of larval feeding.

Several aspects of this procedure were modified in 1958. The sample size was increased to 20 branches, one from each of 20 trees. To facilitate sampling, the trees were sampled serially throughout the plot. Samples were again taken every four days, commencing June 11 and ending August 22. After the first sample, half of the sample was overlapped with the previous sample, i.e. the first sample consisted of branches from trees 1 to 20, the second of branches from trees 11 to 30, and so on. The branches in the overlapping half were sampled from the same height as the branches previously sampled but from opposite sides of the crown. The branches in the other half of the sample were selected at random from the crowns of the trees and determined the position of the branches in the overlapping half of the succeeding sample. Completely defoliated branches were retained in the sample. Field data were recorded as before, and field techniques were the same except that large screw top cardboard cans (Fig. 2) were used for transferring larvae from the field to the insectary.



Figs. 1 - 4 1. Pole pruner head modified for larval sampling. 2. Screw top cardboard container for transporting larvae from the field to the insectary. 3. Rearing cages used for determining percentage hatch. 4. Plastic larval rearing cages: (a) small cages used for rearing early instar larvae; and (b) large cages used for rearing large colonies and fifth instar larvae. (Cut end of branches in plastic cages immersed in water-filled jars suspended from wooden box).

Accompanying laboratory techniques were modified considerably. Special rearing containers (Fig. 3) were made for determining percentage of hatch, because conditions in the shell vials created high humidity which was unfavorable for larval development and the dead unfed larvae were difficult to count. All larvae were reared in the insectary in plastic containers (Fig. 4) until the next sampling period. Mixed groups were counted as accurately as possible before rearing, but homogeneous groups were counted only when the larvae were killed four days later. This procedure least disturbed the larvae and also gave maximum accuracy. Fifth-instar larvae were reared in cages containing a small amount of moist sphagnum moss. This provided a method for determining if larvae had finished feeding, since any found crawling in the moss were assumed to be ready to spin cocoons.

Adjusted population estimates, based on field collections and insectary rearings, were calculated for each sample from the formula

$$P_{ki} = \sum_{j=1}^n X_{kij} - \sum_{j=1}^n Y_{kij} + \sum_{j=1}^n Z_{kij}$$

subject to the condition that $P_{ki} \geq 0$ where P_{ki} is the adjusted population for the k^{th} stage of the insect ($k=1, 2, \dots, 6$) at the i^{th} sampling period; n is the number of branches in each sample;

X_{kij} is the observed number of insects in the k^{th} stage on the j^{th} branch of the i^{th} sample;

Y_{kij} is the number of insects from the j^{th} branch of the $(i-1)^{\text{th}}$ sample remaining in the k^{th} stage during the period between collection of the $(i-1)^{\text{th}}$ and i^{th} samples; and

Z_{kij} is the number of insects from the j^{th} branch of the $(i-1)^{\text{th}}$ sample passing from the $(k-1)^{\text{th}}$ to the $(k+1)^{\text{th}}$ stage during the period between collection of the $(i-1)^{\text{th}}$ samples.

The formula therefore estimates the number of insects that have entered or passed

through any given stage in the 4-day period prior to the collection of any sample. It makes no provision for differential mortality between laboratory and field conditions during the period under consideration. The conditions of non-negativity was imposed to make allowance for sampling variation or differential mortality that could result in negative answers.

3. RESULTS

The work in 1957 was largely confined to developing techniques, mainly removal of branches from the trees without losing too many larvae. Rearing techniques were not satisfactory and with the exception of egg hatch records will not be discussed.

The results to date are considered indicative only, and the current presentation will be largely confined to graphs and tabulations, with a minimum of statistical analysis.

3.1 Seasonal Development

The observed seasonal distribution of eggs and larvae for 1957 and 1958 and the adjusted distributions where estimates of these are available are shown in Appendix Tables 1 and 2. Negative answers are shown in parenthesis. The same distributions are shown in Figs. 5 and 6.

The frequency histograms for number of eggs provide a good illustration of how misleading field collections can be in indicating peak increments to insect populations. The field collections indicate peak oviposition for the four-day period prior to June 30, 1957 and July 9, 1958, a difference of nine days. Adjustment to allow for unhatched eggs shows that the peaks were probably June 26 and July 1, respectively. Nearly half of the time difference in apparent oviposition peaks was therefore due to slower development of the eggs in 1958.

