Durham E-Theses

A population study oncoleophora alticolella zell (lep)

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A POPULATION STUDY

ON

COLEOPHORA ALTICOLELLA ZELL. (lep.)

by

RICHARD C. REAY

- being a thesis presented in candidature for the
Degree of Doctor of Philosophy in the University
of Durham, 1959.

"My purpose is to tell of bodies which have
been transformed into shapes of a different
kind. You heavenly powers, since you were
responsible for those changes, as for all
else, look favourably on my attempts......"

Metamorphoses. Ovid (43B.C. - A.D.17)

ACKNOWLEDGMENTS

CONTENTS

A POPULATION STUDY ON COLEOPHORA ALTICOLELLA. ZELL.

INTRODUCTION.

Although the word 'population' originally referred to
people, biologists have since used it to embrace the numbers
of any plant or animal species and statisticians have further
extended its application to inanimate objects.

Biologists in general, but ecologists in particular,
tend to recognise four major properties of populations. (1).
They consist of a number of individuals. (2). There is a like-
ness of kind among these individuals. (3). There is a criterion
of 'aliveness' . (4). The individuals are limited in space and
time.

A typical example example of this is seen in Pearl (1937)
thus, "A population is a group of living individuals set in a
frame that is limited and defined in respect of both space and
time". Or more recently, Nicholson (1957) ".... a group of inter
acting and interbreeding individuals which normally has no
contact with other groups of the same species".

The study reported in the following pages is on the
numbers of the Tineoid moth, <u>Coleophora alticolella</u>. Zell.,
hence preserving the properties, 'likeness of kind', 'aliveness'

and 'numbers of individuals'.

Two transects were studied (in 1956 and 1957) each being broken up into a number of stations for sampling convenience (see later). The moths on each transect were strictly isolated from each other, there being a geographical separation of several miles between their two nearest points, with the summit ridge of the Pennines (at over 2,700' above sea level - <u>fig 2</u>) intervening. There was also no continuous cover of the insects main food plant, <u>Juncus squarrosus</u>, between these two areas. In the light of property (4) above, it is meaningful to talk of the population of a particular transect as compared with the other, but not of the population of a particular sampling station as compared with the population of another one on the same transect. The latter are in fact local units of the same population, and hence reference has simply been made to the 'numbers' of moths at a particular station.

The study of <u>C. alticolella</u> at Moor House and the neighbouring moorland was actually began by A.M. Jordan in 1952, and continued until 1954. Some of this work has since been published (Jordan, 1958) but in addition, I have had access to other facts presented only in the above authors Ph.D. thesis.

THE LIFE HISTORY OF C. ALTICOLELLA ON J. SQUARROSUS.

In order to facilitate an understanding of the various stages mentioned in the following pages it was thought necessary to give a short account of the life history of the moth when it is in association with its main food plant on the study area, J. squarrosus.

Jordan (1958) gives the life history in great detail and the following account is taken mainly from his work, since in the main his observations have been borne out by the present study.

The adult moths first appear in the field about the beginning of June, or the end of May, emergence probably being stimulated by a spell of warm dry weather. General observations during 1956-7 suggest that the males emerge first. Flying, when it does occur, is only for short periods, the moths in the main being relatively inactive and spending most of their time on the developing host plant.

Pairing occurs soon after emergence and eggs are laid soon after that, a phenomenon associated with the fact that newly emerged females have a large quota of eggs ready for oviposition.

The eggs are ellipsoid, the long diameter being on the

average, .43mm., the short, .23mm. These measurements were done during the present study.

The eggs are laid in sheltered places on the rush plants which as yet bear only poorly differentiated florets. It was also found in the present work that the majority of eggs were laid in the angle between adjacent florets. Thus out of a total of 1.447 eggs laid in 1956, and examined in rush samples, only 104 were taken from places other than this. These other sites were usually under bracts, scales, and the segments of the perianth.

When the eggs are first laid they are creamy-white in colour, but this changes during the next three weeks through a pale red to a dark brown, just before hatching when the head-capsule becomes visible inside the eggshell. This colour change was not reported by Jordan.

Newly emerged larvae move to the now developing seed capsules of the host plant, into which they burrow and begin to feed on the contained seeds. During this feeding period, which may last anything from a few days to four or five weeks, the larvae go through four instars, and in the late third, or early fourth the silken case typical of the Coleophorids is manufactured (see plate 1.). The production of this case pre-ceeds the period of maximum larval activity, a prerequisite

Plate. 1. Final instar larvae (marked 'V') feeding on Juncus squarrosus.

to finding new, undamaged capsules for food.

On completion of feeding the larvae leave the Juncus plants and move down into the moor surface and become part of the litter fauna. Here they seal up the anterior end of their cases and undergo a true diapause as a final instar larva.

Pupation occurs in the following spring, though it has been known for some larvae to feed again in the spring before pupating. The adults emerge about three weeks later.

The above account is of the normal course of events, but on one transect in particular (the Western) this order is interrupted by parasitic Hymenoptera. They are exclusively larval parasites, but as to the species involved and their importance, more will be said later.

The life history is summarised in Fig. 1. which as with the above is partly based on Jordans work.

Fig. 1.

LIFE HISTORY OF *Coleophora alticolella* ON *Juncus squarrosus*
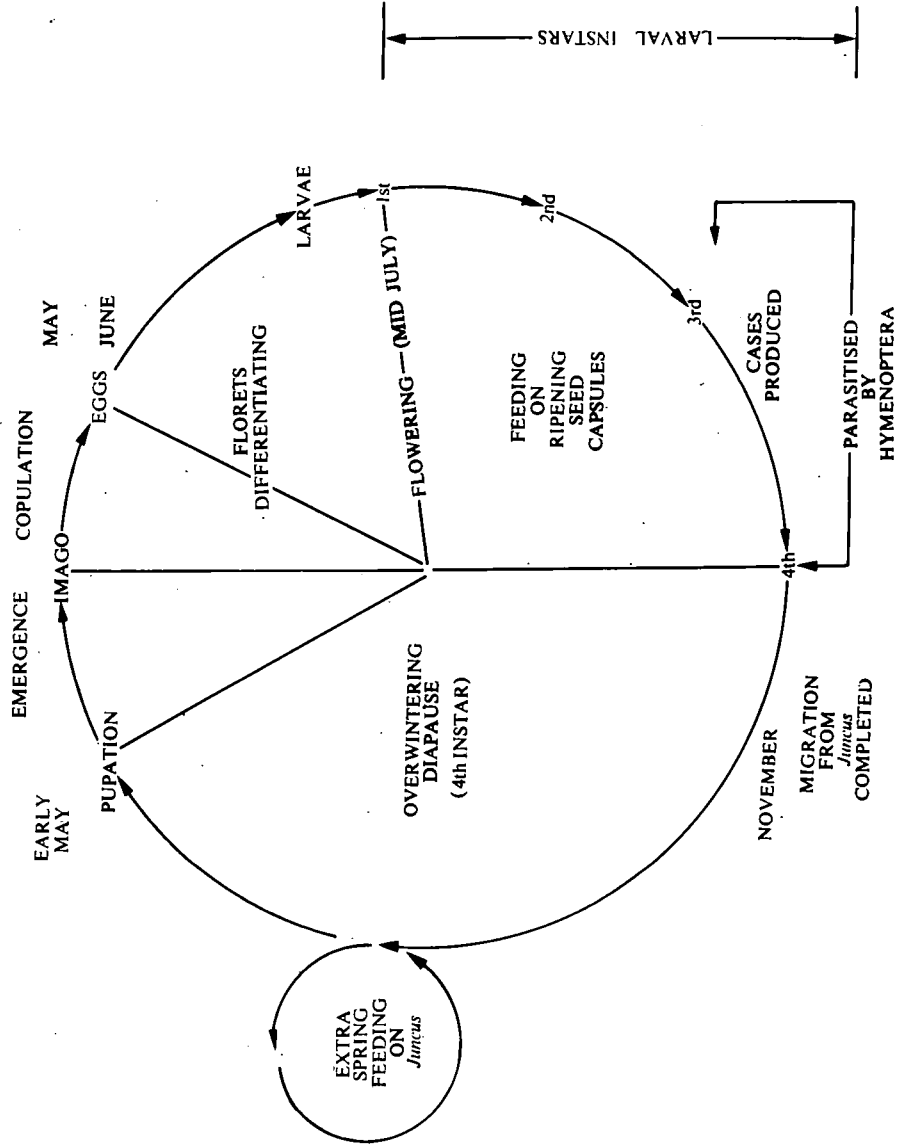
CHANGE OF NAME.

