THE BIOLOGY AND POPULATION DYNAMICS OF *LEUCOPTERA SPARTIFOLIELLA* (HB.) ON BROOM, *SAROTHAMNUS SCOPARIUS*.

By

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ABSTRACT

The biology and population dynamics of Leucoptera spartifoliella Hubner (Lyonetiidae) were studied in a relatively enclosed area of broom, Sarothamnus scoparius (L.) Wimmer at Silwood Park, Berkshire, from October 1963 to August 1966.

L. spartifoliella is univoltine and over winters in the larval stage. The adults emerge between June and July. The females are sexually mature on emergence, but oviposition coincides with flight and extends from June to August. Fecundity is significantly correlated with the weight of females on emergence. There are six larval instars which, except for a short wandering phase in the sixth, mine in the chloroplast-laden outer cortical tissue (collenchyma) of broom twigs. Pupation, in white spindle-shaped cocoons, takes place in May and lasts for approximately four weeks.

The adult stage has a definite flight phase during which flight, within and away from the habitat, occurs mainly in the evenings. The numbers flying are governed by the size and the age of the population, and the temperature at the time of peak flight. Emigration early in the flight period is truly migratory but becomes an extension of the trivial movements later on in this period.

Adult numbers were estimated by shaking eighths of broom bushes over a tray and the immature stages by examining twigs of broom of known weight. Adults exhibited a tendency to aggregation in their distribution.

Losses of the adult population were caused mainly by predation by the webbing and by hunting spiders, and by emigration. Most of the mortality, in the eggs, was due to sterility and predation notably by the Heteroptera (Miridae, Anthocoridae, Nabidae), and in the larvae to winter deaths, predation by birds, deterioration of the habitat and parasitism by the Eulophidae, Tetrastichus

evonymellae galatopus Ratz., Chrysocharis gemma Walk., Pnigalio soemias Walk., Necremnus metalarus Walk., and a Necremnus sp.

Population budgets are presented for 1964-1966.

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L. spartifoliella

x 14

Male

Female

1. INTRODUCTION

This, principally, is a study of the seasonal and annual variations in the population of the Lyonetiid moth, Leucoptera spartifoliella Hubner, on broom, Sarothamnus scoparius (L.) Wimmer. An attempt has been made to estimate the changes, to assess and interpret natality and mortality quantitatively and ultimately to construct a population 'balance sheet' for the moth.

The Leucoptera population was a large one reaching several millions, in the year of peak abundance, in a somewhat clearly delimited habitat of about 1605 broom bushes. The moth is specific to Sarothamnus scoparius; and there are no records of alternative hosts. Population estimates of the adults and also of eggs were obtained by several methods which provided independent and mutual checks on one another. Mortality agents were identified, and their significance assessed quantitatively whenever possible.

The existing information on the biology of Leucoptera spartifoliella, prior to this work, was found to lack in detail and clarity. A fair portion of this study has therefore been assigned to various aspects of the biology of the moth. These include adult emergence, emigration and reproduction; egg distribution and the larval feeding habits. Some observations also were made on the biology of the Eulophid (Chalcidoidea) parasites of the host.

Before this investigation, there were only two published works on Leucoptera spartifoliella. Both studies were performed with a view to finding an insect which could successively control broom in California (U.S.A.) where it is regarded as a serious weed of range and forest lands. The first paper by Parker (1964) dealt with the general bionomics of L.spartifoliella in France, and the moth was considered as promising for introduction into U.S.A. to control broom. The second paper by Frick (1964) is an account of the actual introduction, release and establishment of L.spartifoliella in different broom areas in California. Parker and Frick's works are purely observational and qualitative, and therefore differ from

this study in both substance and detail.

There are 11 species in the genus Leucoptera (Hubner) in Britain alone; only four of these, including L.spartifoliella, are non-leaf miners. The bulk of the literature on the temperate species deals with the more economically important ones, viz. Leucoptera scitella (Zell.) on apple leaves in Italy, Germany and China and L.sinuella (Reutti) on the leaves of the Canadian poplar in Italy. The only published accounts in the tropics again primarily concern species of economic importance, i.e. pests of coffee. These latter include Leucoptera coffeella (Guer) in South America, West Indies and East Africa and L.Meyricki (Ghesq.) in East Africa. Most of these papers deal with either the general bionomics and the parasites or the methods of chemical control of the species, and none with population dynamics. Thus the present work on L.spartifoliella should provide some useful guide lines on which population studies of related species could be based.

2. THE HABITAT

2.1 Description of the Habitat

This study of Leucoptera spartifoliella (Hubner) has been carried out in an area of about two acres of broom, Sarothamnus scoparius (L.) Wimmer located in Gunness Hill at Silwood Park Field Station (Fig.1). The study area is flanked to the north, east and south by park lands of grass interspersed with tall trees, and to the west by a woodland principally of oaks, elms, sycamore and bracken.

The present broom bushes grew from 3 inch high seedlings planted out in March 1957 in 24 rows of unequal lengths. Originally, there were about 80 bushes per row in the first 10 and longer rows, counting from the east, and 60 bushes in each of the last 14 and shorter rows. The rows are so spaced that they appear arranged in pairs. Thus, the two rows of a pair are 4 feet 6 inches apart, but the distance between the pairs of rows is 12 feet. Within a given row, the bushes stand 6 feet apart (Fig.2). The intervening spaces between the broom bushes and rows, respectively, are occupied by various other plants of which the Graminae (Poa pratensis (L)); Dactylis glomerata (L); Agrostis tenuis (Sibth.) and Holcus mollis (L) predominate. Other flowering plants, however, are represented and include meadow thistles (Canduus pratensis (Huds), brambles, stinging nettles (Utica dioica), Rubus ideaus (Raspberry) and Milium effusum (L), spreading Milium.

Many of the broom bushes are more than 6 feet high, with only a few above 8 feet. However, within the time of this study, a marked and progressive reduction in the quality and size of the habitat has been in evidence. Considerable numbers of bushes have died - as would be expected since the life span of a broom plant is usually 10 to 15 years (D.F. Fort in Richards and Waloff, 1961) - so also have some branches and twigs of most of those surviving (Tables 2 and 3a). As will be shown later, it is the broom twigs

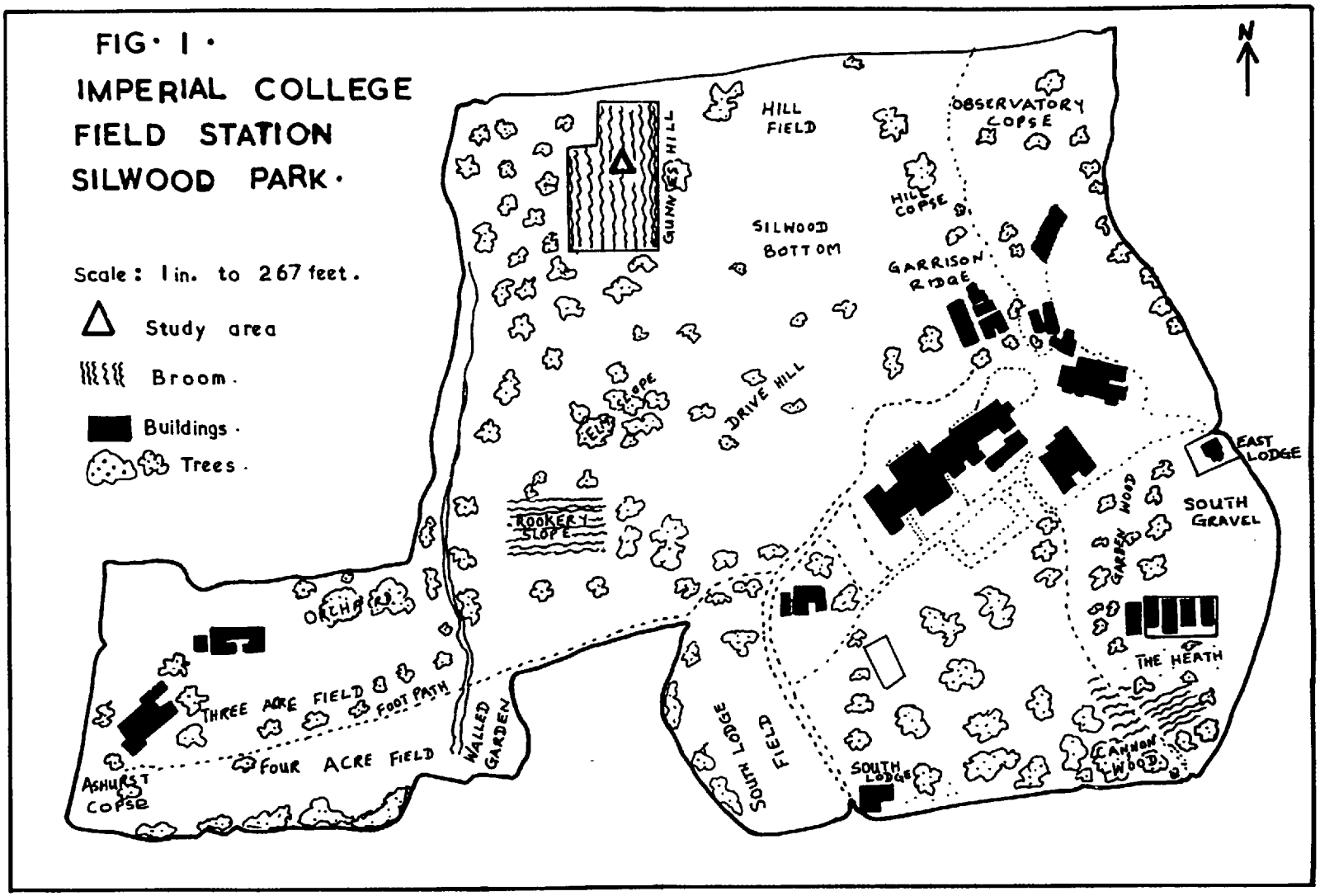
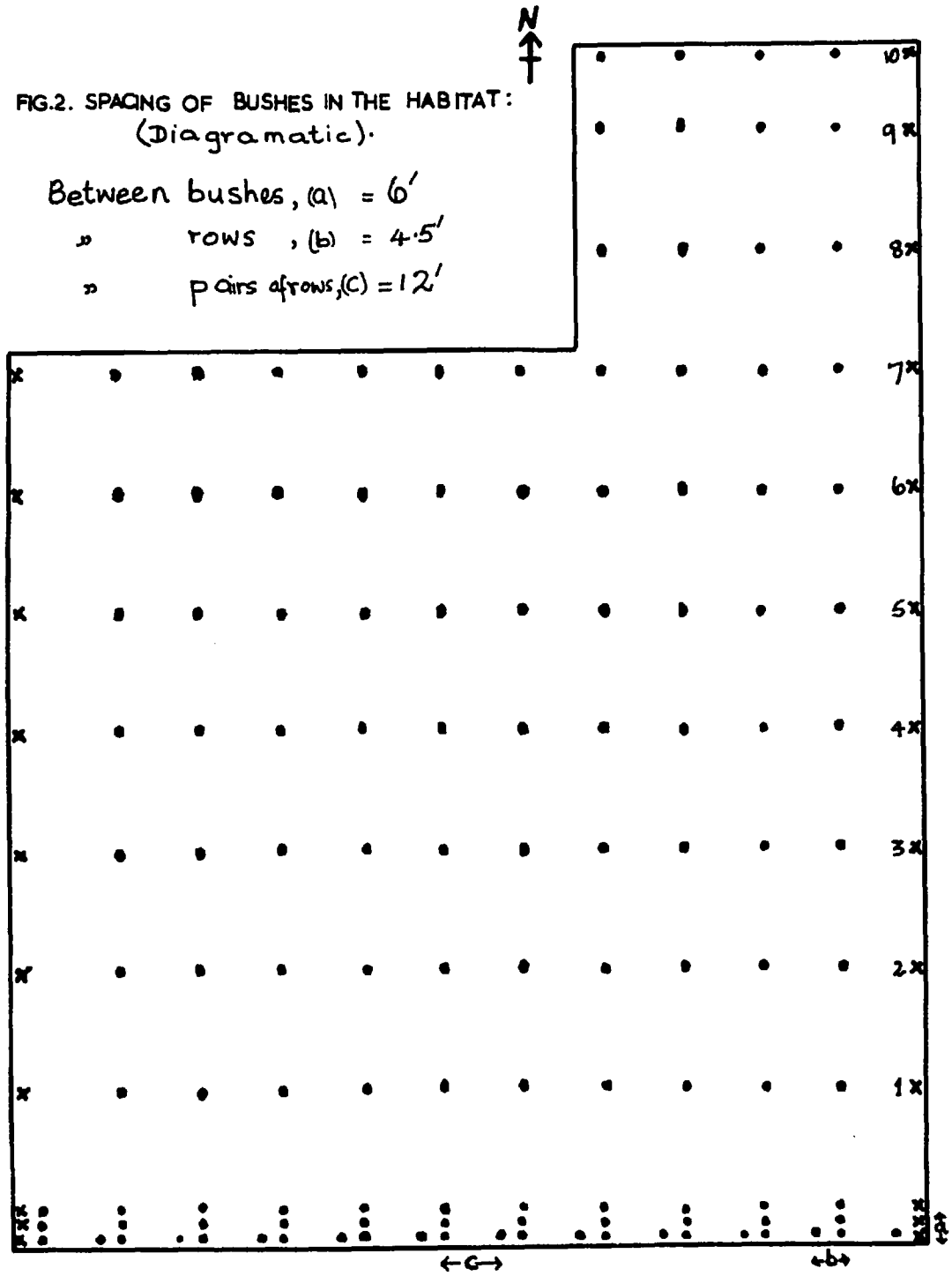


FIG. 1.
IMPERIAL COLLEGE
FIELD STATION
SILWOOD PARK.
Scale: 1 in. to 267 feet.
Study area
Broom.
Buildings.
Trees.
N
GUNN HILL
HILL FIELD
OBSERVATORY COPSE
HILL COPSE
SILWOOD BOTTOM
GARRISON RIDGE
ELM
DRIVE HILL
EAST LODGE
ROOKERY SLOPE
SOUTH GRAVEL
GARDEN WOOD
ORCHARD
THE HEATH
THREE ACRE FIELD
FOOT PATH
WALLED GARDEN
FOUR ACRE FIELD
ASHURST COPSE
SOUTH LODGE FIELD
SOUTH LODGE
CANNON WOOD

FIG.2. SPACING OF BUSHES IN THE HABITAT:
(Diagramatic).

Between bushes, (a) = 6′
» rows, (b) = 4·5′
» pairs of rows, (C) = 12′



Column No.	No. of bushes at each point
1 - 9	8.
10	5.

that provide the sole oviposition sites for the female Leucoptera spartifoliella, and consequently the feeding substrate to the resultant larva in all its stages.

There are other broom areas at Silwood but only two of these attain measurable size : one, on the Rookery Slope, about 300 yards south of Gunness Hill, consists of 138 bushes planted between 1958-59 on about one twelfth of an acre, the bushes lying scattered either in clumps of from 2-8 or sometimes singly. The other is the 'old broom' area on the Heath, about 500 yards south, south-east of Gunness Hill and comprises more than an acre of naturally occuring broom bushes. Most of the broom areas at Silwood, on examination, showed evidence of Leucoptera attack.

2.2 The Host Plant

Sarothamnus scoparius (L) Wimmer is a leguminous perennial shrub with an erect, much branching stem and green 5-faceted twigs. In transverse section, the twigs show an epidermal layer broken in places by stomatal cells, and underlying hypodermal and outer cortical cells heavily laden with chloroplasts - this suggesting a photosynthetic function.

Broom has a wide and extensive distribution in the British Isles, the Islands of Orkney and Shetland being the only exceptions (Clapham, Tutin and Warburg, 1952). Its range in Western Europe extends from Scandinavia to Spain, and as far south as the Canary Islands, and eastwards to Poland and Hungary in Central Europe.

The leaves, small and obovate, appear in spring. This, however, has varied from year to year at Silwood; and is probably influenced by the age of the bushes and the temperature of the habitat. Thus in 1960 the leaves appeared early in February (Parnell, 1962), in 1964-65 late in March, but as late as the first week in April in 1966. Two types of leaves can be recognised - lower petiolate and compound (3 leaflets per leaf) and upper simple

and sessile leaves, respectively. The leaves are deciduous and may start to fall off by mid-September.

Flowering occurs often in May. This as well as its intensity, however, varies with the age of the plant, tending to be later and scantier in older bushes. The flowers (9 to 12.5 m.m.) are yellow and axillary. The pods are green and hairy when young; at maturity they are flat, 1.5-2 inches long and black. Pod dehiscence may start in mid-July and go on for as long as early September.

Broom has two growth cycles a year. The first, the spring growth, precedes flowering and is signalled by the appearance of leaves in March followed by rapid growth of the green twigs in May. It is on this growth that adult female Leucoptera oviposit. The other, the autumn growth, occurring after the summer flowering and fruiting, starts by the middle of August (1st week in August in 1965 at Silwood). It is characterised by a greater growth in length of the twigs and little or no flowering. The autumn growth, therefore, occurs at the end of life of adult Leucoptera in the field.

2.3 Estimation of Total Broom Material in Plantation.

All stages of Leucoptera (egg to adult) are found on broom; therefore, to estimate the absolute numbers of any given stage in the area, it is necessary to know the amount of available broom material (in terms of numbers of bushes and the actual quantity of green and wood) each year.

The quantity of green and wood available is estimated each year from 24 bushes selected at random, one from each of the 24 rows of broom in the plantation. A quarter of each of the selected bushes is cut out right from the base. These quarter bush samples are taken from all four aspects of the bushes : viz, from the north in row 1; east in row 2; south in row 3; west in row 4; north in row 5 and so on till all the 24 rows have been covered. Each of the quarter bushes is divided by eye, and then cut up, into top and

bottom portions; each of these divisions is again sub-divided into an outer top (OT), inner top (IT) and an outer bottom (OB) inner bottom (IB). The wood and green components of each of these portions are weighed separately, and from the weights so obtained the average of green per one-quarter bush can be calculated (Table 1). There is very little green in the lower reaches (IB), most of it being concentrated in the middle region (OB + IT) as compared with the bottom (IB) and top (OT) regions of the bushes. The implication of this will become apparent later on when the height of flight and egg distribution in the habitat are considered.

Table 1 Weight of green per $\frac{1}{4}$ bush at different levels in different years (g.) as per cent of total in bracket.

YEAR	IT	OT	IB	OB
1963	193 (18.33)	469 (44.54)	66 (6.27)	325 (30.86)
1964	197 (16.39)	505 (42.01)	80 (6.66)	420 (34.94)
1965	329 (30.75)	258 (24.11)	106 (9.91)	377 (35.23)
1966	419 (35.54)	312 (26.46)	61 (5.18)	387 (32.82)

The average weight of green and of wood per whole broom bush can similarly be calculated from the 24 quarter-bush samples. This shows a marked variation from year to year; and the progressive decline in the quality of the bushes is shown when the ratio, average weight of green to average weight of wood per bush is computated for each year (Table 2)

Table 2 Average weight (g.) of green and wood per whole broom bush in various years.

Year	No. of bushes in plantation	Wood	Green	Total green in plantation (10^3)	Av.wt. of green / Av.wt. of wood
1963	1605	4168	4210	6757	1.01
1964	1541	5528	4808	7409	0.87
1965	865	6242	4278	3705	0.69
1966	804	7099	4717	3792	0.66

In 1963, counts of the number of live broom bushes in the plantation were made once, and in the autumn. In the subsequent years (1964, 1965, 1966) however, these counts were repeated, but now in each of three seasons (spring, summer and autumn) of the year, as this helped to clarify the variation in the numbers of bushes surviving in the area from season to season, and also the numbers dying over the winter in any given year (Table 3a). The difference between the autumn and spring numbers gives the approximate number of bushes dying over the winter. The 1963 estimates of the quantity of wood and green per bush and also the counts of total number of live broom bushes in the area were supplied by Professor Richards and Dr. Waloff, who also assisted in making similar estimates in 1964.

Table 3a Numbers of live broom bushes in different years.

YEAR	SPRING	SUMMER	AUTUMN
1963	-	-	1605
1964	1570	1560	1541
1965	1503	1414	1388
1966	1349	1289	-

The broom bushes flowered heavily in 1964; in 1965 many of the plants died probably as a result of this since the bushes were already old, and of those bushes that remained alive many branches were dead. Therefore, estimates based on the actual numbers of bushes alive are bound to be too high since a majority of such live bushes fell far below the calculated average weight (in wood and green) of a "whole bush". The actual numbers of live bushes have therefore to be converted into an equivalent number of 'whole bushes'. This was done by choosing, at random, 257 bushes all through the plantation, and scoring the living material left on each of them as fractions of the bush if completely alive. Thus scores such as 0, $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$ and 1 were obtained where applicable,

their sum representing the 'whole-bush' equivalent of the 257 bushes initially chosen. In this particular case, there were 160.25 such 'whole-bushes'; so that the percentage of 'whole-bushes' was computated, viz:

$$\text{The percentage of 'whole-bushes'} = \frac{160.25}{257} \times 100 = 62.35$$

This percentage was applied to the absolute numbers of live bushes counted in 1965 and 1966 to get their respective 'whole-bush' equivalents (Table 3b) employed in the calculation of the initial recruitments of the adult Leucoptera and its instars.

Table 3b 'Whole-bush' equivalents of live-broom bushes in 1965-66 (numbers in brackets = actual numbers of live bushes)

YEAR	SPRING	SUMMER	AUTUMN
1965	(1503) 937	(1414) 882	(1388) 865
1966	(1349) 841	(1289) 804	-

3. LIFE HISTORY OF LEUCOPTERA SPARTIFOLIELLA (HUBNER)

L. spartifoliella is univoltine. The generation commences with the imagines which start to emerge in the second week of June. Emergence in the field is protracted, and many last from 7 to 8 weeks; but maximum emergence occurs quite early in July. There is no correlation between the weight of moths and the date they emerge.

The adult population builds up rapidly, reaching a peak in the first week of July; but, there is then a rapid decline in numbers, so that only a few adults remain by late August or the first week of September. The males precede the females in emergence, but are generally more short-lived; with the result that the tail end of the adult population in the field is composed principally of the females.

The females emerge with about one third of their eggs already mature, but do not start laying until after copulation which begins after the third week in June. Mating takes place in the evenings (7 p.m. - 9.30 p.m.). Most of the eggs are laid within two to three days of oviposition period, but this varies in many individuals. The rate of egg laying is dependent on temperature and is also directly related to the weight of the females at emergence. The eggs are generally laid on the edge of each of the five facets of the broom twig; and their maximum numbers, in the field, are attained within the first fortnight of July.

The incubation period, at normal summer temperatures, is between 13 to 18 days. The small yellowish first instar larvae hatch and eat their way out through the underside of the egg and into the host-plant's tissue. The 'mine' made by the larva is linear, but can bend and cross into the other facets of the twig. The larvae are always solitary in their mines.

There are six larval instars. The first five of these feed within the broom twig. Overwintering is in the third, fourth and fifth larval instars, the bulk of the overwintering population being in the fourth instar. Throughout the winter, feeding and moulting are reduced but not completely stopped. The larval stages overlap, and sometimes three stages may occur simultaneously. The sixth, i.e. the final larval instar appears in the spring and reaches its peak in numbers by mid-April. It continues to mine and feed for 3 to 4 weeks; and then emerges from the mine, approximately in late April and onwards, and assumes a wandering phase. The duration of this phase is variable, but large numbers of wandering larvae can be seen by the end of April and at the beginning of May descending on silken threads to the lower branches of the broom bushes. Then, these larvae spin white spindle-shaped cocoons in which they pupate. The cocoons are open at both ends, but one of the ends is later plugged up by the larval skin cast during pupation.

Pupation commences by the beginning of May, and the greatest numbers of pupae are found in the third week of that month. The length of the pupal period depends on temperature, and lasts approximately 6 weeks. The first adults were seen to emerge on 12th of June 1965. This first emergence is from pupae formed by the earliest wandering larvae. Because of the protracted emergence period, the duration of adult population in the field is long; but, on the average individual adults live only one and a half to two weeks, longevity depending both on temperature and on the size of the moth at emergence.

4. NUMBER OF LARVAL INSTARS AND DEVELOPMENT OF EGG AND PUPAL STAGES

4.1 Methods of Establishing the Number of Instars

The adult of L.spartifoliella was first described by Hübner in 1826. It was re-described by Meyrick in his revision of British Lepidoptera in 1927. Brown's description, in 1952, was not much different from Meyrick's, except that it included some general description of the larva. However, there are no records, as yet, of a definite number of its larval instars. An attempt was therefore, made to ascertain this.

4.1(a) Head-capsule width measurements

Weekly collections of Leucoptera larvae were made from October 1963 to October 1964. In the laboratory, the larvae were removed from their 'mines' and killed in a K.A.A.D. mixture. This mixture induces the intersegmental musculature to swell. The head-capsules are thus pushed out and can be easily measured, unobscured by the prothoracic segment. To prevent larvae bursting, they were transferred after 15 to 20 minutes in the mixture, to 70 per cent alcohol for preservation.

The head-capsule widths were subsequently measured, under a binocular microscope, with a micrometer eye-piece. The measurements were taken across the widest part of the head in the dorsal aspect. A total of 903 larvae was measured. The distribution of the head-capsule widths taken in micrometer eye-piece units, (Fig.3a) shows six clear peaks. Each of these peaks represents a larval stage. A scatter diagram of these head widths and lengths of corresponding dorsal prothoracic shields agreed with this.

Some measurements of the head-capsule widths together with the total lengths of larvae in the successive larval stages are summarised in Table 4. The ratio between the head-capsule widths of successive instars shows reasonable agreement with Dyar's postulate.

Table 4 Width of head capsule and total lengths of larvae in mm. (± 95% Fiducial limits)

Instar	No. of larvae	Mean head width ± 95% Fid. limits.	Head width ratios	Mean body length ± 95% Fid.limits.
I	48	0.091±0.003	-	0.778± 0.029
II	30	0.131±0.010	0.70	1.028 ±0.051
III	29	0.181±0.021	0.72	1.750 ± 0.061
IV	28	0.229±0.007	0.79	2.084 ± 0.063
V	26	0.311±0.012	0.73	3.017 ± 0.106
VI	30	0.456±0.008	0.68	4.874 ±0.146

4.1(b) Larval 'mine' characteristics and recovery of cast head capsules

Early in this study, some changes in width were observed at several points along the 'mines' of Leucoptera larvae. These changes were in the form of horizontal extensions in breadth of the 'mines' (see Fig.3b). When opened, each extension yields a cast head capsule, and so may be regarded as a 'moult chamber'. To see if this could be a reliable means of ascertaining the number of larval instars, broom twigs were collected after the putation of Leucoptera in 1965. Counts revealed five 'moult chambers', each containing a cast cast head capsule, along every 'mine' from which a larva had emerged to spin its cocoon. Since the last instar larva casts its head capsule in the cocoon before pupation, there must be six larval instars. The number of instar stages is thus one in excess of that of the 'moult chambers' along the mines from which larvae had emerged to pupate.

As the table below shows, the 'moult chamber' is quite distinct from other parts of the 'mine', and are easily recognised after some practice.

FIG.3a. NO. LARVAL INSTARS OF L. SPARTIFOLIELLA.

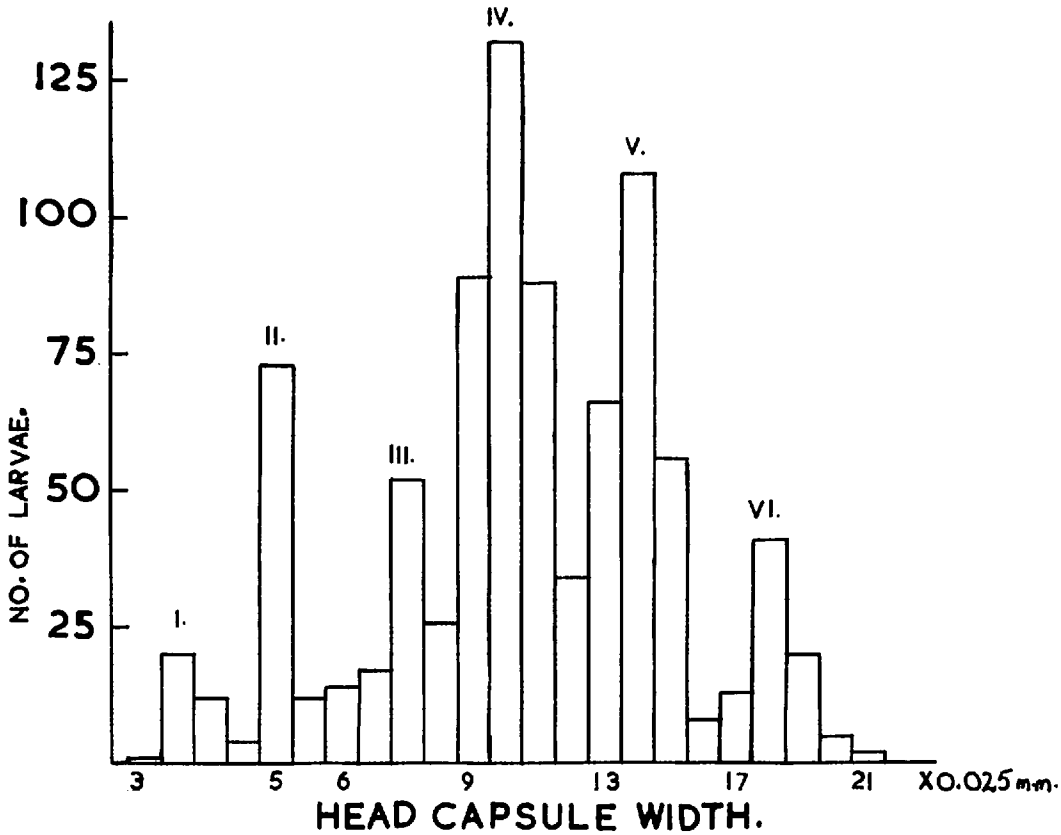


FIG. 3b. SHOWING LATERAL EXTENSIONS OF MINES AT "MOULT-CHAMBERS"

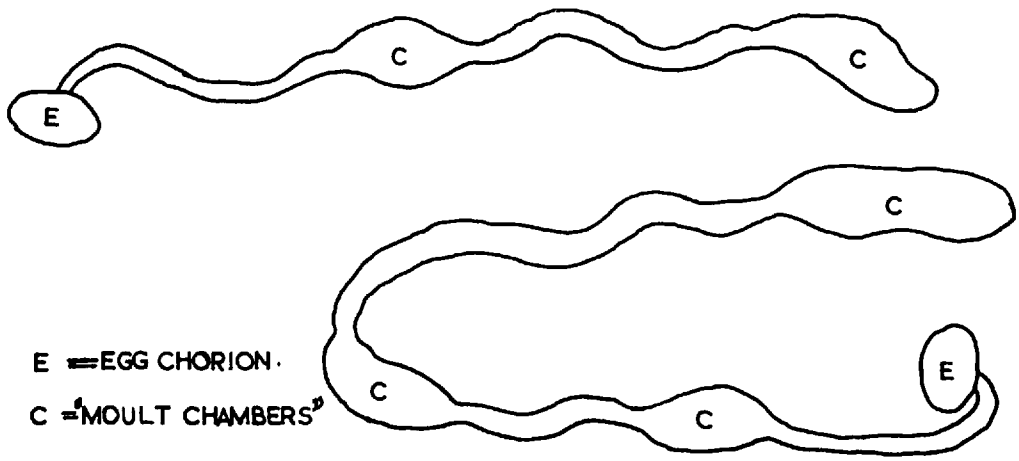


FIG.4. Leucoptera larvae.

Yellow = 5th instar.

Black = 6th instar.

Instar	Breadth of 'mine' (mm.) (mean of 10 'mines')		Length of 'mine' (mm.) (mean of 10 'mines')
	Pre-moult chamber	Moult chamber	
I	0.107 ± 0.049	0.305 ± 0.054	1.461 ± 0.215
II	0.174 ± 0.054	0.399 ± 0.054	2.198 ± 0.100

Larvae in the first four instars can be separated by size only, as they all are yellow and apodous. Three pairs of rudimentary thoracic appendages appear in the fifth instar. In the sixth, these are functional and 3-segmented, and five pairs of abdominal prolegs and the spinneret are in evidence. The two last larval instars can therefore be easily identified. The sixth instar larva is black, whilst the other instars are yellow (see Fig.4). The blackness is due to long black hairs which clothe it. Most of the hairs are lost by the time the larva emerges from the 'mine'. A detailed description of the larvae of Leucoptera lotella Stt., L.laburnella Stt. and L.scitella Zell. are given in a paper by Jayewickreme (1940), and of larvae of L.spartifoliella, in that by Parker (1964). Neither author, however, mentions this larval colour change.

4.2 Development of Egg and the Pupal Stage

Eggs of L.spartifoliella were incubated at five constant temperatures of 10, 15, 20, 25 and 30°C, at 70 per cent relative humidity. The eggs were laid at 20°C and then transferred to the various temperatures within twelve hours of laying. Records were made of the incubation period at the different temperatures. From these data, the mean duration, y, of the egg stage was computated for each temperature regime. Data for the duration of the pupa, at the same constant temperatures and relative humidity, were similarly obtained. The two sets of data are given in Table 5. It can be seen that a rise in temperature reduces the duration of development of the egg and the pupa; and that male pupae develop quicker than the females

Table 5 The incubation period of egg and pupa at constant temperatures.

Temperature °C	Incubation Period (days) ±95% fiducial limits		
	EGGS	PUPAE	
		Male	Female
10	-	96.67 ± 19.93	104*
15	24 ± 0.55	41.92 ± 1.77	46.91 ± 2.02
20	19.42 ± 0.44	19.71 ± 0.48	21.82 ± 0.84
25	13.88 ± 0.33	14.58 ± 0.79	15.86 ± 0.90
30	13.67 ± 0.25	13.45 ± 0.63	14.47 ± 0.51

* based on one female

The rate of development, $1/y$, similarly increases with temperature. The trend of this temperature - rate of development relationship becomes clearer when the values for log. $\frac{K - P}{P}$ are plotted against the appropriate temperatures:

Where K is the inherent rate of development under a given set of conditions, and P is the per cent development per day (i.e. $\frac{100}{y}$). This relationship is linear (see Figs. 5 and 6); the equations for the straight lines are:

for Egg : $\text{Log}_{10} \frac{K - P}{P} = 0.4383 - 0.0118x$

for Pupa

Male : $\text{Log}_{10} \frac{K - P}{P} = 2.0441 - 0.1179x$

Female : $\text{Log}_{10} \frac{K - P}{P} = 2.0421 - 0.1164x$

(where x is the given temperature).

This linearity implies that the relationship between per cent development per day (for the eggs and the pupae) and temperature follows a bisymmetrical logistic curve of the type described by the formula:

$$\frac{100}{y} = \frac{K}{1 + e^{a - bx}}$$ (see Davidson, 1944), where a,

is a constant, and b is the temperature coefficient of per cent development per day.

The calculated values of K, a, and b for eggs and pupae are as follows:

		K	a	b
Egg	:	2.1881	1.1151	-0.0272
Pupa	male:	7.6686	4.7067	-0.2715
	female:	7.1412	4.7021	-0.2671

These values have been substituted in the logistic curve equation to obtain the calculated formula for the temperature-velocity curve for the development of the eggs and the pupae: viz:

for Eggs :- $$\frac{100}{y} = \frac{2.1881}{1 + e^{1.1151 - 0.0272x}}$$

for Pupae: males: $$\frac{100}{y} = \frac{7.6686}{1 + e^{4.7067 - 0.2715}}$$

female: $$\frac{100}{y} = \frac{7.1412}{1 + e^{4.7021 - 0.2671}}$$

These curves imply that from the lowest temperature where complete development is possible to that at which the development rate is fastest, the speed of development of the eggs and the pupae increases to a peak with temperature and then rapidly falls off. The lower and upper temperature limits of development were not accurately determined. However, no eggs hatched at $10^{o}C$, though some embryonic development was observed.

It is worth noting that the temperature coefficients of development, in both sexes of pupae, do not differ very much, but their K values do, suggesting some built-in tendency in the male pupae to develop faster than those of the females.

The temperatures at which the percentage development per day represented by K can be attained, has been calculated for eggs and pupae, and are as follows: Egg $41^{o}C$; male pupa $17.3^{o}C$;

FIG.5. RELATION BETWEEN SPEED OF EGG DEVELOPMENT & TEMPERATURE.