The 1958 histograms for second-, third- and fourth-instar larvae illustrate

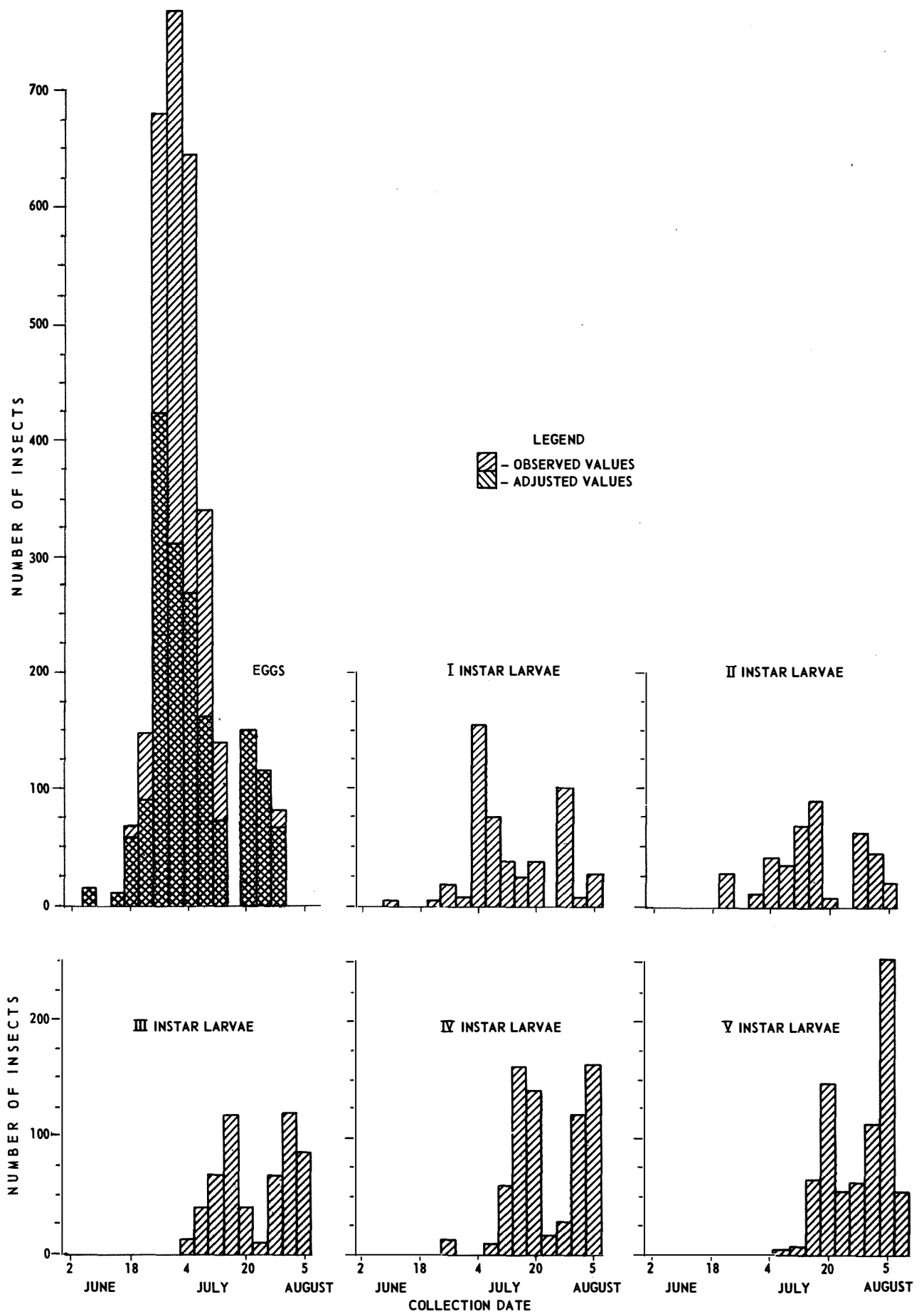


Fig. 5. Seasonal distribution of eggs and larvae in 1957 (number per 10-branch sample).

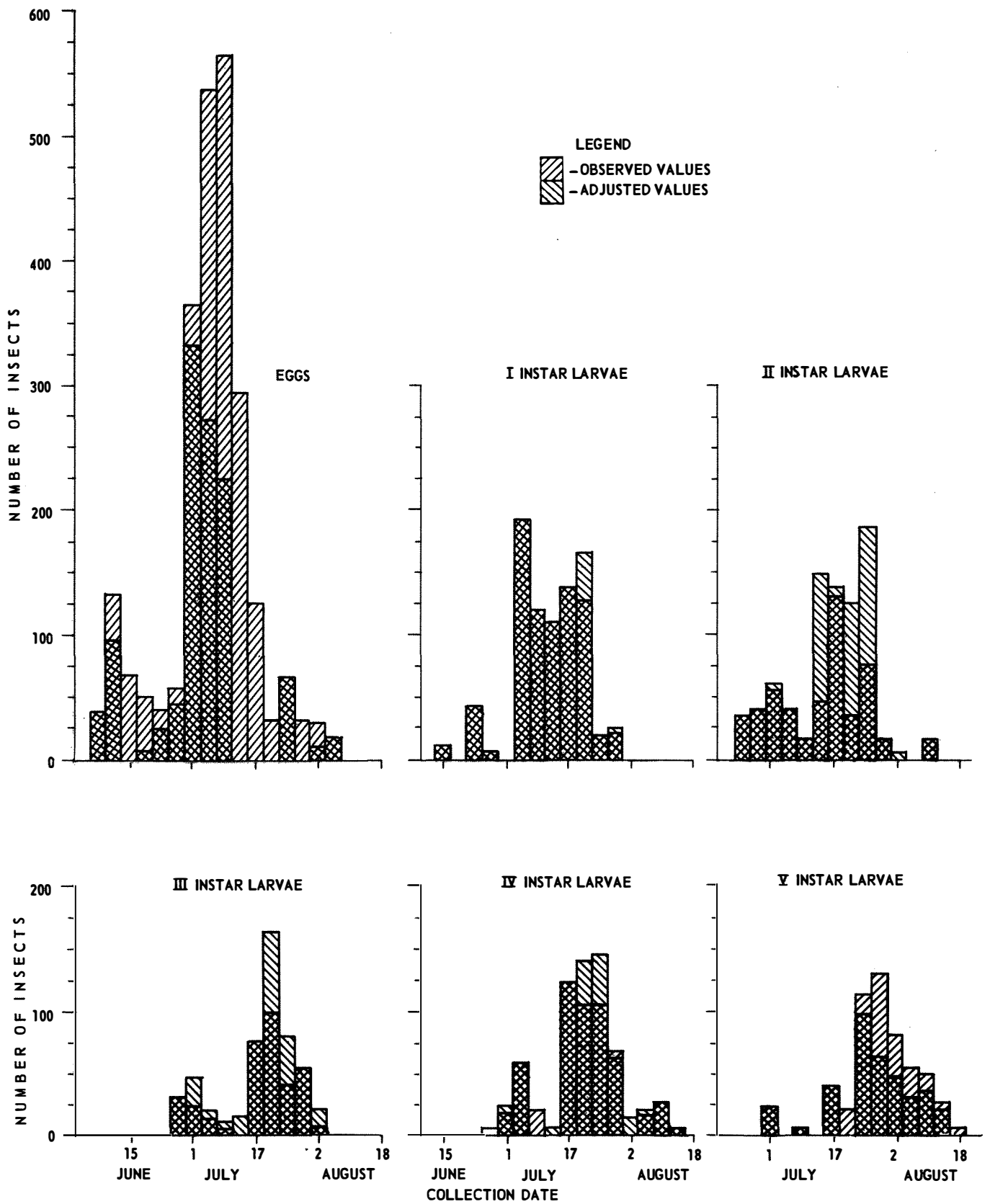


Fig. 6. Seasonal distribution of eggs and larvae in 1958 (number per 20-branch sample).

that a considerable number of larvae in these instars are missed entirely even when sampling is conducted every four days. The histograms for first-instar larvae should probably show a higher proportion of adjustment, but a flaw in technique may have prevented this.¹ The histogram for fifth-instar larvae demonstrates that sampling every four days in effect samples a portion of the larvae in this stage twice.

Except for the slight differences in peak oviposition periods, the general trends for development are similar for 1957 and 1958. In 1957 there was a main peak in oviposition, followed by a secondary peak about three weeks later. This bimodality persisted throughout the larval instars, but because no adjusted population estimates are available it is difficult to determine the relative magnitudes of these peaks. In 1958 the main oviposition period occurred at about the same time as in 1957, but was preceded by a minor peak. The latter persisted through all larval instars. Although the samples are very variable at the present stage of development it appears that they are capable of giving a reasonably accurate picture of development periods for the different immature stages.

3.2 Cumulative oviposition curves

The total oviposition occurring prior to any point in time can be estimated by counting the total egg scars on the branches sampled. Comparison of these values with the cumulative totals of the adjusted oviposition estimates

1

During periods where the work load was heavy on sampling days some of the hatch counts were made after less than four days of rearing. Some of these larvae would undoubtedly have entered the second instar had the rearing been continued for the full four days. This defect will be corrected in future work.

provides a check for gross errors in the latter. The results of this comparison are shown in Figs. 7 and 8 for 1957 and 1958 respectively. The same comparisons are shown in Appendix Table 3. The high variation between samples in the number of eggs makes an accurate check impossible, but the cumulative totals of adjusted values appear slightly higher than they should. Examination of egg clusters from the previous sample was delayed until after the next sample had been completed. When larvae and eggs were abundant this resulted in an extension of several hours beyond the four day period. This extension would probably be sufficient, especially on a hot day, to allow enough additional hatching to account for the discrepancies noted. Examination of egg clusters while field samples are being taken should eliminate this bias. Since the difference noted was small the foregoing explanation is probably correct, but similar effects would occur if the rate of development was more rapid in the insectary than in the field.