The original title of this study was "A population study on _Coleophora caespititiella_. Zell". It now seems however that _C. caespititiella_ , once believed to be the most widely distributed and best known of the rush feeding Coleophorids, has in the course of time assumed a false identity.

Zeller himself (see Stainton 1850) who used external characteristics for classifying the group was not satisfied with this species, thus; "Still nearer is it (i.e. _caespititiella_) to the generally larger _alticolella_ from which it is perhaps not specifically different. _C. alticolella_ has certainly, in general un-annulated antennae; but there are specimens, and indeed not only from the ordinary size, but also from the same size as _caespititiella_ which have more or less distinct traces of dark rings on the basal half of the antennae: moreover I believe positively I have taken both in company".

The fact that the true _C. caespititiella_ is a species of much more localised distribution, and is in fact the species known as _C. agrammella_ Wood., has been shown by Bradley (1955).

Bradley established the correct identity of this species following the dissection of the genitalia of Zellers type material in the British Museum (nat. Hist.). He showed that the species at present known as _C. caespititiella_ should be known

as C. alticolella Zell, and that species known as C. agrammella Wood, should be called C. caespititiella with agrammella Wood as a synonym. This meant that C alticolella, which had lost specific status since Zellers time, was now reinstated as a good species.

Preparations of the genitalia of 50 adults from the study area were made to ascertain the nature of the species there. Following Bradley, a potassium hydroxide method was used, and without exception the adults proved to be C. alticolella. Thus in line with Bradleys findimgs, the males all had a strongly sclerotised sacculus with a series of shallow serrations, while the females had the diagnostic large anchor-shaped signum.

As a final note, it is interesting to note that this mistaken identity goes at least as far back as Barasch (1934), who also used genital characters in his taxonomy, and described C. caespititiella and not C. alticolella as having a many toothed sacculus in the male.

THE SAMPLING SITES.

The initial reason for choosing the two particular transects for sampling was that they were used by Jordan and therefore any results obtained from the present study could be validly compared with his. However, although the two transects were the same, the actual sampling sites were not necessarily so.

These two contrasting areas were both in the northern Pennines, one facing roughly east, the other west. Both are near, and one (the western) actually overlaps, the Moor House National Nature Reserve (N.R.80), whose research station was used as a base for field work.

The intervals between the sample stations were fixed using an aneroid-barometer altimeter, which is the cause of some discrepancy between the stations of the present study, and those of my predecessor.

The Western Transect.

This can be found on O.S. Sheet No. 10, (Alston and Weardale) where it follows Crowdundle Beck. The transect is shown in Fig. 2., and runs from square 1351 (650') upwards in a north-easterly direction to square 1854 (the summit of Little Dun Fell, 2,761'). Only the stations from which Col eophora activity has been recorded are shown in Fig. 2. The
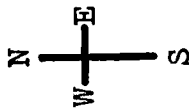
Fig. 2. A photograph of part of O.S. 10,
(Alston and Weardale) showing the W. transect.
Sampling stations marked thus: ●

Scale: Approx. 1½ inches to 1 mile.
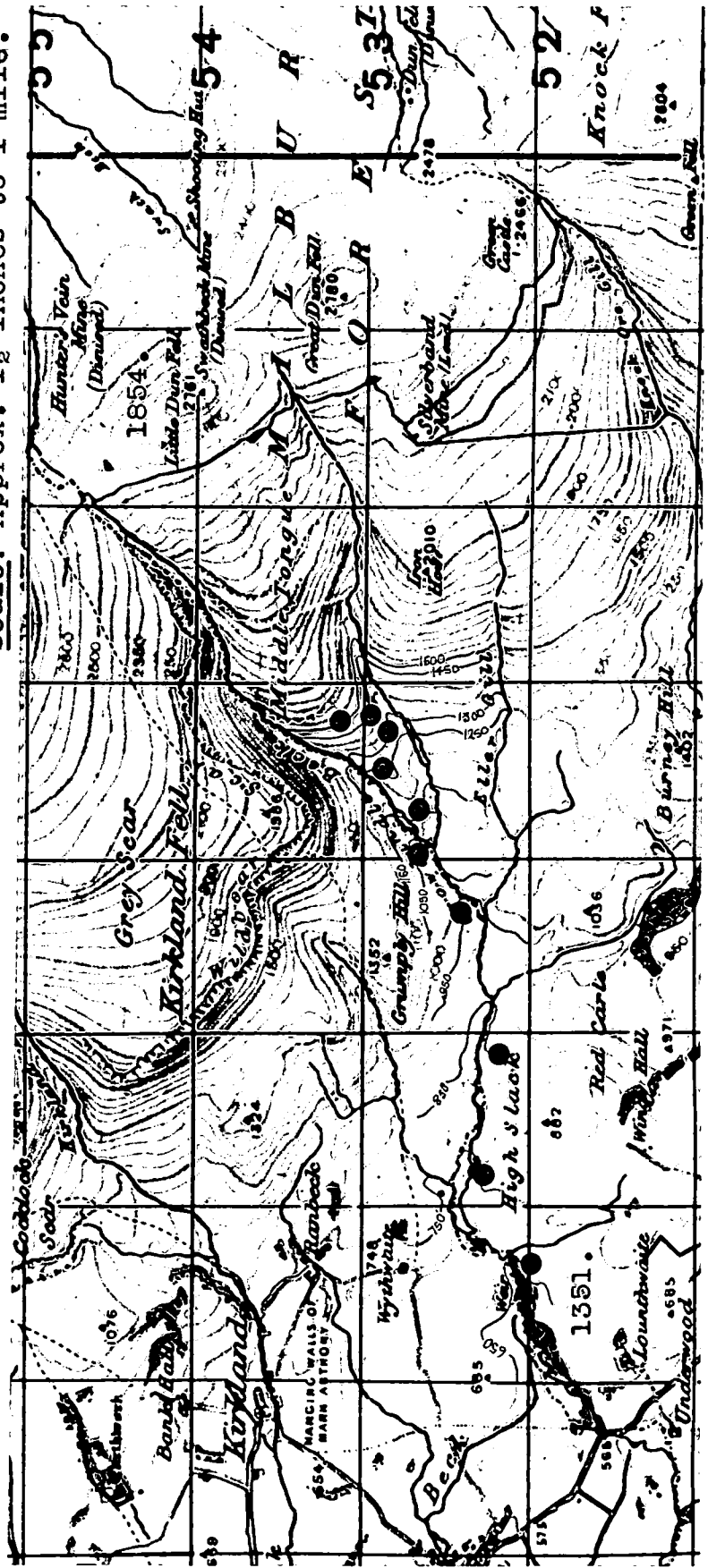
whole transect is by far the longer of the two, running for a distance of some three miles.

The lowest station sampled at 650' (all heights are given in feet above sea level) marks the lowest limit of J. squarrosus and the upper limit of cultivation in that area.