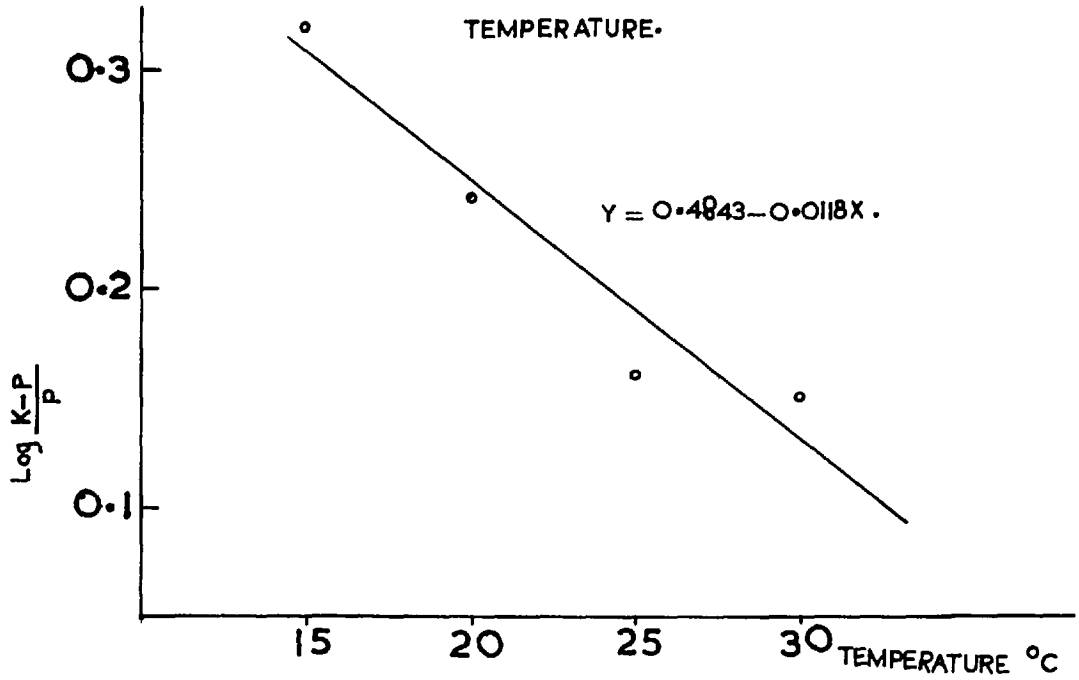
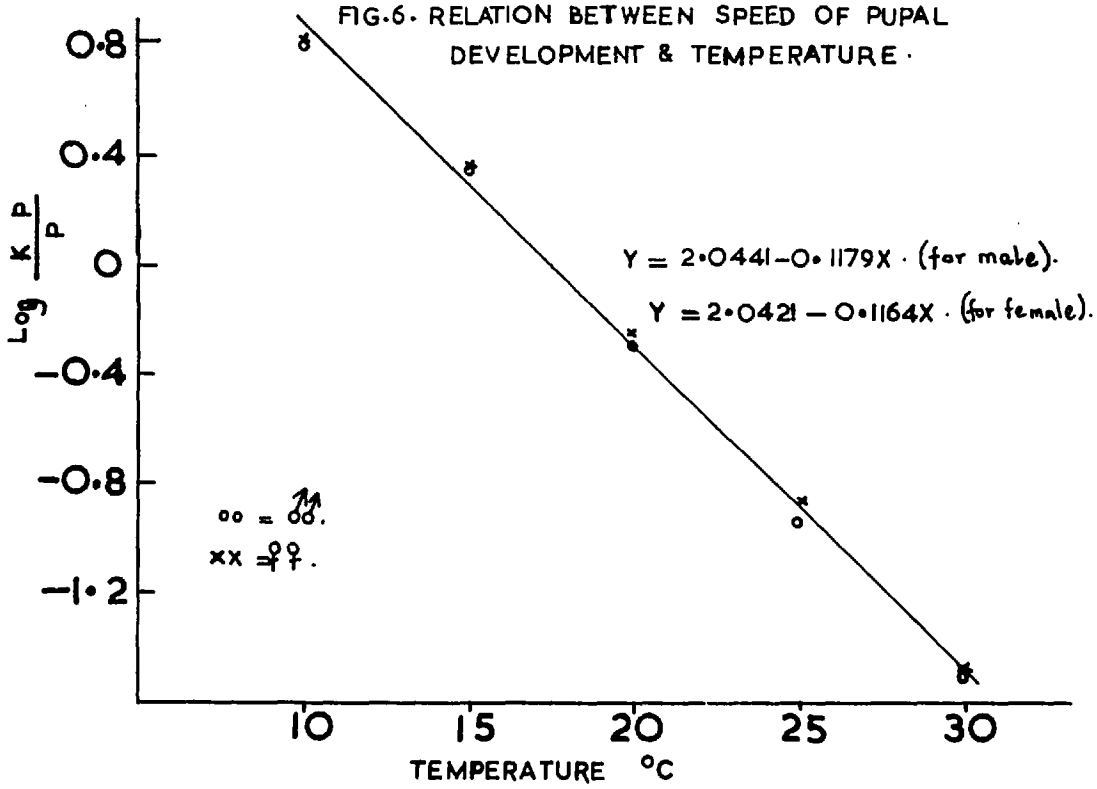


FIG.6. RELATION BETWEEN SPEED OF PUPAL DEVELOPMENT & TEMPERATURE.



female pupa 17.6°C. It should be noted that these temperatures are very near to those at which most of the eggs hatch, and most pupae develop to emerge into adults (see Table 6). The sexes of the pupae have been treated separately because the males precede the females in emergence.

Table 6 Egg hatch; and adult emerged at various temperatures. (Nos. in brackets = actual no. of eggs or pupae incubated).

Stage	Temperature; % hatch and % adult emerged				
	10°C	15°C	20°C	25°C	30°C
Egg	0 (35)	75.6 (41)	83.0 (47)	63.4 (41)	90 (30)
Pupa	12.9 (31)	82.1 (28)	92.6 (27)	79.2 (24)	89.7 (29)

Finally, it must be noted that this type of measurement is useful ecologically, physiologically it is 'inaccurate' as it is sum total of different physiological developmental processes.

5. OVERWINTERING IN L. SPARTIFOLIELLA.

5.1 Overwintering stage

L. spartifoliella is a univoltine species, overwintering in the larval stage. Weekly extractions of larvae from 'mines' revealed that overwintering may be in more than one larval stage. The overwintering population occurs in the third, fourth and fifth larval instar, but the proportions of these vary from year to year. Generally the fourth larval instar is the commonest by December, and the fifth towards the end of winter (see Table 7).

Table 7 Number of instars III, IV and V in the overwintering population.

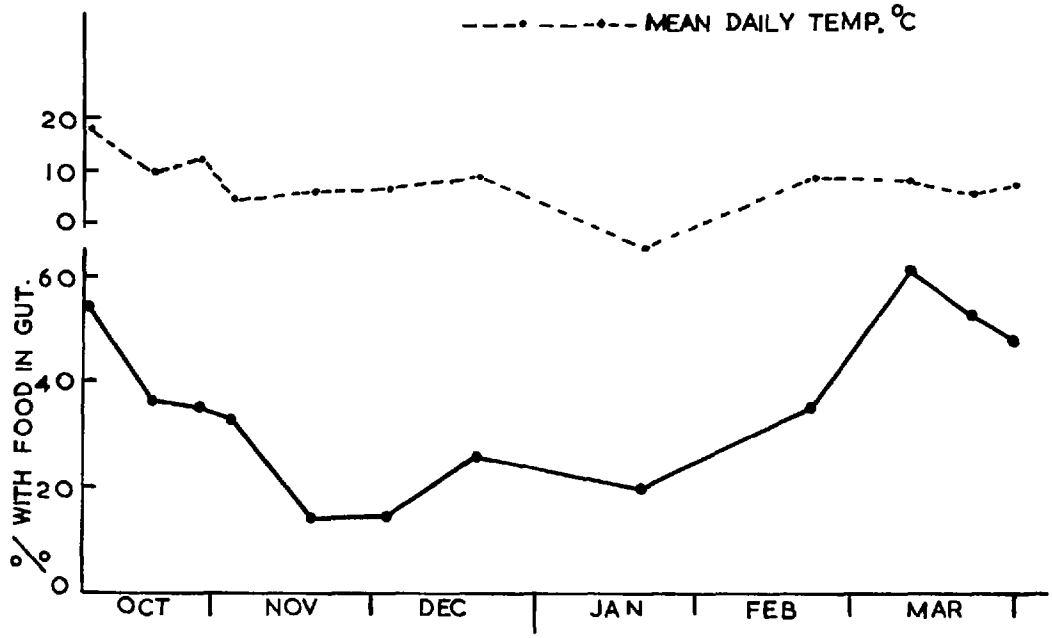
Year	Date	Total larvae in sample	% of the instars		
			III	IV	V
1964/65	16.XII.64	360	26.1	47.5	26.4
	21.1.65	430	10.0	41.2	48.8
1965/66	20.XII.65	209	1.9	60.8	37.3
	20.1.66	288	3.1	46.5	50.4

5.2 Feeding in Overwintering Larvae

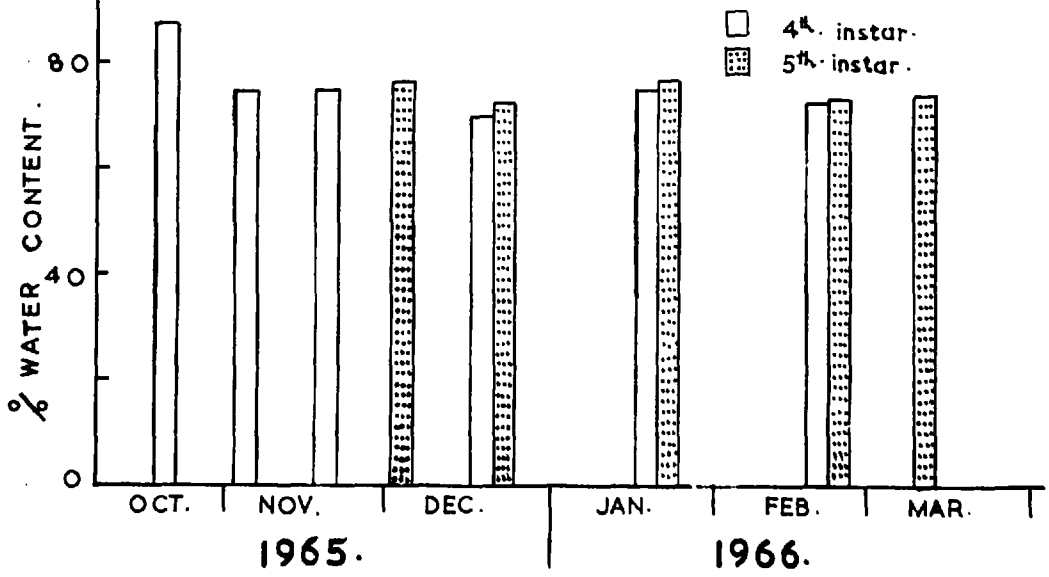
Weekly dissections of the overwintering larvae (except those 'about to moult' or just moulted, which do not feed) were made in 1965 to see if the larvae had fed, i.e. whether there was food in the gut. Fig.7a gives a summary of these observations, and indicates that overwintering Leucoptera larvae do not stop feeding completely, but will readily feed provided the ambient temperature is sufficiently high. The temperature threshold of this winter feeding was not investigated.

The fat deposits in the overwintering larvae are large, but tend to be smaller in larvae that have recently been feeding.

FIG·7a. SEASONAL CHANGES OF PERCENTAGE OF LARVAE FEEDING.



FIG·7b. SEASONAL CHANGES OF WATER CONTENT OF LARVAE.



5.3 Water Content of Overwintering Larvae.

In 1965, an attempt was made to see if overwintering affects the water content of L. spartifoliella larva.

Larvae, from the weekly samples, were weighed in groups in a small glass vial of known weight. The fourth and fifth instars were weighed separately. The ranges of average fresh weight are:

0.08 to 0.2 mg. for the fourth instar, and

0.17 to 0.35 mg. for the fifth instar larvae.

After weighing, the vials were kept in an oven thermostatically set at 108°C. They were brought out, at two day intervals, and weighed after cooling until a constant weight was obtained in two consecutive weighings. From the data, the percentage of total water content was calculated for each of the larval stages (at various times between the autumn of 1965 and the spring of 1966) and plotted against time (Fig.7b). The observations show that there is some reduction in the total water content in each of the overwintering larval instars. The level of the reduction varies from month to month, but is greatest in December. As will be shown later, this is the month in which the overwintering larvae also show the greatest tolerance to cold. The reduction in the fifth larval instar is slightly but consistently less than in the fourth, but the difference is not significant.

5.4 Cold Hardiness in the Overwintering Larva.

5.4(a) Undercooling point determinations

The spring larval population, in an insect overwintering as larva, must be a function of the ability of the overwintering stages to withstand and survive very low temperatures. The lowest tolerable temperature limit is the 'undercooling point' (Salt, 1936). The 'undercooling point' is always below the temperature at which the body fluid freezes, and can be a good index of an insect's cold hardiness. An attempt was made in the winter of 1965/66 to study the ability of Leucoptera larvae to supercool and also to survive varying lengths of exposure to sub-zero temperatures.

The 'undercooling point' investigations were carried out on the fourth and fifth larval instars, as these form the bulk of the winter population. For comparison, in the spring the investigation was extended to the sixth and final larval instar. The larvae were cooled thermostatically in a 'Frigistor' in the way described by Luff (1964); and were brought in from the field and extracted from their 'mines' on the day of the investigation so as to avoid loss in the laboratory of the cold hardiness acquired in the field. To avoid innoculative freezing, care was taken not to pierce the larva with the thermocouple probe, and the glass holder was dried after each determination. The glass holder, containing the larvae and the Thermocouple probe, was gently pushed into the frigistor and the falling temperature of the test larva recorded on a Servograph. The 'undercooling point' was recorded as the point where the temperature suddenly rose as the latent heat of the freezing larva was released. Table 8 shows the undercooling piints (means of ten replicates) for the three different larval instars.

Table 8 Undercooling points of Leucoptera larvae.

Date	Instal Stage	Undercooling point in °C	
		R Ranges	Mean of 10 readings ± 95% Fiducial limit.
4.I.66	Fourth	-13.5 to -21.0	-17.06 ± 1.68
4.I.66	Fifth	-14.5 to -20.5	-17.02 ± 1.43
26.IV.66	Sixth	-7.0 to -17.0	-13.70 ± 2.14

The individual larvae, within each instal stage, varied in their cold tolerance; but the mean undercooling point of the overwintering fourth and fifth larval instars was practically the same. These two, however, were each significantly more coldhardy than the sixth instar (P= 0.01) which occurs in the spring. This increase in the undercooling point, i.e. reduction in cold tolerance, in the sixth larval instar may probably be correlated with the rising ambient temperature in the spring. However, the water contents determination showed that the sixth instar larvae have a slightly higher

total water content (Table 9); also, almost all those dissected had food in their gut. It is probable therefore that reduction in cold hardiness may have been associated with the presence of food in the gut as well as with the increase in live water content (Salt, 1953).

Table 9. The water contents of larval instars, four, five and six.

Larval stage	No. of Larvae	Mean fresh weight (mgm)	Mean % water contents
Fourth	24	0.20	72.9
Fifth	69	0.30	73.3
Sixth	45	0.54	77.6

5.4(b) Larval survival at sub-zero temperatures.

The ability of the overwintering L.spartifoliella larva to survive varying lengths of exposure to sub-zero temperatures was tested in a deep freeze into a small corner of which a small soft-wood cabinet (about 12" x 4" x 4") has been fitted. The cabinet is separated into four compartments with cross-boards of expanded polysterene. A temperature gradient was thus established between the top most and the lowest compartments, and varied from about -4.5°C to -19°C (on one occasion the lowest compartment had a temperature of -21.7°C). Thermocouples leading into each of the compartments helped to measure their respective temperatures by means of a Doran Mini recording potentiometer, the reading of which could be converted to the corresponding temperature (°C) from a 'Voltage - Temperature' table.

Larvae were brought in from the field on each day of the experiment, and placed in equal numbers in four plastic petri dishes which were then put one in each of the cabinet compartments. In an exploratory test, the larvae remained in their 'mines' in about

an inch of broom twigs; but the twigs shrivelled up rapidly, killing the larvae. In later experiments therefore, the larvae were removed from their mines before being placed in the petri dishes. Each petri dish was divided into four cells with plasticine pressed out by hand into thin saucer shapes. This arrangement enabled the exposure of two different larval stages in one cabinet compartment at the same time. The petri dishes were brought out at intervals, allowed to warm up in the laboratory for one and a half hours before the larvae were examined for mortality, and then returned to the deep freeze. A larva was recorded dead when several prods with a fine brush at the last abdominal segment failed to elicit a withdrawal reaction. The mortality of fourth and fifth instar larvae, after a seven day simultaneous exposure to a temperature of $-13.5^{\circ}C$, is shown in Table 10. The stages do not seem to have differed significantly in their ability to survive protracted exposure to very low temperatures; this is in agreement with what has already been said about the similarity of their undercooling points.

Table 10 Survival of larval instars four and five after a seven day exposure at $-13.5^{\circ}C$.

Instar stage	IV	V	Totals	χ^2	P
No. Exposed	25	25	50	0.572	>0.3 but
No. Dead	16	12	28		<0.5

It is probable that the three overwintering stages of L. spartifoliella do not differ markedly in the levels of their cold tolerance.

The overwintering larval stages are found in the field from autumn to spring. To see if their cold hardiness varied within this period, larvae (third instar in autumn and the fifth instar in winter and spring) were brought from the field at intervals of time, and exposed to the sub-zero temperatures. Mortality counts

for the various compartments, were taken after fourteen days. The data are represented graphically in Fig.8. This shows that cold tolerance varied with the time of the year. Cold hardiness was greatest in December, but then decreased towards and during the spring months. Distinct seasonal phases in cold hardiness have also been reported in other species of insects (Yuill, 1934) and Payne, 1926). The overwintering Leucoptera larvae feed and are active during the winter, if the temperature is sufficiently high. The reduced coldhardiness shown in January (see Fig.8) may be partly caused by the food in the gut.

Survival records for fifth instar larvae exposed at the temperatures of -6.02°C, -12.08°C, -16.20°C and -17.9°C for 30 days, but examined at intervals of 2, 3 or 5 days, are represented in Fig.9. This shows an inverse proportional relationship between survival and temperature and duration of exposure. Mortality is highest within the first two days of exposure in the three lower temperature regimes; but then falls to a level and becomes gradual. This may suggest a tendency to acclimatize after the initial shock of the cold. Probably, it may mean that it is the short crisp spells of hard frost that kill Leucoptera larva in the field in the winter. The effect of frost may be less lethal on the larvae in the years when the winter cold gradually builds up in severity.

FIG. 8. SEASONAL VARIATION OF COLD TOLERANCE OF LARVAE.

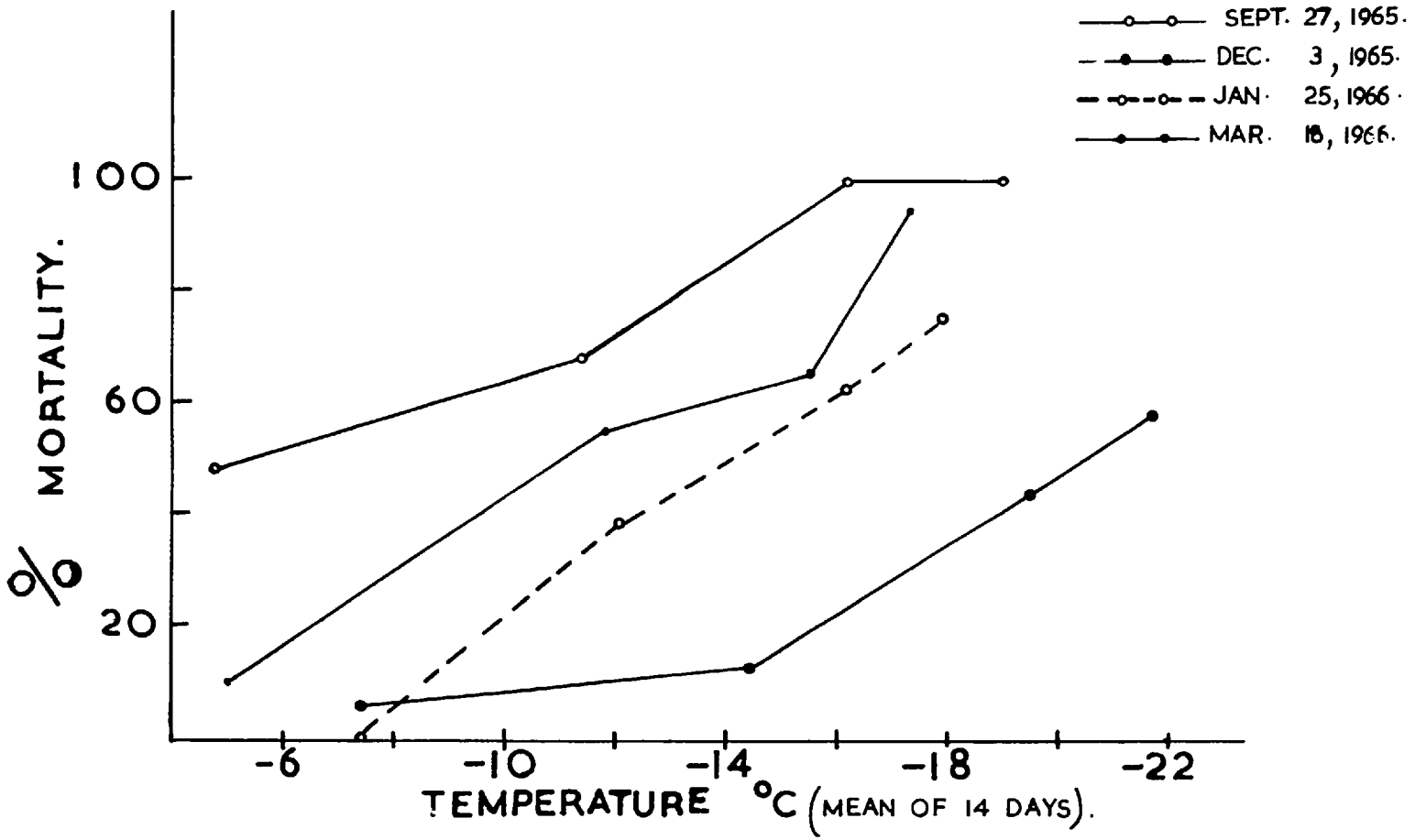
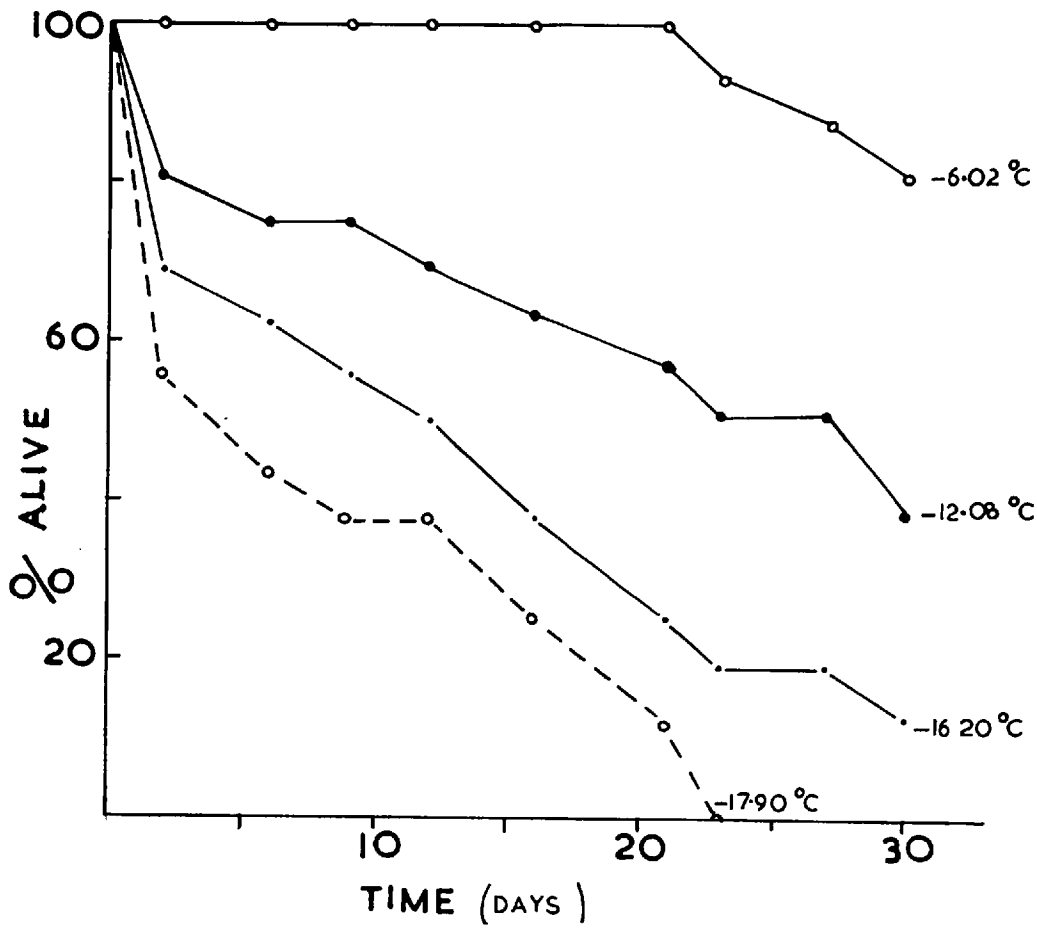


FIG.9. SURVIVAL OF LARVAE AT SUB-ZERO TEMPERATURES.



6. ADULT EMERGENCE

6.1 Adult Emergence in the Field

The appearance of the adults in the field began in about the second week of June in each of the three seasons. The proportion of the total adult population that emerged each week was assessed by the use of emergence bags which covered known quantity of broom bushes (see Section 11, p.91). Fig.10 shows the trend of the weekly emergence in 1964; the emergence patterns in 1965 and 1966 were basically similar. Emergence in the field was at first gradual, but the rate steadily increased for about two weeks before peak of emergence was attained. The average daily maximum temperature in the week preceding that in which the peak emergence occurred was 16.8°C in 1964, 20.2°C in 1965 and 20.1°C in 1966; this may partly explain the agreement in the time of the greatest emergence in years 1965 and 1966 (see Table 11). In 1964, this temperature was low, and the peak emergence was a day later than in 1965 and 1966.

Figs.11 and 12 show the rhythms of emergence when counts of *Leucoptera* adults that emerged from large numbers of cocoons kept in the field in well ventilated plastic cages, were taken at 2-day intervals; they also suggest that there may be some periodocity in the emergence of the adults. As is true of many insects, the emergence of the males preceded that of the females; in *Leucoptera* this difference in time is from three to four days. The rate of emergence of the males was not overtaken by that of the females until the former had attained their peak numbers. The tendency for the males to start to emerge before the female has been shown to be probably inherently determined (see Section 4.2), but it is possible that it could also be associated with the fact that the females, on the average, are larger than the males in size.

FIG·10. EMERGENCE OF LEUCOPTERA IN FIELD, 1964.

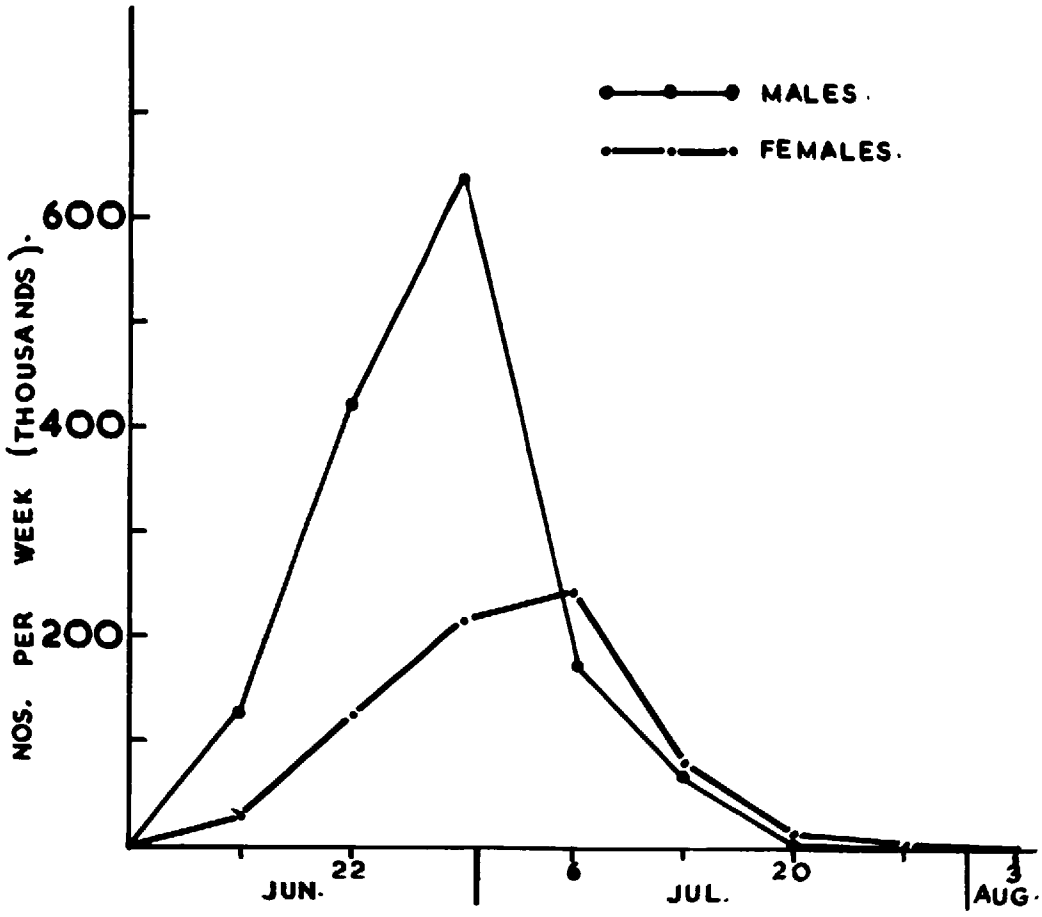


Table 11 Duration of adult emergence period, and the week of maximum emergence, in the three seasons.

Year	1964	1965	1966
First emergence	13.VI.	12.VI.	13.VI.
Last emergence	27.VII.	13.VII.	4.VII.
Max. emergence wk.	22.VI-28.VI	21.VI-27.VI	21.VI-27.VI

The adult emergence period is protracted, and in each of the three seasons exceeded three weeks (Table 11). Richards and Waloff (1946) have shown that the time of emergence of an adult Ephestia elutella (Hbn.), within the emergence period, may be determined genetically as well as by larval size which may be related to the nutritional factors. Table 12 summarises the emergence of the adults from:

(i) eggs laid by Leucoptera females on potted broom plants exposed to the field at various times during the oviposition period, and retained in the field until the adults had emerged; and:

(ii) from the wandering sixth instar larvae collected at different times in spring, and provided with cocooning and pupation sites in 3" x 1" tubes in the field.

It appears from the figures in Table 12 that eggs laid early in one season will give rise to the early moths in the succeeding season. Also, wandering larvae collected early in the spring give rise to adult Leucoptera that are the first to emerge in the summer. These differences in the time of emergence of adult Leucoptera seem likely to be partly genetic, as the females that emerge first usually lay the early eggs from which the earliest females appear in the following year. The size of the larvae may not be directly involved, since the sixth instar larvae that moult late from the fifth, tend to be larger than those that moult earlier (see Table 13); the latter would normally be expected to give rise to the early wandering larvae from which the earliest emerged moths derived.

Table 12 The emergence of adult Leucoptera from eggs and wandering larvae kept in the field.

Date eggs laid(1965)	No. cocoons formed	% adult emerged	Emergence dates and No. adults emerged (1966)									
			13.VI	14-15.VI	16-17.VI.	18-19.VI	20-21.VI	22-23.VI	24-25.VI	26-27.VI	28-29.VI	30.XI 1.VII
14-15.VII	4	25	0	0	1*	0	0	0	0	0	0	0
2-3.VIII	13	30.8	1	1	0	2(1*)	0	0	0	0	0	0
16-19.VIII	11	54.6	0	0	2	2	1*	0	0	0	1*	0
25-28.VIII	11	72.7	0	2	2	2	1	0	1*	0	0	0
Date larvae collected.												
10.IV.	10	20	0	0	0	0	0	1*	0	0	0	1
29.IV.	15	26.7	0	0	0	0	0	1	1	0	2*	0
3.V.	13	30.8	0	0	0	0	0	0	0	0	0	4(1*)
6.V.	3	66.7	0	0	0	0	0	0	1*	1	0	0

* female moth. (1*) a female moth and is included in the main number of moths that emerged.

Table 13 Relative weights of newly moulted sixth instar larvae.

Date	No. larvae weighed	Average weight (mg)	Average wt. + Mean head capsule width
24.III.65	3	0.567	1.206
9.IV.65	5	0.560	1.236
14.IV.65	10	0.590	1.283
21.IV.65	7	0.539	1.190
28.IV.65	6	0.659	1.430
5.V.65	4	0.682	1.436

+ This ratio may be a better index of size.

FIG.11. EMERGENCE OF ADULTS IN FIELD CAGES, 1965.

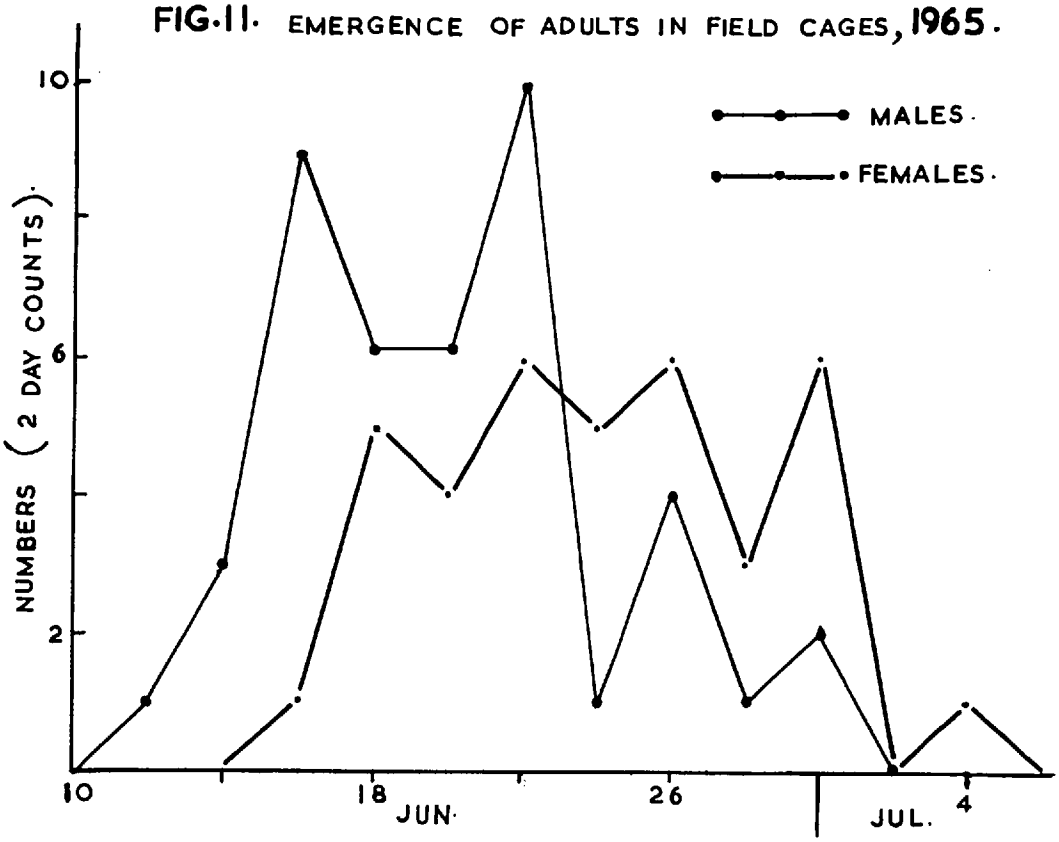
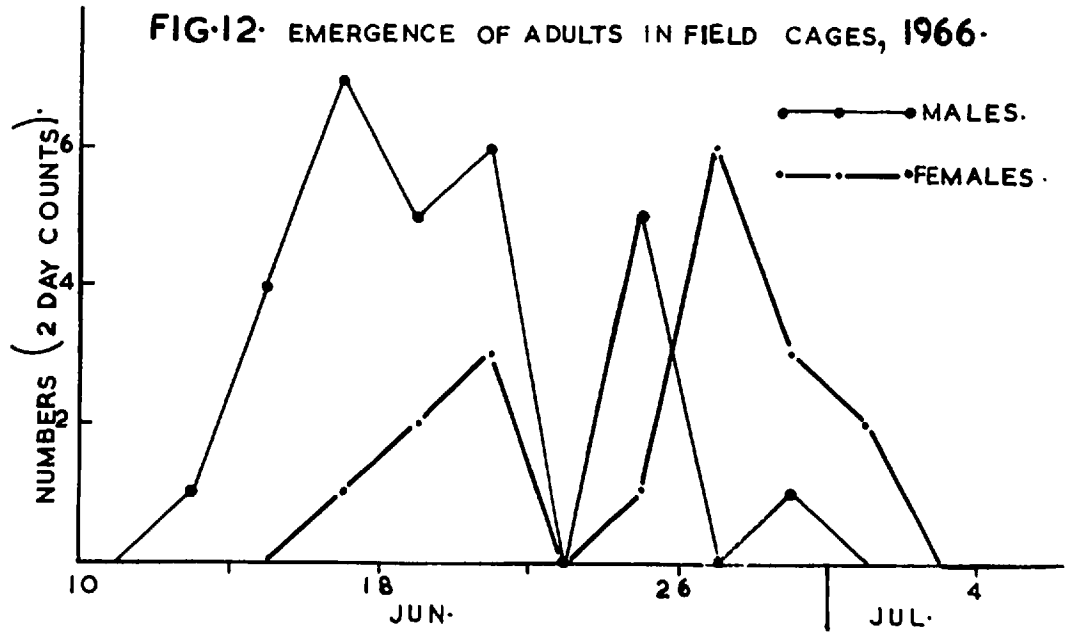
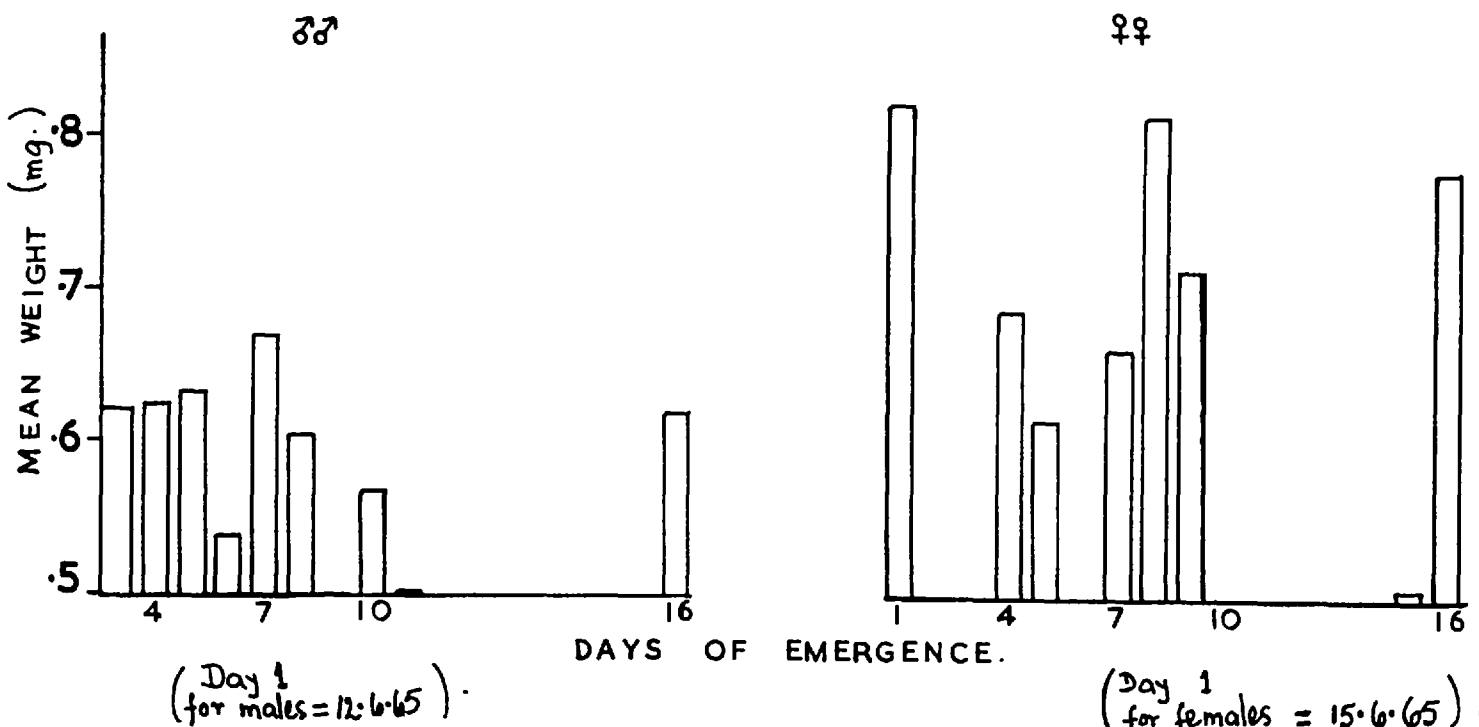


FIG.12. EMERGENCE OF ADULTS IN FIELD CAGES, 1966.