3.3 Estimation of mortality

3.3.1 Cumulative population totals

The adjusted values for eggs and larvae, as shown in Fig. 6, were simply added to give the cumulative totals shown in Fig. 9.

An inconsistency due to sampling variation is apparent in the population estimates because there were more/^{fourth-}than third-instar larvae. It has been assumed that there was no mortality between the third and fourth instars, and the pooled values have been used as the estimate of the number in the fourth instar. On this basis the apparent mortality, in percentages, based on the cumulative number of insects per 20 branches was as follows: egg to first instar - 27.0; first to second instar - 1.3; second to fourth instar - 32.9; fourth to fifth instar - 37.0. The corresponding percentages for real mortality were: 27.0, 1.0, 23.7 and 17.9. It therefore appears that the main periods where mortality occurred were:

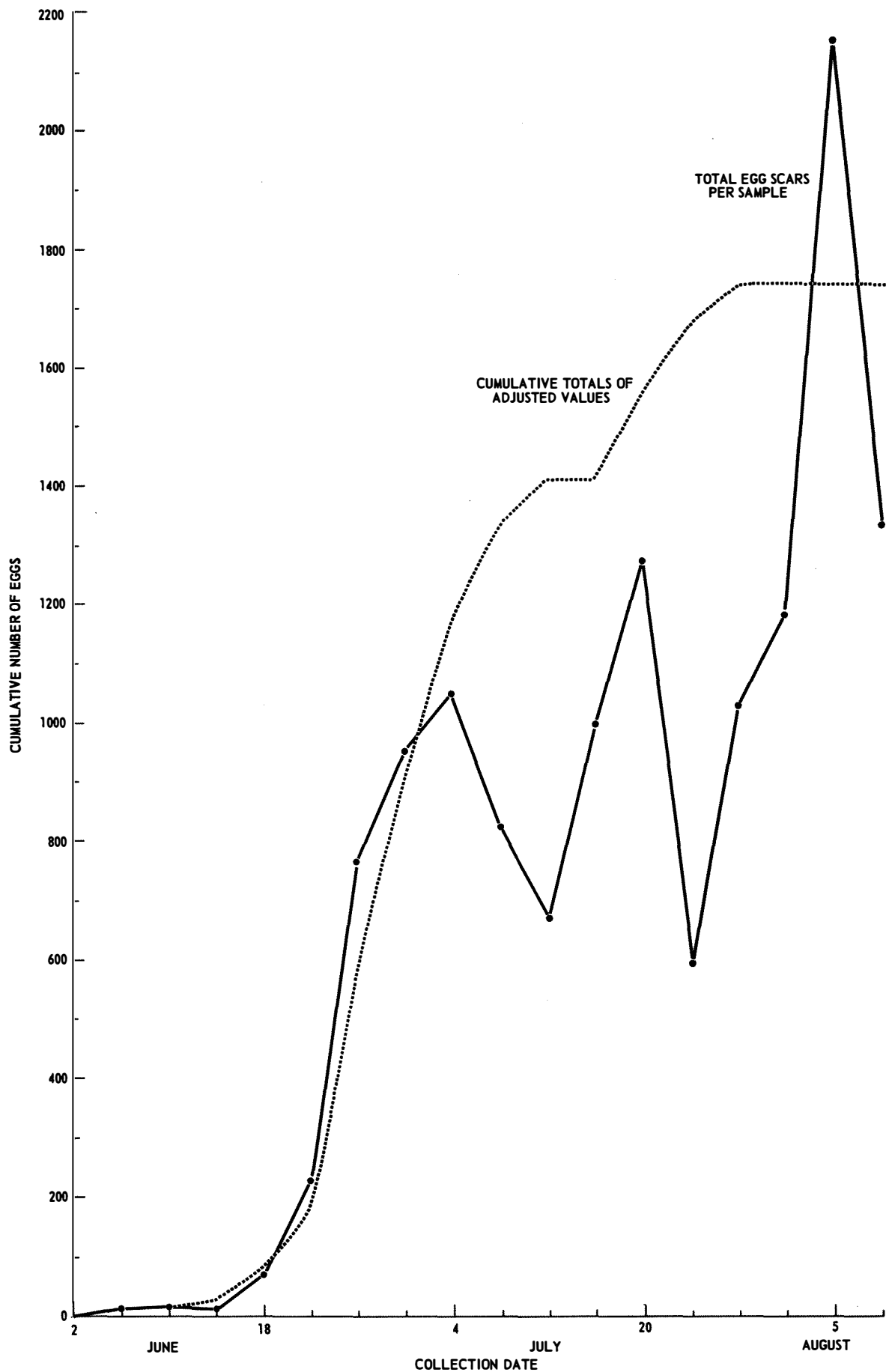


Fig. 7. Comparison of cumulative totals of adjusted egg populations with numbers of egg scars per sample (1957 data).