The slope is quite gentle up to about 1,000', after which it rises with increasing steepness to the summit-ridge of the Pennines.

From 650' upto about 1,400' the J. squarrosus cover is patchy, the intervening dominant plant being bracken, Pteris aquilinum. L. Kuhn., while above this the Juncus is more widespread and the bracken is replaced by heather, Calluna vulgaris L.

The soil is dominantly peat, though when limestone is exposed at the surface, clay loams of the brown earth soil group are developed.

The Eastern Transect.

This is also to be found on O.S. 10., and is in square 2359. Being only about a half-mile long it reaches from 1,500' upwards to just over 2,000'. Once again the lower station marks the upper limit of cultivation.

Each station is separated from the next by a vertical interval of 50; while as Fig.2. shows those of the W. transect

have in the main a 100' vertical separation.

The slope is fairly uniform and has a virtually un-interrupted cover of J. squarrosus. Where the drainage is not so good, clumps of J. effusus are present.

The soil is peat throughout, though some rock out-cropping does occur from 1,850' upwards.

ADULT BIOLOGY.

As was pointed out in the account of the life history the adults emerge in the late spring from pupae present in the plant debris at the base of the previous years J. squarrosus flowering stems. This fact was utilised in an attempt to obtain a measure of the number of adults which emerge per unit area.

Emergence traps were used of the construction shown in Fig.3. The main body of the trap was a cylinder of light gauge metal, rust-proofed with aluminium paint, open at one end and enclosed at the other, either by a fine mesh nylon net or cotton sand-fly netting. The traps were in fact, converted 'Ostermilk' tins (see the acknowledgements).

In 1956 the traps were simply applied to the moor surface and held in place by hoops of heavy gauge galvanised wire. Vigorous plant growth takes place at this time of the year and the traps were thus constantly being lifted from the surface, thus allowing any contained moths to escape. As well as this the traps were continually being overturned by sheep.

In the following year (1957) the traps were sunk into the peat to a depth of about 7cm., and a band of adhesive ('Stictite') placed inside to affix the moths as they emerged. The traps were now low enough however for the sheep to be

EMERGENCE TRAP

WIRE HOOP

FABRIC GAUZE

'STICTITE'

Juncus squarrosus

PEAT
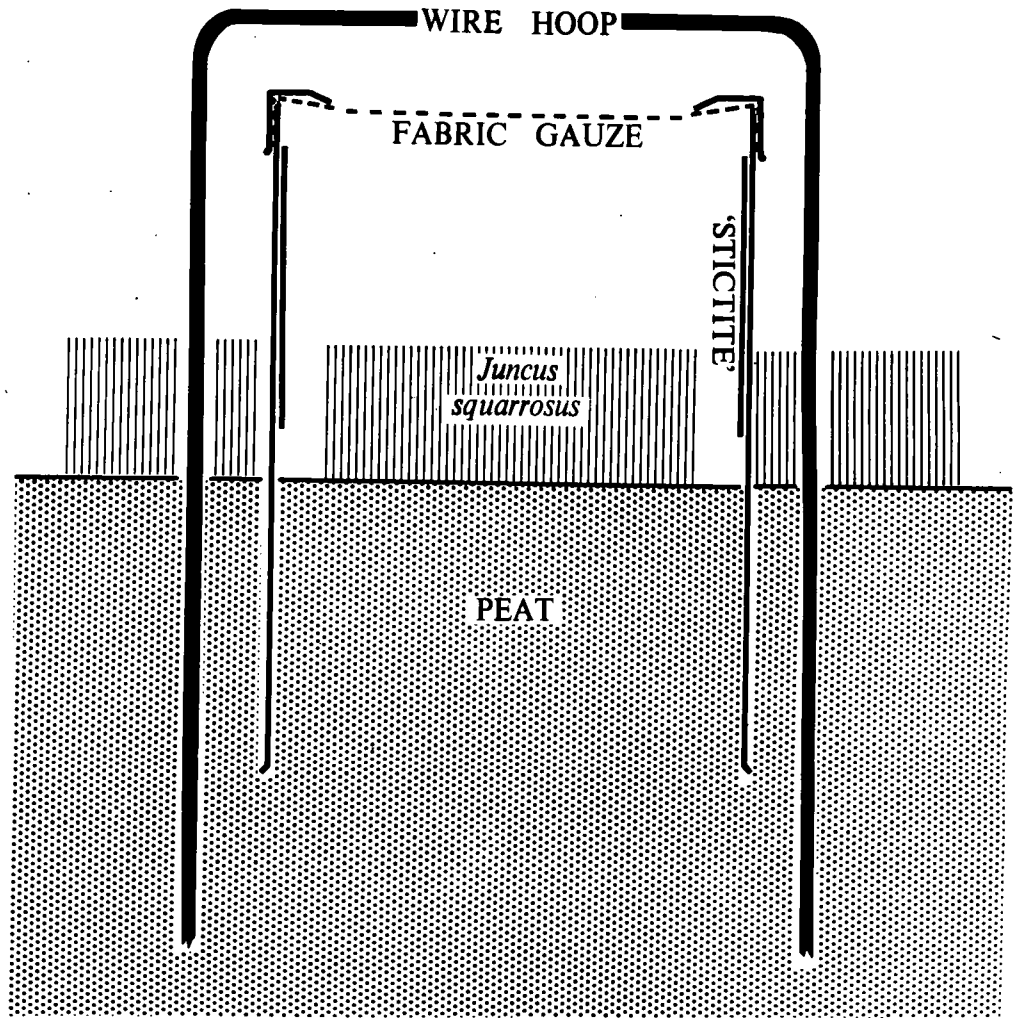
Fig. 3.

Scale: Approx. half-size.

able to stand on them, thus rupturing the febric net and rendering the traps useless. Damage was so extensive that the experiment had to be abandoned in this year.

The only results then are from 1956 when only the E. transect was sampled. In all nine stations were covered from 1,500' upwards by 50' intervals to 1,900'. Altogether 368 traps were used, 44 each at 1,500' and 1,550', while all other stations had 40 each. It was calculated that 44 traps covered a total area of .381 square metres, while 40 covered .364 sq.m.

The traps were placed in the field on June 5th., and examined 17 times, at 2-3 day intervals, until July 17th. when they were removed.

The results may be summarised thus:

1,500' 1 adult; June 11th., and 23rd., July 7th., and 12th., 2 adults; June 28th., giving a total emergence of 15.72 per sq.m.

1,600' 1 adult; June 26th., July 9th., and 15th., giving a total emergence of 8.6 per sq.m.

1,750' 1 adult; June 17th., and July 9th., giving a total emergence of 5.78 per sq.m.

The numbers are probably too low for any significant conclusions to be drawn from them, but they do suggest that

under sheep-free conditions the system could work quite well.

Before any of the above difficulties of trapping in the field had been appreciated, it had been thought that the emergence traps might significantly alter the microclimate of the area they enclosed and hence effect such things as the emergence times of any enclosed pupae.

A field experiment was set up at Durham to test this situation. Temperatures were measured inside the trap and compared with temperatures at the base of the vegetation outside the trap. Readings were taken continuously for a fortnight (from June 13th.,to 27th.) using a 'Cambridge' thermograph. A sample of the results is shown in Fig. 4. All temperatures shown are in ^{o}C.

The daily pattern of events is fairly constant. During the early morning (times are British Summer Time) temperatures both inside and outside the trap were similar (6 a.m.) and as the sun rises higher in the sky the two sets of readings begin to diverge. Thus at 11 a.m. on Sunday, June 23rd., the temperature inside the trap was about 10°C. warmer than in similar conditions outside. Towards the evening (6 p.m.) the differences diminish again, but during the night the temperature inside the trap actually falls below that outside.