FIG·13· DISTRIBUTION OF WEIGHT AT EMERGENCE OF LEUCOPTERA·



The distribution of the weight of the males and the females at emergence with the time of emergence is illustrated in Fig. 13. These data suggest that the average female is heavier than the average male at emergence, but that there is no obvious correlation between the weight of the adult, at emergence, and the time of its emergence.

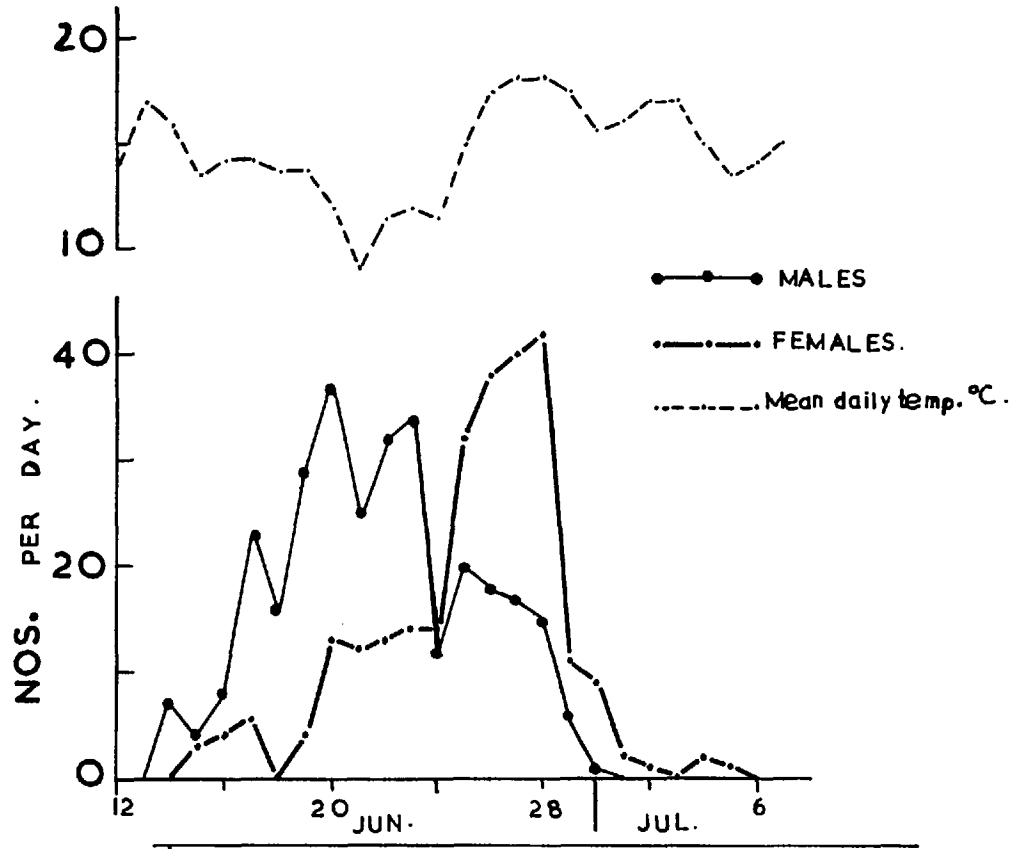
It may be concluded that the first appearance of adult Leucoptera each year is dependent on the time of emergence of the females in the preceding year, as that partly determined the time the eggs were laid; it is also dependent on the developmental period of the immature stages which is effected by temperature (see Table 6).

6.2 Periodicity in the Daily Emergence of Adults.

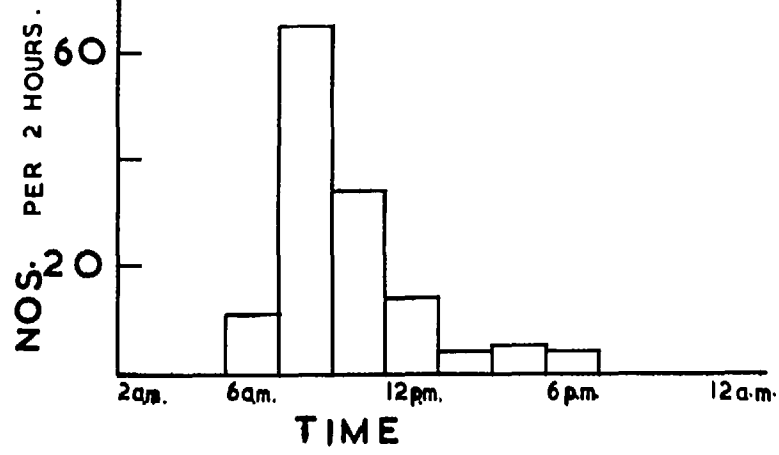
The pattern of adult emergence in the field suggested some periodicity in emergence (Figs.11 and 12). A total of 1068 cocoons, collected from the field two weeks before the emergence of the adults, were kept in clear polysterene boxes, 13 cm. x 6 cm. x 7.9 cm. Each box was ventilated by a pair of one-inch diameter holes bored on each of the two longer sides, and covered with coarse grade muslin. The boxes were placed in an unheated insectary. During emergence, daily records were made of the number of males and females that emerged. Fig.14 shows the trend of emergence in the insectary, and again suggests periodicity in the daily adult emergence.

For a week during this emergence in the insectary, counts were taken at two-hourly intervals of the numbers that emerged in the 24 hours of the day. The result is presented in Fig.15 and Table 14. It can be seen from these that the bulk of the adults emerged in the morning hours, viz., between 4 a.m. and 12 noon, with the peak of daily emergence occurring between 6 a.m. and 8 a.m. The numbers of adults that emerged fell rapidly after 8 a.m.; from 6 p.m. to 4 a.m. no emergence took place. Since the temperature in the insectary was not much different from that

FIG·14· ADULT EMERGENCE IN INSECTARY.



FIG·15· DAILY RHYTHM OF EMERGENCE IN INSECTARY.



in the study area (measured in a Stevenson's screen) in the summer, it may be assumed that the diurnal rhythm of emergence of Leucoptera in the insectary reflects that in the field.

Scott (1936) found that in the insectary Ephestia Anagastar Kuhniella showed a periodicity of emergence in which the peak of emergence was in the evening, and corresponded with the period of peak activity of the adults. This relationship was not seen to hold in Leucoptera spartifoliella in which, as will be shown later, the peak of adult activity was in the evening but most of the adult emergence occurred within the morning hours. It is probable, however, that the diurnal rhythm of emergence of Leucoptera may be connected with the daily fluctuations in temperature (see Fig.14).

Table 14 % emergence at different periods in the day.

Period	Number that emerged	Number that emerged as % of total.
4 a.m. - 12 noon	124	90.5
12 noon - 6 p.m.	13	9.5
6 p.m. - 4 a.m.	0	0
Total	137	100.

7. DISTRIBUTION OF IMMATURE STAGES, THEIR FEEDING HABITS AND TIME OF EMERGENCE OF LARVA FROM THE MINE.

7.1. Distribution of Immature Stages.

The eggs of Leucoptera are usually laid on green shoots of broom; the resulting larvae hatch out from beneath and into the host's tissue. In discussing the occurrence of the immature stages, the distribution of the larvae will be taken as similar to, and determined by that of the eggs. The distribution of the coooons (and thus of the pupae) will, however, be treated separately as it will normally be governed by the behaviour of the wandering sixth instar larvae.

7.1(a) Distribution of eggs.

The chorions of eggs, hatched or sucked, laid in the summer of one year can still adhere to the twigs in the spring of the following year. Thus, the actual oviposition sites can be identified long after oviposition and hatching in the field have ceased. For the standard samples in November 1963, twenty four broom bushes, selected at random, were each divided by eye into an upper and lower region. Two samples of equal weight were taken from each bush, one from each of the portions, and later searched for eggs. A record was made of the number of eggs, and of the twigs with eggs and of those without. The result is shown in Table 15, and suggests that Leucoptera females show a preference for the lower branches of the bushes for oviposition. When the results for 10 sampling occasions were considered, a 't' test revealed that significantly more eggs were laid in the lower branches of the bush than in the upper ($P = < 0.01$).

Table 15. Number of eggs in the bottom (B) and top (T) portions of broom bushes.

Date	Total no. eggs	Eggs laid (as %)		% of twig with eggs		No. of eggs per twig	
		(B)	(T)	(B)	(T)	(B)	(T)
16.XI.63	670	67.2	32.8	42.4	25.6	0.55	0.36
18.XI.63	544	73.3	26.7	42.2	21.9	0.68	0.32
21.XI.63	553	70.3	29.7	36.6	20.2	0.62	0.39

The vertical variation in egg density suggested in Table 15 was investigated further. Ten broom bushes were selected at random, and from widely separated points in the study area. With the aid of a pole marked out at foot intervals, samples were taken from each of the bushes. The pole was stood against each of the bushes in the western aspect, and the springs that touched it at 1, 2, 3....8 foot heights were cut and marked. Only a single cutting was taken at each level. All the 10 cuttings for each height were weighed together, and then searched for eggs. The density of eggs - i.e. number of eggs per 100 g. - at a height was computed from the total number of eggs recorded at that height. The result is represented in Fig.16 in which the logarithm of the number of eggs per 100 g. is plotted against height of the broom bush above ground surface. There is a very significant negative regression between the density of eggs and the heights at different level of the bush ($b = -0.1636$, $P = <0.001$). This relationship is described by the equation:

$Y = 2.8744 - 0.1636x$ where y is the logarithm of the number of eggs per 100 g., and x, the heights at the level of the bush being considered. A closer examination of the points in Fig.16 shows that the egg density increases with the height of bush until about two foot level, but then falls off fairly rapidly towards the top of the bush.

Some of the explanation for the gradient in egg density up the broom bush become apparent when the quantity of green broom at different levels of the bush, and the height of flight of female Leucoptera in the habitat are considered (see Table 16). The figures in Table 16 distinctly show that the density of eggs at any given height of the broom bush may be determined partly by the availability of oviposition sites, and partly by the height of flight of the females.

FIG·16· DISTRIBUTION OF EGGS ON BROOM·

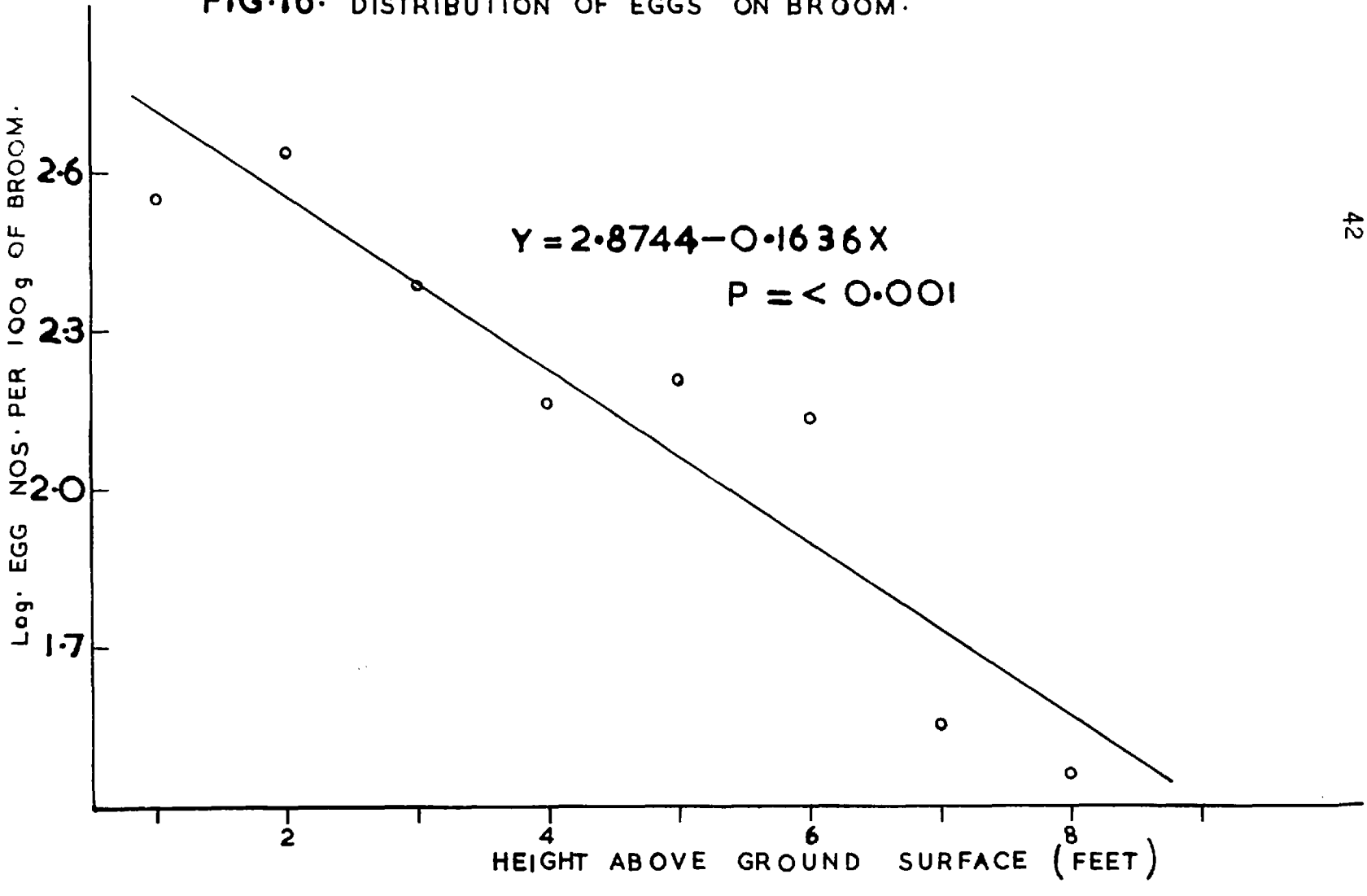


Table 16 Relation between number of eggs at different heights of broom, quantity of green and height of flight of females.

Item	Portion of Bush			Year
	Bottom	Medium	Top	
Number of eggs per 100g. (as %)	22.82	42.64	34.54	1964
Broom green per quarter bush (as %)	6.66	51.33	42.01	
Number of eggs per 100g. (as %)	37.90	41.70	22.40	
Broom green per quarter bush (as %)	9.92	65.97	24.11	1965
Females flying (as % of total)	28.57	61.91	9.52	

The ratio of variance, S^2, to mean, $\bar{x}$, and the value of K (estimated from S^2 and $\bar{x}$), calculated for the egg occurrence in the field, on or near the days of maxima of eggs, are shown below: the parameter K measures aggregation:

Date	$\frac{S^2}{\bar{x}}$	K
18.VII.64	14.2465	2.2293
28.VII.65	8.9482	2.5477

The excess of the variance over the mean, and the low values of K show that the eggs are usually aggregated. It will be shown later (Section 11.4) that adult Leucoptera exhibit an aggregated distribution in the field, and so the aggregation of eggs indicated above may be partly due to this.

The effect of the age of the broom bush on egg distribution in the field was investigated in 1965. The bushes in the experimental area were planted out in 1957; but younger bushes, one to four years old and offspring of the older bushes, can be found in and around the area. The bushes in the study area were classified into four age groups:

1.	1 to 2 years old,	1ft. to 2ft. high
2.	2 to 3 " "	2' " 3' "
3.	3 to 4 " "	3' " 4' "
4.	4 to 10 " "	above 4ft. high.

Twelve bushes were selected at random from each group, and a sample was taken from the middle of each bush in the western aspect. The samples for each age group were weightd together, and the number of eggs on them recorded. In the few cases where the egg shells had fallen off, the number of the mining larvae was taken. The result is summarised in Table 17. The density of eggs is higher in the younger bushes; this is probably because the younger bushes provide more suitable oviposition material than the older ones. The higher egg density in the 2 to 3 year age group, compared with the 1 to 2 year olds, may be a reflection of the preferred height of flight of the females within the habitat.

Table 17 Comparison of the density of eggs and the age of bushes.

Age of bush (years)	No. eggs per 100g.	Number of eggs as % of total
1 - 2	1792	32.22
2 - 3	1972	35.45
3 - 4	1153	20.73
4 - 10	646	11.60

7.1(b) Distribution of Cocoons.

The distribution of the cocoons was studied during the large pupal population of 1964. 24 bushes were selected at random, and a single one-eighth bush sample was taken from each of them. Each sample was subdivided into four portions - inner bottom (IB) outer bottom (OB), inner top (IT) and outer top (OT) - (see section 2). The wood and the green components of each portion were weighed separately. Dead twigs were included in the green, since cocoons are found on both of them. The green in each portion

was examined for cocoons. If, for example, x cocoons were found in the 24 'IB' subsamples, then the average number of cocoons in the 'IB' region of a bush = $\frac{24x}{8}$. Estimates for the mean numbers of cocoons in the OB, IT and OT regions of a bush were similarly obtained. The result in shown in Table 18, along with the estimated density of cocoons expressed as numbers per 100g. of green broom, and suggests that there is a vertical variation in the distribution of cocoons on broom. The density of cocoons is highest in the inner bottom region, but falls off towards the top of the bush; the distribution of green branches on broom does not appear to influence this trend. Turkey's test revealed that the fall in cacoon density with the height of the portion of broom sampled is significant (Table 19).

Table 18 Vertical distribution of cocoons on broom in 1964.

Item.	Portion of Bush			
	IB 0-2.5 ft.	OB 2.5-4 ft.	IT 4-6 ft.	OT 6 ft.
No. of cocoons as % of no. per bush	26.06	64.91	7.29	1.74
No. of cocoons per 100g. green (as %)	49.24	36.34	10.51	3.91
Broom green as % of total per bush, 1963*	6.27	30.86	18.33	44.54

* cocoons are spun on previous year's green.

Table 19 Significance of difference of mean number of cocoons at different heights of broom (Turkey's Test). Critical difference (i.e. t at 5% x std.error) = 5.99.

Portion of bush	Mean no. of cocoons per 100g.	Difference between means
IB	59.11	IB-OB = 15.49*
OB	43.62	OB-IT = 31.00*
IT	12.62	IT-OT = 7.93*
OT	4.69	

* significant since above the critical difference.

The estimated values of the ratio of variance to the mean ($\frac{S^2}{\bar{x}}$) and of K are shown below:

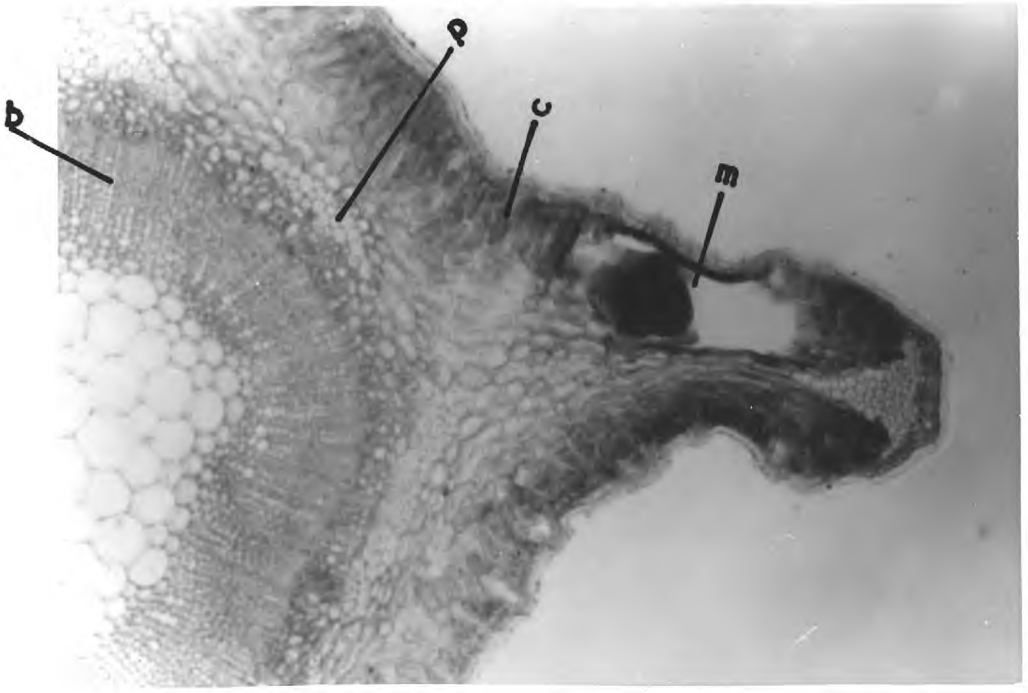
	IB	OB	IT	OT
$\frac{S^2}{\bar{x}}$	41.738	14.011	19.676	33.098
K	1.451	3.353	0.676	0.146

The high values of $\frac{S^2}{\bar{x}}$ and the low K indicate that Leucoptera cocoons are usually aggregated in their distribution on broom. The inverse relation between the direction of increase in density and that of the increase in the degree of aggregation of cocoons on broom (Table 18) is explained when the relative weight and length of the twigs in the top and in the bottom portions of a bush are considered. The bulk of the twigs at the top part of the bush represents the autumn growth. Observations showed that twigs at top of the bush are generally heavier than those at the bottom; a given weight of green broom from the top portions of the bush may therefore, contain fewer number of twigs, and so fewer cocooning sites, than the same weight of green from the lower regions of the bush. The reduced degree of aggregation of cocoons in these lower regions of the bush may be due to greater availability of cocooning sites in them.

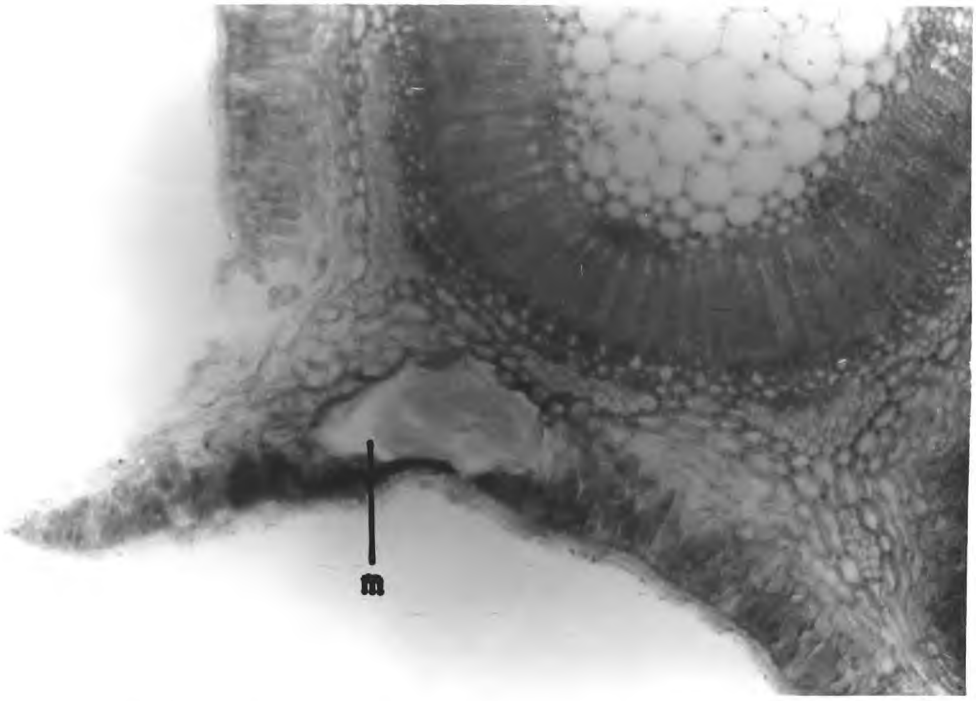
7.2 Type of Tissue Mined by Larvae.

The larval stages, except the wandering sixth instar, mine in the broom twig. To identify the tissue in which the larvae mine, transverse sections of the twig were cut. A two inch length of fresh twig containing a mining larva was embedded in pith and reasonably thin transverse sections were cut from it by hand. The sections were mounted in water and examined under a microscope. More permanent sections were prepared by fixing the twigs in acetic alcohol for 24 hours, hand-sectioning them in pith and then staining in Safranin and Light Green botanical stain. The procedure was to stain the sections in Safranin alcohol for 2 to 3 minutes, rinse in water, and counterstain in Light green in Clove oil after dehydrating in alcohols - ascending to absolute. The sections were cleared in Clove oil, and then mounted in Balsam

FIG.17. Tissue mined by larvae.



m = mine c = collenchyma



p = pericyclic fibres b = vascular bundle

after rinsing in xylene. Sections were cut from all parts of a 'mine'.

Fig.17 shows the tissues of the broom twig and the position of the 'mine'. The epidermis is broken in places by stomates, and the underlying outer cortical cells are heavily laden with chloroplasts. This outer region of the cortex was distinctly green in the fresh sections; the walls of its cells were stained green in the permanent preparations, indicating the presence of cellulose. The Leucoptera larval 'mine' was usually restricted to this region of the cortex. Occasionally, the 'mine' extended one or two cell layers into the inner cortical region but never into the pericyclic fibre region.

Mclean et al. (1962) state that the chloroplasts in the outer cortical cells (Chlorenchyma) are functional, and in broom and some other Xerophytes are true palisade tissue comparable with that in the leaf and undertake photosynthetic function. The nutritive value of the collenchyma cells to Leucoptera larvae is outside the scope of this work.

7.3 Emergence of Larva from 'Mine'

7.3(a) Period of emergence from 'mine'

The end of the 'mine' usually bulges out three to four days before the sixth instar larva emerges from it. In 1964, five potted small broom plants 1.5 feet to 2 feet high were exposed in the field during the adult oviposition period. They were left in the field, but were brought into a glass insectary early in the spring in 1965. The temperature in the insectary was measured with a Six's maximum and minimum thermometer. 28 'mines', as soon as they showed the 'bulge', were each marked and numbered with a spot of white non-toxic paint about 0.5cm. from their ends. Observations were then taken daily to record the number of the sixth stage larvae that emerged at six hourly intervals. The result is presented in Table 20. The analysis of the result revealed a very significant association ($P = < 0.001$) between the time of day and the emergence

of Leucoptera larvae from their 'mine'. Most of the larval emergence from 'mine' occurred within the morning hours (i.e. 6 a.m. - 12 noon). This has already been shown to be true of adult emergence in the field (see Section 6).

Table 20 The period of emergence of larva from 'mine'

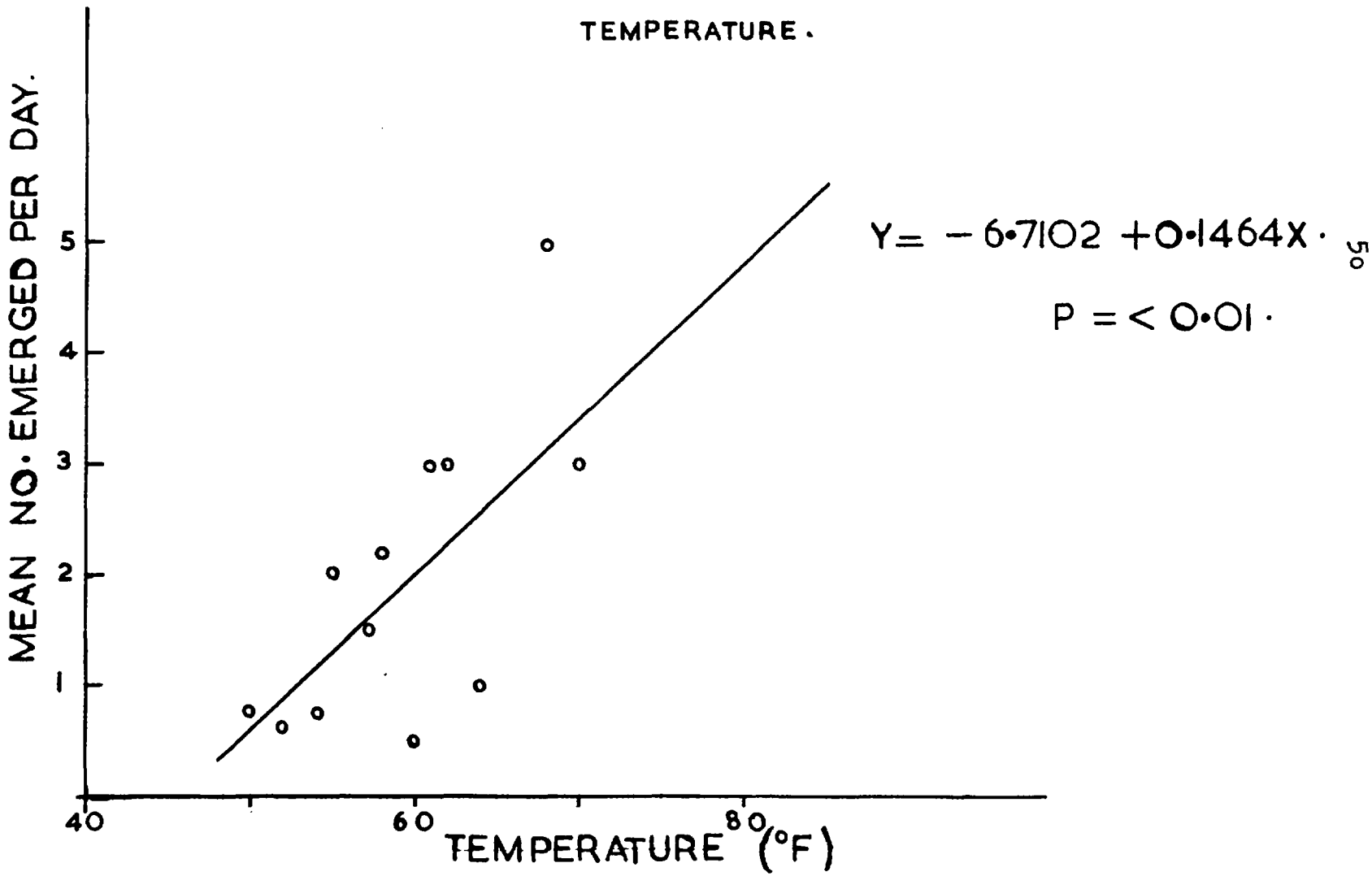
Emergence	Time and No. emerged				χ^2
	6 a.m.- 12 noon	12 p.m.- 6 p.m.	6 p.m.- 12 a.m.	12 a.m.- 6 a.m.	
Expected	7	7	7	7	=62.0
Observed	25	2	1	0	P=<0.001

7.3 (b) Effect of Temperature on Larval emergence from 'mine'

Observation showed that the sixth stage larva may cut its emergence hole but still remain in the 'mine'. This, and the fact that many wandering sixth instar larvae were usually seen on warm sunny days, suggested some temperature effect on the larval emergence from mine. A simple experiment was set up to investigate this.

The mining larvae were obtained by a process similar to that described in Section 7.3(a). The potted plants were brought into the glass insectary early in April, 1965. The daily maximum temperature in the insectary was recorded from Six's thermometer. The plants were examined at 6 a.m. each day, and all the sixth instar larvae that had emerged recorded and removed. 51 larvae emerged in the 24 days that the records were kept. Where the same daily maximum temperature, t, occurred for p days, the mean number of larvae that emerged at t was obtained by dividing the sum of the larvae that emerged from mine on those p days by p. The maximum daily temperature taken was that on the day preceding that on which the count was made. The result revealed that larval emergence from mine is significantly correlated with temperature ($r = 0.7493$, $P = <0.01$). The linear relationship between larval emergence from mine and temprature (Fig.18) is described by the regression equation:

FIG·18· RELATION BETWEEN LARVAL EMERGENCE FROM MINE & TEMPERATURE.



$Y = 6.7102 + 0.1464$ where y is the number of larvae that emerged, and x, the maximum daily temperature.

7.4 Effect of the Mining on the Host-plant.

Heavy infestation by Leucoptera larvae cause serious damage to the twigs, and possibly the death of the host-plant. It has been shown (p.46) that the mining larva destroys the chlorenchymatous cells which in broom are photosynthetic in function. The importance of the Chlorenchyma tissue to the broom plant, particularly from autumn, when its leaves fall, to the spring when new leaves appear, cannot be over emphasized. Many of the broom bushes, or parts of them, died after the heavy larval population in 1964. An attempt was therefore, made to see if 'mining' contributed to the death of the twigs.

12 broom bushes were selected at random in the experimental area. Two samples, one of living twigs and the other of dead ones, were taken from each bush. Only one aspect of each of the bushes was sampled, and the samples were taken from the same point at the middle of a bush. In the laboratory, the lengths of all the twigs dead and of those alive were measured and recorded separately. The number of mines in each group of twigs was counted and also recorded. The density of 'mines', expressed as the number of mines per cm., was calculated for the live and the dead twigs and the mean 'mine' densities were compared by the t-test (see Table 21). It can be seen from this that the density of 'mines' on the twigs that die is significantly higher than that on the living ones. This, and the fact that 95.2% of the dead twigs were mined (in contrast to the only 61.1% in the live twigs) indicates that the mining Leucoptera larvae may cause serious damage to, and possibly the death of their host plant. It is of relevance that in California, where broom is considered as a weed, Leucoptera is the insect which is used to check its spread.

Table 21 The density of 'mines' on live and dead twigs of broom.

State of twigs	Total No. of 'mines'	Mean No. of 'mines'per cm.	$t_{(22)}$ and P
Live	152	0.1637	t=2.3877
Dead	284	0.3598	P=<0.05

8. OBSERVATIONS OF FEMALE REPRODUCTION.

8.1(a) Laboratory studies on oviposition.

The adults used in the determination of oviposition in the laboratory, in 1964, were obtained from cocoons taken in the routine weekly samples, and stored in an unheated outdoor insectary. In 1965, some of the cocoons were obtained from broom bushes in the Rockery Slope, about 350 ft. from the study area (see Fig.1); these were incubated at a 20°C constant temperature room until adult emergence. The moths were isolated in pairs (a male and female) in 3-inch by 1-inch glass tubes fitted with coarse-grade nylon topped bored corks. Each tube was marked, and the female provided with a piece of green broom twig, about 2.5 cm. long, for oviposition (Fig.19). Water to drink was supplied to each pair of moths from a strip of moist filter paper inserted so as to adhere to the side of the tube. The twigs were removed for examination between 10 a.m. and 11 a.m. daily, and fresh ones supplied. The number of eggs laid in 24 hours was recorded. Males were replaced if they died. In 1964, the adults were segregated into 'the pairs' two to three days after emergence, and 5 pairs were kept in each of four constant temperatures of 10, 20, 25, 28.5°C; counts of the number of eggs laid each day were made. The details are summarised in Table 22. The number of females used is too low, but a trend for more eggs to be laid at 20°C was evident. The average of the daily mean temperatures and of the daily maxima calculated for a month (i.e. 27 June-26 July) of the oviposition period in the field was very close to 20°C. The oviposition period decreased where as the average daily rate of oviposition increased with temperature.

Table 22. Number of eggs laid at different constant temperatures; average of daily mean and of daily maximum temperatures for a month of oviposition in the field, 1964.