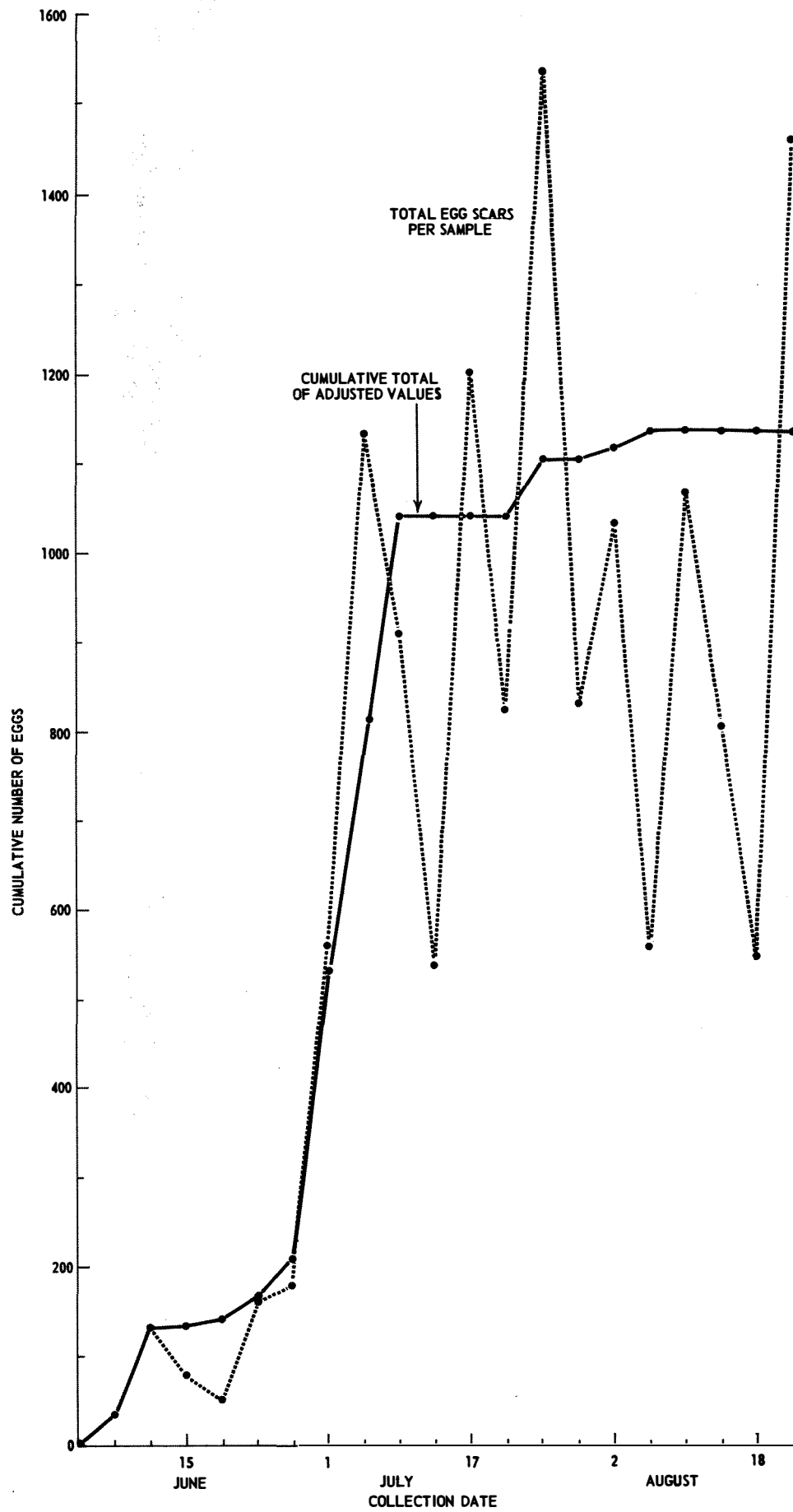


Fig. 8. Comparison of cumulative totals of adjusted egg populations with numbers of egg scars per sample (1958 data).

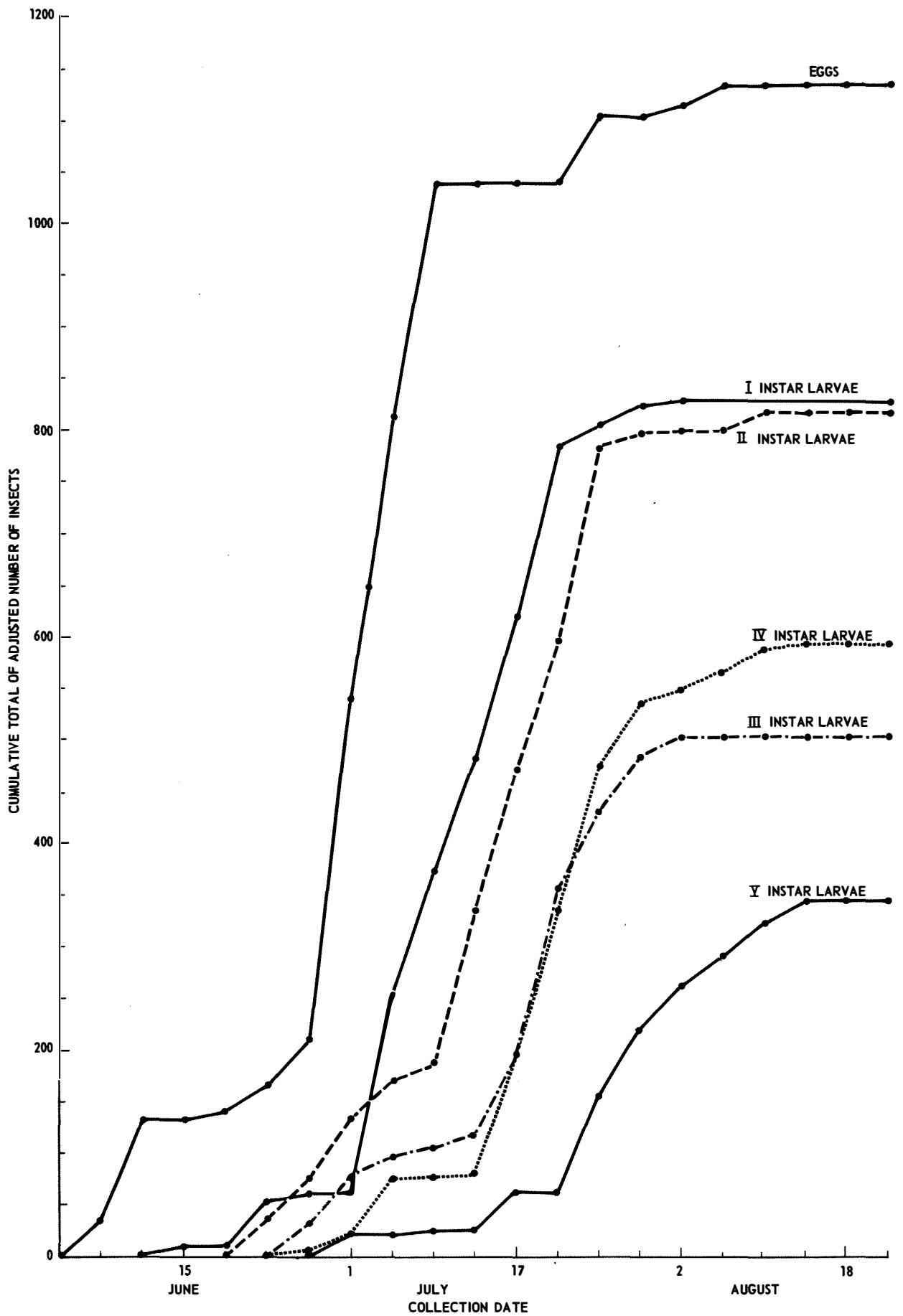


Fig. 9. Cumulative totals of adjusted population estimates for eggs and larvae (1958 data).

(1) between the egg stage and the middle of the first instar; (2) between the middle of the second and middle of the third instars; and (3) between the middle of the fourth and middle of the fifth instars. It should be emphasized, however, that these conclusions are based on data which is very variable and may therefore be erroneous.

3.3.2 Hatch records

Shoots containing eggs were reared to obtain records of hatching. To determine if insect predators were attacking the eggs, the records were divided into two groups based on the time interval between collection and hatching, those that had hatched or were hatching in four days and those that took longer (Appendix Tables 4 and 5). The percentages of hatching in the two groups were 78.9 and 93.4 in 1957 and 77.7 and 83.2 in 1958. These differences probably can be attributed to insect predation, as rearing conditions were identical. The differences do not represent the total insect predation, for some of the first group would normally have been exposed to predation for up to four days longer, and some of the second group had also been exposed to predation for a number of days before collection. Furthermore, if all of the eggs in a shoot had been destroyed it would not be included, as it was impossible to determine when the eggs had been laid. The differences probably represent approximately half of the total predation since the 4-day period is about half of the incubation period.

Early in the season it was usually possible to determine if there had been any feeding on or near a scarred shoot. If there was little or none the eggs or newly hatched larvae may have been destroyed by insect predators. A complete tally of all oviposition scars was therefore made, covering the period when it was possible to associate most of the scarred shoots with colonies of larvae (Appendix Table 6). Assuming that predators had destroyed all the eggs in the column headed

"apparently predatorized", the percentages of losses are not large, amounting to 8.9 and 4.5 for 1957 and 1958, respectively. However, if they are added to the differences between the hatch figures for the two groups the amount of mortality that may be due to insect predators is 23.4 per cent in 1957 and 10.0 per cent in 1958. The percentage of mortality in the "not hatched in four days" group was 16.8 in 1958. Some of this mortality is probably due to insect predators, the remainder to infertility, failure of larvae to escape from egg slits and other causes. Adding the 1958 figures of 10.0 and 16.8 gives a figure (26.8) that is in very close agreement with the mortality figure (27.0) for the interval between the egg and first instar larva, as calculated from the cumulative number of insects.