In summary then, the inside of the trap both heats up
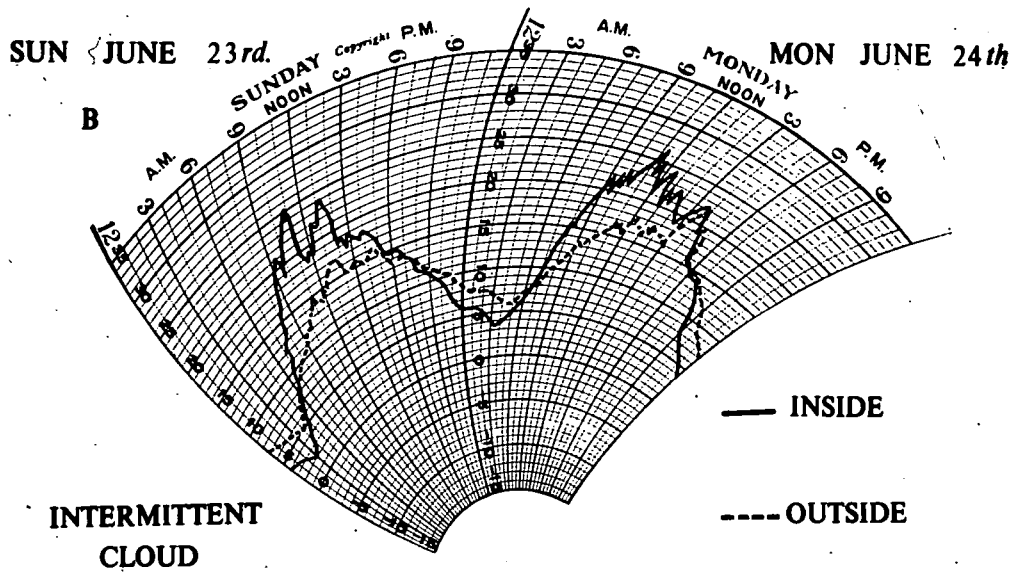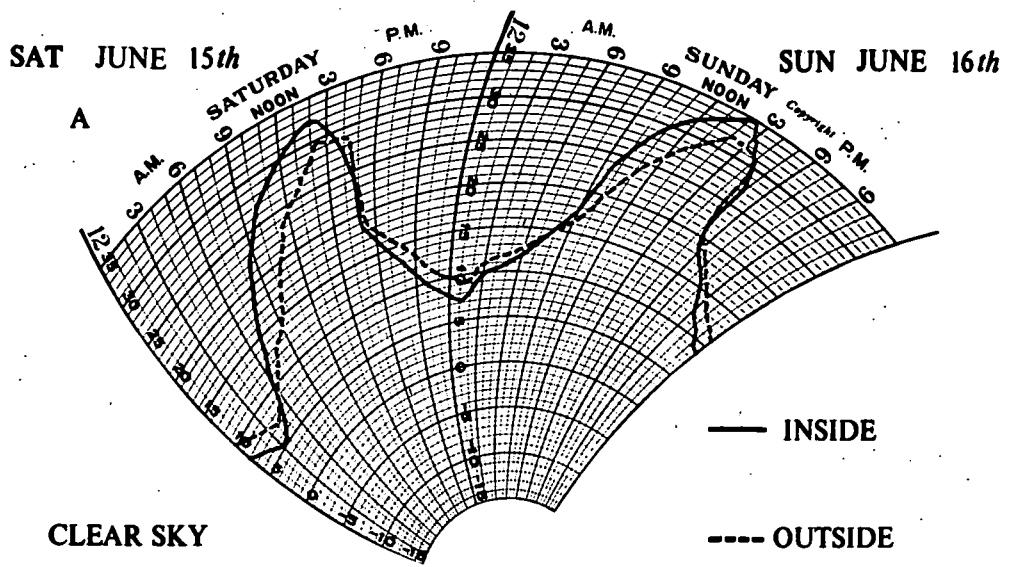
Fig. 4.

'Cambridge' Thermograph Records.

faster and cools down more quickly, and reaches both higher and lower temperatures, than in the more normal conditions outside. It should be emphasised that these measurements were not done on the study area, where probably the maximum temperatures are not so high as at Durham, and the minimum temperatures lower, at this time of the year.

It is only after more accurate emergence estimations have been made however, that the real effect of these differences on the moths biology can be assessed.

THE POPULATION STUDY. (PART 1).

INTRODUCTION.

Whereas the adult season is relatively short in duration
the egg and larval stages embrace by far the greater period
of the insects active life. Both eggs and larvae are found
on the flowering and fruiting heads of J. squarrosus and it
is actually the latter that are sampled.

The sampling method used, was to randomly select twenty
stems from each station at regular intervals throughout the
known months of the insects life history. These stems were
sealed into polythene bags and kept in the deep-freeze (at
-15°C. to -20°C.) until they were required for examination.
This method of preservation has obvious advantages over that
used by Jordan, who kept his material in formalin. No drying
is required before examination and no unpleasant fumes are
experienced. Even after several months, such delicate str-
uctures as newly laid eggs were found to be in excellent
condition.

The more accessible, and hence the more frequently
sampled transect was the Eastern one. Sampling dates for both
here and the W. transect, for the years 1956 and 1957 are given
below. Those for 1955 and 1958 are dealt with later.

Sampling Dates, E. Transect.

1956.

June. 5, and alternate days to 20, 23, and 26.

July. (3), 7, (9), (12), (18), 20, (24), 26, and (28).

Aug. 3, (14), and 20.

Sept. 11, and (25).

Oct. 17, and (23).

Nov. 12.

1957.

June. 5 (no J. squarrosus), 12, 19, and 25.

July. 2, 9, 16, 23, and 29.

Aug. (7), 21, and (26).

Sept. 5, 17, and (25).

Oct. 11.

( ) indicate dates on which only the 1,500' station was sampled

Sampling Dates, W. Transect.

1956.

June. 21.

July. 11, and (25).

Aug. 9, amd (21).

Sept. (4), and 18.

Oct. 9, and (25).

1957.

June. 5, and 19.

July. 2, and (18).

Aug. 7, and 26.

An out break of foot-and-mouth disease in this area of the Pennines prevented further access to this transect until early November, by which time all Coleophora activity had ceased.

( ) indicates dates on which the 950' station only was sampled.

After removal from the deep-freeze, the rush heads were affixed to strips of 'Sellotape' to facilitate handling. This adhesive strip was pinned to a cork sheet for examination under a binocular microscope where the Juncus material was dissected out, and the following groups of observations made:

1. Undifferentiated florets

    (a). The numbers per stem.

2. Ripe seed capsules.

    (a). The numbers per stem.

3. Damaged seed capsules.

    (a). The numbers per stem.

4. Eggs.

     (a). The numbers per stem

     (b). Their position.

5. Larvae.

     (a). The numbers per stem.

     (b). The numbers per capsule.

     (c). The numbers with cases.

     (d). The number with parasites.

From the above groups of information it was possible to build up a picture of the numbers of the moth, and of the quantity of food available to it.

Tables 1 and 2, summarise the results from the two years under consideration and represe nt both the egg and larval numbers in relation to each stem of J. squarrosus. These tables show only the results from those days when all stations were sampled, the extra data from the more frequently sampled 1,500' station are dealt with in appendix 1.

Table 1. E. transect, 1956.