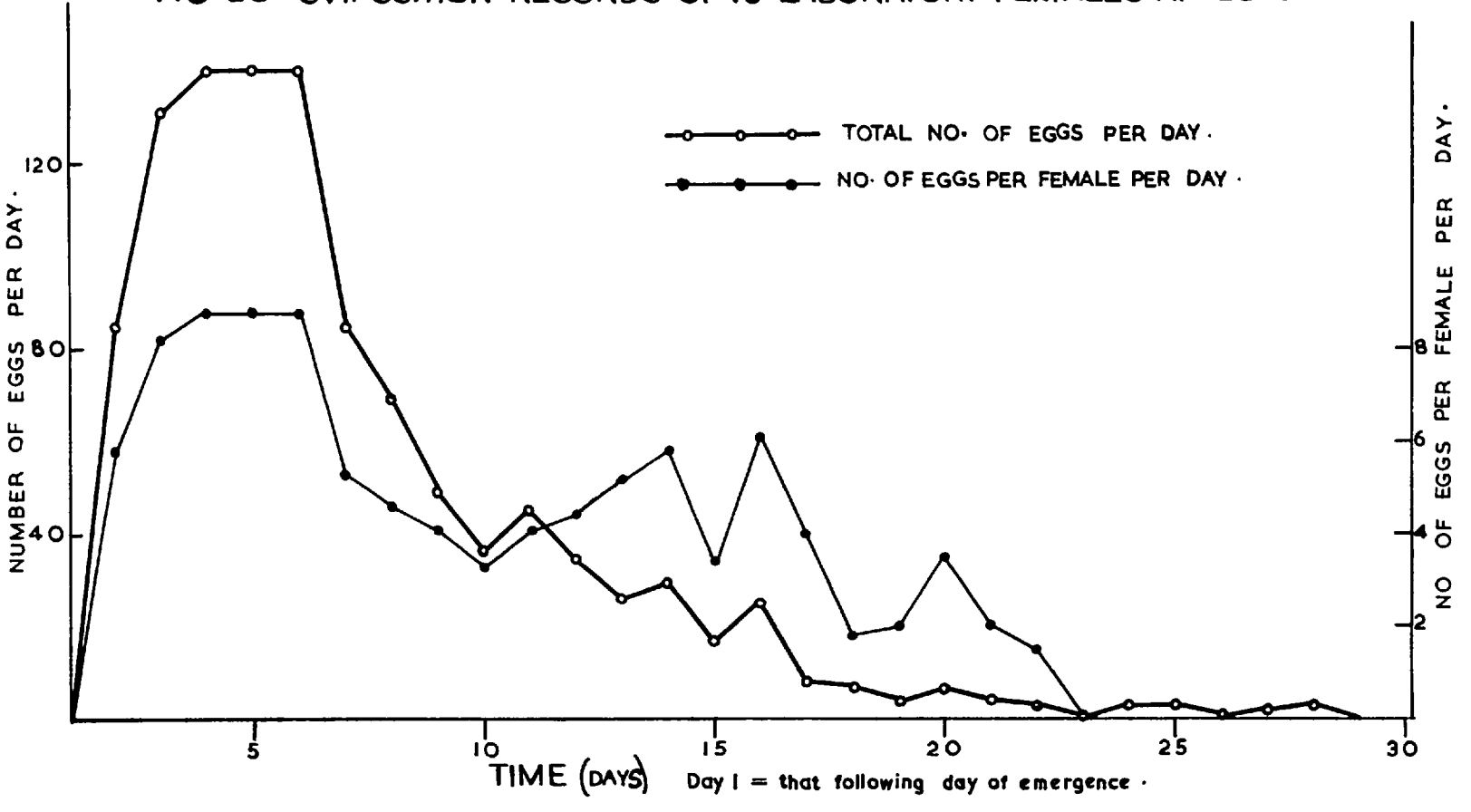
	Number of eggs per female (for 5 females)		Average of mean daily temperature (a) and of daily max. temperature (b) in the field. °C.
Temperature	Mean	Range	
10	26	1-77	(a) 16.8
20	72	55-139	
25	58	26-100	(b) 21.9
28.5	51	0-80	

In 1965, 36 females were used. 16 of these emerged from cocoons from the Rookery Slope, and 20 from cocoons from the study area at Gunness Hill. The moths were weighed and each was paired with a male within 12 hours of emergence, and then kept in 20°C constant temperature room. The pre-oviposition period averaged 3.6 days (limits 2 - 7 days). Daily oviposition records were kept separately for the two groups of females. The two populations from which the females were drawn differed in their average fecundity as follows:

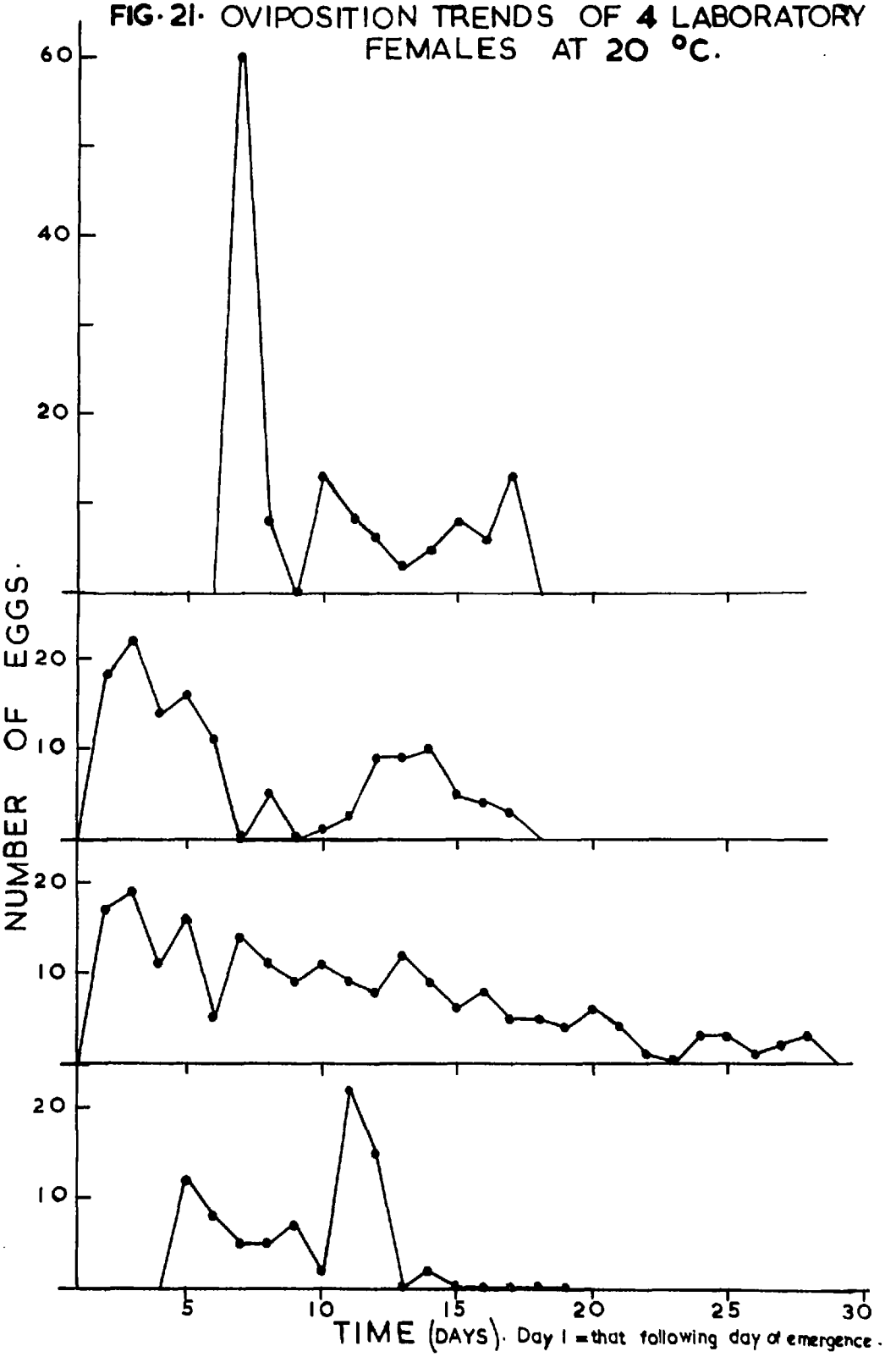
Location	No. of females	Weight (mg.)		Fecundity	
		mean	limits	mean	limits
Gunness Hill	20	0.73	0.37-1.04	43	0-103
Rookery Slope	16	0.79	0.38-1.26	68	6-202

When the total number of eggs laid by the Rookery Hill females per day was plotted against the oviposition period, most of the eggs appeared clearly to be laid in the first two to six days of oviposition, but the total number of eggs laid per day fell off after this (Fig.20). A plot of the daily oviposition rate per female against the oviposition period (see Fig.20) reveals that bursts of oviposition are usually followed by periods of relative

FIG·20· OVIPOSITION RECORDS OF 16 LABORATORY FEMALES AT 20°C ·



FIG·21· OVIPOSITION TRENDS OF 4 LABORATORY FEMALES AT 20 °C.



rest. This trend suggests periodic maturation of eggs from the oocytes. This periodicity becomes more apparent when the daily oviposition pattern of four of the females, selected at random, is considered (Fig.21). The pattern is again that in which most of the eggs are laid early in the oviposition period, days of much egg laying usually preceding those of relative rest. The short lived females lay most of their eggs within a few days; the long lived ones, however, lay almost continuously throughout the period of oviposition (Table 23). The greatest number of eggs laid by a female in one day was 60, but lower numbers are more frequently laid in 24 hours, the commonest numbers lying between one and five.

Table 23 The frequency of the number of eggs laid per day by 16 laboratory females, 1965.

No. of eggs per 24 hours.	0	1-5	6-10	11-15	16-20	21-25	26-30
Frequency	74	55	32	19	11	4	0

No. of eggs per 24 hours.	31-35	36-40	41-45	46-50	51-55	56-60
Frequency	1	2	0	0	0	1

It is clear from Figs.20 and 21, that the daily oviposition rate, y, falls off with the age of the ovipositing female, x. An analysis of the effect of age on the oviposition rate revealed that there is an inverse and linear relationship between the number of eggs laid by a female in a day and the age of the female. This linearity is expressed by the regression equation:

$$y = 1.2952 - 0.0266x \quad (P = <0.001)$$

8.1(b) Effect of fertilisation on oviposition rate.

The females used were bred from cocoons isolated singly in 3" x 1" tubes until the adult emerged. 30 females of the adult that emerged were divided into two groups of 10 and 20. Individuals

in the group of 10 females, (A), were paired, i.e. a female with a male, on emergence and supplied with green broom twigs for oviposition. The second group of females were also reared singly, and supplied with broom twigs but no males. After four days, this group was sub-divided into two groups, (B) and (C), each of 10 females. Females in (B) were each paired with a male; females in (C) were never paired. The group (B) females were dissected at death. All the three groups were kept in the laboratory (21 ± 1.5°C), fresh oviposition materials being supplied daily, and records of the number of eggs laid made.

The result is presented in Fig.22. The daily oviposition rate is distinctly depressed in the group (B) and (C) females, far below that of group (A), initially. When the males were supplied to group (B), the oviposition rate of the females immediately rose, far above that of the females in the cnntrol (A); but the oviposition rate in (C) still stayed low, increasing later on towards the end of oviposition. The average fecundity of the group (A) females was 53, 93.4 per cent of the eggs being fertile. The average fecundity in (C) was 25 and all eggs were sterile. The average fecundity in group (B) females was 28; 97.6 per cent of these eggs were laid after the males were supplied and 87.8 per cent of them were viable. 24.4 per cent of the eggs laid by the group (B) females on the day they were supplied with males were sterile. Post mortem dissection of the (B) females revealed presence of sperm in their bursa. It may be concluded that the fertilised females of Leucoptera lay more eggs than the virgin females. Unmated females also lay eggs, but these are non-viable.

8.1(c) Total fecundity

A distinction is made here between the potential fecundity, i.e. the number of eggs and egg rudiments produced in the ovary of a female (whether these are laid or not), and the mean number of eggs actually laid by a female.

In 1965, 32 females were weighed individually on emergence, and then divided into two equal groups. One group was dissected and the number of mature eggs and oocytes recorded. Each of the 16 females in the other group was paired with a male, supplied with oviposition material, and kept in the 20°C constant temperature room. The eggs laid were counted daily, and fresh broom twigs were supplied. The females were dissected at death to record the mature and immature eggs still unlaid. The details are shown in Table 24. The two groups of females are practically comparable in weight, but both the average number of eggs actually laid and the potential fecundity in the laying females exceeded the potential fecundity on emergence. This suggests that the full compliment of eggs and egg rudiments are not present on emergence, and more oocytes become differentiated during the life of the female. The excess of the potential fecundity of the laying females over the total of eggs and oocytes on emergence is 24.2%, but this difference is not significant. It is also likely that there is no resorption of egg rudiments by the fertilised females.

Table 24. Weight on emergence and the potential and actual fecundity of 16 laboratory females, 1965.

Group of female	No. of females	Weight (mg.)	Mean No. of eggs and oocytes	
			Eggs laid	Eggs and Oocytes
Dissected on emergence.	16	0.76	-	66
Kept to lay	16	0.79	68	82

8.1(d) Weight of females on emergence, longevity and fecundity.

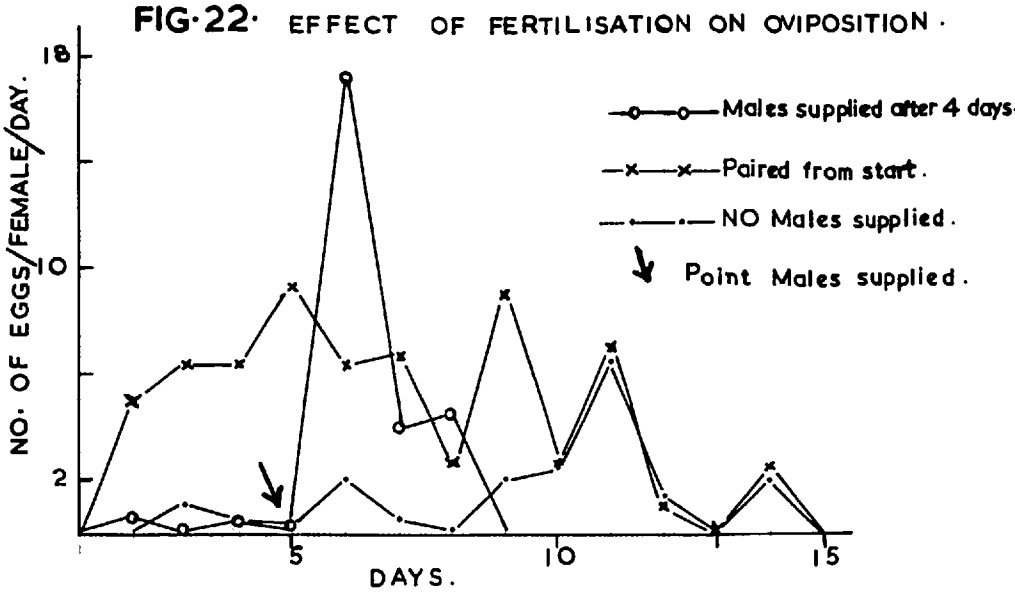
In 1965, 19 females weighed on emergence were paired singly with males, and kept at 20°C constant temperature room for egg laying. Daily counts and records of the eggs laid by each female were made. The dates of death of the females were also taken, and their longevity thus calculated. Analyses of the effects

of these two factors on the average fecundity of the females reveal a clear and a significant correlation between weight on emergence and fecundity ($r = 0.5346$; $n-2 = 17$; $P = < 0.02$). The correlation of fecundity with longevity of the females was not significant, ($r = 0.3992$; $P = < 0.1$; $n-2 = 17$). The estimated regression coefficient of fecundity on weight of females on emergence is 71.5894. This suggests that an increase of 1 mg. in the weight of a female on emergence would ideally increase its fecundity by about 72 eggs.

8.1(e) Number of mature eggs and oviposition rate in the field.

20 females and 20 males were captured each week from the study area, and introduced into two cylindrical cellulose acetate cages, 12" long and 9" in diameter. About half of the sides of each cage was cut away, and the opening sealed over with coarse-grade nylon sheet for ventilation. A small branch of a broom bush was introduced into each cage, and secured in position by tying off the sleeved end of the cage round its base (Fig.23). The branches caged were sleeved before adult emergence to ensure that no eggs were laid on them. 10 females and 10 males were put into each of the cages; the branches were cut after seven days and examined for eggs. The cages were transferred to fresh branches each week, and the male and female moths changed. Every week 10 to 12 females taken from the beating samples were dissected, and records made of the number of mature eggs in their ovaries. The results are compared in Fig.24. The trend in the daily oviposition rate in any given week follows closely that of the ripe eggs available in the field that week. The relationship between these two trends becomes apparent when the logarithm of the daily oviposition rate, y, is plotted against the logarithm of the average number of mature eggs in the week, x (see Fig.25). This indicates that daily rate of oviposition in the field depends significantly on the number of eggs maturing in the females in that week.

FIG·22· EFFECT OF FERTILISATION ON OVIPOSITION·



FIG·24· RELATION BETWEEN NO· OF MATURE EGGS, OVIPOSITION RATE &POPULATION AGE.

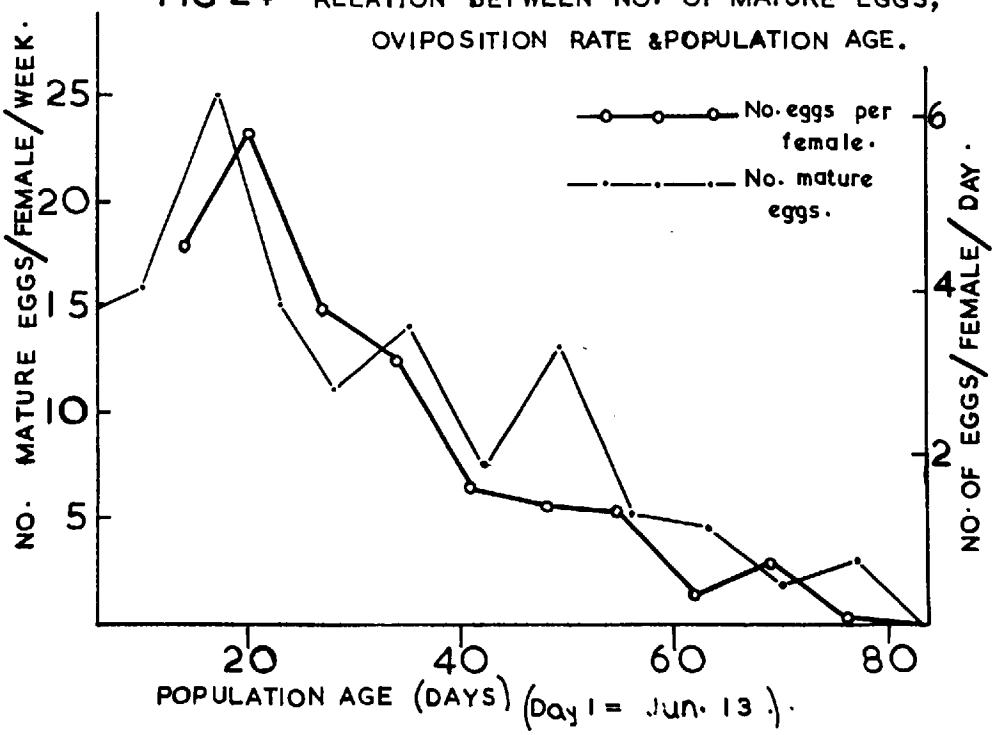
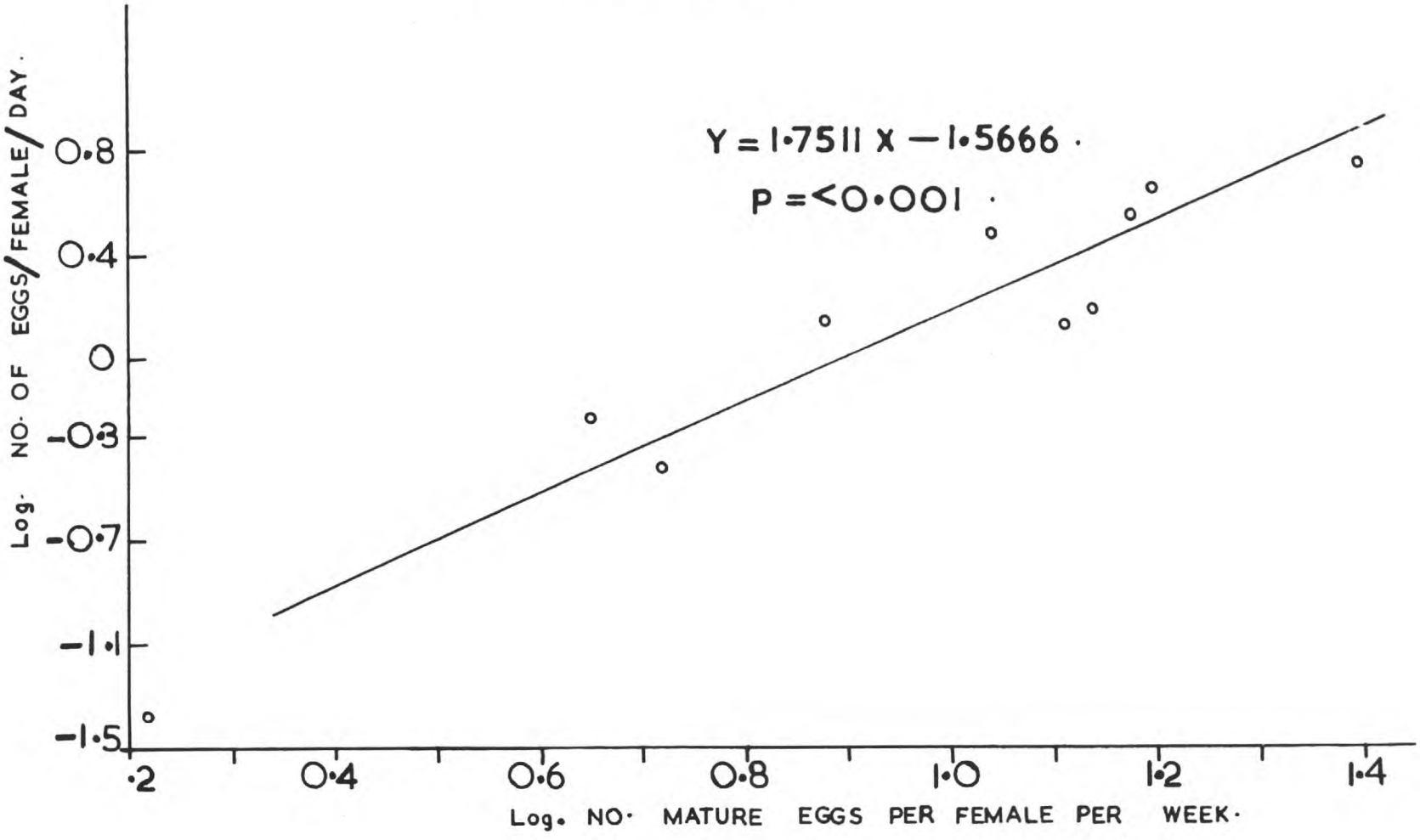


FIG.23. Field oviposition cage.

FIG·25· RELATION BETWEEN OVIPOSITION RATE & NO· OF MATURE EGGS



8.2 Changes in the Female Reproductive System.

The changes that take place in the female reproductive organs will be partly discussed in connection with emigration from the habitat (see Section 9, p.75). The ovary of L.spartifoliella is bilateral, each ovary comprising four ovarioles. In dissections of young and newly emerged females, some of the ripe eggs have already passed into the oviduct at the time of emergence of the female; however, the corpora lutea are not readily discernable until later in the oviposition period. In such young females, the lower section of each ovariole is occupied by mature eggs, the upper section by oocytes. 14 females dissected on emergence in 1965 had on the average 21 ripe eggs (limits 12 to 32), and 44 oocytes (limits 19 to 83). In general the number of mature and immature eggs decreases as oviposition progresses (See Fig.26). The relationship between the logarithm of number of ripe eggs, y, and age of the female (in days), x, in the field is linear and can be described by the equation:

$$y = 1.5325 - 0.0148x \quad (P = < 0.001).$$

The fat body also undergoes progressive changes in size in the ovipositing female. It is large in the newly emerged females, but decreases rapidly after oviposition commences. The assessment of fat body levels in the dispersing Leucoptera females will be discussed in section 9.3. Changes in the values of the fat body were similarly determined for the females all through the 1965 season. The result is shown in Fig.31. The knowledge of the value of the fat body can be a useful index in the assessment of the relative age of an insect population.

FIG·26· RELATION BETWEEN NO· OF EGGS; OF OOCYTES; FAT BODY & AGE OF FEMALES IN THE FIELD·

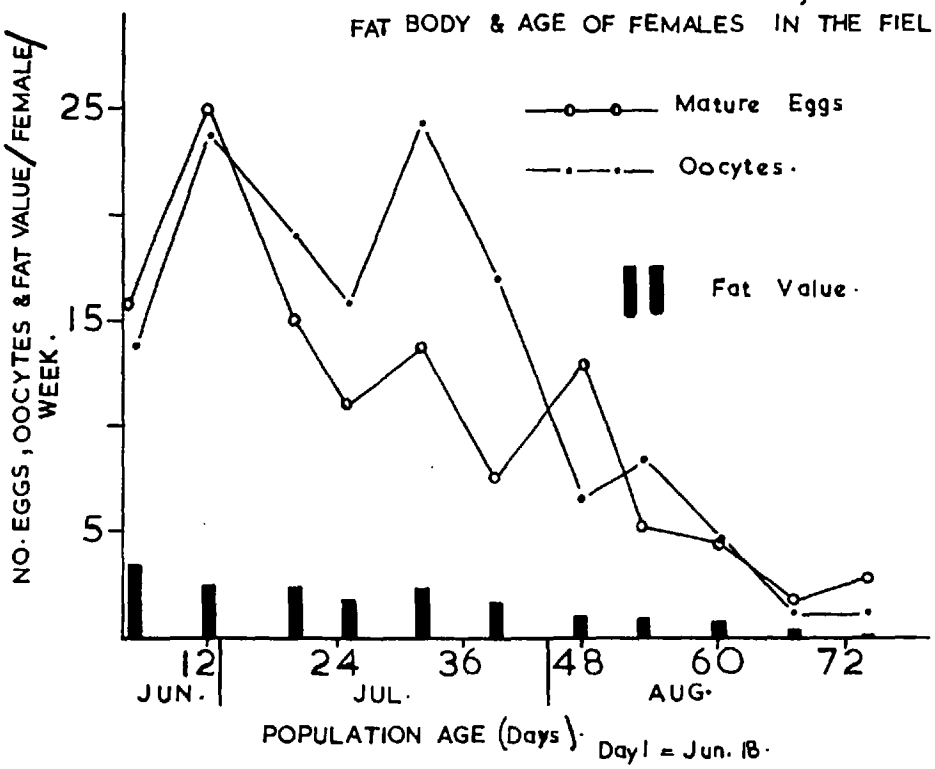


FIG.19. Egg laying tubes.

9. FLIGHT ACTIVITY OF L.SPARTIFOLIELLA

9.1 Adult Movement within the Habitat

The movement of adults from one bush to another is by flight, but within a bush active walking is undertaken by the males as they seek the females, and by the females when they search for suitable oviposition sites. The time and height of flight in the habitat were investigated.

9.1(a) Periodicity of flight

The time of flight within the broom plantation was studied in 1964. For five days in succession observations were carried out, in the centre of the study area at two hourly intervals, on the numbers of flying Leucoptera. Throughout every 24 hours, at intervals of 2 hours ten observations (each lasting 30 seconds) were made on the numbers of moths flying across a chosen field of vision. To obtain a more uniform field of view, two blinkers were cut from Bristol board and worn one on each ear. Each blinker was 9" x 3", and when worn projected outwards for about six inches. At night, a torch light was used. This did not disturb the result since Leucoptera adults are not attracted to light in the dark, since no moths were taken in a light trap 20 feet away from the study area.

The results of these observations are presented in Fig.27, and suggest that flitting can continue for the most part of the 24 hours. However, no flight occurred between 2 a.m. and 6 a.m., and there was very little flight in late morning and early afternoon (i.e. 6 a.m. to 2 p.m.). The numbers of flitting moths steadily increased in the evening, attaining a peak between 6 p.m. and 8 p.m., but then falling off rapidly as shown below

	2a.m.-6a.m.	6a.m.-2p.m.	2a.m.-6p.m.
No. flitting (as % of 608 moths)	0	3.5	11.8

	6p.m.-8p.m.	10p.m.-12p.m.
No. flitting (as % of 608 moths)	82.4	2.3

As is shown later the dispersive flights outside the habitat closely follow this daily rhythm.

9.1(b) Height of flight

The height of flight within the habitat was assessed with the aid of sticky traps (Broadbent and Doncaster, 1948). The trap was modified and consisted of a wooden pole, cubical in cross section and 7 feet high. 12 thin expanded steel plates, each six inches square, were fixed in pairs to the pole, and at foot intervals. Six inches were allowed at the end of the pole to be pushed underground. If the plates of the pair at one foot level face north and south respectively, the plates at two feet will face east and west, the pair at three feet north and south, and so on to the last pair at six feet. In this way the four aspects, north, east, south and west, were each covered three times (see photograph Fig.28). Grease bands were spread out and fastened to each of the plates. These bands were removed for examination every two days and replaced with new ones.

Table 25 which summarises the result shows that flight within the habitat takes place at different heights. Most of the flight (67.9%), however is concentrated between the heights of three to five feet. The males tend to fly mostly at five feet, and the females at four feet; but, there is no significant difference between their mean height of flight. It was shown in Section 7.1(a) that the height of flight of female Leucoptera is partly determined by the distribution of the green shoots on broom. It is probable that within the habitat, the males will fly mostly at heights likely to lead to the females.

Table 25

Heights (ft.)	1	2	3	4	5	6	Total No.
No. male flying (as %).	6.25	9.37	15.63	25.00	31.25	12.50	32
No. females flying (as %).	4.76	23.81	19.05	28.57	14.29	9.52	21

FIG.28. The sticky trap.

The proportion of the males to the females caught flitting in the habitat differed from the sex ratio of Leucoptera caught outside it on a pair of trap plants 27 ft. away from the plantation, and in an 18 inch suction trap 300 ft. south of the plantation (see Table 26). This suggests that more males than females flit within the habitat; the excess of the males over the females caught by the sticky traps is more than can be accounted for by the estimated population size of the two sexes. Outside the habitat, however, more females than males fly. This is of relevance when colonisation of new habitats is considered.

Table 26 Number of males and females (as %) caught on sticky trap within the plantation, and on trap plants and suction trap outside the plantation in 1965.

	Population estimate (in the habitat)	Sticky trap	Trap plant 27' away.	Suction trap 300' away.
Male :	58.1	60.4	39.5	44.5
Female:	41.9	39.6	60.5	54.5

The numbers of Leucoptera caught at the different aspects of the sticky traps within the habitat were as follows:

	North	East	South	West
No. flying towards (as % of 53 moths).	30.2	24.6	22.6	22.6

This indicates clearly that flight within the habitat is non-directional. The orientation of flight outside the area occupied by the population is different, and will be discussed later.

9.2 Dispersal of Adult L.spartifoliella

The flight activity outside the population source was assessed in three ways:

(1) By the use of broom trap plants (Waloff and Bakker, 1962)
(2) Suction traps (Johnson and Taylor, 1955)
(3) Sticky traps (Broadbent and Doncaster, 1948)

9.2 (a) Trap plants

These consisted of six pairs of small broom bushes, 2.5 to 3.5 feet high, planted at different distances away, and south of the plantation. The pairs were planted on a logarithmic scale of 3, 3^2, 3^3 ----- 3^6 feet, the first pair only three feet away from the plantation. The bushes in each pair are nine feet apart. These bushes were sampled daily between 9.30 a.m. and 10 a.m., and the numbers of Leucoptera shaken off each pair was recorded. Plants 1a and 2a, i.e. the two pairs nearest the plantation, died after a few beats in 1964, and had to be replaced several times during the flight period; this must have affected the data for that year. In 1965, all the bushes were examined in May and cocoons seen on them removed to ensure that any adults seen on them must have arrived by emigration from the plantation. The dispersive flights lasted for eight weeks in 1965, i.e. from 25 June to 13 August. A total of 643 Leucoptera adults were caught on the trap plants, 83.1% of the catch occurring between the third and fifth weeks of flight. The details of the catch in the 1965 season are as shown:

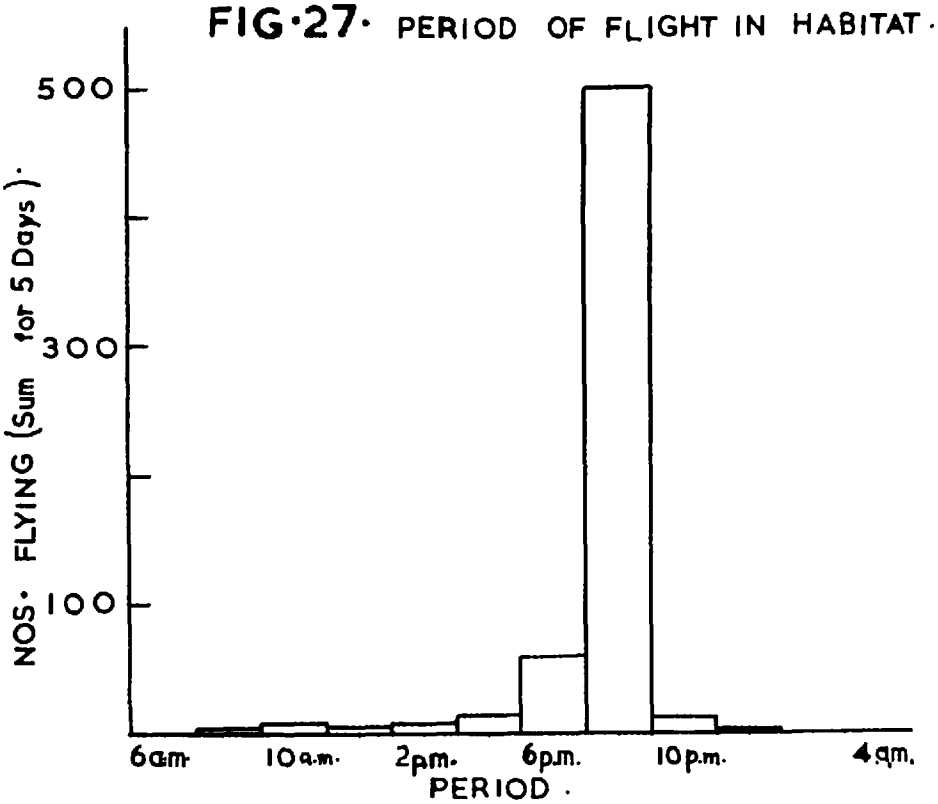
Distance from habitat (ft.)		3	9	27	81	243	729
No. Leucoptera caught	male	109	56	30	18	6	5
	female	191	118	46	40	15	9

It can be seen that the total number of the moths captured in the successive pairs of flight plants tend to fall off with the distance from the plantation. The numbers caught on the plants in 1964 and 1966 seasons showed similar trends. A linear relationship was found between the logarithm of the number of the moths, y, caught on the trap plants and the logarithm of the distance, x, away from the plantation. This linearity is described by the regression equation:

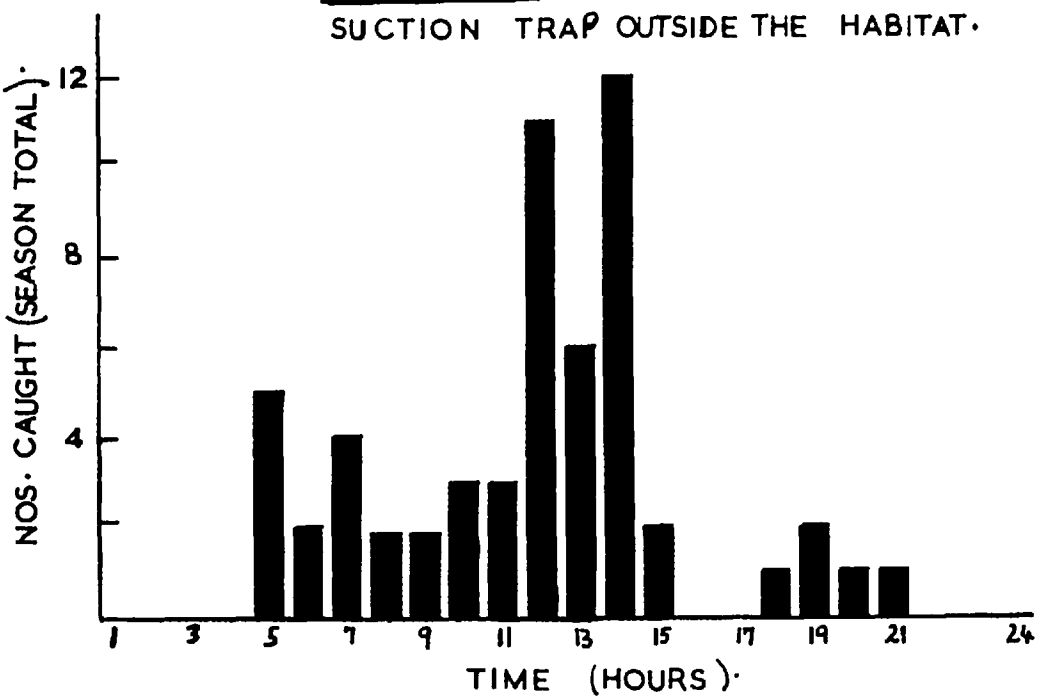
$$y = 2.7577 - 0.5705x. \qquad (P = < 0.001).$$

The inverse relationship between the density of the dispersing individuals and the distance from the population source has been demonstrated in Culicoides imperfectus (Kettle, 1951), and in a number of other insects.

FIG·27· PERIOD OF FLIGHT IN HABITAT·

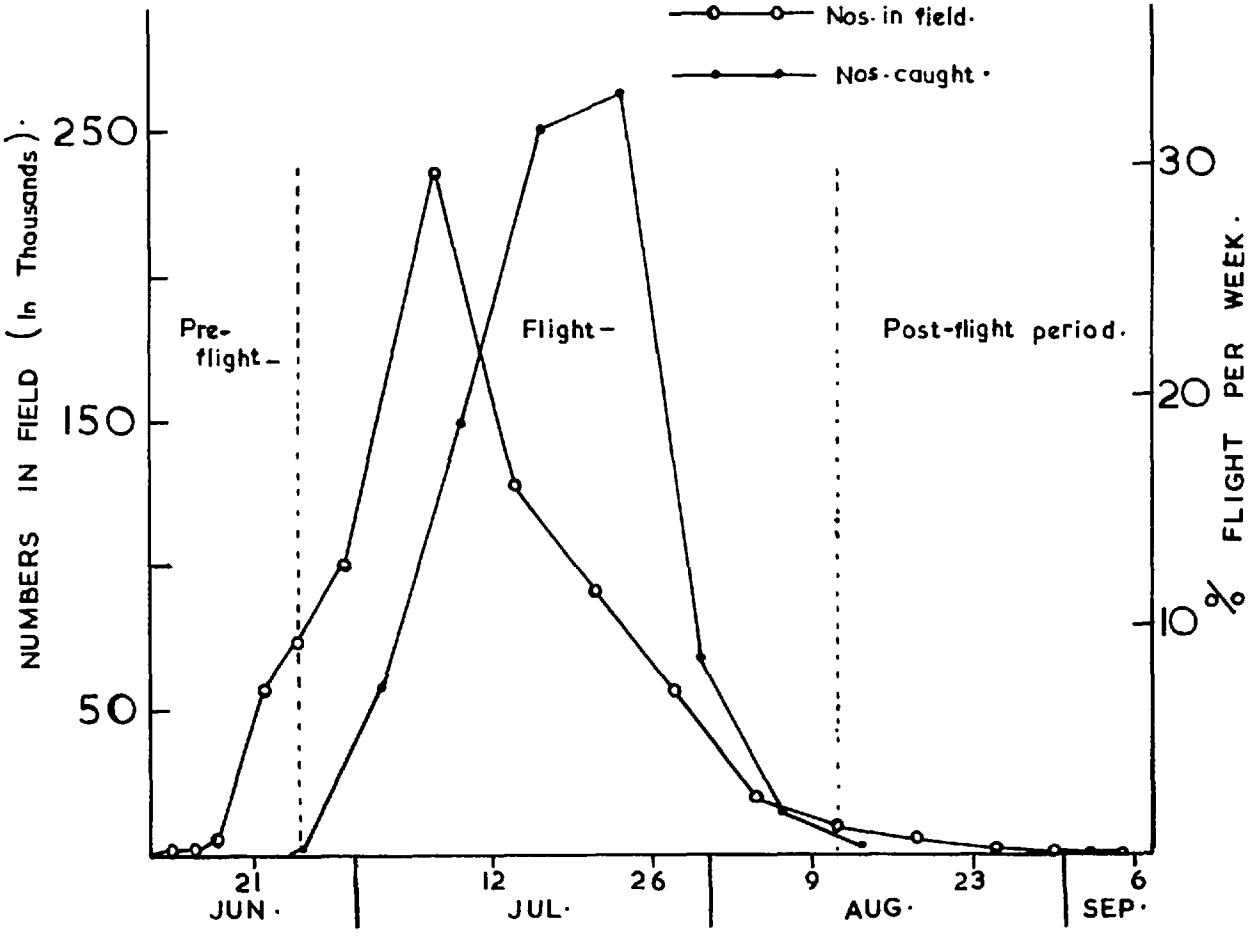


FIG·30· LEUCOPTERA CAUGHT IN DISC DROP SUCTION TRAP OUTSIDE THE HABITAT·



(1 = 6a.m. .. . . . . 7 = 12p.m. . . . 24 = 5a.m.)

FIG·29· RELATION BETWEEN NOS. OF LEUCOPTERA CAUGHT ON TRAP PLANTS & NOS. IN THE PLANTATION



The relationship between the number of Leucoptera captured on the trap plants, and the weekly estimates of the population trend is presented in Fig.29. There is a distinct flight phase during which the numbers dispersing tend to increase as the adult population builds up. The peak of the dispersive movement lagged behind the population peak by about two weeks; this is probably due to variations in readiness to migrate, which may also be associated with variations in the dates of emergence of adults (see Section 6).