3.3.3. Associated larvae and egg scars

The estimates of mortality based on association between larvae and egg scars have one major weakness. If all of the larvae in a colony are destroyed no estimate is available. The chances of this happening should increase with time and one would expect a greater under-estimation for later instars than for earlier instars. Another weakness is that no association is usually possible for fifth-instar larvae because of larval wandering. Nonetheless, the method does serve as a check on other mortality estimates by providing a lower bound. The number of scars and numbers of associated larvae for the first four instars for 1957 and 1958 are shown in Appendix Tables 7 and 8. The percentages "pseudo-real" mortality for 1958 are 38.6, 30.0, 43.9 and 50.3 for instars I, II, III and IV respectively. (The mortality has been called "pseudo-real" because it approaches the definition of real mortality but errs by an unknown amount because the eggs from colonies in which all larvae have been destroyed are not included.) There is another anomaly here which also occurred in 1957: the mortality to the second instar is less than that to the first instar. This anomaly may be due to sampling variation. If so,

the best estimate of the mortality to the first instar is the pooled data for the first and second instars. Comparison of this pooled result for 1958 (35.8) with the cumulative insect estimate (27.0) indicates a disagreement of 8.8 per cent. However, if there is a mechanical source of error² in the estimates of mortality to the first instar, and in fact the true mortality to the second instar is in the neighbourhood of 30 per cent, the appropriate comparison is 27.0 plus 1.0 or 28.0 per cent and the two estimates are in reasonably close agreement.

Assuming 30.0 per cent to represent the mortality to the second instar, association between shoots and larvae gives an estimate of 13.9 per cent mortality between the second and third instars and a further 6.4 per cent between the third and fourth instars in 1958. The total "pseudo-real" mortality to the fourth instar, 50.3 per cent, is in close agreement with the real mortality estimated from the cumulative adjusted population figures, 51.6 per cent. It therefore appears that fewer colonies were completely destroyed than had been anticipated, although this agreement could be due to fortuitous circumstances.

3.3.4 Collections versus insectary rearings

Estimation of mortality by comparing the number of insects in each instar reared from the previous collection, with the number collected from the field has a number of disadvantages. The mortality is not estimated for any fixed number of instars, but for the interval between the collection of the two samples. The estimate is also subject to bias if the rate of insectary development differs from that in the field. Sampling variation also may greatly affect the estimates, as shown in Appendix Table 9, where fewer second- and fourth-instar larvae occurred in

²

Such an error is quite possible. Larvae were not counted (in 1958) until the conclusion of rearing. If dead first-instar larvae were mistaken for cast skins, or missed, the results would over-estimate mortality to the first instar.

the reared population than in the field population.

However, no check on the mortality between the fourth and fifth instars is available from other sources. Both this estimate and the one to be checked are based on insectary rearings, but the approach is different. The apparent mortality for the 4-day period prior to collection for the fifth-instar larvae is estimated as 36 per cent. This period approximately covers the late fourth and early fifth instars. The estimate therefore compares favorably with that of 37 per cent apparent mortality between the mid-fourth and mid-fifth instars as estimated from the cumulative adjusted population figures.

3.4 Sampling variation

Sampling variation has not been discussed in the previous section because the sample sizes were small and confidence intervals would be too wide to be of any value. However, examination of the variability will prove helpful in planning future work.

The 1957 data provides some information on the relative magnitudes of inter- and intra-tree variability, although inclusion of small and defoliated branches would undoubtedly have increased these variations (Appendix Table 10). The intra-tree variation, with some exceptions, is as large as the inter-tree variation for all stages sampled. Stratification of the sample by crown level and crown class has been shown to reduce the intra-tree variation in number of scarred shoots (Ives, 1955). Such stratification should also prove useful in larval sampling, but all crown levels probably could not be sampled from each of the trees since the number of trees would then be too small. Each stratum could be constructed to include two branches from one crown level of a group of trees having a similar crown class. In this way all crown levels and crown classes could be represented in each sample, although no estimate of inter-crown level or inter-crown class variability

would be available. However, the error mean square should be reduced appreciably.

The 1958 data provides information on the variances and covariances for samples taken from the same trees at 4-day intervals (Appendix Table 11). With a few exceptions, the larval stages are apparently too transient to be able to demonstrate any appreciable continuity between successive samples, even when these samples consist of paired branches. The eggs and total scars show that some continuity is achieved by overlapping the samples, but the results are inconsistent. Mechanical difficulties would likely be encountered if two branches from a crown level were overlapped with a preceding sample of two branches (i.e. it would be difficult to ensure that removing the first two branches would not injure or dislodge larvae on branches to be included in the second sample). It therefore appears that the gain in continuity does not justify overlapping the samples. Independent samples would also simplify the estimation of variances, since no covariances would be involved between successive samples.

A further aspect of variation that is of concern in estimating larval populations is the amount of variation at different population levels. The available data are rather inadequate to determine the relationship between variability and population density, since only two years' collections are available and the populations were not high. However, examination of the data shows clearly that the variation increases as the population increases for all stages sampled in this project (Fig. 10).

The relationship between mean and standard deviation appears to be linear, although the egg data for 1958 suggests the possibility of a curvilinear relation. The accuracy of estimates at different population levels is roughly proportionate to the mean for the range in densities encountered. If this relationship holds over a wider range it will simplify the estimation of larval populations, since a fixed sample size can be used with equal efficiency throughout the season.