The mean number of Coleophora eggs (E) and larvae (L) per stem of J. squarrosus.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850		T
June 23	.70 ± .31	-	-	.03 ± .01	-	-	-	-	E	
										3
June 26	1.1 ± .29	.40 ± .18	.50 ± .20	.60 ± .20	.30 ± .13	.55 ± .15	.15 ± .01	.10 ± .07	E	
										11
July 7	2.1 ± .39	1.3 ± .37	1.1 ± .22	.95 ± .33	.85 ± .16	.80 ± .25	.26 ± .12	.05 ± .049	E	
										13
July 20	2.9 ± .55	1.2 ± .25	1.4 ± .35	1.0 ± .32	.95 ± .20	.95 ± .30	.25 ± .10	.10 ± .09	E	
	.15 ± .07	-	-	.10 ± .09	.10 ± .09	.05 ± .049	-	-	L	
										6
July 26	1.4 ± .32	1.3 ± .28	1.1 ± .23	.75 ± .22	1.4 ± .25	.65 ± .21	.20 ± .12	.05 ± .049	E	
	1.6 ± .33	.70 ± .22	.25 ± .12	.45 ± .13	.70 ± .27	-	.10 ± .07	.05 ± .049	L	
										8
Aug. 3	1.8 ± .25	1.0 ± .28	.95 ± .27	.70 ± .18	.85 ± .22	.60 ± .22	.10 ± .09	.05 ± .049	L	
										17
Aug. 20	2.7 ± .30	1.0 ± .25	.85 ± .26	.90 ± .19	1.1 ± .28	.40 ± .15	-	.10 ± .068	L	
										22
Sept 11	2.1 ± .28	1.5 ± .31	1.0 ± .24	1.4 ± .21	1.1 ± .30	.60 ± .20	.20 ± .12	.05 ± .049	L	
										36
Oct. 17	1.3 ± .28	.65 ± .20	.40 ± .21	.85 ± .21	.95 ± .11	.55 ± .15	.20 ± .12	-	L	
										26
Nov. 12	.35 ± .13	.55 ± .15	.40 ± .13	.20 ± .12	.40 ± .13	.30 ± .11	.20 ± .12	-	L	

'T'. The number of days between samples.

- The absence of C. alticolella.

Table 2. E. transect, 1957.

The mean number of eggs (E) and larvae (L) per stem.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850		T
June 12.	1.25 ± .27	-	.30 ± .30	-	-	-	-	-	E	7
June 19.	56.2 ± 5.5	67.8 ± 9.5	33.4 ± 2.8	39.1 ± 4.7	29.7 ± 2.8	30.2 ± 2.6	9.6 ± 1.7	12.4 ± 1.0	E	6
June 25.	59.9 ± 5.8	49.2 ± 5.5	48.0 ± 3.7	60.3 ± 4.0	36.9 ± 4.8	40.7 ± 3.0	18.4 ± 2.3	14.3 ± 1.7	E	7
July 2.	62.4 ± 5.2	42.6 ± 5.1	39.6 ± 3.2	31.9 ± 3.4	26.0 ± 3.1	25.4 ± 3.0	15.6 ± 1.3	8.3 ± 1.4	E	
July 2.	7.5 ± 1.0	4.8 ± .76	5.4 ± 1.0	5.0 ± .86	4.7 ± .58	4.5 ± .74	1.7 ± .27	.60 ± .19	L	7
July 9.	17.7 ± 2.4	12.5 ± 2.1	9.1 ± 1.2	10.0 ± 2.3	11.4 ± 2.0	8.8 ± .76	5.0 ± .99	4.5 ± .56	E	
July 9.	10.8 ± 1.6	8.1 ± 1.1	5.4 ± .77	7.9 ± 1.3	5.7 ± .77	7.5 ± .78	4.6 ± 1.0	3.4 ± .63	L	7
July 16.	7.2 ± 1.3	6.0 ± 1.0	4.0 ± .74	3.0 ± .47	2.5 ± 1.2	NOT SAMPLED ON THIS DATE.			E	
July 16.	10.1 ± 1.5	3.6 ± .99	4.0 ± .51	4.8 ± .85	4.3 ± 1.4				L	7
July 23.	.25 ± .09	.09 ± .03	0	.15 ± .11	0	.35 ± .15	.15 ± .11	.06 ± .04	E	
July 23.	5.6 ± 1.0	2.3 ± .77	.85 ± .20	.60 ± .22	.60 ± .35	3.9 ± .88	1.0 ± .43	1.5 ± .62	L	6
July 29	.05 ± .049	0	0	0	0	0	0	0	E	
July 29	4.3 ± .90	1.3 ± .63	.55 ± .25	.80 ± .33	.30 ± .21	2.1 ± .54	.40 ± .19	.84 ± .60	L	9
Aug. 7	1.2 ± .38	NOT SAMPLED ON THIS DATE.							L	14
Aug. 21	.25 ± .12	-	.13 ± .13	.15 ± .12	.10 ± .10	1.1 ± .42	.25 ± .16	.15 ± .12	L	5
Aug. 26	.50 ± .26	NOT SAMPLED ON THIS DATE							L	10
Sept. 5	.20 ± .11	-	.13 ± .09	0	-	.50 ± .18	.05 ± .049	.60 ± .19	L	12
Sept. 17	0	-	0	0	-	.15 ± .08	.05 ± .049	.14 ± .09	L	8
Sept. 25	.15 ± .08	NOT SAMPLED ON THIS DATE							L	16
Oct. 11	0	-	0	0	-	0	0	0	L	

'T'. The number of days between samples.

0   The absence of C. alticolella

–   The absence of J. squarrosus.

In these two tables (as in all others) the top row of figures refers to the altitude of the sampling station.

In each case the earliest date shown is the first on which eggs appeared in a sample of 20 stems. Reference to the complete list of sampling times given previously (pp. 16 & 17) shows that samples were taken well before these dates so that they must represent, to within a few days the time when eggs were first laid in the field.

The maximum height shown indicates the upper limit of the moths distribution, but in general ripe seed capsules were produced above this height, but not utilised by the moth. (See later)

Tables 1 and 2., are pictorially represented in Figs 5 and 6. The distance between each of the columns shown there is proportional to the time between successive samplings, the actural duration of these being given in section 'T' of the above two tables. Where eggs and larvae appear together in the same sample their totals have been combined in calculating the height of the column for that particular date.

Fig. 5, shows that in 1956 there was more or less a regular fall in numbers with increasing altitude, the 1,500' station having by far the greatest infestation, while at 1,800' and 1,850' numbers were so low as to indicate the moths presence as a trace only. Certain anomalies do occur

-21-

Fig. 5.

EASTERN TRANSECT

1956

ALTITUDE

(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)

MEAN NUMBER OF EGGS & LARVÆ PER STEM.

Fig. 6. 'T' shows a trace.

EASTERN TRANSECT
1957

Juncus EXTINCT

Juncus EXTINCT

MEAN NUMBER OF EGGS & LARVAE PER STEM.