9.2(b) Suction traps

Suction traps give the best and the most unbiased estimates of aerial densities of small insects. Two 18-inch propeller type suction traps are run 300 and 350 feet from, and south of the study area every year. One trap samples the air at 4 feet, and the other at 30 feet above the ground. In 1965, a 9" vent-Axia disc release type, which segregates catch into hourly samples, was also used, and provided additional information on the daily rhythm of the despersive flight.

Data for the suction trap catches are shown in Tables 27 and 28. The dispersive phase is protracted, and lasts approximately four weeks. A greater number of females than males tend to fly outside the habitat. The figures in the tables suggest that the density of Leucoptera in the air decreases with height, and so support recent views on the aerial distribution of insect populations (see Johnson, 1957).

Table 27 Leucoptera caught by 18-in. suction trap, 4' above ground on the days of first, peak and last catch; and the season total catch.

	1964			1965	
Catch	Date	Male	Female	Date	Male	Female
First	26-28.VI.	9	29	27.VI.	1	-
Peak	2.VII.	6	23	8.VII.	3	5
Last	24-26.VII.	1	1	28.VII.	-	5
Season total		30	90		20	24

Table 28 *Leucoptera* caught in 18-in suction trap at 30 ft. above ground.

1964			1965		
Date	Male	Female	Date	Male	Female
26-28.VI.	-	2	5.VII.		
30.VI.	-	1	8.VII.		1
14.VII.	-	3	9-11.VII.	1	1
17-19.VII.	1	-			
TOTAL	1	6		1	2

The data from the disc drop suction trap are presented in Fig.30, and indicate that dispersive flights from the habitat take place for the greater part of the day; however, no catches were obtained at 9 p.m., 10 p.m., and 3 a.m. to 9 a.m. Most dispersal occurred in the evening, with a peak between 5 p.m. and 8 p.m. This agrees closely with the daily pattern of trivial movements within the habitat (see Fig.27).

9.2(c) Sticky traps

The construction of, and the acquisition of data from these traps were described in section 9.1(b). Three traps placed 9', 81' and 702' respectively away from, and south of the plantation in 1965, provided information on the direction of flight outside the population area. The result is summarised in Table 29. The figures are too low to be conclusive, but it can be seen that the numbers of the moths flying out, i.e. eastwards, and the numbers returning to the plantation, i.e. westwards, are nearly equal near the habitat. This suggests that there is a tendency for non-directional flight near and around the plantation. Displacement farther away from the area of population appears directional, and may be influenced by the direction of wind (see Table 30).

Table 29 Direction of flight outside the habitat.

Distance from plantation (ft.)	Numbers flying towards				Total
	N.	E.	S.	W.	
9	1	7	6	6	20
81	1	-	1	-	2
702	-	-	1	-	1
Total	2	7	8	6	23

Table 30 Direction of flight and wind direction outside the plantation.

Distance from plantation (ft.)	Date	No. caught	Flying towards	Wind direction
81	14.VII.65	1	south	south
"	15.VII.65	1	north	north
702	12.VII.65	1	south	south-west

9.3 Reproductive state of females caught on trap plants.

Many migratory flights in insects are made by sexually immature and young adult females before or just immediately after the tenereal period (Johnson, 1960 a, b, c; Southwood, 1962; Johnson, 1963). In Leucoptera, the ovaries and about one-third of the eggs are mature at emergence. This makes it somewhat difficult to identify precisely the relationship between age and migratory movements in the females. In cases such as this, however, the relative numbers of mature and of rudimentary eggs in the ovarioles, the number of spermatophores in the bursa corpolatrix and the state of the fat body can be useful indicators of the physiological age of a lepidopteran population (Waloff, 1956). The age of the dispersing females in 1965 was assessed by this method.

Forty-nine Leucoptera females shaken off the trap plants during the flight period were dissected. Counts and records of the number of ripe eggs and differentiated oocytes in ovarioles were

made. The amount of the fat body, in comparison with that of females dissected immediately on emergence, was recorded as very high, high, medium, low and nil. These categories were scored as 4, 3, 2, 1 and 0. The spermatophore sac was usually digested within the bursa, but the presence of sperm in the latter was taken as evidence of mating. Females whose ovarioles showed corpora lutea were also noted as having oviposited. These data are summarised in Table 31a, and show that although all the dispersing females were sexually mature, 6.1% of them were still virgin. Females flying later in the flight period were older, were all fertilised and had all oviposited. The number of differentiated oocytes and the quantity of the fat body decreased as the flight period progressed.

Table 31a Reproductive state of females caught on trap plants in 1965.

Date	No. dissected.	Mean No. of mature eggs.	Mean No. of oocytes.	Mean value of fat body.	No. with sperm in bursa.
25.VI.	1	5	43	4	1
30.VI.	5	12	39	3.5	3
3.VII.	6	16	35	2.5	5
5.VII.	6	8	34	2.3	6
13.VII.	8	10	14	1.67	8
17.VII.	6	8	27	1.83	6
28.VII.	7	9	26	1.43	7
6.VIII.	4	8	19	0.50	4

The state of sexual maturity of the emigrating females is compared with that of the females in the field population in Table 31b. It can be seen that the emigrating females contain relatively more oocytes and fat body than those in the habitat. This suggests that, at least at the beginning of the migratory period, it is the younger individuals that tend to emigrate.

Table 31b Comparison of state of maturity of females caught on trap plants, (b_1) and of females from the field samples (b_2), 1965.

Date	No. dissected	No. mature eggs (Average)	No. oocytes (Average)	Fat body (Average)	Location
30.VI.	5	12	39	3.5	(b_1)
29.VI.	10	25	24	2.4	(b_2)
5.VII.	6	8	34	2.3	(b_1)
5.VII.	9	15	19	2.3	(b_2)
12.VII.	6	9	15	1.80	(b_1)
12.VII.	12	11	16	1.75	(b_2)

9.4 Factors affecting flight of Leucoptera

The physiological age of dispersing Leucoptera females has been discussed (see Section 9.3). The other factors considered were climate, the size of the population and the age of the population.

The relative level of flight from the population source was assessed by the number of Leucoptera shaken off daily from the trap plants. The climatic factors measured were the mean daily air temperature, mean daily air temperatures at the peak hours of flight (i.e. 3 p.m. to 9 p.m.), relative humidity, hours of sunshine at daily peak of flight and rain fall. These measurements were obtained in a Stevenson Screen in the centre of the plantation. The size of the population on each day of the flight period was read off from the graph of the weekly population estimates (see Fig.29). The age of the population was measured from the day preceding that on which the moths were first caught on the trap plants. The data on the eight variables were put through the College computer for analysis by Dr. G. Murdie. For this analysis, the data, n, on the numbers flying and on the daily population size were transformed into log. n + 1. These calculations included an

intercorrelation and a multiple regression analysis, and a β coefficient analysis for the predictor variables. These are illustrated in Tables 32, 33 and 34

Table 32 The mean and the standard deviations (s.) of the variables which may effect flight activity of L.spartifoliella. No. of observation = 50.

	Variables	Mean	s.
a	Age of population (days)	25.500	14.577
b	No. of Leucoptera in population ($\log_{10}$ n+1)	4.858	0.406
c	Temperature °C at 3 p.m. - 9 p.m.	16.138	1.903
d	Mean daily temperature °C.	14.716	2.335
e	Relative humidity (%)	77.020	10.794
f	Sunshine hours, 3 p.m. - 9 p.m.	1.416	1.630
g	Rainfall (m.m.)	0.560	1.599
h	Nos. flying per day ($\log_{10}$ n+1)	0.831	0.546

Table 33 Correlation matrix (i.e. Intercorrelation of the variables, a to g as in Table 32).

a	b	c	d	e	f	g
-0.8142***						
0.2262	-0.3819**					
0.1343	-0.1603	0.7326***				
-0.0486	0.2232	-0.2385	0.0188			
0.5423***	-0.5218	0.3488*	0.0665	-0.3292*		
0.1207	-0.0187	-0.2926*	0.1280	0.3919**	-0.1237	
-0.3755**	0.7125***	0.0180	0.1543	-0.1423	-0.2630	-0.1804

Level of significance : * = 5%; ** = 1%; *** = 0.1%

Multiple regression coefficient, R_9 = 0.8893

R^2 = 0.7908

F ratio (at degrees of freedom $n_1 = 7$, $n_2 = 42$) = 22.6761 ($P < 0.001$).

The figures in Table 33 show that the numbers of Leucoptera flying are significantly correlated with the size and, negatively, the age of the population in the plantation. Some of the other variables are significantly intercorrelated, viz: sunshine hours and population age, mean daily temperature and temperature at peak flight (3 p.m. - 9 p.m.), temperature and sunshine hours at 3 p.m. - 9 p.m., relative humidity and rainfall; and significant negative correlation between population size and age of the population, population size and temperature (3 p.m. - 9 p.m.), population size and sunshine hours (3 p.m. - 9 p.m.), temperature (3 p.m. - 9 p.m.) and rainfall and relative humidity and sunshine hours (3 p.m. - 9 p.m.).

The multiple regression coefficient, R, of 0.8893 is highly significant ($P < 0.001$), and is a clear indication that a good prediction of the numbers of Leucoptera flying on any given day can be obtained from the chosen variables. The R square ($R^2 = 0.7908$) shows that 79% of the variability of the numbers flying can be explained in terms of these variables. The regression equation for predicting the number of Leucoptera flying on any day of the flight period may be written as:

$$y = 0.0290X_1 + 1.9578X_2 + 0.1108X_3 - 0.0027X_4 - 0.0011X_5 - 0.0225X_6 - 0.0460X_7 - 11.0237$$

where $y = \log_{10}$ n+1 of numbers flying, and X_1, X_2 ..... X_7 = the predictor variables

Table 34 β coefficients of the predictor variables, a to g as in Table 32.

Predictor variables.	a	b	c	d	e	f	g
β coefficients	0.775	1.457	0.386	-0.012	-0.022	-0.067	-0.135

The β coefficients (Table 34) are measures of the predictive values of the seven chosen variables, and show that size and the age

of the population and temperature at the daily peak hours of flight, in that order, are the most important factors affecting flight activity in L. spartifoliella. Rainfall appears to be the most important variable in inhibiting flight. The estimated initial numbers of adults in the plantation, and the calculated proportions of the populations which had emigrated in the three successive years are as follows:

Year	Initial Nos. of adults in plantation	% that emigrated	No. that emigrated
1964	5,514,665	20.50	1,130,438
1965	2,710,487	16.75	454,077
1966	89,392	15.86	14,182

It will be seen that the numbers of emigrants fell in the years in which the sizes of the populations decreased.

10. SOME OBSERVATIONS ON THE BIOLOGY OF THE PARASITES OF L. SPARTIFOLIELLA.

The records of the parasites of L. spartifoliella in literature are summarised in Table 35. There are no previous records of the parasites of Leucoptera in the British Isles.

Table 35 Parasites of L. spartifoliella recorded in literature.

Parasite	Recorded by	Country recorded	Stage of host attacked	Reference
Entedon parvicalar (Thoms.)	Wagner	Germany	-	Rev. Appl. Ent. (A) 19, p. 127 (1931)
Tetrastichus crassinervis (Thoms.)	"	"	-	"
Tetrastichus punctiscuta (Thoms.)	"	"	-	"
Tetrastichus evonymellae (Bouche)	Parker	France	Chrysalids during pupal stage	J. Econ. Ent. 57, (1964), p. 566
I. evonymellae (Bouche)	Frick*	Calif. U.S.A.	Coccons	J. Econ. Ent. 57 (1964), p. 589

* the author suggests that the parasite was apparently introduced from Europe with its host.

The parasites bred from L. spartifoliella at Silwood Park were all Eulophidae (Hymenoptera). They were kindly identified by Mr. G.I. Kerrich of the British Museum and by Dr. M.W.R. Graham of the Hope Department of Entomology, Oxford. They include Tetrastichus evonymellae (Bouche) species near galactopus' (Ratz.); a Necremnus spp.; Pnigalio soemias (Walk.), Chrysocharis gemma (Walk.)

Necremnus metalarus (Walk.) and Achrysocharis lanassa (Walk.), A brief account of the biology of these parasites is given here. A recently revised key to the British Eulophidae is given in a paper by Graham (1959).

The Tetrasticnus evonymellae from L.spartifoliella were determined by Dr. Graham as "sp. near galactopus" (Ratz.). "They differ from the latter in having longer flagellar segments and a rather shorter gaster. It is possible they represent an undescribed species".

T.evonymellae, sp. near galactopus (Ratz.) is endoparasitic and passes its entire development, i.e. from egg to pupa, in the larval and pupal stages of Leucoptera. The eggs are usually laid in the first instar larva of the host; but, as indicated in Table 36, they can still be seen in the fourth instar host larva. The eggs are ovate, and are usually found floating in the abdominal haemocoele of the host larva. In 1964 and in 1965, some of the eggs were seen to be half-inserted into the dorsum or into the dorso-lateral aspect of one of the last three abdominal segments. This, presumably, is the general oviposition site of the parasite.

Table 36 Occurrence of eggs of T.evonymellae in host larvae, dissections in 1965 (Aug. 24 to Oct. 13)
No. dissected = 1045.

Stage of Leucoptera larva	I	II	III	IV	V
Total eggs (Tetrastichus)	41	37	27	3	-
Total eggs (as % of larva of the host stage)	38.3	14.1	6.6	1.3	-

The newly hatched larvae are usually found in the abdominal haemocoelic cavity of the host. Clausen (1940) states that many species of Tetrastichus oviposit from 8 to 20 eggs in a single host. One to three eggs or larvae were usually found in the Leucoptera larva in 1965 (see Table 37) but the usual number of parasitic larvae

that survive to the fifth larval stage of the host is one. Supernumerary larvae usually die in the third or fourth instar of the host. Two larvae per host were seen on 22.IX.65, 29.IX and 6.X.65, but in each case one of the parasite larvae was dead. In one case a Tetrastichus larva was attached to another probably cannibalising it.

Table 37 Occurrence of Tetrastichus per host larva, 1965 dissections.

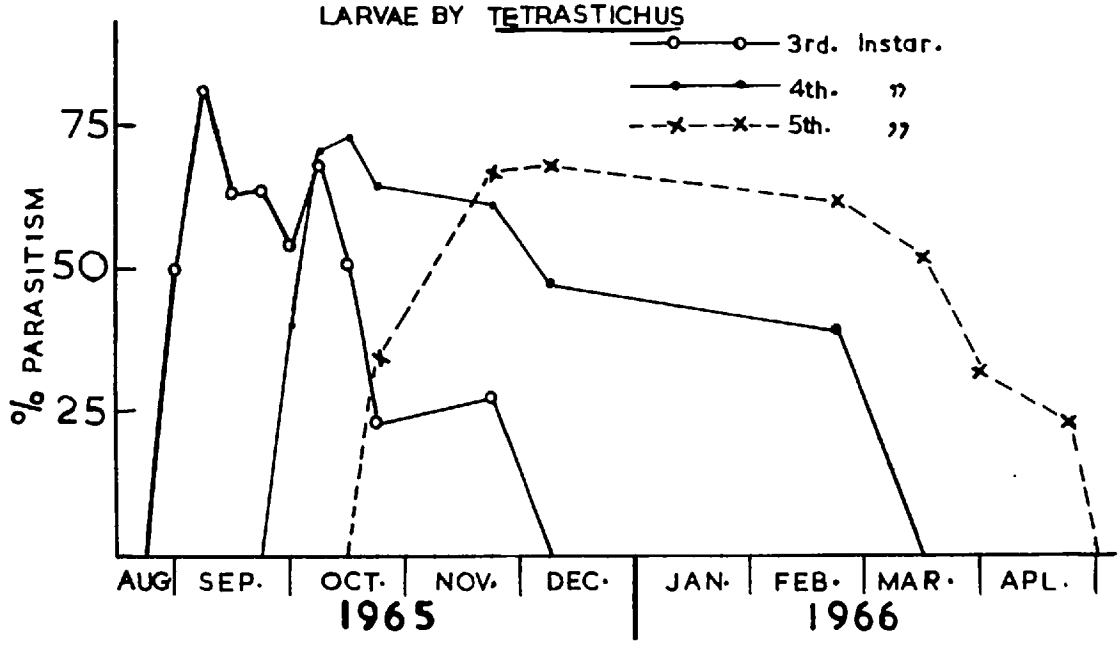
No. of Tetrastichus per host larva.	No. of occurrences in caterpillars of Leucoptera				
	Instar I	II	III	IV	V
1	44	149	201	50	33
2	12	30	21	5	-
3	3	1	1	1	-

The parasite overwinters as larva. The parasite larvae in summer and in the winter are shown in Figs. 31a and 31b. Most of the development of the parasite takes place when the host reaches the pupal stage. Pupation takes place usually in a cell constructed within the host pupa, and lasts for about four weeks. In the field, the adult Tetrastichus start to emerge in about mid-July. Only one wasp emerges per host. The emergence, from 643 and 164 Leucoptera cocoons kept in well ventilated plastic cages in the field in 1965 and 1966, was spread over approximately four weeks (see Table 38).

Table 38 Dates of emergence of Tetrastichus in the field.

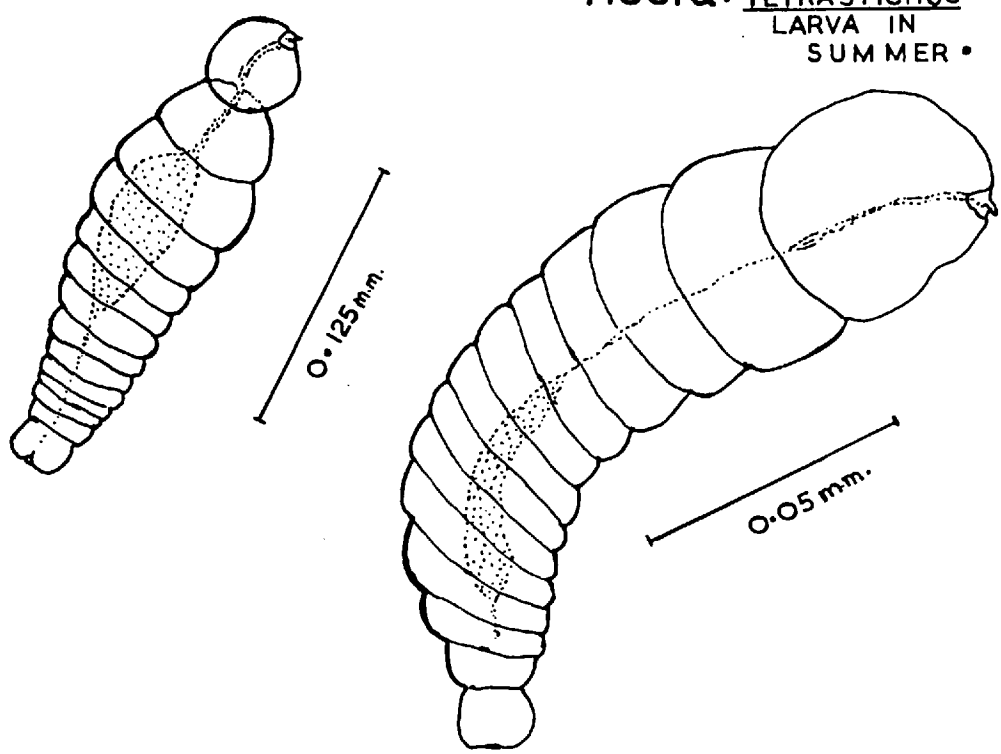
Cocoons Collected	First parasite emergence.	Last parasite emergence.	No. of Leucoptera cocoons.
17.V.65	20.VII.65	19.VIII.65	643
30.V.66	14.VII.66	16.VIII.66	164

FIG·32· CHANGES IN PERCENT PARASITISM OF LEUCOPTERA LARVAE BY TETRASTICHUS



FIG·31b. TETRASTICHUS LARVA IN WINTER.

FIG·31a. TETRASTICHUS LARVA IN SUMMER.



The emergence of the adult parasites is later than that of adult Leucoptera (see Tables 39 and 40). It is, however, well synchronised with the hatching of the first instar larvae of the host. In 1965 and 1966, eggs laid by the field females of Leucoptera were stored in plastic petri dishes in the field. A comparison of the time of egg hatch with the time of emergence of the wasps from the cocoons in the field (Table 41) suggests that Leucoptera larvae that hatch late in the season are the least parasitised by Tetrastichus, since the wasps live for only 10 to 12 days in the field. Since the percentage parasitism depends on the relatively short oviposition period of the parasite, the highest level of parasitism by this Eulophid occurs early in the larval instar of the host (see Fig.32).

Table 41 Dates of egg hatch, emergence of Tetrastichus, in the field cages.

Year	First egg to hatch	First Tetrastichus to emerge.	Last egg of Leucoptera to hatch
1965	20.VII	20.VII	8.X.
1966	25.VII.	14.VII.	13.IX.

The wasp is univoltine. The details of the first appearance in the field of the different stages of the parasite in 1965-66 are given below:

Egg	Larva	Pupa	Adult emergence
28.VII.65	11.VIII.65	20.VI.66	14.VII.66

T.evonymellae galactopus is hyperparasitised by a Eupelmus sp.(Hymenoptera) just before it attains the pre-pupal state in the host pupa.

One specimen of Chrysocharis gemma (Walk.) was bred from Tetrastichus, i.e. hyperparasitised this Eulophid.

Necremnus sp.

The Necremnus sp. (Eulophidae) is ectoparasitic on Leucoptera larva in late fifth instar which is about to moult into the sixth. The parasite eggs are placed on the dorso-lateral aspect of one of the last five abdominal segments. The larvae are solitary, and develop entirely outside the host. The caterpillars appear to be killed by the oviposition wound, and in dissections were seen to turn dark brown and liquify before the parasite larva had completed its development. Some of the Leucoptera larvae parasitised by this Necremnus sp. were found, on dissection, to contain a Tetrastichus larva as well, but the latter was invariably dead. The fully fed parasite larva crawls away and pupates a little distance away from the remains of the host. In the field the larval development appears to be completed in about two weeks, as is shown below:

Year	Egg first seen	Larva first seen	Pupa first seen
1965	31.III.	14.IV.	6.VI.
1966	10.III.	17.III.	16.V.

Adult emergence in the field was not observed, but the average duration of the pupal period in the laboratory was 10 days. The shortness of the life cycle suggests that there is an alternative host of this parasite, but this remained undiscovered.

Chysocharis gemma

An account of the general biology of Chrysocharis gemma (Walk.) as a parasite of the holly leaf miner, Phytomyza ilicis Curt. (Diptera:Agromyzidae) is given in a paper by Cameron (1939) The following observations will therefore provide additional information on the parasite.

C. gemma is an endoparasite of the sixth instar larva of L.spartifoliella. The host is attacked about two weeks after it

has moulted from the fifth larval instar. The eggs are elongated and kidney shaped, and are generally found in the host's abdominal cavity. The parasitised host larva is impaled and bloated, but later becomes flaccid and pale in colour. Superparasitism was occasionally encountered in dissections, but only one larva usually developed. Fully fed parasite larvae emerge from the hosts, and pupate some distance away from their remains. The adults begin to emerge in the field early in June, after a pupal period of about 20 to 23 days. In the field the life cycle is apparently short, and takes about 8 to 9 weeks to complete. The dates of the first occurrence of the stages in 1966 are as follows:

egg	larva	pupa	adult emergence
31.III	18.IV.	16.V.	8.VI.

A comparison of the adult emergence with that of Leucoptera adults is given in Table 40. A single specimen was bred as a hyper-parasite of Tetrastichus evonymellae galactopus in 1965. Out of 24 sixth instar Leucoptera, parasitised by Chrysocharis, dissected on April 22, 1966, 33.3% contained a Tetrastichus larva, usually dead. This indicates that the Chrysocharis female may not discriminate very much in its choice of host.

Pnigalio soemias

Pnigalio soemias (Walk.) (Eulophidae) is an external parasite of the sixth instar Leucoptera larvae the parasite eggs being laid just before the caterpillars emerge from their mines. The eggs are placed on the dorsum of an abdominal segment of the host, and the host is usually paralysed. The larva is not restricted in its feeding to the oviposition site, but when fully grown leaves the host and pupates nearby. The last larval exuviae envelops the tip of the abdomen of the pupa, and thus serves to attach it to the wall of the mine. The pupal period is short, and in the laboratory lasts between 7 and 9 days. Only one adult

emerged from the parasite pupae kept in the field in 1966 (see Table 40). The first occurrence of the different stages in samples taken in 1966, and the date of emergence of the adult in the field are shown below:

Egg	Larva	Pupa	Adult emergence
7.IV.	18.IV.	23.V.	8.VI.

Necremnus metalarus

Necremnus metalarus (Walk.) (Eulophidae) is ectoparasitic on the sixth instar Leucoptera larva that has emerged from its mine and spun its cocoons, but has not assumed the full pupal state. The eggs were usually found on the dorsum of the abdominal segments of the host. Commonly they were one per host, except on 2.V.66 when two eggs were seen on a host; however only one of these hatched. The host is completely consumed by the time the parasite completes its larval development. The pupation period in the field is short. Adult emergence in the field begins early in June, and is perfectly synchronised with that of Leucoptera (see Tables 39 and 40). The whole life cycle in the field may be completed in about eight weeks. The dates of the first appearance of the different stages of the Eulophid in field samples are given below:

Egg	Larva	Pupa	Adult emergence
26.IV.66	2.V.66	30.V.66	8.VI.66

Table 39 Emergence of adults of Leucoptera (a), Tetrastichus (b) and Necremnus metalarus (C) in field cages, 1965.

	Date and nos. emerged				
	12-21.VI.	22-28.VI.	29.VI.-5.VII.	6-12.VII.	13-19.VII.
(a)	48	22	8	-	-
(b)	-	-	-	-	-
(c)	12	8	-	-	-

Table 39 continued.

	Date and nos. emerged.			
	20-26.VII.	27.VII.-2.VIII.	3-9.VIII.	10-19.VIII.
(a)	-	-	-	-
(b)	47	64	29	8
(c)	-	-	-	-

Table 40. Emergence of adults of Leucoptera (a), Chrysocharis (b) Pnigalio (c), N. metalarus (d) and Tetrastichus (e) in field cages 1966.

	Dates and nos. emerged.				
	8-VI.	9-13.VI.	14-20.VI.	21-27.VI.	28.VI-4.VII.
(a)	-	1	25	17	6
(b)	1	1	-	-	-
(c)	1	-	-	-	-
(d)	1	2	11	5	2
(e)	-	-	-	-	-

continuation of above columns of dates and nos. emerged.

5.11.VII	12-18.VII	19-25.VII	26.VII-1.VIII	2-8.VIII	9-16.VIII
-	-	-	-	-	-
-	1	-	-	-	-
-	-	-	-	-	-
-	-	-	-	-	-
-	8	32	34	15	3

One Achrysocharis lanassa (Walk.) (Entedontinae) was bred as an internal parasite of third instar Leucoptera larva. It is probably an aberrant parasite of Leucoptera.

11. METHODS OF SAMPLING POPULATION.

11.1 Methods of Sampling Adults

Three methods of sampling were used in the estimation of the population size of adult Leucoptera in the study area.

11.1(a) The beating method.

A quantity of broom measuring about one-eighth of a whole bush was shaken over a muslin tray of approximately one metre square. The adult Leucoptera, thus shaken off, were collected, sexed and their numbers recorded. Most of the sexing, in 1964, was done in the laboratory under a binocular microscope. By 1965, the sexes were easily recognised; sexing was therefore, done in the field and the adults were released after this. Thirty one-eighths of bushes were beaten on each sampling day in 1964 when there were relatively more broom bushes. The bushes were chosen systematically so as to cover the whole study area, and the distribution pattern of the broom bushes. This was reasonably similar to Milne's (1959) Centric-Systematic area sample.

Most of the broom bushes had died in 1965; those that lived had many of their branches, or parts of these dead (see Section 2, p.7). To minimise further destruction of the habitat by beating, the number of bushes beaten each week was reduced to 24 in 1965 and 1966. It was, however, increased to 48 towards the end of life of the moths in the field (i.e. last week in August in 1965 and 1966) when the population density had greatly declined, and the adult distribution had become patchy.

Beats were one per bush and from only one aspect of each selected bush. The aspect sampled was changed in each row of broom bushes, viz.: north in row 1; east in row 2; south in row 3 and west in row 4. This was repeated in all the subsequent rows. Records of the aspect and fraction of each bush beaten per week were made. Thus, the quantity of broom shaken each week was known; and from the number of moths collected from this, estimates of the adult Leucoptera population were made, since the total number of broom bushes was known (see Section 2, p.7).

11.1(b) Marking and recapture method.

Leucoptera adults are small and fragile; and so individual handling and marking with some nitro-cellulose paint is unsuitable. Consequently, mass marking with finely divided dust of a dye was adopted. This is the method that has been successfully used by Macleod et al. (1957) in their studies of the Caliphorinae.

The dye used was Rotor Brilliant Red R. A number of the moths were put into a conical flask in which a pinch of the powder of the dye was suspended. The conical flask was connected by rubber tubing to a cylinder of carbondioxide. By gently blowing in a small amount of carbondioxide, the moths were dusted with the powder. Since the moths become temporarily immobilised by the carbondioxide, they were allowed to recover sufficiently before being taken back and released at various points in the study area. After 72 hours, a sample of 100 of one-eighths of bushes was taken by the beating method. The marked and recaptured individuals were identified by placing all the adults captured on a white filter paper, and then brushing them with a few drops of acetone. Thus treated, marked moths gave a red mark on the filter paper. From the number of marked moths recaptured, an estimate of the population size was made using the modified version of the Lincoln index (Bailey, 1952).

11.1(c) Emergence trap method.

The traps used for the estimation of adult emergence consisted of white muslin bags, each 6 feet long and 4 feet in circumference. Each one of these bags tapered to a point from about a foot at one end. Two wire rings, approximately of the same circumference as the bags, and suitably placed in each bag, helped to distend this cage; two four-foot lengths of wire tied to the rings provided an additional support. Branches of broom amounting to about one-eighth of a whole broom bush, were enclosed in each bag which was then tied off with a string at the lower end (Fig.33). The bushes were chosen systematically so as to cover the whole broom area, and the choice of the aspect of a bush to bag

FIG.33. Emergence bag.

was made as described in the Beating method. A different set of bushes were chosen every week so that the adult emergence in as much of the habitat as possible was covered.

The emergence bags were always put out in the study area before the adults started to emerge. In 1964, 15 bags were used, but from 1965 onwards the number was increased to 20, as this tended to increase the reliability of the result. During the emergence period, the enclosed broom branches were shaken into the bags once a week. The content of each bag was then poured out onto the beating tray, and all the emerged Leucoptera adults that were thus trapped were collected, sexed and their numbers recorded. Some of the moths were retained for observations on their oviposition, and the rest were released. From the number of adults that emerged from the known quantity of broom bagged an estimate of the total adult emergence per week was obtained. Thus, if x represents the number of adults that emerged from each one-eighth of the 20 bushes bagged, then the total adult emergence in the week is:

$\frac{8\sum x}{20} \cdot y$ where y is the total number of broom bushes in the study area. The estimated total adult emergence in the season is:

$$\frac{8}{20}\left(\sum x + \sum x_1 + \sum x_2 \ldots\ldots\ldots \sum x_n\right) y$$

where n is the duration, in weeks, of adult emergence period.

11.2 Comparison of Results from the Different Methods of Sampling Adults.

The estimates of the number of Leucoptera adults by the three sampling methods are shown in Table 42. The population estimates from marking and recapture are very low. The discrepancy between the estimates from beating and from the weekly emergence is not as wide; the accumulated emergence, however, is much greater than that obtained from the beats. This may suggest a rapid disappearance of the adults from the habitat at some time after emergence (see Fig.36).

The discrepancy may also arise from the fact that whereas the emergence data measure the absolute emergence, they do not take account of emigration and mortality. By contrast, the beating estimates are measures of the numbers of the moths actually present in the study area on the occasion of beating. The difference between the two estimates may, therefore, represent the combined effects of emigration from, and mortality in the habitat.

The reliability of beating as a method of sampling the adults is presented in Table 43. Better results are obtained at or around the peak periods of adult occurrence in the field. As the population level declines estimates by beating tend to be less reliable. An increase in the number of beats in 1965 towards the end of adult life in the experimental area failed to be effective. It will be shown later that the Leucoptera adult population is generally over dispersed and the patchiness of the distribution increases as the population density declines. This inevitably results in some parts of the study area having an abundance of the moths whereas others become depleted. Beating samples will therefore tend to over- or under-estimate the population size according to whether they are sampled mainly from one or the other of these parts.

The adult period can be divided into pre-flight, flight and post-flight phases. At the flight phase the moths fly off readily from the beating tray, and some may be missed in the counts.

The marking and recapture method was tried once in 1964 and again in 1965. Since the identification of the marked from the unmarked moths required the killing of all Leucoptera caught on the recapture date no further marking was undertaken. The efficiency of the marking-recapture method depends on the marked insects, after release, remaining available for recapturing, i.e. the population experiencing no deaths, or emigration. The low estimates obtained by this method in the present study is probably not caused by mortality since a set of moths similarly

marked, but kept in 3" x 1" tubes survived for over seven days in the field. It is improbable that the dye rendered the marked insects more conspicuous to predators. The Leucoptera population, however, is not a closed one as the moths fly readily and actively. The estimates have been calculated from the formula:

$$P = \frac{a(n+1)}{(r+1)} \qquad \text{(see Bailey, 1952)}$$

where P is the population size; a, the number of moths marked; n, the number taken on the recapturing date and r, the number marked and recaptured. No obvious explanation can be given for the marking estimates which are too low, as the number of trials with the method is probably not enough to be conclusive.

Table 42. Population size of Leucoptera in the field on, or near to the days of their maxima; estimates by three methods.

Date of Sample	Estimate by Beating	Estimate by Marking and Recapture	Estimate by Emergence Traps	
			Weekly emergence	Accumulated emergence to date
25.6.64	359,840	11,093 ±4420*	736,654	944,863
7.7.64	630,656	-	568,049	2,675,320
14.7.64	164,320	-	185,578	2,860,898
28.7.64	50,336		6,789	2,885,227
25.6.65	73,176		149,497	151,935
7.7.65	235,986		219,780	852,303
21.7.65	91,250	8,972 ±1244	1,626	915,272
28.7.65	56,426			

* Fiducial limits calculated as described by Bailey (1952).

Table 43. The reliability of the beating method for sampling Leucoptera adults.

	Number of 1/8 bush beats	Mean number of Leucoptera per beat ± 95% Fiducial limits	Standard error	Standard error as % of mean
25.6.64	30	28.40 ± 1.52	0.742	2.61
7.7.64	30	50.90 ± 12.62	6.170	12.12
14.7.64	30	13.17 ± 5.04	2.466	18.73
11.8.64	30	0.63 ± 0.27	0.131	20.73
25.6.65	24	10.38 ± 4.20	2.028	19.54
21.7.65	24	12.96 ± 6.79	3.283	24.56
4.8.65	24	2.83 ± 1.46	0.706	24.95
25.8.65	48	0.29 ± 0.32	0.160	54.79
30.8.65	48	0.60 ± 0.07	0.035	55.56

Table 44a. The reliability of estimates of the numbers of Leucoptera from the emergence trap data.

	Number of emergence traps	Mean number of Leucoptera per trap ± 95% Fiducial limits	Standard error	Standard error as % of mean
22.6.64	15	43.40 ± 14.93	6.959	16.04
6.7.64	15	33.47 ± 17.81	8.303	24.81
20.7.64	15	1.13 ± 0.96	0.446	39.47
21.6.65	20	9.20 ± 4.37	2.088	22.70
5.7.65	20	13.65 ± 4.97	2.376	17.41
13.7.65	20	3.45 ± 2.10	1.001	29.02

The weekly and the accumulated emergence estimates have been computed from the proportion of the adult population trapped as it emerged from the cocoons. The reliability of these estimates are summarized in Table 44a. The variation of the percentage error about the mean is reasonably close to that in the beating method (Tables 43 and 44a). The estimated totals of emergence throughout the seasons, however, are lower than the similar estimates based on the beating data (see Table 44b).

Table 44b. Comparison of estimates of total number of adults

Year	Estimated emergence in the whole area in the season.	Estimate based on beating data *
1964	2,888,622	5,514,665
1965	915,272	2,710,487
1966	67,181	89,392

A possible explanation for this is that the wandering sixth instar larvae spin their pupation cocoons on living, as well as on dead and dried twigs. In 1964, 1965 and 1966, the broom bushes had much of the latter (especially at the lower parts of branches) most of which broke off as the emergence bags were being placed in position. A rough and approximate estimate is that about 26 percent of the pupae could have been missed in this way. This estimate is probably conservative as many other workers were sampling in the same broom area, particularly in 1964 and 1965.

11.3 Method of Sampling Immature Stages

Weekly census of eggs and larvae were obtained by examining known weights of broom cuttings under a binocular microscope. Any eggs or larvae found were carefully removed with a mounted needle.

At the start of this work in 1963, preliminary test samples taken to determine the best sample size, revealed that the accuracy of estimates increased with the number and not the size of

cuttings. However, samples of 24 cuttings or more were adequate, and the difference in the coefficient of variation from the mean expressed here in percentages for comparison, was very small (Table 45).

To sample eggs and larvae, 36 cuttings were taken weekly from broom bushes chosen at random, and at points widely distributed over the study area. The bushes were each divided by eye into top, middle and bottom portions. One portion only of a selected bush was sampled on any one occasion. The samples were taken from the four aspects : north, east, south and west, a single aspect per bush. This stratification of the broom bushes for sampling purposes was found to increase the accuracy of the population estimates ($P = <0.001$). The cuttings were weighed together; and on wet days were dried before being weighed. When present, i.e. from mid May to July, flowers and green pods were removed before the cuttings were weighed, as both together increased the total sample weight by approximately 18 per cent. The cuttings were then each searched under the binocular microscope for eggs and larvae. Eggs sucked by predators and sound eggs were recorded separately, and the latter were kept in the laboratory for observations on hatching, sterility and parasitism. The larvae, extracted from their 'mines' were recorded separately and then the instars noted. Periodically, they were dissected to obtain a measure of parasitism. From the numbers of eggs and or larvae occurring in the known weight of a sample, the population estimates expressed as numbers per 100 g of green broom were obtained.

The pupae were sampled and estimated in the same way as the eggs and larvae. In this case, however, the binocular microscope was used only when the cocoons - and the pupae within - were to be dissected for parasitism. A record of the number of mines from which the sixth instar larvae had emerged to pupate was also kept and provided a check on the estimates of pupal population.