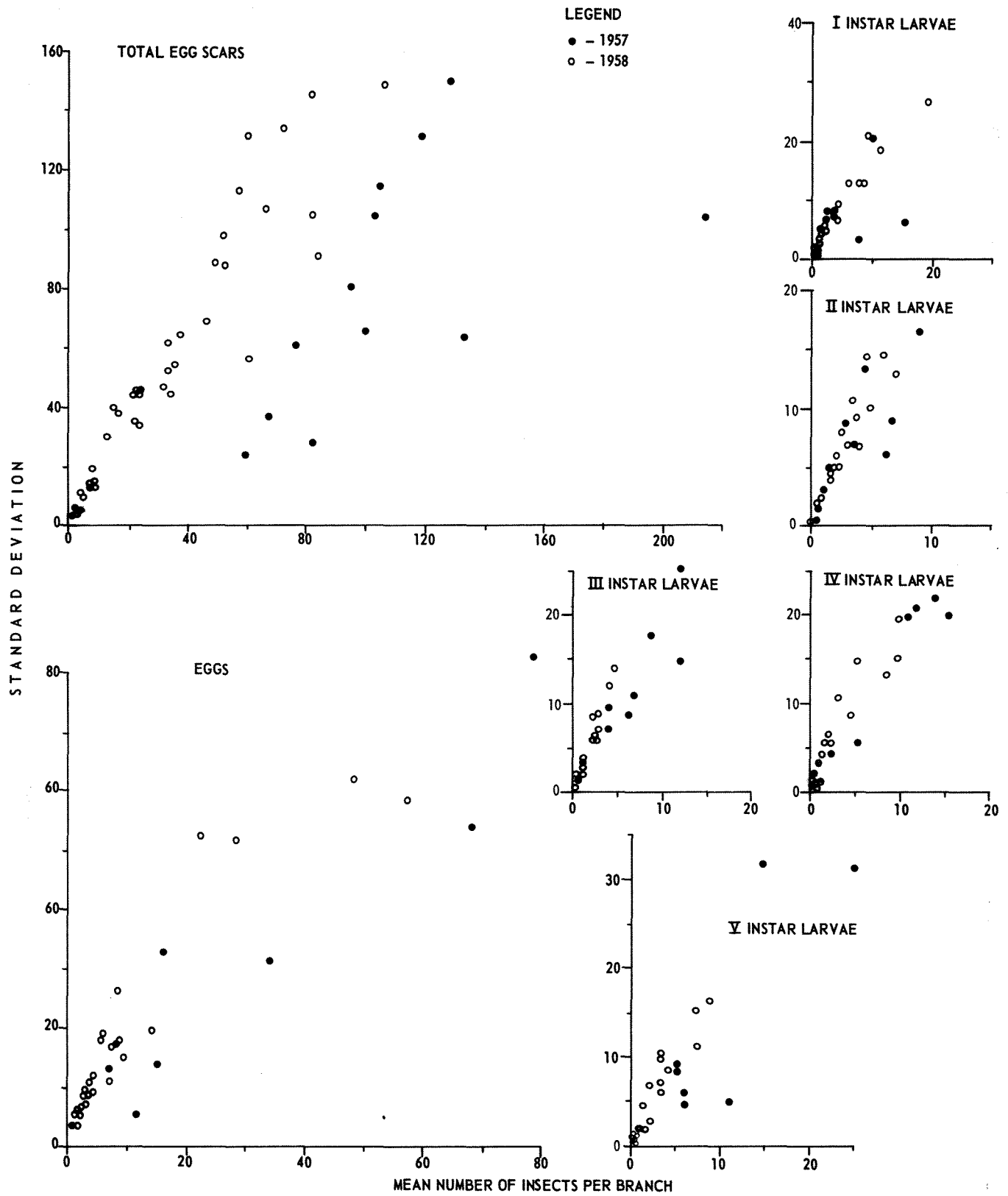


Fig. 10. Relationship between means and standard deviations in 1957 and 1958.

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5. APPENDIX

Table 1

Seasonal Distribution of Eggs and Larvae in 1957
(number per 10-branch sample)

Date	Eggs		I Instar	II Instar	III Instar	IV Instar	V Instar
	Observed	Adjusted					
June 2*	0	0	0	0	0	0	0
6	15	15	0	0	0	0	0
10	0	0	2	0	0	0	0
14	11	11	0	0	0	0	0
18	68	57	0	0	0	0	0
22	158	90	3	28	0	0	0
26	681	423	16	0	0	11	0
30	783	311	6	10	0	0	0
July 4	646	267	154	41	12	0	0
8	339	161	74	34	39	6	1
12	139	73	36	68	67	55	4
16	0	0	22	89	118	158	62
20	149	149	35	6	40	138	146
24	114	114	0	0	8	12	52
28	81	66	100	62	64	24	61
Aug. 1	0	0	6	45	121	117	110
5	0	0	26	16	86	159	252
9	0	0	0	0	0	1	52

Table 2

Seasonal Distribution of Eggs and Larvae in 1958 (number per 20-branch sample).
Negative answers for adjusted values are shown in parenthesis.

Date	Eggs		I Instar		II Instar		III Instar		IV Instar		V Instar	
	Observed	Adjusted	Observed	Adjusted	Observed	Adjusted	Observed	Adjusted	Observed	Adjusted	Observed	Adjusted
June 3*	0	0	0	0	0	0	0	0	0	0	0	0
7*	37	37	0	0	0	0	0	0	0	0	0	0
11	133	96	0	0	0	0	0	0	0	0	0	0
15	67	0(-40)	11	11	0	0	0	0	0	0	0	0
19	51	7	0	0	0	0	0	0	0	0	0	0
23	41	25	42	42	34	34	0	0	0	0	0	0
27	57	44	6	6	39	39	30	30	3	3	0	0
July 1	365	332	0	0	55	59	23	45	14	19	21	21
5	537	273	193	193	41	40	13	20	54	53	0	0(-21)
9	565	226	120	120	15	14	5	10	18	0(-7)	3	3
13	294	0	111	111	45	147	0	13	0	3	0	0(-3)
17	126	0(-63)	138	138	130	138	75	75	119	119	38	38
21	30	0(-39)	127	165	36	126	98	162	103	137	18	0(-12)
25	66	66	18	18	75	185	39	77	103	143	109	94
29	29	0(-7)	20	22	16	16	53	53	64	61	127	63
Aug. 2	28	11	0	3	0	4	6	20	1	13	78	44
6	18	18	0	0	0	0	0	0	15	17	52	29
10	0	0	0	0	16	16	0	0	23	23	47	33
14	0	0	0	0	0	0	0	0	3	2	24	21
18	0	0	0	0	0	0	0	0	0	0	4	0(-9)
22	0	0	0	0	0	0	0	0	0	0	0	0(-1)

*Interpolated from June 11 sample.

Table 3

Comparison of Cumulative Totals of Adjusted Egg Populations with
Numbers of Egg Scars per Sample

1957			1958		
Date	Cumulative Adjusted egg population	Number of egg scars per sample	Date	Cumulative Adjusted egg population	Number of egg scars per sample
June 2	0	0	June 3	0	0
6	15	15	7	37	37
10	15	15	11	133	133
14	26	11	15	133	79
18	83	68	19	140	51
22	173	227	23	165	162
26	596	763	27	209	182
30	907	952	July 1	541	560
July 4	1174	1052	5	814	1132
8	1335	823	9	1040	908
12	1408	671	13	1040	537
16	1408	997	17	1040	1203
20	1557	1276	21	1040	823
24	1671	592	25	1106	1538
28	1737	1027	29	1106	830
Aug. 1	1737	1180	Aug. 2	1117	1033
5	1737	2140	6	1135	558
9	1737	1330	10	1135	1064
			14	1135	807
			18	1135	546
			22	1135	1459