80
70
60
50
40
30
20
10
0

1,500   1,550   1,600   1,650   1,700   1,750   1,800   1,850

ALTITUDE

(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)
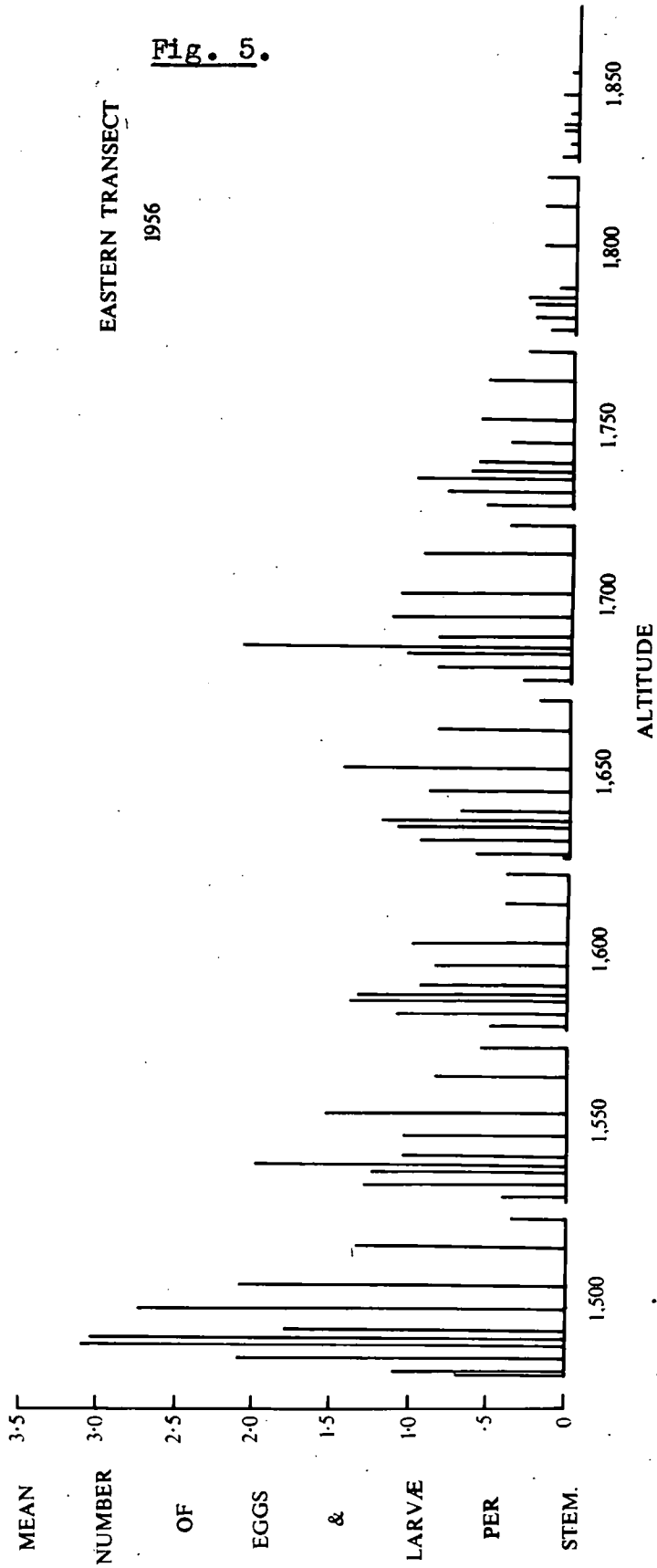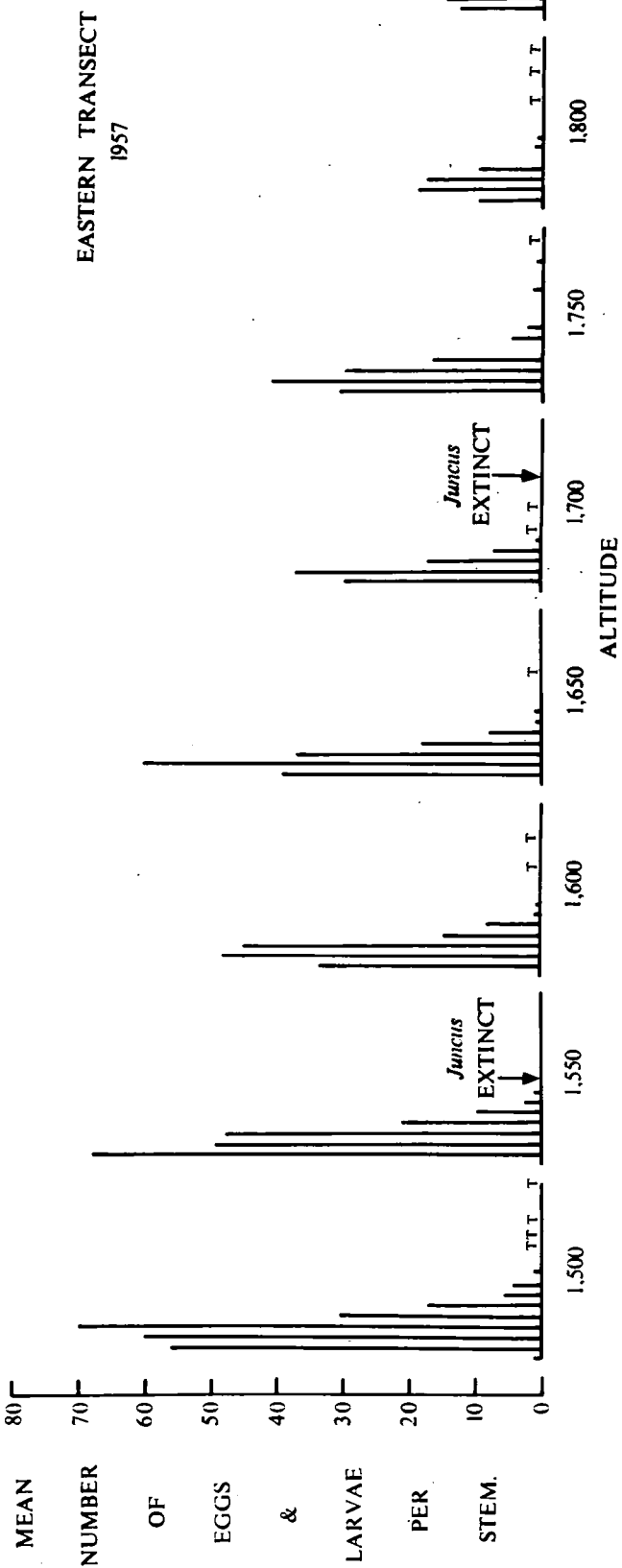
however, the 1,600' maximum for instance, being slightly less than its neighbours, while at 1,700' it is more.

As in 1956, the lower stations in 1957 have the highest numbers per plant, while the uppermost limits of the moths' distribution give the lowest readings. The regular altitudinal effect was not so well marked however due to high numbers at both the 1,550' and 1,650' stations.

It has already been mentioned that on this transect the 1,500' station was the most frequently sampled one. It is thus fair to assume that any conclusions drawn from the results of these greater number of samples will be nearer the true explanation of the numbers of C. alticolella than those from elsewhere. Bearing this in mind, this station will be considered separately and in greater detail than any other.

Note.

The 'error' estimate presented with the mean in some of the tables of this thesis is a StandardError.

THE DETAILED SITUATION, E. TRANSECT, 1,500'. 1956.

1. Egg results. (See graph 1.)

The emergence trap data given previously (p. 12) indicate that adults were present in the field as early as June 11th., and yet although rush heads were then present as well, the first eggs did not appear until June 23rd. The only other height at which eggs were also present was 1,650&.

(This appears to contradict the idea that eggs are laid soon after emergence. However there are two reasons as to why this should happen. The first is that the males emerge first, the early specimens in the traps being males, the second is, that probably the conditions in the trap effect the actual time of emergence.)

For the next three weeks or so the numbers of eggs per stem (e.p.s.) rose fairly rapidly and regularly until they reached a maximum of 3.3 e.p.s. on July 12th. This rise simply shows that the rate of egg-laying was outstripping the egg mortality (and latterly the hatching) rates. Since some mortality (and hatching) could have taken place during the intervals between samplings, the maximum of 3.3 e.p.s., will be an underestimate.

In the subsequent three weeks after June 12th., (i.e. to between July 2oth. and Aug. 3rd.) egg numbers decreased

Graph. 1. The dotted line shows the sum of the egg and larval numbers.