300 to 650 g of green broom were examined on each sampling occasion. Larger samples were taken as the density of the immature

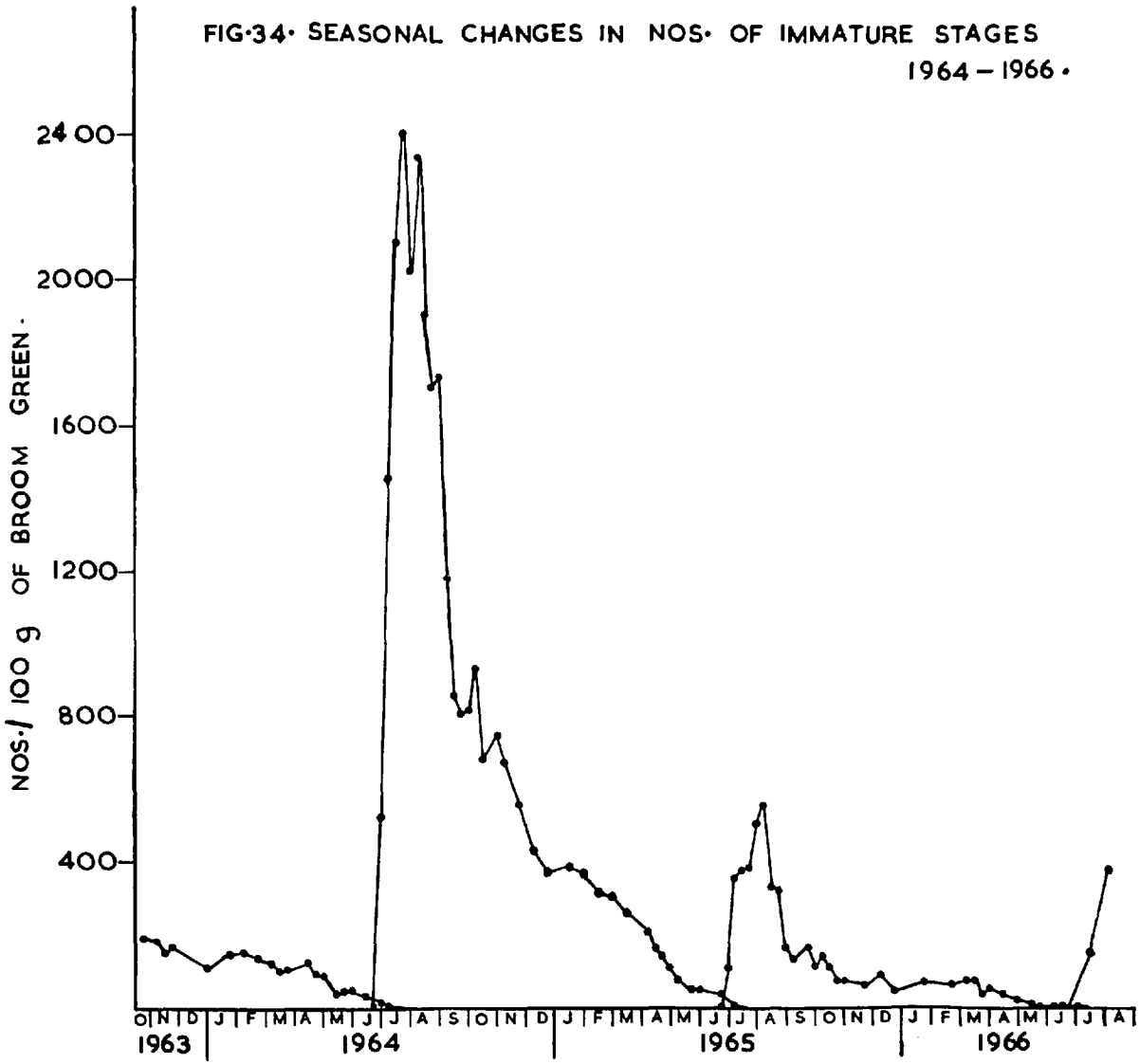
stages decreased. The number of cuttings was also increased to 40 for the same reasons. In 1965, many of the broom bushes had died (see Table 3a); to avoid extensive depletion of the habitat, the number of cuttings was reduced to 24 early in the season, but was increased to 40 from the first of September onwards, as the larval population density fell.

The frequency of sampling was once a week in Summer, autumn and spring when the stages were changing rapidly. In the winter, the samples were taken every two weeks.

Table 45: Effect of number and size of cuttings on the reliability of egg samples.

Number of cuttings	Weight per cutting (g)	Number of eggs per cutting ±95% Fiducial limits	Standard error as % of mean.
10	10	40.20 ± 19.39	21.33
12	10	39.25 ± 17.10	19.79
24	10	31.33 ± 10.06	15.51
36	2.9	7.36 ± 2.15	14.41
60	2.8	7.20 ± 1.63	11.33

The reliability of this method of sampling for the eggs of L.spartifoliella is presented in Table 46. The general seasonal changes, in the total population of the immature stages for two and a half years, as established by this method, are shown in Fig. 34. The reliability of the population estimates based on cutting increases with the number of cuttings (see Table 45). This increase is slight at high population densities. When the ends of the egg stage are considered, it is seen that an increase in the number of cuttings may not lead to a proportionate increase in the reliability of the estimates. The general trends in the populations of the immature stages are basically similar in each of the three seasons, the peak numbers obviously occurring at the egg stage. The changes that occur are due to moulting and mortality; but changes in the host plant, such as loss of leaves in autumn or a reduction in weight


FIG·34· SEASONAL CHANGES IN NOS· OF IMMATURE STAGES
1964 – 1966 ·
NOS·/ 100 g OF BROOM GREEN·
2400
2000
1600
1200
800
400
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1963
1964
1965
1966

of the twigs in the winter, may lead to estimates higher than the number of larvae actually occurring in the field (c.f. September and December, Fig.34). The successive generations of the immature stages overlap from year to year at the egg and pupal stages.

Table 46 The reliability of the method of sampling eggs of Leucoptera.

Date	No. of cuttings	No. of eggs per cutting ± 95% Fiducial limits	Standard error	Standard error as % of mean
30.6.64	36	15.33 ± 3.98	1.959	12.78
8.7.64	36	29.53 ± 6.94	3.417	11.57
15.7.64	40	53.80 ± 11.14	5.507	10.24
5.8.64	40	2.65 ± 1.04	0.512	19.32
14.7.65	24	22.21 ± 7.32	3.538	15.93
28.7.65	24	20.25 ± 5.69	2.748	13.57
11.8.65	24	10.88 ± 5.01	2.420	22.25
1.9.65	40	1.30 ± 0.75	0.369	28.39

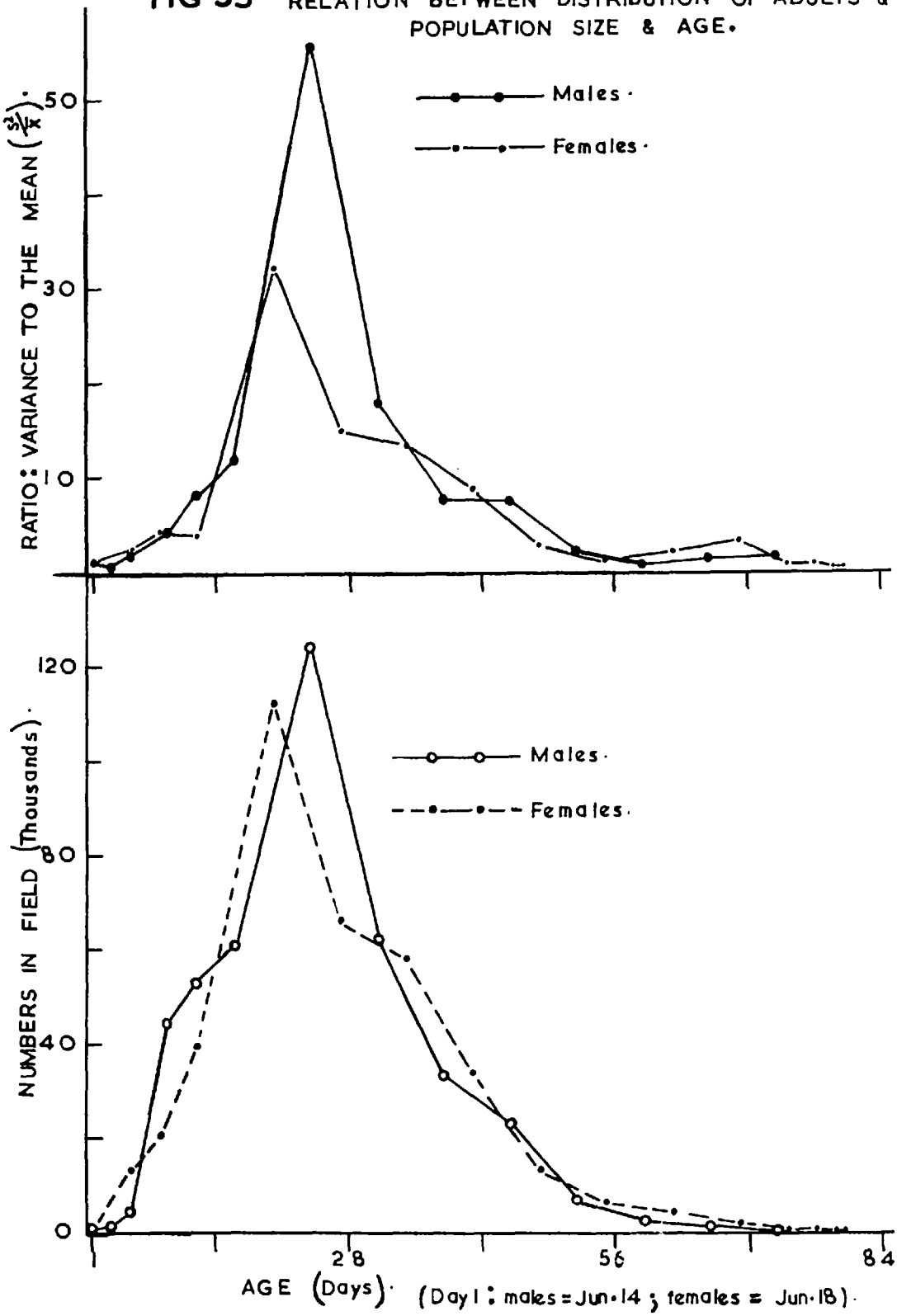
11.4 Distribution of Adult L.spartifoliella in the Field.

The relationship between the pattern of distribution and the size and age of the population was studied and analysed. The data in the adult period in 1965 were obtained from the number of individuals beaten weekly from 24 one-eighths of bushes. The number of adult moths counted per beat varied on each sampling occasion. If the moths were randomly dispersed, the observed variance (S^2) of the count would be equal to the mean ($\bar{x}$) (Bliss and Owen, 1958; Fisher and Bliss, 1953). The ratio of the observed variance to the mean : $\frac{S^2}{\bar{x}}$, therefore provides a good test for the randomness of distribution, since it is unity when conditions of randomness are satisfied. Values of $\frac{S^2}{\bar{x}}$ significantly above or below unity indicate aggregation or under-dispersion (Hutchinson, 1962).

The ratio of the variance to the mean was estimated for each set of data related to adult occurrence in 1965. This was plotted, along with the corresponding population estimates, against the age of the population in the study area (see Fig.35). The sexes were treated separately, and the first day of life for each sex was taken as that on which the adult male or female was first seen in the samples. The trend of distribution was similar in the two sexes. It is evident from Fig.35 that the adults were mostly aggregated, i.e. over-dispersed, the level of over-dispersion varying with the size and the age of the population. The over-dispersion was greatest at the peak period of adult occurrence. When adult numbers were low, as at the beginning and the end of the adult population, the distribution tended towards randomness, and in a few cases to under-dispersion (i.e. where $\frac{S^2}{\bar{x}} < 1.$). The males were under-dispersed on days 3 and 59; $\frac{S^2}{\bar{x}}$ and the females on days 74, 77 and 79. The χ^2 test showed that the values of $\frac{S^2}{\bar{x}}$ on these five days did not differ significantly from the Poisson series. However, the population size, and therefore the mean number of moths per beat, was relatively low at the beginning and towards the end of adult life in the field; at such low values of the mean, departures from randomness may remain undetected and so the significance indicated by the χ^2 test becomes suspect (Healy, 1962). For the rest of the data, the observed variance was much larger than the mean, the χ^2 test giving the value of P as < 0.001. On these occasions over-dispersion was far too large and the population could not be considered to be randomly distributed. An attempt was made to find a description of its distribution.

The distribution depicted by the negative binomial is generally regarded to be applicable to a wide variety of biological data - especially those relating to insect populations (Fisher and Bliss, 1953). The data on 28 July, 1965, for the females have been transformed into a frequency series, with the number of beats yielding 0, 1, 2, 3, 4 ------ n moths shown (Table 47). The variance, S^2, calculated from the observed frequencies is more than

FIG·35· RELATION BETWEEN DISTRIBUTION OF ADULTS & POPULATION SIZE & AGE.



eight times larger than the mean, $\bar{x}$. χ^2 test based on the variance and the mean, viz: $\chi^2 = (n-1)\frac{S^2}{\bar{x}}$ where n is number of observations, gives the value of P which is < 0.001. The observed frequency distribution does not fit the Poisson series. Estimates of the expected negative binomial frequencies are shown in the table and come very close to the observed values.

The goodness-of-fit of the expected negative binomial, ϕ, to the observed frequencies, f, was tested by χ^2. The observed frequencies have been pooled to values of, or above five, to avoid expectations of ϕ less than 5. The χ^2 at one degree of freedom, i.e. three less than the number of $\frac{(f-\phi)^2}{\phi}$ summed, was 0.5039, and with the P equal to .50 approximately, indicated a good fit with the negative binomial. The value of K, estimated from the variance and the mean by the approximate method, was 0.6186 (with a standard error of 0.3262). The exponent K is a valid measure of the amount of aggregation, Its value can vary from zero, where aggregation is maximal, to infinity which will indicate pure random distribution. Generally, large values of K indicate an approach to randomness. Since the K values for most of the Leucoptera data were less than one, it seems likely that the adult populations were more commonly aggregated than randomly distributed. The size of the aggregation may be partly explained by the tendency of the adult females to lay most of their eggs on young current year's twigs. Observations showed that broom bushes with more green growth on them yielded more moths than those with dying or senescing growths. It was mentioned in section 7.1(a) that this aggregated distribution of the adults is reflected on the distribution of their eggs.

Table 47. Fitting the negative binomial to counts of Leucoptera on 28.7.65.

No. of Leucoptera per beat x	Observed frequencies, f.	Expected negative binomial frequencies ø	$\frac{(f-ø)^2}{ø}$
0	7	6.28	0.0825
1	4	3.44	0.1401
2	1	2.47	
3	1	1.91	
4	3	1.55	
5	1	1.25	0.0003
6	3	1.04	
7	0	0.87	
8	0	0.73	
9	0	0.62	
10	0	0.53	
11	0	0.45	
12	0	0.39	
13	0	0.34	
14	1	0.29	
15	0	0.25	
16	1	0.22	0.2810
17	1	0.19	
18	0	0.16	
19	0	0.14	
20	0	0.12	
21	0	0.10	
22	0	0.09	
23	0	0.08	
24	1	0.07	
25+	0	0.44	
TOTALS	24	24	0.5039= χ^2

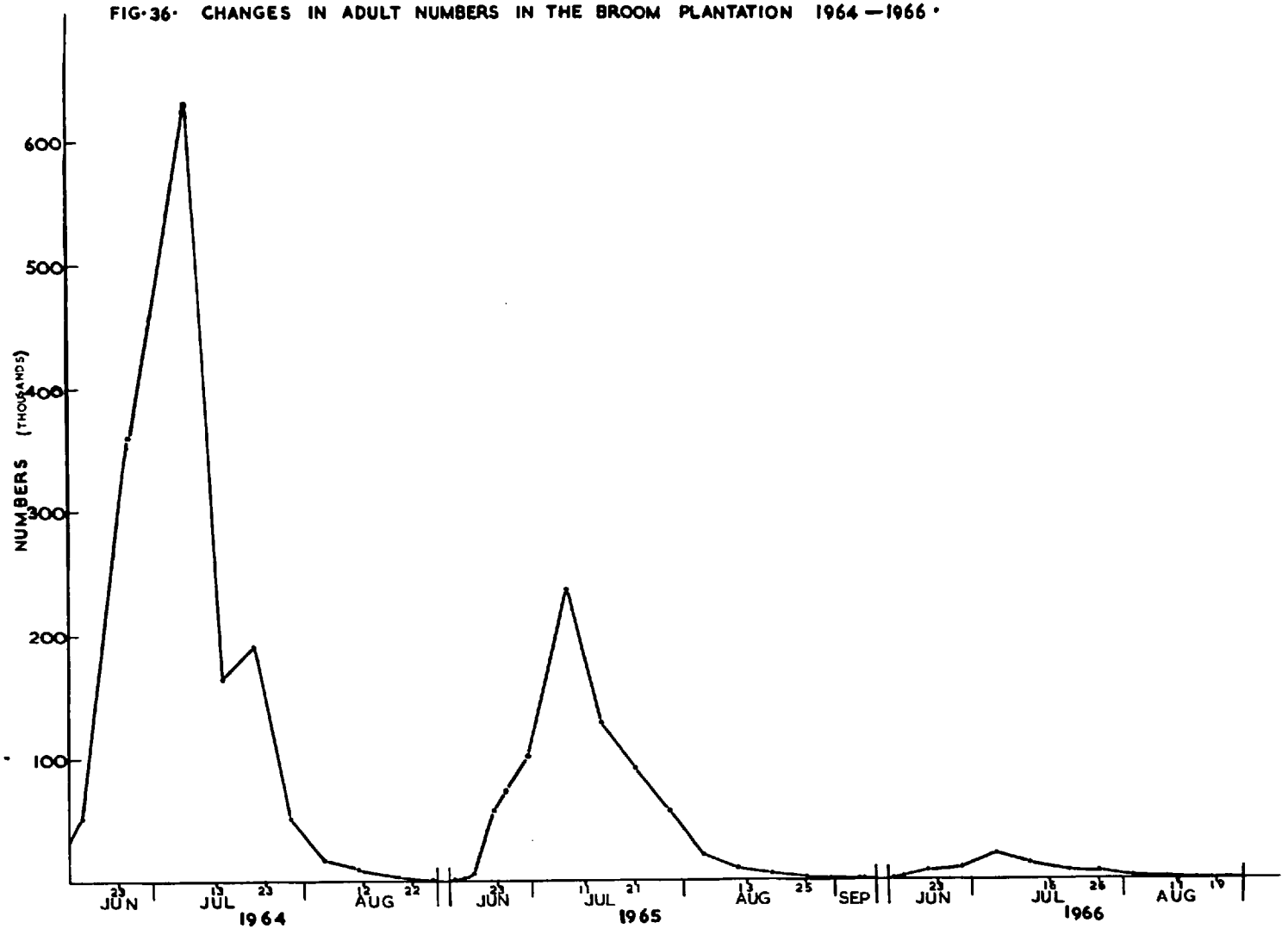
$\bar{x}$ = 4.7917; D.f. = 1; Std. error of mean = 1.3214. P = .50 approx.
Variance (S^2) = 41.9113; $\frac{S^2}{\bar{x}}$ = 8.75; K = 0.6186; Std. error of K = 0.3262.

12. ANALYSIS OF POPULATION DATA

12.1 Survivorship and Mortality of the Adults from peak numbers.

The rapid decline in numbers of adults at some time after emergence is the combined effect of mortality and emigration. The duration of time of the fluctuations in adult numbers in the three seasons are presented in Fig.36 which shows that the build up in adult numbers to the peak was rapid in each of the three successive seasons. However, the decline after the peak was less gradual in 1964 than in 1965 and in 1966. This suggested some difference in the emigration and mortality rates of the adults in the three years. A clearer idea of the trend in survival and mortality of the moths in the three years was obtained when the logarithm of the numbers that survived at given age interval was plotted against the age of the adults in the field. To simplify the calculations, the mortality before the peak in numbers in the field has been treated as negligible and has been ignored. All survival in these calculations is known to depend on two processes, i.e. mortality and emigration. Age 0, is taken as the day on which peak numbers occured in the field. In 1964 and 1965, this date was 7th July. The initial population size at age 0 was taken arbitrarily as 1000 individuals born more or less simultaneously, and the survivorship, lx, was obtained by the successive subtraction of deaths in the age intervals from the survivors at the beginning of the interval (See Deevey, 1947). With regard to the Leucoptera data, the mortality between two age intervals, 0 and 1 was calculated from the fraction of the population at '0' that die between the age interval 0 to 1. Thus if at ages 0 and 1, the population estimates are x and y respectively, then the fraction of the population that disappeared between 0 and 1 = $\frac{x - y}{x}$. On the per 1000 basis, the mortality rate at 0 will be $\frac{x - y}{x} \cdot 1000$. This subtracted from 1000, i.e. the assumed population size at age 0, gives the number of survivors, S, at the beginning of age 1. A similar

FIG·36· CHANGES IN ADULT NUMBERS IN THE BROOM PLANTATION 1964 — 1966 ·



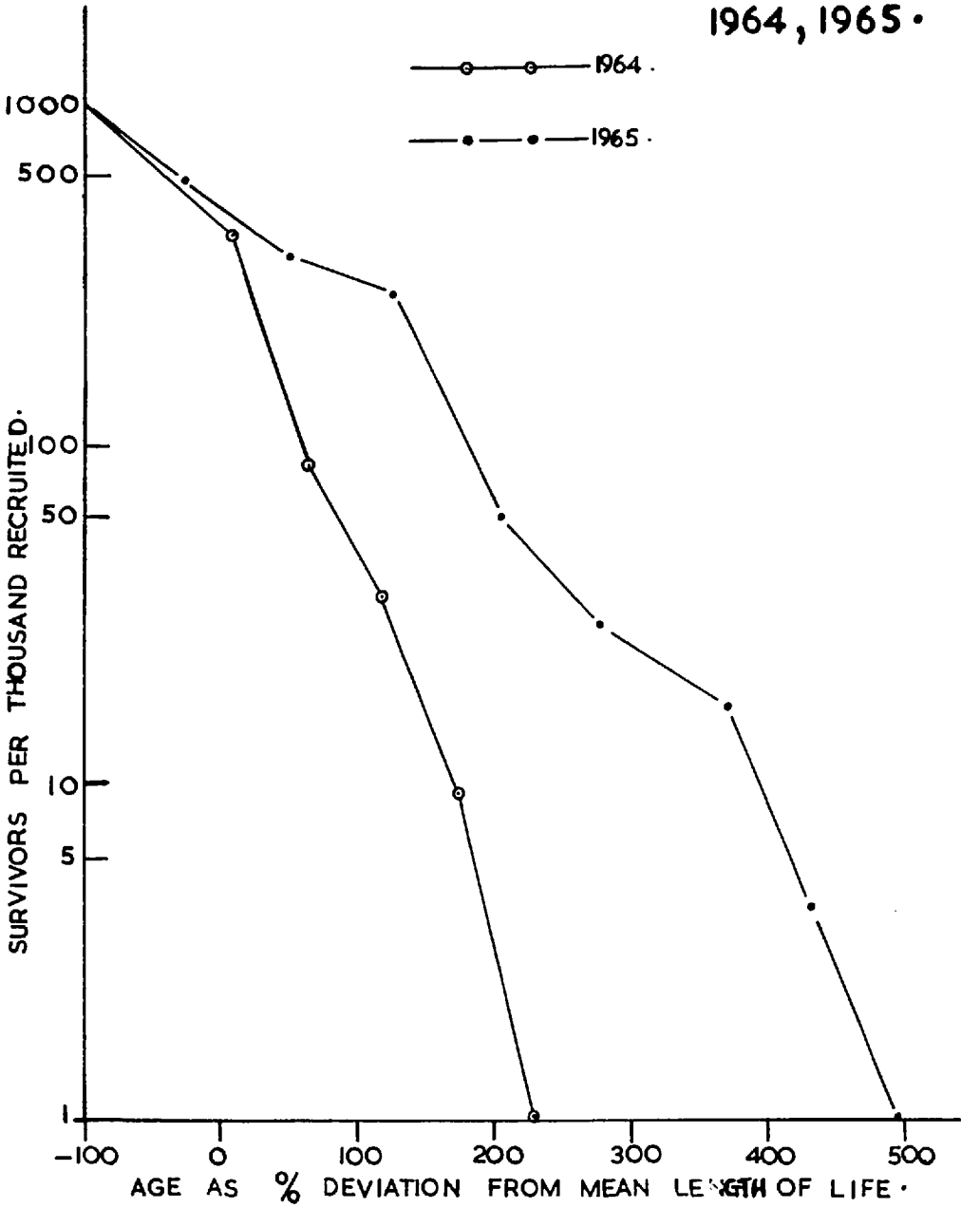
calculation from the population estimates at ages 1 and 2 (multiplied by S_2 and the product then subtracted from S) gives the number of survivors at the beginning of the age, 2, and so on.

The survivorship curves for the adults in 1964 and 1965 are shown in Figs.37 and 38; in which the logarithm of survivors at the beginning of given age intervals is plotted against adult age in the field. The sexes are treated separately, since they differ in their mean length of life. To facilitate comparison between the two sexes, and also between the same sex in the two years, in which the mean life span differed, the origin of the age axis was shifted from zero to the mean length of life of each of the sexes, and the age scale expressed as percent deviations from the mean length of life (see Pearl in Deevey, 1947). From Fig.37, it is evident that the curve for the males is much steeper in 1964 than in 1965. The same is true of the females. This indicates that the rate of survival, in both sexes of the adults, was higher in 1965 than in 1964. The curves also suggest that mortality in early life is low, but increases with the age of the population in the field. A comparison of the survivorship of the males and the females in the two years, reveals that the latter have a higher rate of survival than the males of comparable age. The implication of this will become apparent when the changes in sex ratio with the population age in the field is discussed. The greater survival of the adults in 1965 than in 1964 partly explains the much longer duration of adult life in the field in the former year (see Fig.36). The generally higher survivorship of the females, compared with males, may be partly accounted for by their larger size on emergence, since longevity in adult Leucoptera is significantly correlated with weight on emergence ($r = 0.5691$, $P = < 0.001$, $n - 2 = 30$)

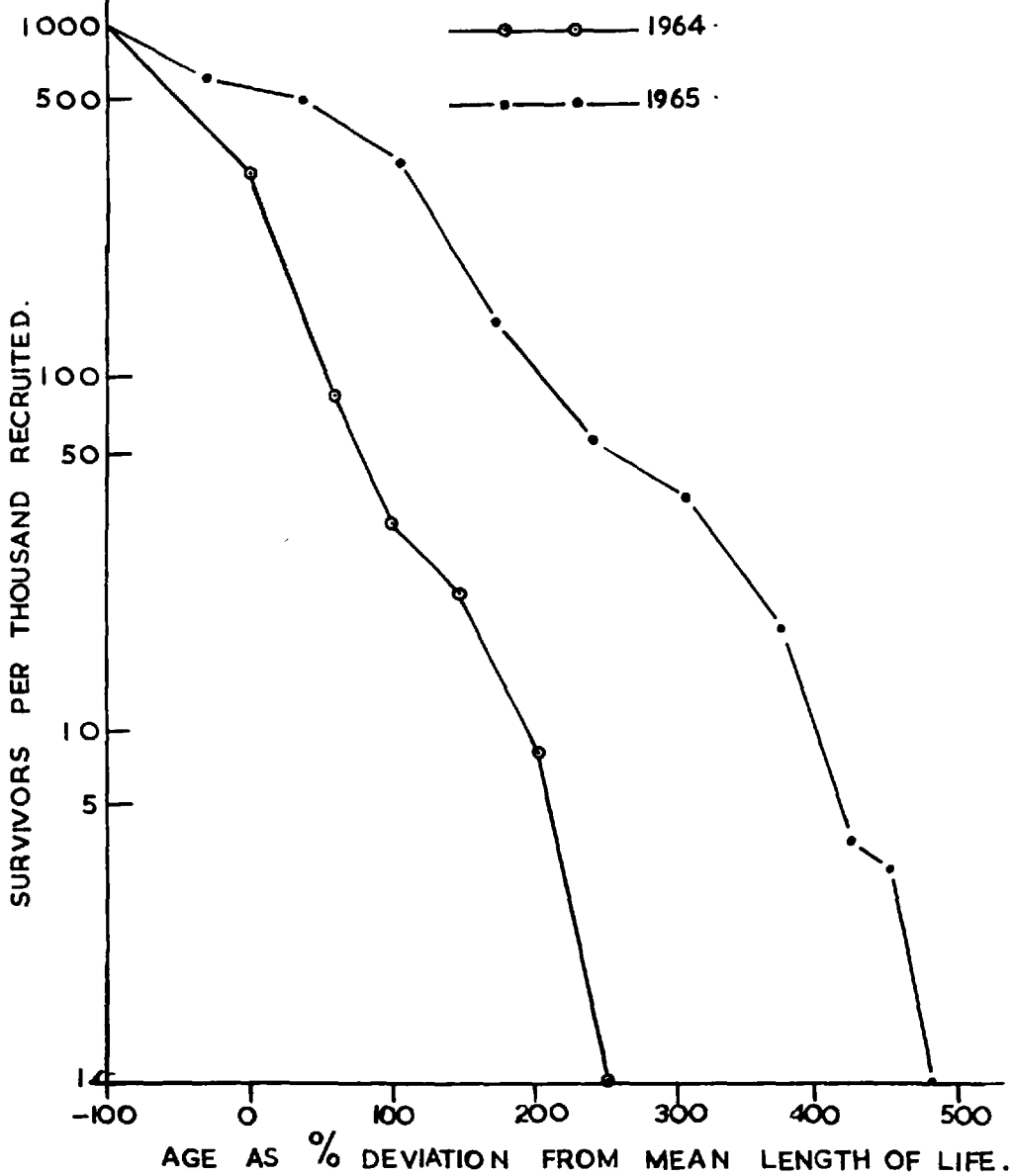
12.2 Sex Ratio

The sex ratio in each of the seasons was assessed from the emergence trap data. The sex ratios obtained in 1964, 1965 and 1966 are summarised on the following page.

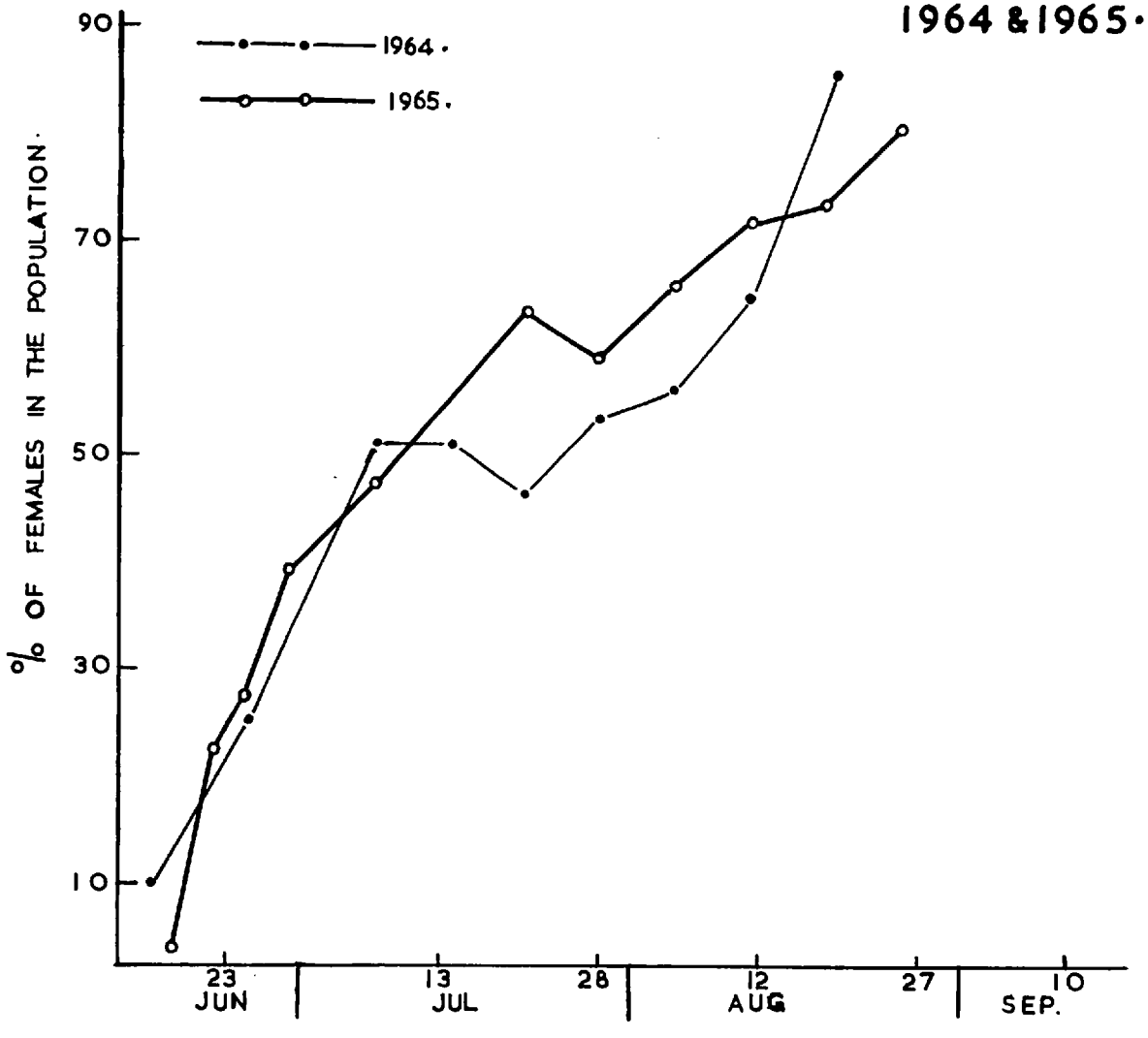
FIG·37· SURVIVORSHIP (lx) CURVES (MALES) 1964, 1965·



FIG·38· SURVIVORSHIP (lx) CURVES (FEMALES)
1964, 1965·



FIG·39· CHANGES IN SEX RATIO WITH POPULATION AGE 1964 & 1965·



1964	1965	1966
5♂ :2.44♀	5♂:3.61♀	5♂:4.88♀

The total number of males that emerged in each of the three seasons was distinctly greater than that of the females, notably so in 1964. This disparity in the total emergence of the sexes was smaller in 1965, and the sex ratio was very close to 1:1 in 1966. The variation of the sex ratio with the age of the population in 1964 and 1965 is presented in Fig.39, with the proportion of the females in the population expressed as percentages. The proportion of females in the population was similar in the two years, increasing with the increased age of the population. This probably was partly due to the females emerging later than the males, but it is also a result of the greater longevity of the females. It should be noted that the fall in the proportion of females on July 21, 1964 is repeated on July 28, 1965. This may not be due to sampling errors. However, calculations of survival rates showed that 77% and 70.3% of the males, as against 69.2% and 60.5% of the females, died by these two dates. It is therefore probable that greater emigration of the females from the habitat was mainly responsible for the fall in the proportion of the females on the two dates.