Table 4

1957 Hatch Records

Eggs hatched (or hatching) in 4 days

Eggs not hatched in 4 days

Date col- lected	No. egg scars	No. larvae	Date col- lected	No. egg scars	No. larvae	Date col- lected	No. egg scars	No. larvae	Date col- lected	No. egg scars	No. larvae
26/VI	27	21	4/VII	29	22	14/VI	11	9	26/VI	17	17
	27	21	(Cont'd)	21	21	18/VI	25	24	(Cont'd)	36	34
	38	26		26	26		28	24	30/VI	21	19
	18	13		31	24		15	15		20	19
	7	6		31	24	22/VI	25	25		30	29
	14	10		42	39		23	23		17	17
	33	19		16	16		20	19		23	22
	30	26		22	22		26	25		25	25
30/VI	22	11		12	10		40	39		23	23
	19	17	8/VII	18	6	26/VI	20	19		16	16
	24	24		35	21		30	30		22	21
	26	26		23	7		32	31		18	16
	28	27		19	17		14	13		21	21
	21	12		16	6		15	15		25	19
	36	34		12	6		19	19		34	33
	30	22		8	3		22	21		22	21
	15	14		32	30		28	24		22	22
	17	17		51	25		11	11		20	19
	26	20		32	21		29	27	4/VII	25	25
	17	17		27	25		45	44		15	13
	19	13		46	37		13	13		12	11
	16	16	12/VII	28	19		21	18		12	1
	27	26		46	46		16	14		6	6
	20	16		29	23		34	33		24	22
	22	18		21	19		40	35		21	16
	19	18		15	6		15	12	8/VII	20	18
	20	19	20/VII	47	44		30	29	24/VII	15	13
4/VII	20	18		15	14						
	31	21		20	16				Total	1209	1129
	12	11		24	22						
	29	25		15	3						
	20	17		28	17						
	13	3	24/VII	14	11						
	11	8		27	27						
	17	5		15	9						
	22	10		16	6						
	16	16		11	11						
	25	23		16	14						
	24	22	28/VII	12	12						
	24	24		19	13						
	22	18		6	4						
	15	13		44	41						
			Total	1936	1528						

Table 5

1958 Hatch Records

Eggs hatched (or hatching) in 4 days

Eggs not hatched in 4 days

Eggs hatched (or hatching) in 4 days			Eggs not hatched in 4 days								
Date col- lected	No. egg scars	No. larvae	Date col- lected	No. egg scars	No. larvae	Date col- lected	No. egg scars	No. larvae	Date col- lected	No. egg scars	No. larvae
11/VI	7	7	9/VII	44	42	11/VI	24	24	5/VII	34	32
	19	17	(Cont'd)	9	8		25	22	(Cont'd)	42	3
15/VI	15	13		35	24		19	19		37	35
	8	7		15	15		5	4		14	12
19/VI	17	16		22	17		6	6		10	10
	18	18		7	7		28	25	9/VII	10	5
23/VI	28	24		12	11	15/VI	20	16		22	19
27/VI	24	20		21	19		15	8		31	17
1/VII	32	30		17	14		9	7		17	13
	19	3		13	12	19/VI	16	16		40	40
	33	28		11	11	23/VI	13	12		34	31
	22	22		14	5	27/VI	33	33		16	14
	32	22		26	13	1/VII	21	17	13/VII	20	20
5/VII	10	7	13/VII	10	6		12	11		32	30
	21	16		12	6		46	43		36	3
	27	6		28	16		28	26		34	29
	19	17	17/VII	38	26		29	29		40	35
	10	10		14	12		25	25		30	28
	31	28	21/VII	30	28		28	28		36	30
9/VII	7	4	25/VII	22	22		17	9		16	12
	27	18		9	8		10	10	17/VII	31	24
	15	8	29/VII	12	4		11	9		38	33
	47	43	2 VIII	6	5	5/VII	40	36		5	5
	44	32		16	4		31	30	25/VII	8	7
	16	8		6	6		23	19		27	24
							27	17	29/VII	17	17
							42	36			
			Total	997	775				Total	1280	1065

Table 6

Complete egg scar tally for portion of sampling period
(Association becomes impractical after last dates given).

Collection date	Associated with eggs	Associated with larvae	No association*	Apparently predatorized	Totals
1957					
June 10	0	9	0	6	15
14	0	11	0	0	11
18	68	0	0	0	68
22	134	75	0	18	227
26	681	45	0	37	763
30	783	45	0	124	952
July 4	646	374	0	32	1052
8	339	378	0	106	823
12	139	465	0	62	666
16	0	675	210	112	997
Totals	2790	2077	210	497	5574
Percentages	50.0	37.3	3.8	8.9	100.0
1958					
June 11	133	0	0	0	133
15	67	12	0	0	79
19	51	0	0	0	51
23	41	121	0	0	162
27	57	117	0	8	182
July 1	365	180	0	15	560
5	476	638	0	18	1132
9	565	252	21	70	908
13	294	223	0	20	537
17	126	757	227	93	1203
Totals	2175	2300	248	224	4947
Percentages	44.0	46.5	5.0	4.5	100.0

* The larvae from most of these egg scars had apparently completed feeding, or had been destroyed in later instars.

Table 7 (Cont'd)

Date	I Instar		II Instar		III Instar		IV Instar	
	Scars	Larvae	Scars	Larvae	Scars	Larvae	Scars	Larvae
July 24	-	-	-	-	5	5	10	6
28	6	2	12	11	21	21	19	12
	14	13	16	8	16	14	19	7
	24	17	20	10	27	10	-	-
	30	28	8	4	23	19	-	-
	26	21	17	12	-	-	-	-
	9	4	17	16	-	-	-	-
	30	11	5	5	5	-	-	-
Aug. 1	4	2	30	16	16	8	16	12
	10	4	15	11	23	13	18	12
	-	-	25	10	8	8	27	20
	-	-	-	-	20	16	32	16
	-	-	-	-	14	11	-	-
	-	-	-	-	4	2	-	-
5	31	26	21	19	27	6	15	13
Totals	<u>971</u>	<u>523</u>	<u>643</u>	<u>384</u>	<u>620</u>	<u>360</u>	<u>822</u>	<u>423</u>

Table 8

Numbers of egg scars and associated larvae for 1958

Date	I Instar		II Instar		III Instar		IV Instar	
	Scars	Larvae	Scars	Larvae	Scars	Larvae	Scars	Larvae
June 15	12	11	-	-	-	-	-	-
23	28	15	13	6	-	-	-	-
	9	7	22	19	-	-	-	-
	36	20	13	9	-	-	-	-
27	6	6	26	19	40	26	14	11
	-	-	14	10	-	-	17	6
July 1	-	-	20	14	29	24	-	-
	-	-	27	13	-	-	-	-
	-	-	33	20	-	-	-	-
5	16	5	20	17	13	7	59	14
	19	16	21	2	11	1	20	14
	22	1	15	12	-	-	17	11
	19	19	23	10	-	-	19	13
	108	68	-	-	-	-	11	6
	45	18	-	-	-	-	-	-
	23	7	-	-	-	-	-	-
	26	13	-	-	-	-	-	-
	35	20	-	-	-	-	-	-
	42	14	-	-	-	-	-	-
	25	7	-	-	-	-	-	-
	29	5	-	-	-	-	-	-

Table 8 (Cont'd)