EASTERN TRANSECT

1,500 FEET

1956

LARVÆ

EGGS

MEAN NUMBER OF EGGS & LARVÆ PER STEM.
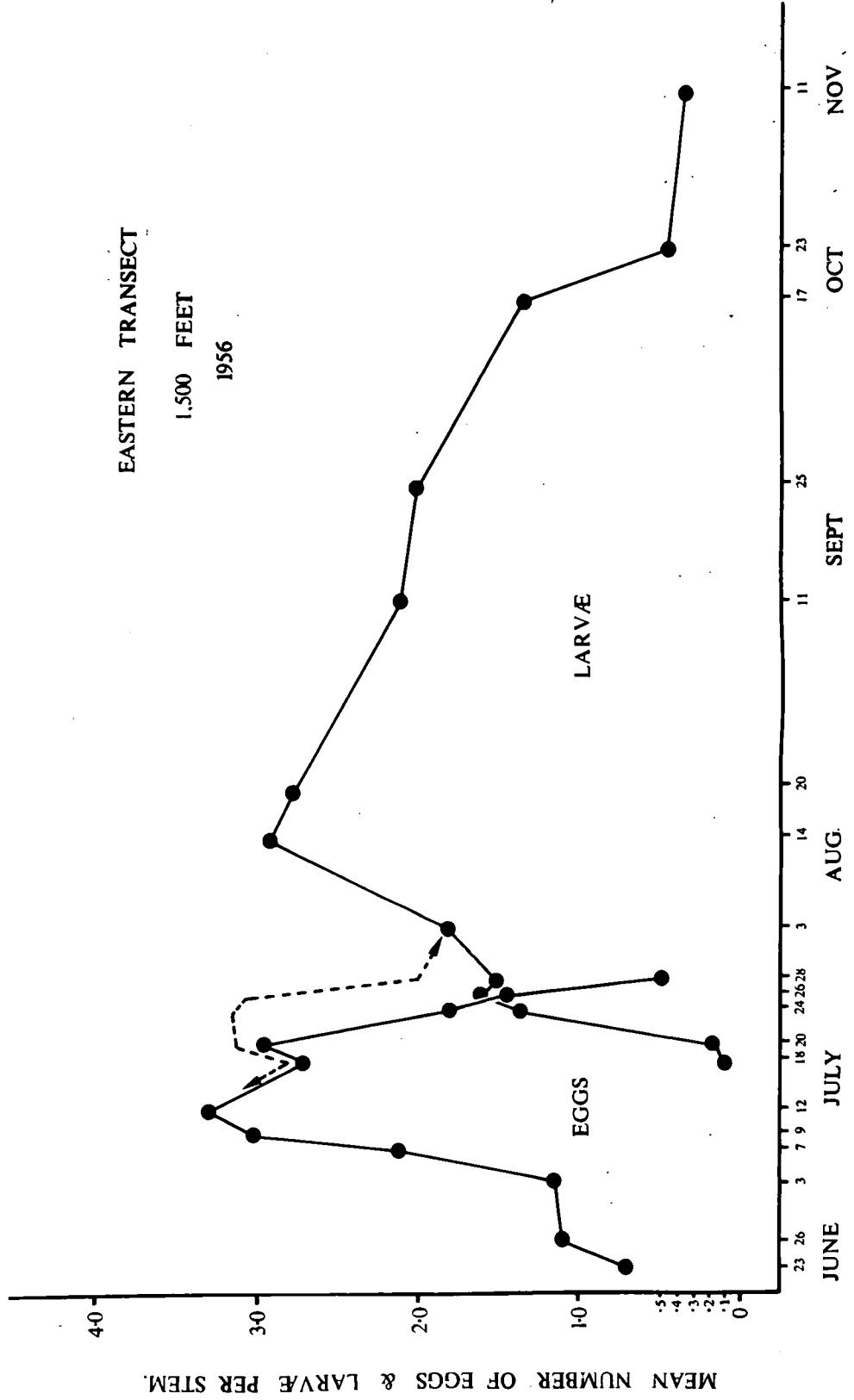
fairly rapidly due to a combination of egg mortality, adult mortality, and the hatching of eggs into larvae. The adult mortality, of course, makes itself felt in a reduction in the number of egg-laying females.

Not much is known of the causes of egg mortality. No predators have been seen in the field, but predation could neverthe less be an important source of mortality. Nothing is known as to what percentage of the eggs laid are viable. but it is probably fair to assume that this would not be an important source of mortality. Actual mechanical removal of the eggs , such as washing out by rain, would be unlikely in this year (see later) as the oviposition sites are all fairly well sheltered.

The results from the whole transect are more or less consistent withtthe above plan, though in general the max-imum is reached slightly later. On the whole, Jordans hypo-thesis that egg-laying commences at about the same time at each statton regardless of altitude, seems to have been con-firmed.

2. Larval results. (See graph 1.)

At first sight the pattern of larval development is similar to that of the egg. Larvae first appear on July 18 th. so that the first hatching in the field probably took place

a day or two before this. Their numbers rose to a maximum in about four weeks, when on Aug. 14th., there was an average of 2.9 l.p.s. There was a subsequent reduction in numbers until on Nov. 12th., (90 days later) the last day sampled, there was only a mean of .35 l.p.s. This figure probably represents those atypical larvae which overwinter on the J. squarrosus.

It is only when one examines the reasons for these changes in numbers that it becomes evident that the situation is more complex than that of the egg stage.

The initial increase in larval numbers is a simple product of the hatching rate being greater than larval mortality at this stage. Decrease in numbers however is not just due to mortality and the fall-off and eventual cessation of hatching rate. It will be recalled that on completing their feeding, final instar larvae move away from the rush stems, and hence out of the possibility of occuring in this sampling technique. It is this third factor, migration, which complicates the interpretation of falling larval numbers.

Larval mortality then, can only be assessed upto the time that this migration begins to make itself felt on the census data. In order to fix the onset of migration as accurately as possible, two methods have been used.

A characteristic of the late instar larvae is that they produce an easily recognisable case. Appendix 1. shows that no larvae possessed cases on Aug. 20th., while all larvae present on or after Oct. 17th., had them. It seems also that a few (14% only) larvae had entered their final stages by Sept. 11th., but as the number was so low probably very few if any had left the stems. By Sept. 25th., however considerably more (65%) had cases, so that this period (11-25th. Sept.) is probably the one in question. Figures for the rest of the transect are given below.

Table 3. E. transect, 1956.

The percentage of larvae with cases.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
Sept. 11	14.0	6.0	-	14.0	18.0	-	-	-
Oct. 17	100.0	76.0	87.0	100.0	78.0	73.0	75.0	-
Nov. 12	100.0	86.0	75.0	75.0	100.0	83.0	100.0	-

Coleophora larvae actually feed on the developing rush seed capsules, and certain data on the percentage of these capsules damaged is also shown in App. 1. It can be seen that there was a considerable increase in the percentage damaged between Sept. 11th., (only 24%) and Oct. 17th. (58%). This indicates that between these two dates numbers of final instar larvae have been produced, since it is a characteristic of

this stage to move actively from one capsule to another in search of food. Also by Oct. 17th., feeding had in fact almost ceased, since the percentage damaged then is very little different from the Nov. 12th., figure of 53%, when all moth activity had ceased.

This evidence supports the above contention that migration commences between approximately Sept. 11th., and 17th., since the presence of late instar larvae indicates the period of the migration phenomenon.

Capsule data for other stations are given below, from which similar conclusions may be drawn.

Table 4. E. transect, 1956.

The percentage of ripe capsules showing damage.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
July 20.	6.0	0	0	12.0	33.0	100.0	0	0
July 26.	23.0	11.0	6.0	14.0	16.0	0	100.0	0
Aug. 3.	18.0	8.0	8.0	8.0	11.0	8.0	3.0	2.0
Aug. 20.	25.0	8.5	12.0	10.0	14.0	6.0	0	4.0
Sept. 11.	24.0	14.0	12.0	16.0	11.0	7.0	5.0	2.0
Oct. 17.	58.0	29.0	22.0	31.0	34.0	14.0	6.0	0
Nov. 12.	53.0	32.0	26.0	26.0	35.0	23.0	9.0	2.0

From all of the egg and larval results presented above an attempt has been made to give some idea of the extent of egg and larval mortality.