12.3 Estimation of Recruitment and Mortality in the Immature Stages.

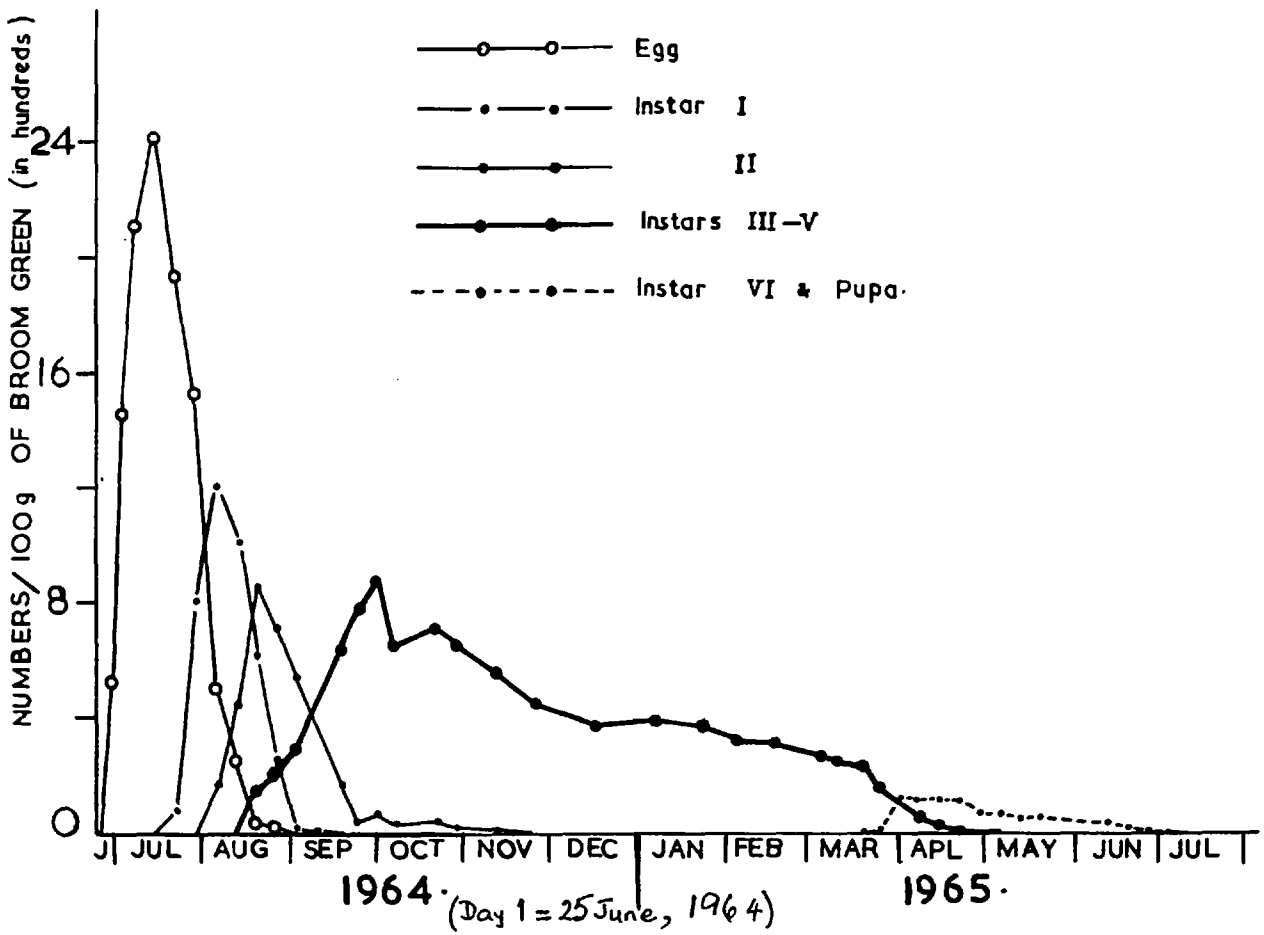
It has been shown that the emergence of adult Leucoptera in the field is protracted (see Section 6.1). Because of this and the long period of oviposition and egg hatching, many of the immature stages overlap. In a population of this kind the number of individuals in each developmental stage is simultaneously being decreased by moulting and mortality, and also increased by fresh oviposition, hatching and moulting, A number of methods have been developed for the estimation of recruitment and mortality of individuals in each stage of such population. Each of these methods has its own weaknesses and makes various assumptions. Three of these were described by Richards and Waloff (1954); Richards, Waloff and Spradbery (1960) and Dempster (1961). A fourth method

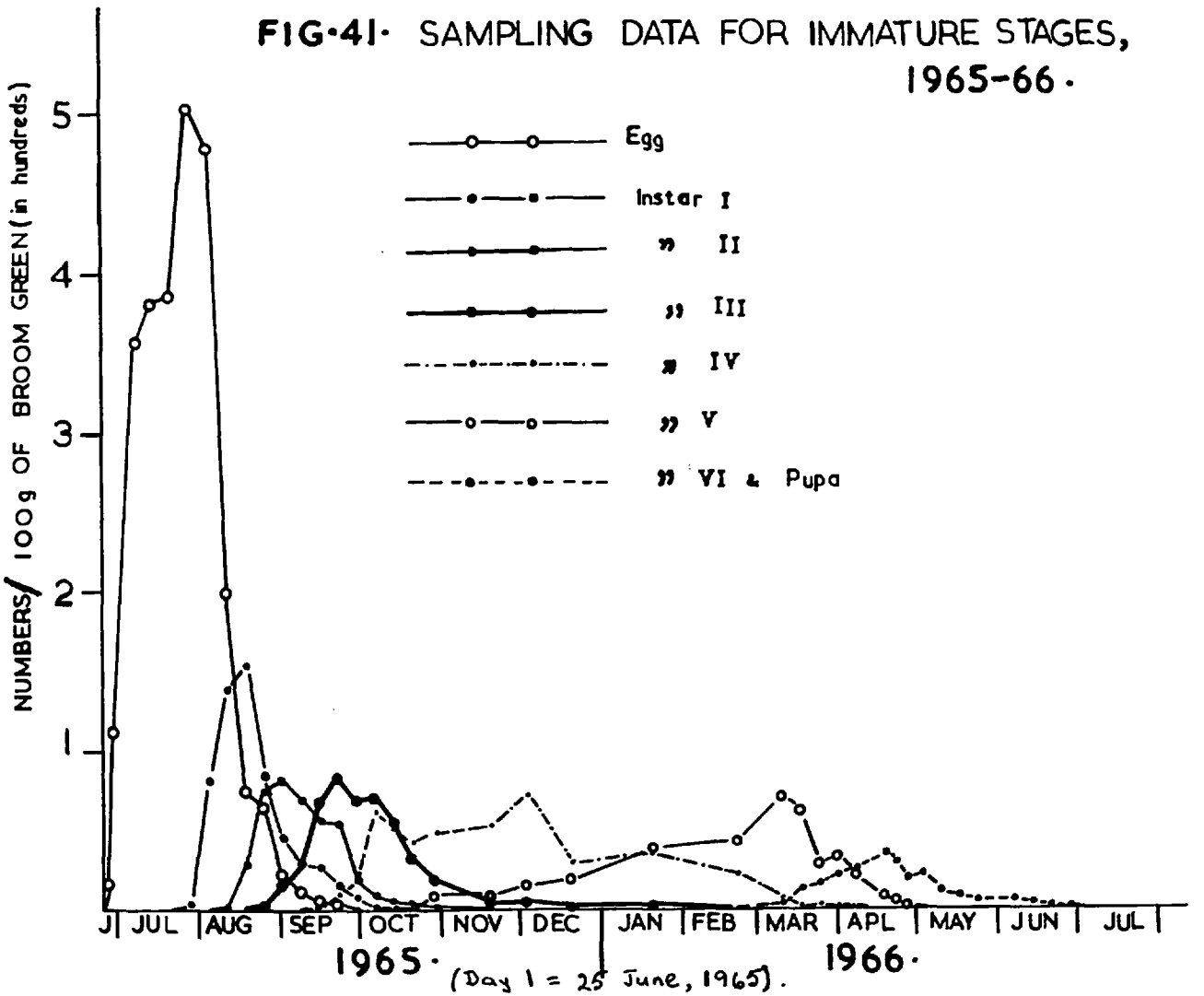
method, Southwood and Jepson (1962), the crudest, is useful for data unsuitable for analysis by the other methods, and usually gives under-estimates. The methods by Richards, Waloff and Spradbery (1960) is applicable to data from a population with long oviposition period and no well-defined peak. The simultaneous equation method (Dempster, 1961) is applicable to insects in which the same stages in successive generations are distinct and do not overlap. The method of Richards and Waloff (1954), the regression method, proved the most suitable for the analysis of the Leucoptera data. This method assumes an approximately steady mortality rate once oviposition and hatching are completed, and a fairly symmetrical emergence peak. If these conditions are satisfied, then the trend of the population can be represented by the equation $y = nk^x$, where y is the population on day x, n, the total number of eggs laid or larvae hatched, and k is the fraction of the population surviving per day. The logarithm of y (for population estimates after the peak in numbers) should follow a straight line, since $\log y = \log n + x \log k$. The values of the logarithm of successive population estimates and of x can be used to determine a linear regression equation; the regression coefficient is the logarithm of the average fraction of the population surviving per day. The initial size of the population, i.e. the population size at time 0, can be calculated from this equation. Estimates of the initial recruitments into each development stage can thus be made. The difference between the total recruitment of any two successive stages gives the mortality occurring in the earlier of the two stages. A calculation for the population less the eggs (i.e. for successive accummulated totals of the first instar) gives an estimate of the total number of individuals recruited into the first instar. The total numbers entering each of the subsequent stages are similarly estimated.

In the analysis of the Leucoptera data, the population estimates based on sampling by taking cuttings of broom were used. Since the cutting samples were usually taken at weekly intervals,

the value of x (at time 0) for any particular stage, was taken as that of the day half-way between the last sampling day and that on which the stage was first encountered. The best estimates of recruitment into a stage were obtained when calculations for the initial numbers entering that stage were based on the part of the curve for the whole population which corresponded to the time that stage was available. The trends in the occurrence of the egg and larval stages in 1964 to 1965, and 1965 to 1966 are shown in Figs.40 and 41. It will be seen that the numbers in each stage rapidly build up to a well defined peak and then fall off, and that the stages overlap considerably. Sampling in 1963 was started on October 25, and so the egg, the first instar larvae and part of the second instar stage were missed. The other stages could not be clearly identified for separate individual treatment. The second to the fifth instars were, therefore, grouped as one stage, and the sixth instar to the pupa as another. Regression equations were then calculated for the total number of larvae recruited into instar two and into instar six. Recruitment into the first instar stage was estimated from the number of hatched eggs in known weight of broom cuttings. The difference between the initial number of the first instar larvae and the initial number of the second instar larvae gave the mortality in the first instar stage. The difference between the total numbers entering instar two and instar six gave the mortality in instars two to five. Similarly, the mortality in instar six to pupa was estimated as the difference between the recruitment into the sixth instar stage and that of the adults (estimated by regression method). Since the date of first occurrence of the second instar larvae in 1963 was not known, day x for the estimation of recruitment into the larval stages two to five was taken as a day earlier than the first occurrence of the same stage in 1965. This conclusion was arrived at from the fact that the sixth instar larvae first appeared on 23rd and 24th March in 1964 and 1965, respectively.

FIG·40· SAMPLING DATA FOR IMMATURE STAGES, 1964 — 65·




FIG·41· SAMPLING DATA FOR IMMATURE STAGES, 1965-66·
NUMBERS/ 100 g OF BROOM GREEN (in hundreds)
Egg
Instar I
" II
" III
" IV
" V
" VI & Pupa
J
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APL
MAY
JUN
JUL
1965·
1966·
(Day 1 = 25 June, 1965).

The data for 1964 to 1965 were more detailed and included all stages from the egg to the pupae. They were not, however, consistent enough for the stages to be analysed separately. Therefore instars three to five were grouped as one stage, and similarly the instar six to the pupal stage. Regression calculations based on each of these stages gave the initial number of individuals recruited into the egg, the first instar, the second instar, the third instar and the sixth instar. The difference between the initial numbers entering the egg stage and those entering first instar stage gave the mortality in the egg stage, the difference between the initial numbers in first instars and that in second, the mortality in first instar. The mortality in the second stage larvae was similarly derived. The mortality in the third to the fifth instar is the difference between the initial numbers in the third instar and the initial numbers in the sixth. The mortality in the sixth instar to pupa was obtained from the difference between initial numbers entering the sixth instar and the numbers of the adults recruited. The data in 1965 to 1966 were much more detailed and consistent, and this allowed all the developmental stages to be treated separately. Regression equations were based on each of the stages, and the initial number of individuals recruited and the mortalities in each of the stages were estimated in the manner already described. The chorions of eggs sucked by Hemiptera and other enemies appear in samples right from the first day of occurrence of eggs in the field. These chorions increase in numbers, as more eggs are laid and remain on the twigs long after the adults have died out and oviposition had ended. They, therefore, give a false idea of a prolonged duration of the egg stage. Hence in the regression calculation for eggs, the sucked eggs were not included. The percentage of eggs sucked by Hemiptera was separately calculated from the total number of eggs (i.e. hatched, unhatched and sucked) recorded in the samples from the start of oviposition to the day adult females were last seen in the samples

taken by beating broom. From the percentage of eggs sucked, an estimate of the total number of eggs preyed on by Hemiptera was made. Thus if the percentage of eggs sucked is Q, and the estimate of unsucked eggs in a whole season is P, then the total number of eggs, Z, sucked in the season was calculated from the equation:

$$\frac{Z.100}{P + Z} = Q$$

The estimates of sucked eggs in 1964 and 1965 are as follows:

1964	7,270,100
1965	3,821,579

These figures were added to egg estimates to get the real total number of eggs laid in 1964 and 1965. Tables 48, 49 and 50 summarize the estimates of the initial numbers in each of the larval stages, along with those of the adults estimated by the regression method, for the three years.

Table 48 Estimates of recruitment and mortality in the developmental stages, 1963-1964.

Stage	No. recruited	Mortality in Stage (%)
Egg	———	———
Instar I	19,852,213	19.3
Instar II - V	16,020,966	43.5
Instar VI - Pupa	9,044,808	39.0
Adult	5,514,665	

Table 49 Estimates of recruitment and mortality in the development stages, 1964-1965.

Stage	No. recruited	Mortality in Stage (%)
Egg	89,791,455	8.7
Instar I	81,943,353	52.0
Instar II	39,332,640	14.8
Instar III - V	33,511,716	65.4
Instar VI - Pupa	11,611,121	76.7
Adult	2,710,487	

Table 50 Estimates of recruitment and mortality in the developmental stages, 1965-1966.

Stage	No. recruited	Mortality in Stage (%)
Egg	17,774,786	68.3
Instar I	5,637,110	23.5
Instar II	4,312,117	49.9
" III	2,158,778	22.7
" IV	1,669,020	21.8
" V	1,306,142	65.4
" VI	451,756	68.6
Pupa	141,909	37.3
Adult	89,392	

12.4 Fecundity

The estimates of fecundity in the field were obtained in three ways. The first method was based on the initial number of eggs, N, laid in the whole study area, calculated by the regression method. This was divided into the number of females recruited in the whole season. The number of females was estimated from the total number of adults in each season, determined by regression calculations, since the sex ratio was known (see Section 12.2). Thus in 1964, fecundity in the field, $\frac{N}{n} = \frac{89,791,000}{1,808,573} = 49.6$

In 1965, $\frac{N}{n}$ was $\frac{17,774,786}{1,136,428} = 15.6$ (n = number of females recruited).

The second and the third methods consisted in the pairing of the moths on emergence in 3 in. x 1 in. tubes containing a length of broom twig (see Fig.23). 20 pairs were kept in an unheated outhouse in which the temperature was very close to that in the field, another 20 pairs were kept in the field in ventilated Watson and Doncaster cylindrical cellulose cages. Records of oviposition were made at one or two day intervals, and the twigs of broom

renewed. The same females were used until they died, and so the resultant fecundity can be considered as the absolute fecundity of the moths. The males were usually replaced if they died. As there was much variation in the number of eggs laid by the individual females, the 95% fiducial limits of the observed mean fecundities of the moths were calculated. Thus the average fecundity in the insectary and in the field were as follows: 35 ± 21.56 and 27 ± 23.15 (1964); 26 ± 10.43 and 20 ± 8.78 (1965) and 31 ± 8.91 and 28 ± 16.10 (1966).

Table 51 summarises, and also compares, the fecundity estimates by the three methods. The regression method probably over-estimated the fecundity in 1964, as the emigrating females may not lay most of their eggs in the study area.(see Tables 31a and 31b). The other two methods should, therefore be expected to give higher values of fecundity than the regression estimates, as was true in 1965. The higher fecundity values in the insectary, than in the field may be accounted for by the more settled conditions in the former. Some of the factors such as weight of females on emergence, age, availability of mature eggs in the females and temperature, that affect fecundity have already been discussed (see Section 8)

Table 51 Fecundity estimates by the three methods.

Year	Regression	Insectary	Field in 3" x 1" tubes.
1964	49.6	35	27
1965	15.6	26	20
1966	-	31	28

The estimates of the total number of eggs laid in each of these seasons, based on the fecundities computed from the three methods are shown in Table 52. The female used in these calculations, are derived from the total adult recruitment for each year, determined by the regression method (Section 12.3). It will be seen that for

each of the years the estimates of the initial egg population, based on the three methods of fecundity assessments are reasonably close, particularly in 1965 and 1966. The calculated fecundities in the laboratory is much higher than that occurring in the field(see Section 8.1(c)) and has not been included in these estimates, since the conditions in the former widely differ from those in the field.

Table 52 Estimates of the total egg numbers in the field by the three Fecundity Methods.

Year	Total Number of Eggs by the three methods			No. of Females
	Regression	Insectary	Field (3"x 1" tubes)	
1964	89,705,220	63,300,055	48,831,471	1,808,572
1965	17,728,277	29,547,128	22,728,560	1,136,428
1966	-	1,368,743	1,236,284	44,153

The variations in the annual fecundities (Table 51) may not be due to annual changes in the weights of females on emergence as these varied very little in the three years, but there is some correlation between fecundity and the mean longevity of the females.

An attempt was made in 1965 and 1966, to investigate the trends in the weekly oviposition in the field, and from this, the number of eggs added each week to the egg population during the oviposition period. 20 different females were used each week; in this way a good cross-section of the female population, at various stages of adult life in the field, was used. The method was described in Section 8.1(e). Records of oviposition were taken once a week. The average weekly oviposition rate was multiplied by the number of females in the field (estimated from the weekly beats) to get the number of eggs added each week. The eggs laid each week were kept in the field and records of the number that hatched were made. This provided additional information about the proportion of

the first instar larva added to the population each week. The results are summarised in Tables 53 and 54. The weekly rates of oviposition in 1965 and 1966 are compared in Fig. 42. There is close agreement in the trends of oviposition which, in the two years, rose rapidly to a peak and then fell off with the age of the population. The extended oviposition period evident in Tables 53 and 54 is partly due to the protracted emergence periods of Leucoptera in the field. The total egg sterility was higher in 1965 than in 1966, and tended slightly to increase with the age of the population. Similarly, the population of eggs that failed to hatch was higher in 1965 than in 1966. The details are as follows:

Year	% Sterility	% not hatched	% hatched
1965	49.1	8.1	39.8
1966	5.3	1.5	87.5

When this is considered together with the figures in Table 51, it becomes evident that the balance of the population is determined each year by the average fecundity of the females and the level of viability of the eggs.

It must be noted that the number of eggs, i.e. the sum of all the weekly totals (Column 4, Tables 53 and 54) recruited is far below those estimated by the other methods (Table 52). An explanation for this is that the females in the field cages were more exposed to rain and sun than those living naturally in the field. Thus a number of them might have died within a week.

FIG·42· COMPARISON OF WEEKLY OVIPOSITION RATES OF 1965 & 1966.

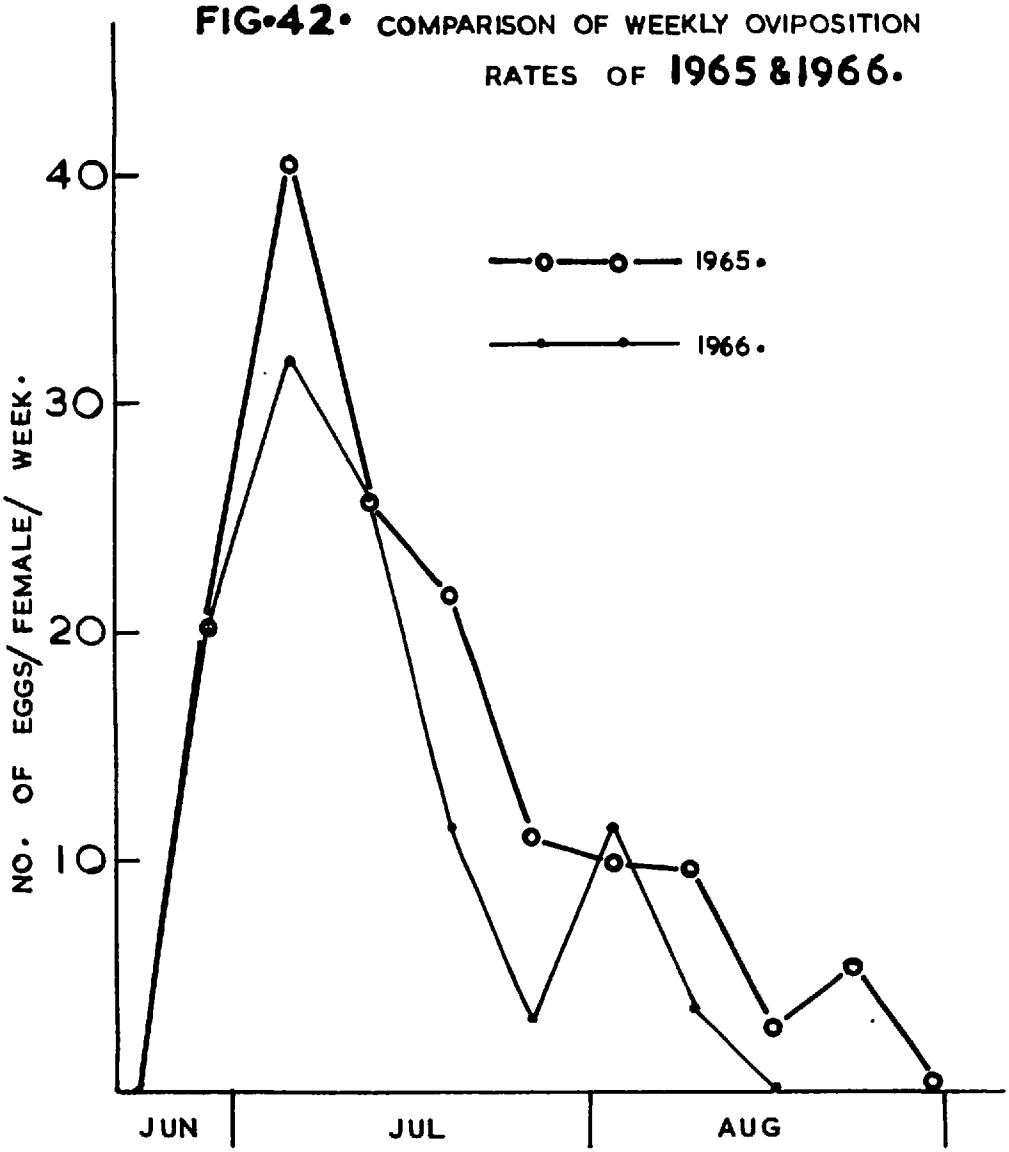


Table 53 Weekly oviposition; and eggs that hatched in field cages, 1965.

Date*	Estimated No. of females in field	No. of eggs per female	Total No. of eggs laid	% sterile	No. of eggs sterile	% not hatched	No. not hatched	% hatch	No. hatched
22.VI	13,099	19.7	258,050	49.0	126,445	14.0	36,127	28.4	73,286
29.VI	39,233	40.4	1,585,013	23.5	372,478	9.6	152,161	66.1	1,047,694
7.VII	112,116	25.7	2,881,381	95.1	2,740,193	1.2	34,577	0.4	11,526
14.VII	65,976	21.5	1,418,484	9.6	136,174	12.7	180,147	76,4	1,083,722
21.VII	57,895	10.9	631,056	10.7	67,523	9.8	61,843	77.1	486,544
28.VII	33,503	9.9	331,680	31.1	103,152	35.0	116,088	18.9	62,688
4.VIII	13,225	9.6	126,960	4.7	5,967	4.7	5,967	89.6	113,756
11.VIII	6,245	2.7	16,862	80.4	13,557	2.0	337	0	0
18.VIII	4,114	5.3	21,804	20.0	4,361	5.0	1,090	69.0	15,045
25.VIII	1,544	0.3	463	0	0	0	0	16.7	77
	Totals		7,271,753		3,569,850		588,337		2,894,338

Table 54 Weekly oviposition; and eggs that hatched in field cages, 1966.

Date*	Estimated No. of females	No. of eggs per female	Total No. of eggs laid.	% sterile	No. sterile	% not hatched	No.not hatched	% hatch	No. hatched
21.VI	1,473	20.2	29,755	1.9	565	2.8	833	85.9	25,560
28.VI	5,224	31.9	166,646	6.9	11,499	1.9	3,166	90.1	150,148
5.VII	10,314	25.9	267,133	4.3	11,487	1.2	3,206	87.4	233,474
12.VII	7,903	11.4	90,094	6.6	5,946	1.1	991	86.9	78,292
19.VII	3,349	3.1	10,382	11.6	1,204	2.3	239	83.7	8,690
26.VII	2,947	11.4	33,596	2.6	874	1.0	336	80.9	27,179
2.VIII	1,071	3.5	3,749	3.6	135	3.6	135	75.0	2,812
	Totals		601,355		31,710		8,906		526,155

* Beginning of week.

13. CAUSES OF CHANGES IN POPULATION OF L. SPARTIFOLIELLA.

13.1(a) Predation

The adult Leucoptera populations in the three years were large and existed along with an equally large predator fauna comprising various Hemiptera (Miridae, Anthocoridae and Nabidae), Araneida, Acarina, Dermoptera and Coleoptera (Coccinellidae, Staphylinidae and Carabidae). However, the most obvious predators of the moths in the field were spiders. In 1964, 1965, 1966, numerous spider webs were found on the broom bushes during the period when Leucoptera was adult. Frequently many Leucoptera were found caught in the dense webs and being devoured by the spiders. On a number of occasions many crab spiders (Thomisidae) were seen on the beating tray feeding on Leucoptera adults. Mr. D.J. Clark of the British Museum has kindly identified these spiders. The thomisids that feed on the moths in the field are the immature stages of Xysticus cristatus (Clerck) and adults of Philodromius aureolus. Some immature stages of Tibellus sp., probably oblongus (Walck.) were also taken, but it is not certain that they feed on the moths. The commonest of the web-spinning spiders that feed on Leucoptera are the immature stages of Linyphia triangularis (Clerck) (Linyphidae). The others are Meta segmentata (Clerck), Araneus sp. probably gibbossus (Walck) (Argiopidae) and Linyphia clathrata (Sund.) (Linyphidae) which spins its webs on the graminaceous undergrowth in the broom area. Simple laboratory tests to see which other predators feed on Leucoptera were made by confining the moths with suspected predators in 3" x 1" tubes. Of those tested only Forficula auricularia L. (Dermoptera) fed on Leucoptera.

Since a Leucoptera adult, or parts of it, caught in a spider web was easily visible, it was possible to estimate the size of the Leucoptera population destroyed by the web forming spiders. These estimates were made by counting the number of spider webs on eighths of broom bushes chosen at random, and recording the number of Leucoptera seen in the webs. The one-eighths of bushes were

then beaten over a tray and the number of Leucoptera was recorded. With the data collected, estimates were made of the numbers of Leucoptera caught in them in the whole study area. In each of the three seasons, the maximum predation by web spiders occurred in, or near to the week of peak numbers of Leucoptera in the field. Table 55 summarises the data on or near the dates of the greatest numbers of Leucoptera and the incidence of predation by the web spiders in 1964, 1965 and 1966. The greatest proportion of the moths was destroyed in 1964 when the population was very high. In 1965, and 1966, this proportion fell with the fall in the population size of the moths. Simultaneously the numbers of webs were low in 1965 and 1966 when Leucoptera numbers were low, but were high in 1964 when the moths were more abundant.

Table 55 Estimated Nos. of Leucoptera in spider webs, No. of spider webs on or near weeks of Leucoptera maxima in the field.

Date	No. of Leucoptera (a)	No. of spider webs	No. of Leucoptera in webs (b)	(b) as % of (a)	Calculated initial Nos. of Leucoptera in the field
*21-28.VII.64	190,112	60,450	22,100	11.63	5,514,665
7-14.VII.65	235,986	40,186	6,612	2.80	2,710,487
5-12.VII.66	20,226	17,547	268	1.33	89,392

* Two weeks after the peak Nos. in 1964.
Peak No. Leucoptera in 1964 = 630,656.

The exact contribution to the changes in the population of the moths by the other known predators could not be evaluated, as in the web spiders. However, some idea of their relative importance was gained from a comparison of the trends of their occurrence in the field in relation to that of the prey in 1965 (see Table 56). The

trends in the numbers of the Argiopid and of Lyniphid spiders appear to follow those of Leucoptera fairly closely, the date of their peak numbers synchronising perfectly with that of the moths. The same correlation does not appear to obtain in the other predators. The web spiders can therefore be considered to be important predators of the moths. None of these predators feeds exclusively on Leucoptera. Neither are these spiders confined to broom, but probably accumulate in large numbers near an abundant source of food. Other sources of prey are available, as Watmough (1963), using the precipitin test, showed that the Thomisid, the Argiopid and the Lyniphid spiders feed extensively on psyllids. Forficula auricularia L. in the broom area are known to take immature stages of the chrysomelid beetle, Phytodecta olivacea (Forster) (see Richards and Waloff, 1961).

Table 56 Occurrence of Leucoptera and its known predators in 1965

Date	No. Leucoptera in the field (a)	% of (a) in spider webs	No. Web-spiders in the field	No. of Thomisids in the field	No. of F. auricularia in the field
14.VI.	588	-	17,632	-	-
25.VI.	73,176	0.40	31,150	-	588
7.VII.	235,958	2.80	40,186	-	1,763
28.VII.	56,426	2.60	20,426	-	2,057
4.VIII.	19,895	1.47	20,130	-	1,029
11.VIII.	8,669	-	16,310	3,784	2,645
18.VIII.	5,584	-	16,750	5,216	3,306
25.VIII.	1,911	-	5,877	4,482	4,482
2.IX.	294	-	4,702	4,775	2,351

In the 1964 season, mites were noticed to be attached to the sides, or under the wings of Leucoptera adults. Mr. D. Macfarlane of the British Museum identified them as Typhlodromus (Amblyseius) reticulatus Oudemans (Phytoseiidae). This species of mites is

known to be abundant in Southern England on broom (Chant, 1959). The same author (1958) states that the family Phytoseiidae are primarily predators of phytophagous, orchard-living mites. In the case of L.spartifoliella, moths with these mites appeared exhausted and when the mites were removed, under a microscope, lesions were seen at their point of attachment to the moths. Occasionally five to six large mites were attached to one moth; and this increased weight would reduce the moth's flight. In 1965 Leucoptera sampled by beating were examined to estimate the importance of this mite (see Table 57). The mite appeared to attack more female than male moths, but there was unfortunately no time to investigate the effects of these mites on the fecundity or life span of the moths.

Table 57 Occurrence of the mite, Typhlodromus reticulatus on adult Leucoptera, 1965.

Date	No. of Leucoptera collected	No. with mite	As %	% of the moths, with mites, that were females.
25.VI.	221	3	1.36	33.3
7.VII.	601	8	1.33	75.0
14.VII.	334	9	2.69	66.7
21.VII.	242	9	3.72	77.8
28.VII.	136	10	7.35	70.0
4.VIII.	64	1	1.56	100
11.VIII.	28	-	-	-
18.VIII.	17	-	-	-

The effect of birds on population of the adult Leucoptera are unknown, but since they certainly feed on aphids and psyllids, they may also take some Leucoptera.

13.1(b) Emigration.

Emigration contributed considerably to the changes in the size of the population of Leucoptera in the three seasons. The

number of adult moths which had emigrated from the broom plantation in each of these seasons was estimated graphically (see Waloff and Bakker, 1963). This method was applicable to the Leucoptera data since the adult life was clearly divisible into a pre-flight, a flight and a post-flight period. The size of the pupal population, P, corrected for the known percentage of parasitism by Tetratichus evenymellae galactopus on the sampling date before adult appearance in the field, was estimated. The pre-flight weekly population estimates of Leucoptera were transformed into percentages of P, then into probit values, and plotted against the age (in days) of the population. The post-flight weekly population estimates were similarly treated. The straight lines joining the pre-flight and post-flight points were produced to intercept a vertical straight line, from a point (along the time axis) representing the date of completion of adult Leucoptera emergence from the pupae, at n_1 and n_2 respectively. The probit values of n_1 and n_2 were retransformed into percentages. The values of these percentages of P were calculated. The difference between n_1 and n_2 was taken as the number that had emigrated from the plantation. This method gives a crude approximation of emigration, but was found to suit the Leucoptera data satisfactorily. The calculated emigration from the broom plantation were as follows:

Year	Estimated initial nos. recruited	Nos. which had emigrated	As %
1964	5,514,665	1,130,438	20.5
1965	2,710,487	454,077	16.75
1966	89,392	14,182	15.86

13.1(c) Numbers taken for dissection in Laboratory.

Some adult Leucoptera were taken from the beating tray each week and dissected for evidence of parasitism. The numbers of moths dissected were 3,351 (1964), 386 (1965) and 43 in 1966. No evidence of parasitism was found in all the dissections, and no

parasites emerged from the adults collected throughout each season and kept in 3" x 1" tubes for twelve weeks. These dissections thus involved the removal of a fraction of the adult population, and therefore are considered to have contributed in a small degree to the changes in the numbers of the moth.

The individual contributions of these mortality factors to the adult population of Leucoptera from year to year are summarised in Table 58. Most of the mortality was caused by factors, the effects of which have not been evaluated quantitatively These other factors are considered to include old age, and climate which also interacts with predation and emigration. No adults survive to the following year.

Table 58 Comparison of the contributions of known mortality factors to changes in adult Leucoptera populations (as % in brackets).

	1964	196565	1966
Initial No. of adults.	5,514,665	2,710,487	89,392
No. which emigrated.	1,130,438(20.50)	454,077(16.75)	14,182(15.86)
No. killed by spiders.	641,356(11.63)	75,894(2.8)	1,189(1.33)
No. killed by dissection.	3,351(0.06)	386(0.01)	45(0.05)
Other factors	3,739,510(67.81)	2,180,130(80.44)	73,978(82.76)

13.2 Mortality Factors in the Immature Stages.

13.2(a) Causes of mortality in the eggs.

The factors responsible for mortality in the eggs of L.spartifoliella are sterility and predation.

Egg sterility.

There is considerable sterility in the eggs of Leucoptera. The sterile eggs are usually pale yellow, and easily recognisable as the top of the chorion collapses inwards. In 1964 eggs from

the field samples were kept in plastic petri-dishes, and examined at later dates for hatching, sterility and parasitism. Altogether 423 eggs were examined. 21 of these were sterile (i.e. 4.7% sterility). The rest hatched, and there was no egg parasitism. In 1965 and 1966, sterility in the eggs was determined from the eggs laid by females in the field oviposition cages (see Section 12.4., p. 122). The percentage of sterile eggs was calculated from the estimated total number of eggs laid, and the total number of sterile eggs throughout the season (see Tables 54 and 55). The calculated percentages of sterility in 1965 and 1966 were 49.1 and 5.3 respectively. The number of sterile eggs in field was thus:

Year	Initial no. of eggs	% sterility	No. sterile in field
1964-65	89,791,455	4.7	4,220,198
1965-66	17,774,786	49.1	8,727,420

As was shown in Tables 54 and 55, there were weekly variations in the levels of sterility in the eggs laid by the field females: these levels tended to be slightly greater in the eggs laid by the older females. It is also possible that sterility may result from non-fertilisation of the females which may arise when the female fails to mate (see Section 8.1(b)) or runs short of sperm. There was, however, no evidence of the latter in post mortem dissections of some of the females. The reasons for the high percentage of sterility in 1965 remains unexplained.

Predation on eggs.

An important cause of mortality of the eggs of Leucoptera spartifoliella is predation. As was described in section 12.3, the chorions of eggs sucked by Hemiptera and other enemies are buff white and appear very early in the oviposition period in the field. To identify these predators, labotatory tests were carried out in which a known number of Leucoptera eggs was exposed (for 24 hours) to a suspected predator. The predators tested, and the results of

the test are presented in Table 59. Hemiptera, notably anthocorids and the mirids appeared to be the most important predators of Leucoptera eggs. Coccinellids did not feed on the eggs.

Table 59 No. of Leucoptera eggs taken by predators in 24 hours.

Insect tested	No. of individuals	No. of Leucoptera eggs supplied	No. eggs eaten or sucked	as %
Forficula auricularia L.	5	20	1	5
Heterocordylus tibialis Hahn.	10	20	6	30
Orthotylus concolor Kirsch.	10	20	4	20
O. viriscens Douglas & Scott	10	20	-	-
O.adenocarpi Perris	10	20	1	5
Nabis apterus Fab.	10	20	2	10
Anthocoris nemorum L.	10	20	15	75
A. nemoralis Fab.	10	20	-	-
A. sarothamni Douglass & Scott.	10	20	3	15
Coccinellids	8	20	-	-

This list cannot be considered as exhaustive, as there are many other well known predators of insect eggs, for example Anystis on psyllid eggs (see Watmough,1963) and on Sitona eggs (Danthanarayana, 1965), present in large numbers in the study area that must have fed on Leucoptera eggs.

The method of estimating the percentage of Leucoptera eggs destroyed by predators, from the total number of eggs (i.e. hatched, unhatched and sucked) recorded in weekly samples from the beginning of the oviposition to the date when adult females were last seen in the samples, has already been described in section 12.3. The calculated percentages of eggs sucked by Hemiptera and other insect enemies were 8.1 in 1964 and 21.5 in 1965. Estimates of the total numbers of sucked eggs, based on the calculated initial numbers of eggs laid in the season, were then made; and the data on the mortality

of Leucoptera eggs in 1964 and 1965 are summarised in Table 60.

Table 60 Data on mortality of Leucoptera eggs in the field.

	1964	1965
Estimated No. of eggs in the season.	89,791,455	17,774,786
No. of eggs sterile.	4,220,198 (4.7%)	8,727,420 (49.1%)
No. of eggs preyed on.	7,270,100 (8.1%)	3,821,579 (21.5%)
Calculated No. of eggs that hatched.	78,301,147 (87.2%)	5,225,787 (29.4%)

The effect of these mortality factors overlap. For example, some of the eggs destroyed by predators may have been non-viable. This will tend to give a high estimate of egg predation. It has not been necessary to make correction for this in the egg mortality estimates, since any increase in the actual level of predation is counter-balanced by a corresponding decrease in the estimated level of sterility in the eggs. A better evaluation of predation would have been obtained by serological tests (see Dempster, 1960), but it was impossible to conduct them in the time available for this study.

13.2(b) Causes of mortality of larvae and pupae.

The mortality in the larval and pupal stages of L.spartifoliella is considerable. As has been shown in section 3, the greater part of the larval life is passed in the mine, with only a short wandering phase between this and pupation in cocoons outside the mine. Most of the larvae die in mines. The small first and second instar larvae are well protected in the mines from predators, however a great majority of them die when they are about to moult. Such larvae rapidly turn blackish brown and then liquify. Dr. M.F. Madelin of the Department of Botany, the University of Bristol, eliminated fungus as the cause of death. In the Botany Department at Imperial College, only the saprophytic fungus,

Penicilium, grow on specimens of larvae kept on Agar medium. Mr. D.E. Pinnock of the Department of Bacteriology of Imperial College suspected the presence of the bacterium, Bacillus lentus, in specimens sent to him, but suggested that further confirmation may be needed as to whether the bacterium is the cause of death. Breed and Murray et al. (1957) described Bacillus lentus as a bacterium showing no liquifaction on gelatin slab, and which thrives in aerobic conditions and is probably common in the soil. This description would exclude Bacillus lentus from causing the death of the Leucoptera larvae, unless it can be shown to be present in plant sap. An idea of the magnitude of this mortality was gained by examining the routine samples on 25.VII.65, when 132 out of 460 first and second instar larvae (i.e. 28.7%) died from this cause. On an estimated initial recruitment of 5,637,110 into the first instar (see Table 51) about 1,617,851 Leucoptera larvae must have so died. 23.88% (about 1,346,142 of the initial recruitment) of the mortality was in the first instar, and 4.82%, i.e. 271,709, in the second instar. Thus, the numbers dying from this cause diminished in the later instars. Only very few of the fourth and the fifth instars were found to die from this cause. In these later stages, however, other mortality factors operated; these will now be treated one by one.

Parasitism.

A certain cause of mortality in the Leucoptera larvae is parasitism by chalcid wasps. These wasps, all Eulophidae, are Tetrastichus evonymellae Bouche, sp. near galactopus (Ratz.), a Necremnus sp., Necremnus metalarus Walk., Chrysocharis gemma Walk. and Pnigalio soemias Walk. Some aspects of their biology in relation to that of the host larvae, have already been discussed in section 10. Each parasite attacks a definite developmental stage of L. spartifoliella. Although Tetrastichus evonymellae attacks the first instar larvae, it does not kill the host until the pupal stage. Thus, it has often been wrongly described as a parasite of the pupal or cocoon stage of Leucoptera (see Parker, 1964; Frick, 1964). Of the remaining four

parasites, the Necremnus sp. attacks the fifth instar Leucoptera larvae which are about to moult, Chrysocharis gemma and Pnigalio soemias the sixth instar in mine, and Necremnus metalarus the sixth instar larvae in cocoons.

The level of parasitism by each of these Eulophids was assessed by dissections of mines and of larvae in the routine weekly samples. Cocoons and pupae were also dissected to determine the degree of parasitism by Necremnus metalarus and Tetrastichus evonymellae. The results of these dissections for the three seasons are presented in Tables 61, 62 and 63. The percentage of parasitism by each species of parasite was based on the numbers of sound and parasitised hosts in known weights of broom samples. The estimates based on dissections of the early instars of the host gave a higher degree of parasitism by Tetrastichus (see Fig.32) The calculated percentage of parasitism by Tetrastichus has been based on dissections of pupae, since some of the early instars of the host larvae survive the attack by this Eulophid. In 1963-64 the estimates of the percentage of parasitism by Necremnus metalarus and by Tetrastichus were determined from the numbers that emerged from 736 cocoons kept in an unheated outhouse.

Table 61 Parasitism of Leucoptera larvae and pupae, 1963-64.

Date	Parasite	Estimated No. of host in field.	% parasitism	Calculated No. of host killed.
13-20.IV.64	Necremnus sp.	3,635,335 +	0.76	25,268
3-10.V.64	Chrysocharis	1,556,545	14.94	232,548
"	Pnigalio		1.14	17,745
9.VI. to 20.VII.64	Necremnus metalarus	-	9.51*	-
"	Tetrastichus	-	13.72*	-

* Estimated from cocoons in an unheated outhouse.
\+ Fifth instar of Leucoptera.