Date	I Instar		II Instar		III Instar		IV Instar	
	Scars	Larvae	Scars	Larvae	Scars	Larvae	Scars	Larvae
July 9	10	7	34	15	15	5	35	18
	10	7	-	-	-	-	-	-
	11	7	-	-	-	-	-	-
	38	29	-	-	-	-	-	-
	44	31	-	-	-	-	-	-
	10	10	-	-	-	-	-	-
	30	21	-	-	-	-	-	-
	15	8	-	-	-	-	-	-
13	29	21	59	45	-	-	-	-
	41	38	-	-	-	-	-	-
	30	10	-	-	-	-	-	-
	35	28	-	-	-	-	-	-
	29	14	-	-	-	-	-	-
17	13	11	29	27	61	45	98	36
	22	20	21	16	31	27	33	28
	30	19	13	13	-	-	33	13
	25	14	52	41	-	-	25	18
	15	9	-	-	-	-	-	-
	28	27	-	-	-	-	-	-
	15	14	-	-	-	-	-	-
	12	10	-	-	-	-	-	-
21	23	15	29	17	23	15	24	19
	9	2	15	15	35	18	70	40
	13	4	-	-	24	3	10	10
	11	7	-	-	26	22	5	2
	32	28	-	-	21	10	-	-
	24	5	-	-	-	-	-	-
	29	19	-	-	-	-	-	-
	13	5	-	-	-	-	-	-
	47	35	-	-	-	-	-	-
	19	12	-	-	-	-	-	-
	18	13	-	-	-	-	-	-
25	19	14	27	25	29	27	30	5
	-	-	37	25	20	4	31	5
	-	-	36	26	16	17	-	-
29	15	5	18	16	21	1	32	16
	17	15	-	-	19	8	20	9
	-	-	-	-	34	14	15	14
	-	-	-	-	28	18	-	-
	-	-	-	-	19	7	-	-
Aug. 6	-	-	23	16	-	-	25	11
10	-	-	-	-	-	-	41	21
Totals	<u>1281</u>	<u>786</u>	<u>640</u>	<u>448</u>	<u>515</u>	<u>289</u>	<u>684</u>	<u>340</u>

Table 9

Numbers of larvae in field collections and in insectary rearings of previous collections

Date	I Instar		II Instar		III Instar		IV Instar		V Instar	
	Reared	Collected	Reared	Collected	Reared	Collected	Reared	Collected	Reared	Collected
June 15	24	11	0	0	0	0	0	0	0	0
19	13	0	18	0	0	0	0	0	0	0
23	34	42	0	34	0	0	0	0	0	0
27	24	6	42	39	34	30	0	3	0	0
July 1	20	0	2	55	21	23	47	14	8	21
5	68	125	1	71	40	13	31	54	34	0
9	178	120	73	15	35	5	53	18	18	3
13	245	105	6	45	104	0	15	0	24	0
17	37	138	92	93	50	76	0	116	0	38
21	0	122	66	36	168	111	108	99	178	18
25	49	18	15	75	120	39	94	108	153	109
29	36	20	12	16	75	53	42	57	153	104
Aug. 2	1	0	19	0	6	6	52	1	110	78
6	10	0	15	0	0	0	5	15	24	53
10	0	0	0	16	0	0	0	23	39	47
14	0	0	0	0	15	0	1	3	25	24
18	0	0	0	0	0	0	0	0	16	4
22	0	0	0	0	0	0	0	0	1	0
Totals	739	707	361	495	668	356	448	511	783	499

Table 10

Inter- and intra-tree mean squares
(1957 data)

Date	Eggs	I Instar	II Instar	III Instar	IV Instar	V Instar	Total Scores
June 10*	0	0	<1	0	0	0	22
	0	0	<1	0	0	0	22
14	12	0	0	0	0	0	12
	12	0	0	0	0	0	12
18	89	0	0	0	0	0	89
	163	0	0	0	0	0	163
22	752	1	78	0	0	0	1324
	1101	1	78	0	0	0	2090
26	4256	26	0	0	12	0	5945
	2914	26	0	0	12	0	3672
30	10393	2	10	0	0	0	11591
	6827	3	10	0	0	0	6585
July 4	6804	710	74	12	0	0	16023
	7354	42	93	12	0	0	13261
8	885	69	40	75	4	< 1	1254
	992	12	50	90	4	< 1	830
12	795	50	254	357	240	2	23143
	392	66	83	126	35	2	1354
16	0	43	147	218	330	79	10755
	0	44	272	216	415	37	4355
20	872	36	1	28	208	789	16687
	198	53	2	50	511	1036	22603
24	229	0	0	2	3	50	4431
	29	0	0	3	3	88	589
28	212	407	313	82	13	64	9026
	300	416	39	72	22	24	10950
Aug. 1	0	2	170	452	537	648	30279
	0	2	177	644	448	28	17338
5	0	68	26	256	385	930	42866
	0	68	26	314	394	1012	10910
9	0	0	0	0	< 1	23	19640
	0	0	0	0	< 1	71	4072

*The first number in each pair is the inter-tree mean square, the other is the intra-tree mean square.

Table 11

Estimated variances and covariances for 1958

Date*	Eggs	I Instar	II Instar	III Instar	IV Instar.	V Instar	Total Scars
June 11	237	0	0	0	0	0	237
	-14	0	0	0	0	0	<1
	117	12	0	0	0	0	175
15	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
	29	0	0	0	0	0	29
19	116	0	0	0	0	0	116
	0	0	0	0	0	0	0
	87	0	0	0	0	0	87
23	0	86	116	0	0	0	885
	0	0	0	0	0	0	0
	325	4	86	37	0	0	1475
27	0	0	<1	<1	1	0	29
	0	0	1	4	4	0	149
	706	0	24	53	20	49	1946
July 1	2716	0	51	0	0	0	2930
	1396	0	10	0	0	0	4704
	3884	698	46	14	228	0	22301
5	372	0	0	0	0	0	368
	0	0	0	0	0	0	-23
	0	5	4	0	0	1	208
9	3435	344	22	0	32	0	8431
	680	269	0	0	0	0	3277
	293	443	6	0	0	0	1992
13	2771	20	202	0	0	0	2651
	506	42	0	0	0	0	2557
	309	167	217	200	116	116	17473
17	143	173	171	73	186	2	3120
	0	23	16	-9	-12	0	3050
	90	171	36	143	236	22	7649

Table 11 (Cont'd)

Date	Eggs	I Instar	II Instar	III Instar	IV Instar	V Instar	Total Scars
July 21	44	47	17	8	2	<1	2178
	0	0	0	24	<1	0	5685
	51	0	62	72	3	43	21256
25	73	32	101	4	389	253	18077
	0	26	0	2	0	18	5046
	29	23	0	35	32	58	4701
29	14	0	24	38	77	283	4269
	0	0	0	0	0	-1	-440
	0	0	0	0	0	2	2020
Aug. 2	78	0	0	4	<1	135	11005
	50	0	0	0	0	5	752
	32	0	0	0	<1	5	1128
6	0	0	0	0	12	79	3865
	0	0	0	0	24	4	5613
	0	0	26	0	48	5	12826
10	0	0	0	0	0	102	7953
	0	0	0	0	0	6	7455
	0	0	0	0	<1	11	11530
14	0	0	0	0	0	<1	1634
	0	0	0	0	0	0	-519
	0	0	0	0	0	0	.1979
18	0	0	0	0	0	1	1212
	0	0	0	0	0	0	1246
	0	0	0	0	0	0	9657

* The first figure in each group of three is the variance for the random half of the previous sample, the third is the variance for the overlapping half of the sample for the date given, and the middle figure is the covariance between the two.