Table 62 Parasitism of Leucoptera larvae and pupae, 1964-65.

Date	Parasite	Estimated No. of host in field.	% parasitism	Calculated No. of host killed
14-20.IV.65	Necremnus sp.	908,829	2.82	25,629
21-28.IV.65	Pnigalio	10,532,718	1.40	147,458
5-12.V.65	Chrysocharis	4,330,842	11.11	481,157
25.IV. to 2.VII.65	Necremnus metalarus	3,670,065	11.36	416,919
"	Tetrastichus		28.03	1,028,719

Table 63 Parasitism of Leucoptera larvae and pupae, 1965-66

Date	Parasite	Estimated No. of host in field.	% parasitism	Calculated No. of host killed
17-24.III.66	Necremnus sp.	1,069,473	1.88	20,106
2-8.V.66	Pnigalio	522,481	5.52	28,841
"	Chrysocharis		27.61	144,257
20.VI.66	Necremnus metalarus	103,838	19.23	19,968
	Tetrastichus		57.69	59.904

It will be seen from the figures in Tables 61, 62 and 63 in conjunction with the preceding paragraph, that the greatest mortality due to parasitism occurred each year in the sixth instar larvae and in the pupae. This pupal mortality was caused by Tetrastichus which attacked the host in its first larval instar. The data for 1963-64 are incomplete. However, in 1964-65 and 1965-66 when the numbers of the sixth instar Leucoptera in the field were 10,532,718 and 522,481 respectively, 2,074,253 and 252,970 were parasitised. This suggests that the number of the host individuals parasitised depends directly on the numbers of the host available in the field. Also the number of the parasitic wasps in each succeeding season is determined by the numbers of the host larvae in

the preceding year. The number and quality of the broom bushes were higher in 1964 than in 1965 (see Section 2), and the larval population in the later year was concentrated on the few available suitable broom bushes. This larval concentration is probably responsible for the higher percentage of parasitism in 1965-1966 than in 1964-1965. The fact that these parasites can diminish the larval and pupal populations by several thousands each year indicates that they exert considerable regulatory effect on Leucoptera populations. There were clear indications of this in the three seasons of this study.

Predation.

The larvae in the broom twigs are not easily visible in the field until the spring, when the sixth instars begin to appear. The increase in the size of the larvae in the sixth instar causes the mine to bulge. These bulges become more conspicuous as the larvae feed and increase in size, and it is at this stage that Leucoptera suffers considerable mortality from birds which slit open the 'bulges' and remove the larvae. The signs of bird feeding are characteristic and easily recognised. Further, bird predation was shown experimentally with a group of ten potted broom plants (2 to 2.5 feet high) which had been exposed to oviposition in the field during the adult Leucoptera period in the previous year (1965). The number of larvae on each plant was counted early in the spring of 1966. Four of the plants containing 100 larvae were removed into a cage in the field; this cage was 6' x 4' x 4' in volume and covered by a half inch wire mesh. The other six plants contained 178 larvae and were left exposed at various points in the study area (see Fig. 43). The plants were examined for evidence of bird feeding a day after the sixth larvae were last seen in the weekly routine samples. The result may be summarised in the following synopsis:

FIG.43. Field bird predation cage.

Plants exposed in	No. of larvae in plants (a)	No. of bird feeding signs and as % of (a)	No. of mines from which larvae emerged (b)	No. of cocoons formed, and as % of (b)
Field	178	9 (5.1%)	99	85 (85.9%)
Wire cage	100	0 (0%)	45	38 (84.4%)

It is thus clear that the larvae were preyed on by birds, as there was no evidence of bird feeding on the broom plants from which they had been excluded by the wire netting. Hering (1951) states that "birds are the main enemies of mining insects in Europe" since they peck out the larvae or pupae from the mines. The same author reports that Bear (1906) discovered pieces of spruce needles containing the larvae of Epinotia nanana Tr. in the stomachs of tits, Parus ater (L.). Flocks of blue tits are usually present in the broom area at Silwood Park in the spring, and it is possible that they remove Leucoptera larvae from their mines. Since the mines from which the caterpillars had been pecked out were easily identified, estimates were made of the numbers of the sixth instar larvae thus destroyed in the spring of each of the three seasons. The results are shown in Table 64, and are based on the numbers of such 'mines' found in known weights of broom cuttings of the week in which the sixth instar larvae were last seen in the routine samples. There is close correlation between the numbers of Leucoptera larvae available in the field and the numbers taken by birds.

Table 64 No. and percentage of larvae killed by birds.

	Calculated No. of larvae killed in the field	Estimated initial No. of larvae in the field.	% of the initial No. of larvae killed
10-17.V.64	868,633	9,044,808	9.60
12-20.V.65	5,189,108	11,611,121	44.69
16-23.V.66	69,172	451,756	15.31

The sixth instar larvae of Leucoptera are also exposed to predation by birds and to insect enemies during their short wandering phase before pupation in cocoons. As shown in the synopsis, the numbers of the larvae that emerged from their 'mines' were higher than those that finally formed cocoons and pupated. The difference bears a relation to the number of wandering larvae that are killed by predators. It was not possible to estimate the magnitude of mortality from predation of the wandering sixth instar larvae; but some idea of the possible effect of insect predators was gained from a simple laboratory experiment in which the larvae were confined with suspected enemies in plastic petri-dishes. In these tests the following predators took Leucoptera larvae : Anthocoris nemorun L., Anthorcoris nemoralis Fab. (Anthocoridae), Heterocordylus tibialis Hahn.; Asciodema obsoletum Fieber (Miridae); Coccinella septempunctata (L); Adalia decempunctata (L) (Coccinellidae), Gabrius nigritulus Gr., Xantholinus fongiventris Heer. (Staphylinidae), Dromius linearis Ol. (Carabidae), the ant, Lasius brunneus Latreille (Hymenoptera) and Forficula auricularia L. (Dermaptera). These predators were all collected on broom, and occurred in fairly large numbers. However, it is not known whether they all feed on the sixth instar Leucoptera larvae in the field.

Finally, the pupae, in their white cocoons, are conspicuous and exposed to predators in the field. Forficular auricularia L. ate them in captivity in the laboratory; it is also possible that birds, small mammals and other predators may take a few in the field.

Winter disappearance.

The sizes of larval populations were much greater at the beginning of winter than at commencement of spring. The difference between the size of the overwintering larval population at the beginning of winter and that at the beginning of spring gave the estimate of the numbers which had died during the winter. The calculated winter mortalities are summarised in Table 65.

Table 65 Winter mortality in larvae of Leucoptera.

Year	No. of larvae at beginning of winter. (a)	No. of larvae at beginning of spring.	Winter disappearance (b)	(b) as % of (a)
1963-64	10,355,010	7,555,544	2,799,466	27.0
1964-65	9,099,519	6,333,041	2,766,478	30.4
1965-66	1,633,190	1,364,629	268,561	16.4

The factors responsible for the winter losses are difficult to identify; a number of probable factors, however, can now be discussed. The survival of an overwintering insect depends partly on the degree of its cold tolerance and on its ability to withstand long exposures to low temperatures. The cold hardiness of the overwintering Leucoptera larvae has already been discussed in section 5.4. The cold-death point of the overwintering population, the bulk of which occurred in the fourth or fifth larval instar (see section 5.1), was shown to average -17.04°C (limits -13.5°C to -21.0°C). This, the undercooling point of the caterpillars, represents the limit of the lowest tolerable temperature. Exposures to temperatures below it will be lethal to the larvae. Deaths will result in winters when the temperatures fall below this range. At Silwood the daily mean, maximum and minimum temperatures in the study area are measured every year in a Stevenson's screen. These records show that the daily minimum temperatures never fell below -9.3°C during the period of this study. It has not been possible to measure the winter temperature within the broom twigs, but this probably did not vary considerably from that of the study area. Since the undercooling point of the larvae is so far below 0°C, freezing can be eliminated as a cause of winter mortality.

In the winter of 1964, it was observed that on warm days some Leucoptera larvae became exposed and had fallen off from their mines, or killed by some insects feeding on broom twigs. Sitona regensteinensis Hbst. is known to feed on broom on warm winter days

and hence its disturbing activity was implicated. Sixty five Leucoptera larvae (in twigs) in petri dishes were exposed to S.regensteinensis collected from the field on 5 January 1965. The petri dishes were kept in a constant temperature room at 20°C. Examination after five days revealed that the beetles, by their feeding, had exposed and caused seven Leucoptera larvae to fall out of their mines. Four of the caterpillars were half eaten by the beetles in the process of feeding on the twigs. In other words a mortality of 16.9% of the larvae was caused by the feeding of this phytophagous beetle in the laboratory. S.regensteinensis has been shown to emerge from litter and feed on broom on winter days when the temperature is above 8°C (Danthanarayana, 1965). The frequency of days in which the daily maxima of temperature rose above this in January 1965, was 10. It is therefore, probable that some of the winter mortality of the Leucoptera population may result from the feeding by this beetle and by other phytophagous insects that come up to feed on broom on warm days in winter.

Some of the mortality of the caterpillars in winter must result from the death of the host plant. This will be discussed more fully later, but briefly the numbers of the broom bushes in the plantation at the beginning and the end of winter in 1964 and 1965 were as follows : 1541 and 1503 (1964-1965), 865.4 and 841.1 (1965-1966), (see Tables 3a and 3b). It cannot be pretended that the factors here discussed accounted for the size of winter mortalities shown in Table 65. Some of the larvae died from no apparent causes; others were found to die from the factor already described as ? Bacillus lentus.

Changes in the habitat.

The life span of the broom plant is 10 to 15 years (see section 2.2). The broom bushes in the study area were planted out in 1957, and were nearing this age at the time of this study. A progressive reduction in the number and quality of the bushes was evident during the three years of this work. Age, excessive

flowering and attack from many broom feeders, especially Leucoptera, contributed to the decline of the habitat. It is the death and the reduction in quality of the broom bushes between the summer of one year and the spring of the following year (i.e. when the larvae are in their 'mines') that result in the mortality of Leucoptera larvae on broom. The relative losses in numbers of the host plant in the plantation in the three seasons are as follows:

1963 to 1964	1605-1570	=	35
1964 to 1965	1541-1503	=	38
1965 to 1966	* 881.6-841.1	=	40.5

* measured as 'whole bush' equivalents (see Section 2.3).

After the heavy attack by Leucoptera larvae in 1964-1965, the number of bushes was greatly reduced. A corresponding decline in the quality of the bushes has already been shown (see Table 2). Part of the heavy mortality of the immature stages of Leucoptera in 1964-1965 and 1965-1966, undoubtedly resulted from the depletion of the habitat.

14. POPULATION BUDGETS, 1964-66.

The population budgets for the years 1964-65 and 1965-66 (for which the data are complete) are presented in Tables 66 and 67. The budgets are of the type proposed by Richards and Waloff (1961), and summarise the changes in the population size and the variations in the mortalities of the successive developmental stages of Leucoptera in the two seasons. The causes of the population changes were discussed in details in Section 13.

The mortalities are expressed, in these budgets, as percentages of the total initial number of eggs recruited, and where possible as percentages of the number entering the stage. Table 68 illustrates the distribution of the mortalities and indicates that the greatest mortality occurs in the eggs and in the first and second larval instars. Thus, with respect to the total egg numbers, the highest deaths occurred in the larval instar I and II in 1964-65, but in the eggs in 1965-66. The accumulated mortalities in these three stages, i.e. the egg, the first and the second larval instars, amounted to 62.7% and 87.9% in the two seasons. However, when the individual stages are considered, it is seen that the mortalities in the fifth and in the sixth larval instars are also high.

In a species with an average fecundity of 100 a mortality of 98% is necessary for population stability, if the sexes occur in equal proportions. The sex ratio in L.spartifoliella was approximately 2♂ : 1 ♀ (1964) and 1♂ : 1 ♀ (1965) (see Section 12.2). With corresponding average fecundities of 49.6 and 15.6 (estimated from the regression equations, section 12.4) mortalities equivalent to 93.95% and 87.82% respectively, would have resulted in stability of the population. Mortalities above this would have produced a decrease, and those below an increase in the population. The estimated (actual) mortalities of Tables 66 and 67 and those that would have given stability with each year's average

Table 66

BUDGET 1964-65

Stage	No. entering stage (nearest thousand)	No. dying within stage (nearest thousand)	% of that stage which died	Mortality of that stage as % of total egg no.	Accumulated mortalities % of egg no.
Adults in summer, 1964	5,515,000				
Eggs.	89,791,000	7,848,000	8.7	8.7	8.7
Larval instar I	81,943,000	42,610,000	52.0	47.5	56.2
Larval instar II	39,333,000	5,821,000	14.8	6.5	62.7
Larval instars III - IV.	33,512,000	21,901,000	65.4	24.4	87.1
Larval instar VI - Pupa.	11,611,000	8,901,000	76.7	9.9	97.0
Total adults, summer 1965.	2,710,000				

Table 67

BUDGET 1965-66

Stage	No. entering stage (nearest thousand)	No. dying within stage (nearest thousand)	% of that stage which died	Mortality of that stage as % of total egg No.	Accumulated mortalities % of egg No.
Adults in summer, 1965	2,710,000				
Eggs	17,775,000	12,138,000	68.3	68.3	68.3
Larval instar I	5,637,000	1,325,000	23.5	7.5	75.8
Larval instar II	4,312,000	2,153,000	49.9	12.1	87.9
Larval instar III	2,159,000	490,000	22.7	2.8	90.7
Larval instar IV	1,669,000	363,000	21.8	2.0	92.7
Larval instar V	1,306,000	854,000	65.4	4.8	97.5
Larval instar VI	452,000	310,000	68.6	1.7	99.2
Pupae	142,000	53,000	37.3	0.3	99.5
Total adults in summer, 1966.	89,000				

fecundity are examined in relation to the changes in the adult population in Table 69. The 1964-65 percentage of mortality was greater than that which theoretically would have resulted in stability in the following year, and this is reflected in the fall in the number of adults in the summer of 1965. In 1965-66, the actual mortality was again considerably above that which would have produced stability; this again is supported by a much greater fall in the numbers of Leucoptera in 1966, to less than half the number in 1965.

Table 68 Distribution of mortality in the different developmental stages of Leucoptera (Mortalities as % of initial egg Nos.)

Year	1964-65	1965-66
Mortality of eggs	8.7	68.5
Mortality of larval instars I and II	54.0	19.6
Mortality in larval instars III-V	24.4	9.6
Mortality in larval instar VI-Pupa	9.9	2.0

Table 69 Annual deviations of mortality from those necessary for stability.

Year	1964	1965	1966
Adults from eggs of previous generation.	5,514,665	2,710,487	89,392
Mortality necessary for stability (%)	93.95	87.82	
Actual mortality (%)	97.0	99.50	
Difference (%)	-3.05	-11.68	

15. DISCUSSION

This work on a natural population of Leucoptera spartifoliella has revealed continual changes in the numbers of the adults and in the immature stages from year to year. These changes are quite considerable, and in the adults amounted approximately to a seven-fold reduction in numbers, from 5,514,665 in 1964 to 89,392 in 1966 (see Table 58). Corresponding changes in the levels of the population of the immature stages were also evident The factors likely to influence the sizes of an insect population fall into several, rarely independent, groups. These include climatic factors, (locally weather), factors of the habitat, (i.e. the food plant), intra-specific factors and the effect of other organisms. If considered in relation to a particular organism, in this case Leucoptera, these factors can be represented as the components of the environment, where the effective environment of an organism is depicted as everything in the universe that affects the successful establishment of the organism (Andrewartha and Birch, 1954; Allee et al., 1949; Milne, 1957).

It is proposed in this discussion to examine these factors in the light of the present study, and then to show how they have either singly or severally contributed to the variations in the observed population levels of the moth within the period of study. It is not pretended that a study of so short a duration - 2.5 years - should be conclusive as to the general regulation of Leucoptera populations, for as Richards (1961) has pointed out at least a minimum of five year period is required to get any useful idea about the population dynamics of an insect in Great Britain. Attempts will also be made to draw general inferences as to how Leucoptera is adapted to maintain its population despite the odds against its achieving this in a temperate climate.

The limits of the geographical distribution of an insect are known to be determined by climatic factors; but these (weather) factors alone cannot control the abundance of the insect,

(see Nicholson 1933, 1958; Varley, 1956; Milne, 1957; Richards, 1961). The main effect of weather factors on a population is to accelerate or retard its reproductive rates, and influence its survival. Climate may also cause a high percentage of mortality (though this is difficult to demonstrate in the field), and thus may by interacting with emigration and immigration determine the abundance of a species.

The component of weather that most affected the Leucoptera population was temperature. The oviposition rate and fecundity of the moths were affected by temperature (see Table 22). Temperature also influenced the movement of moths within, and also the emigration from the habitat. It was found to affect the rate of development of the immature stages (see Table 5 and 6) and also the emergence of the last instar larvae from the mines. The duration of the wandering larval phase before pupation seemed to depend on temperature; since this phase is vulnerable to predation, temperature can be said to influence its length of exposure to predation. Rainfall not only inhibited flight, but also often drowned these small and fragile moths.

A cause of mortality that must be discussed in conjunction with temperature effects is what has been described in Section 13 as 'winter-disappearance'. During the period of this study the loss to the larval population due to this amounted to 27.0% (1963-64) 30.4% (1964-65) and 16.4% (1965-66) of the estimated numbers entering the overwintering population (see Table 65). One is tempted to ascribe most of this mortality to weather factors in the winter when changes in temperature could be critical for the survival of a hibernating population, for most insects in the temperature region are known to suffer heavy mortalities in the winter whilst the direct effects of weather during the summer months can be considered relatively unimportant (Richards, 1961). It is interesting to note, at this juncture, that Varley and Gradwell (1960) found that the key mortality factor in the larvae of the winter moth, Operophtera brumata L. is winter disappearance, and

that this was probably due to weather factors. Varley and Gradwell did not determine the undercooling point of the larva, but it is known that the cold death-point of an insect is a measure of its ability to survive exposures to low temperatures (see Salt, 1936; Stenseth, 1965; Mellanby, 1939). It is not considered that the heavy mortality of overwintering Leucoptera larval population is due mainly to weather factors, for as has been shown (see Section 4.4) their cold death-point (i.e. the undercooling point) is far below zero, and since within the period of this study temperature never fell below this point, freezing can be excluded as the cause of mortality. Evidence was obtained that some of the winter deaths were due to phytophagous insects that come up to feed on broom on warm days in winter. The proportion of the days warm enough for this feeding to occur was comparatively small, and larval mortality from this cause probably constituted only a minor part of the total winter-disappearance. Some of the winter deaths were due to no apparent cause and some to a pathogenic organism that has tentatively been described as ? Bacillus lentus. However, a great deal of the winter mortalities appear to have resulted from the deaths of the host plants in the winter. These winter deaths increased as the broom bushes aged and became more susceptible to the reverses of climatic conditions, and can be taken to contribute considerably to the winter-disappearance of the over-wintering population.

On the whole there is a general agreement among entomologists that it is intraspecific competition for food or space that sets the upper limit to the population density of any species (Nicholson, 1933, 1958; Milne, 1961; Solomon, 1964). It is hardly conceivable that food shortage could have had any marked influence on the population densities of Leucoptera observed in the two and a half years of this census. For although a progressive deterioration in quality of the broom bushes was evident, the quantity of food did not fall below starvation level that would cause the death of the mining larvae. It is, however, possible that the poorer quality

of the twigs on which the larvae feed may indirectly affect the fecundity of the resultant adults in the summer. Thus the average fecundity of the moths was 49.6 in 1964 and only 15.6 in 1965. This is a variation by a factor of about three; this reduced fecundity greatly affected the population level in 1965. It is difficult, however, to see how this could have resulted from a defficiency in the food of the larvae since the average weights of the females (0.73 mg. in 1964; and 0.68 mg. in 1965) were not significantly different, and since in Leucoptera fecundity is very highly correlated with the weight of females on emergence (see Section 8.1(d)). The effect of space was more interesting. Though the adult females could not have competed for oviposition sites which were in ample supply in the field, some of the larvae were occasionally observed to die from cannibalism when their mines coalesced. This is not intraspecific competition in the conventional sense, for according to Milne (1961) the criterion for competition is the insufficiency of the resource for the number of competitors. The twigs in which cannibalism occurred did not seem insufficient for the numbers of larvae mining on them. However, it is conceivable that situations in which the number of broom bushes is far reduced in proportion to the number of Leucoptera females in the field would lead to an increased number of larvae mining on a particular twig. In such a case, the incidence of cannibalism would increase and then contribute much more significantly to the fluctuations in the population. Fortunately, such a situation has not yet arisen at Silwood.

A great impact on the population of Leucoptera was undoubtedly attributable to the host-plant. The effect of the host plant is likely to be more marked on the larvae. Apart from a short wandering phase of the sixth instar larvae and the pupation in cocoons outside the mines, the entire larval life is spent within the twigs. Thus the broom twig provides both space and food to the larva. Consequently, the survival of the larvae and also the size of the resulting adult population will depend partly

on the quality of the host plant. It is also true to say that the poor quality of larval food may show itself not only as mortality of the larvae, but also in the reduction of egg production in the resulting adults. In this connection, it is interesting to note that the Leucoptera population decreased with the ratio of green material to wood on the broom bushes (see Tables 2, 49, 50 and 51). The larvae are restricted in their feeding to the outer cortical cells, the collenchyma, which are laden with chloroplasts and according to Mc clean et al. (1962) photosynthesise. These cells therefore must be full of nutritive materials on which the larvae draw. It is probable that the nutritional level of the twigs would decrease as the broom bushes get older, and this reduced the fecundity of the adult females. The progressive reduction in the numbers and quality of the broom bushes was quite marked in 1964 and 1965. The bushes were dying from age, excessive flowering and damage from insect feeders, particularly Leucoptera larvae (see Section 7.4). Most of these deaths occurred whilst the larvae were still in their mines, and indubitably took considerable tolls of the larval population. Frick (1964) recorded evidence that the introduction and establishment of L. spartifoliella in California resulted in an appreciable damage and death of parts or of whole broom bushes, in some instances the feeding of the larvae causing a significant lowering in seed production.

The possible effect of changes in the habitat on the adult Leucoptera population was seen in the concentration of eggs, and therefore of the resultant larval stages. This followed the reduction in the numbers of suitable broom bushes. The depletion in the quantity of broom will also tend to concentrate the predators and parasites of Leucoptera along with the moth, and lead to greater predation and parasitism. This was clearly evidenced in 1965-66 when the parasitism of the larval and the pupal stages was proportionately higher than in 1964-65, even though the initial recruitment into the larval population in the former was only about a fifth of that in the latter season (see Tables 62 and 63).

A greater control of the Leucoptera population was exerted by other organisms, in the same habitat, chiefly the Eulophid parasites of the larvae and the various predators of the adults, eggs and larvae.

The collective effect of the parasites on the Leucoptera population was considerable; hundreds of thousands of the larvae were killed by parasitism each year. Parasitism in this regard may be recognised as one of the major factors regulating Leucoptera population at Silwood. A comparison of the numbers of larvae destroyed in each of the two seasons (1964-65 and 1965-66) for which the data were complete showed that greater numbers of individuals were destroyed in the year in which the size of the host population was higher. However, the percentage reduction of the population by parasitism was higher in the year with the smaller population level (see Tables 62 and 63). Thus, it appears that the degree of parasitism is inversely related to the host population size. This may be the beginning of a delayed density - dependent relationship in the sense of Varley (1948, 1953), but it is impossible to be sure of this in a three year study. However, no firm conclusions can be drawn from only two year data, since the increased level of parasitism in 1965-66 could have been due to the concentration of the Leucoptera larvae which had resulted from the decline in the quality of the host plant. The relative effectiveness of the parasites depended on the stage of, and the time the host was attacked. Parasites effectively regulate the population of their host if their life-cycles are synchronised with that of their host, and if their mortality is not high (see Thalenhorst in Varley, 1953). In this regard, Tetrastichus evonymellae, sp. near galactopus was the commonest and the most effective parasite. Its life-cycle was perfectly synchronised with that of the host, and its effect was greatest when the host was rare. Thus in 1965-66 parasitism by Tetrastichus was 57.69%. In other words, more than half the pupal population in that generation was destroyed by this parasite. This

means that the reduced size of the adult Leucoptera population in 1966 was largely attributable to the influence of Tetrastichus. The numbers of the Necremnus sp. are usually low as this parasite attacks a declining population of the fifth instar Leucoptera larvae. These larvae were usually among the last set that moult into the sixth instar, and may represent the larvae derived from the later hatched eggs of the host.

It is interesting to note that in the population budgets (see Table 66 and 67) the heavy mortalities occurred in the fifth and sixth instars. These are the stages most attacked by the parasites. Therefore the heavy percent mortality in them probably partly reflects the impact of parasitism.

As with parasitism, predation was a major factor regulating the Leucoptera population. The Heteroptera, notably the common mirid bugs and the anthocorids were shown to be the most important predators of Leucoptera eggs. It was also indicated in the laboratory tests that the anthocorid bug, Anthocoris nemorum Fab. fed most on the eggs. Although these bugs suck Leucoptera eggs, they do not depend exclusively on them; since the bugs can also feed on broom aphids and psyllids (see Dempster 1960; Richards and Waloff, 1961). It should be recalled, however, that the estimated predation on Leucoptera eggs in 1964 and 1965 were as follows:-

Year	1964	1965
Initial Egg Nos.	89,791,455	17,774,786
No. of Eggs destroyed by predators.	7,270,100(8.1%)	3,821,579(21.5%)

These figures have been extracted from Table 60, p.134 . They show that predation was more intense in the year when fewer Leucoptera eggs were laid. This situation in which the effect of the predator or parasite is inversely proportional to the numbers of the host available has been described as inverse-density relationship

(see Solomon 1964, Holling, 1961). In this instance this relationship could have been produced by the declining habitat, and the consequent concentration of predator and prey in relatively more restricted space. Predator effects on the early larval instars of Leucoptera are practically nil; the mine apparently provides an adequate protection. The occasional losses in the overwintering population, due to the feeding of some phytophagous broom feeders such as Stiona regensteinesis is not considered to have an important effect on the Leucoptera population. The sixth instar larvae still in their mines suffered heavy predation from birds. The actual species of bird involved was not identified. As Richards (1961) aptly pointed out, a collection of an appreciable number of vertebrate predators in order to study their gut contents would often alter the whole situation, since these animals are relatively rare. Moreover, it will not be easy to recognise a particular species of insect in the gut contents. The comparative destruction of the sixth instar larval population by birds in the field, for 1964-66 was presented in Table 64. The number of birds was unknown, but it appears that the total number of the host larvae killed was correlated with the numbers available in the field. Two kinds of predatory responses are known. These are: the functional response, where the number of the prey destroyed increases with density of the prey; and numerical response: where the number of predators increases in response to increase in density of the prey (see Solomon, 1949; Holling, 1961). Bird predation of the sixth instar Leucoptera larvae appears to be of the functional type. However, further studies are needed to see if this response agrees with the characteristic s-shaped curve - representing the functional response of vertebrate predators (see Holling, 1959).

The wandering phase of the sixth instar larvae, and the pupae in cocoons are the two stages in Leucoptera population that are also vulnerable to predation, and it was shown that the common mirids, anthocorids, coccinellids, staphylinids and broom carabids can take the wandering larvae. However, a quantitative assessment

of predation is needed in order to ascertain the actual size of the loss in the Leucoptera population due to this cause of mortality The serological method which has proved useful in the quantitative estimation of the predation on the immature stages of the Chrysomelid beetle, Phytodecta (see Dempster, 1960; Richards and Waloff, 1961; Dempster, Richards and Waloff, 1959) could be utilised here.

The adult Leucoptera population was subjected to predation by spiders. The commonest of them, and the one that caught the largest numbers of the moths in its webs was the lyniphid, Linyphia triangularis (Clerck). Since most of this predation occurred during the peak of the egg laying period, it must be considered as important.

Another factor in the interspecific complex that needs to be discussed is that of insects, other than the parasites and predators, that occupy the same habitat. As has already been stressed the life cycle and survival of Leucoptera are intimately connected with its mining habit on broom. Consequently, the other stem miners will be of relevance to Leucoptera population, since their presence would introduce interspecific competition for oviposition sites, mining space and food, particularly if their adult stages are concurrent with that of adult Leucoptera. Only one other insect, the larval stages of Trifurcula immundella Zeller (Nepticulidae) was found to mine on broom at Silwood Park. The adult period of this nepticulid usually coincided with the tail end of occurrence of adult Leucoptera (i.e. after mid-August), and when the latter had laid most of its eggs. Therefore interspecific competition, if any, between Leucoptera and Trifurcula for oviposition sites must be considered as negligible. Competition for food or space was also unlikely since broom twigs were in sufficient supply. Only once (i.e. on 17.2.65) during this study were two larvae, one of Leucoptera and the other of Trifurcula, found dead when their mines met. However, the feeding of the larvae of the nepticulid moth may have helped to accelarate the progressive deterioration of the habitat, and thus indirectly contributed to the concentration of

the immature stages of Leucoptera on broom in 1965-66. It should be recalled that this concentration was partly responsible for the higher proportion of parasitism and predation of Leucoptera in 1965-66. On the other hand, the Trifurcula larvae were parasitised by the Necremnus sp. which also attacked the fifth instar larvae of Leucoptera, and was preyed on by birds. Thus by serving as alternative food, Trifurcula may have released some of the pressure on the Leucoptera population.

Another factor that contributed to the changes in Leucoptera abundance was egg sterility. The estimated egg sterility for 1964 and 1965 can be summarised as follows:

Year	1964-65	1965-66
Estimated initial egg numbers	89,791,445	17,774,786
Average fecundity of females	49.6	15.6
No. of sterile eggs(and as % of total egg Nos.)	4,220,198(4.7%)	8,729,420(49.1%)
Larval density (taken as the peak nos. per 100g.)	1229	153

Thus egg sterility was clearly high in 1965-66. It is convenient at this juncture to refer to the population budgets for the two seasons, 1964-65 and 1965-66 (see Tables 66 and 67). The most noticeable difference between the two years is in the degree of mortality of eggs and of the first larval instar. When egg mortality was low, the mortality of the first instar larvae was high, and vice versa. The two mortalities seemed, therefore, to be mutually compensatory. Similarly, the percentage of egg sterility was low in 1964 when the overall egg mortality was low, but was high in 1965 when the total egg mortality was high. It appears, therefore, that the main mortality factor in the eggs was sterility. When this is considered together with the average fecundities in 1964 and 1965, it becomes apparent that the abundance of Leucoptera each year is largely determined by the average fecundity of the females and the level of viability of the eggs. Mortalities of the other

stages, however, are also important, but tend to counter-balance the combined mortalities of the eggs and the first larval instar. Thus, when the accumulated mortalities of the egg and the first larval instar were 56.2% in 1964, those of instar two to pupa were 40.8% (total = 97%); similarly, in 1965 the accumulated mortalities of egg and first larval instar were 75.8%, and those of instar two to pupa 24.7% (total = 99.5%).

Klomp and Gruys (1965) and Klomp (1966) have produced evidence (in the pine looper, Bupalus piniarius L.) of an inverse relationship between the fecundity and viability of offspring and the larval density of the preceding generation. When the Leucoptera data are examined in the light of this concept it appears that the greatly reduced fecundity and the high egg sterility in the generation 1965-66 may be explained by the very high larval density in 1964-65. This, however, remains a subject for further experimentation.

Finally, emigration also contributed to the changes in the adult population levels in the field. Flight in Leucoptera was shown to have two components. These are: (a) movements within the habitat (flitting); this component is also referred to as trivial movements (see Southwood, 1962) associated with mating and oviposition; (b) movements away from the population. This is dispersal or emigration, and was the component principally affecting the numbers of adults in the habitat. Losses to the population caused by emigration were shown to be 20.5% (1964), 16.75% (1965) and 15.86% (1966), and to be significantly correlated with the size and the age of the population. Southwood (1962) sees migratory movement as an evolutionary development to enable a species to keep up with the changes in the location of its habitat. This appears to be true of the emigration of Leucoptera as broom, which grows readily on disturbed ground and is usually replaced as the natural vegetation regenerates, can be considered as a relatively temporary habitat. On the other hand, the proportion of the population which had emigrated was not less in 1964 when there were more broom bushes

than in 1965 and 1966 when the bushes deteriorated in numbers and in quality (see Tables 3a and 3b). This indicates that emigration in Leucoptera is not strictly a response to current changes in the habitat, and therefore supports Johnson's postulate (see Johnson, 1960a, b). Only a very slight increase in emigration was noted when the population was extremeley dense (1964). Almost the same proportion of the population emigrates irrespective of the population size. This still further supports Johnson's concept that migration is an inherent activity. The special features which characterise true migratory movements are simultancity, undistractedness and occurrence only in young and sexually immature females (see Johnson 1960 a, b, c, 1963, 1965; Kennedy 1961). This study has established that although emigrating Leucoptera are sexually mature at emergence, those emigrating early in the flight period are young and some virgin; whereas females emigrating later in the flight period are older, fertilised and have all oviposited. It appears, therefore, that the dispersive movements in Leucoptera are truly migratory at the beginning of emigration, but are extensions of the trivial movements later on in the flight period.

According to Johnson (1963, 1965) the migratory activity of insects are partly controlled by humoral and neorophysiological factors, since processes which prolong or abolish the pre-oviposition period tend also to encourage or teminate migratory flight. This is probably why in Leucoptera the pre-oviposition period is prolonged so that oviposition coincides with the commencement of emigration.

It is intended to discuss here how Leucoptera seems to be adapted to live and reproduce in its environment. The whole life cycle is spent on or in the broom plant which is a deciduous perennial. Adult emergence, oviposition and part of the larval development occur in the summer. The entire life cycle, with the exception of the short wandering phase before pupation, is passed within the mine which affords protection to the early and more vulnerable larval instars from predation. There is a larval dispause

which ensures survival in winter, and which assists in the synchronisation of the life cycle with both the seasonal weather and the growth cycle of the host plant, for oviposition in the summer is largely on the spring growths (see Section 2, p. 7). The overwintering population is equipped with an under-cooling point far below zero, and this ensures against mortality from freezing. The advantages of overwintering in more than one larval stage are, however, not clear since these stages are not dissimilar in their cold tolerance (see Section 5.4(a)). There is a colour change from yellow (larval instars one to five) to black (sixth instar larvae). The latter have to emerge from the mines and pupate, and so this colour change may act as a device for rendering the larvae less conspicuous to predators at the wandering phase. The pupation cocoons lie exposed on the green twigs, and it is perhaps surprising that white cocoons which contrast strongly with the background melieu and are easily visible to predators, should have been selected. The protraction of adult emergence is probably genetically determined (see Section 6.1, p. 33) and enables the oviposition period of the population to be prolonged much more than that of the individuals. This probably ensures that at least some parts of the population are excluded from the full pressure of parasitism and predation; for instance, the highest percentage of parasitism by Tetrastichus evonymellae sp. near galactopus Ratz. occurs early in the larval instars of Leucoptera (see Section 10).

Summarising, the population of L.spartifoliella at Silwood Park fluctuated between 1963 and 1966. The initial total egg number of the generation 1963-64 was unknown, since this study commenced when that stage had passed; but the size of the resultant adult population was high. There after the population fell in generation 1964-65, and fell still further in the generation 1965-66. The main reasons for the downward trend in population size are variations in natality and increased mortality. The former was caused by the reduction in the fecundity of females, and the latter principally by a much greater egg sterility and

predation. There is no obvious explanation for the high percentage of egg sterility in 1965-66. The other mortality factors, notably predation, parasitism, and winter-disappearance in the larval stages, and emigration and predation in the adults, which contributed substantially to the changes in the population size are also important.

The biology of the main parasites, viz. Tetrastichus evonymellae sp. near galactopus Ratz., Necremnus metalarus Walk., Chrysocharis gemma Walk. and Pnigalio soemias Walk., can be said to have been studied in some details and their effects on the Leucoptera population more or less quantified. These parasites, it should be recalled, are contemporaneous on the sixth instar larvae of the host. As Morris (1965) has shown the effect of any mortality factor on population trend can be influenced by other factors which operate contemporaneously within the same age interval of the host. It has not been possible in the time available for this study to determine the extent to which these parasites interact with each other, and further studies may be needed to estimate their interaction coefficients.

Predation is another mortality factor that requires further investigations, since it has not been possible in this relatively brief study to make a full quantitative determination of its effects. In this regard the serological method (see Dempster, 1960) can be used to identify the predators and the number of meals of Leucoptera individual predators have taken. With such data and the estimates of the total number of the predators in the field, the number of Leucoptera destroyed by predation could be calculated. This information is essential for the accurate determination of the type of prey-predator interaction operating in any given generation of the host.

One other factor that needs further investigation is one that has been designated as ? Bacillus lentus, since a considerable proportion of the mortalities in the earlier larval instars were

were caused by it. Similarly, it will be interesting to probe further into the reasons for the heavy winter disappearance of larvae despite the high cold tolerance of the overwintering larval populations.

Finally, this work can be said to have given reasonable information on the trends of Leucoptera population within the time of study, and on the factors responsible for these trends. It has not been possible, within the time available, to investigate all facets of the problem in detail; nevertheless, it is possible to conclude that the study has provided the main indications along which future work on Leucoptera and related species can be planned.

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APPENDIX 1

Survival of adults after peak numbers in 1964

Table of the fall-off of numbers with time, based on a fixed number, e.g.1000

x = age

d_x = number dying in age interval out of the 1000.

l_x = number surviving at the beginning of age interval, x (out of the 1000 'born')

$1000q_x$ = mortality rate per 1000 alive at the beginning of age interval.

	x (days)	dx	lx	1000qx
Males	0-14	669	1000	669
	14-21	225	331	770.4
	21-28	53	76	697.4
	28-35	14	23	608.7
	35-43	8	9	888.9
	43-50	1	1	1000
Females	0-14	727	1000	727
	14-21	189	273	692.3
	21-28	56	84	666.7
	28-35	11	28	392.9
	35-43	9	17	529.4
	43-50	8	8	1000

APPENDIX 2

Survival of adults after peak numbers in 1965

Table of fall-off of numbers based on a fixed number e.g. 1000.

Males	0-7	497	1000	497.0
	7-14	234	503	465.2
	14-21	84	269	312.3

APPENDIX 2 cont.

	x (days)	d_x	l_x	$1000q_x$
Males	21-28	130	185	702.7
	28-35	35	55	636.4
	35-42	8	20	400.0
	42-49	9	12	750.0
	49-54	3	3	1000
Females	0-7	412	1000	412.0
	7-14	72	588	122.4
	14-21	217	516	420.5
	21-28	181	299	605.4
	28-35	62	118	525.4
	35-42	19	56	339.3
	42-49	23	37	621.6
	49-54	10	14	714.3
	54-57	1	4	250.0
	57-60	2	3	666.7
	60-62	1	1	1000