The difference of 12% between the highest egg figure

of 3.3 e.p.s., and the highest larval estimate of 2.9 l.p.s., is a measure of the mortality during the late egg and early larval, transition period. Since newly hatched larvae must leave the relatively safe oviposition site in search of a food source this period, one would have thought, would be one of high mortality. The figure of 12% then, is perhaps an underestimate.

Probably a more accurate mortality estimate is that for the period, Aug. 14th. (maximum larvae at 2.9 p.s.) to a short while after Sept. 11th. (the onset of migration at about 2.1, l.p.s.). This gives a figure of about 27%, which however could be a slight overestimate if there had been some migration before the time suggested.

Finally a word of explanation about the results from samples collected on July 28th., and Aug. 3rd., as indicated by the dotted line in graph 1. The combined egg and larval estimates (2.0 and 1.8, respectively) on both dates are well below the maximum larval figure of 2.9 l.p.s., and hence must be underestimates.

The explanation probably lies in the hand-sorting technique. During this period of the life history some of the few eggs present could have easily been missed during

examination because the seed capsules need to be fairly heavily mutilated in the search for larvae. On the other hand the larvae themselves vary greatly in size, from newly hatched to larvae two to three weeks old, hence some of the smaller ones could easily have been overlooked.

These are conditions which apply with less force earlier in the season when there are more eggs and the larvae do not vary greatly in size, or later, when there are no eggs and the larvae are larger and more easily found.

THE DETAILED SITUATION, E. TRANSECT, 1957.

1. Egg results. (See graph 2.)

Field observations show that upto June 5th., of this year there were very few J. squarrosus stems available, not enough in fact to yield a sample of even ten stems from any station.

A week later however (June 12th.) stems were present both at the 1,500' and 1,600' stations, and it is then too that the first eggs were recorded. This is eleven days before the first eggs appeared in the 1956 samples.

During the next week there was an astronomical rise in numbers of 450%, giving a mean of 56.2 e.p.s. This was followed during the next fortnight by a less rapid rise to the egg maximum of 62.4 e.p.s., on July 2cd. This figure does not quite represent the seasons true maximum since it can be seen that larvae were also present on that date. The combined total of eggs and larvae gives a mean of 69.9, which means that this figure was the minimum that the maximum number of eggs could have been. It also means that the real egg maximum must have occured some time before that suggested above (July 2cd.)

As might be expected, the eggs were extremely crowded during this period and it was common to find groups of 6, 7,

Graph. 2. The dotted line shows the sum of the
egg and larval numbers.

EASTERN TRANSECT

1.500 FEET

1957

LARVÆ

EGGS

MEAN NUMBER OF EGGS & LARVÆ PER STEM.
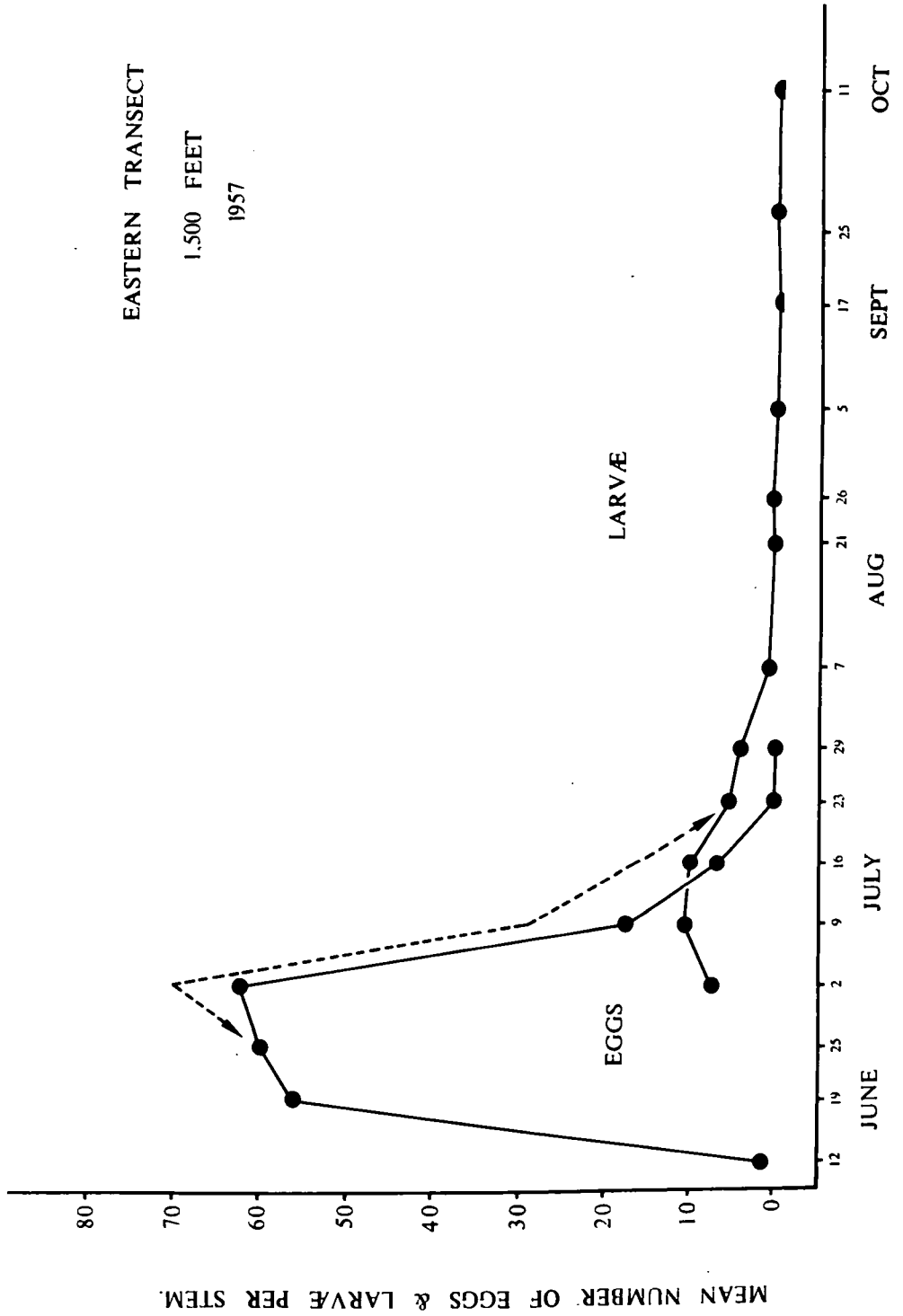
and 8 eggs in a single angle between two florets, and on one occasion there were as many as 11 eggs in this position. Where the eggs occured in a mass, they were usually stuck together in strings, giving the impression that they had been laid by the same female in one act of oviposition. During 1956 it was rare even to find two eggs in the same position, but as in that year, the majority of eggs in 1957 were laid in the angle between adjacent florets. The reason for this difference in the two years probably is as follows.

During the egg period of 1956, the maximum number of florets per stem at 1,500' was about 16. Since the florets usually occur in pairs, and the space between them utilised as oviposition sites, this gives a potential of approximately 8 sites per stem. (See append. 111.). Since the maximum number of eggs was only about 3 per stem, it is no wonder that two eggs were only found very rarely in the same place.

On the other hand, comparable figures for 1957 (again in append. 111.) show that the maximum number of florets at 1,500' was about 22 per stem, and hence the number of potential sites about 11. When the number of eggs per stem is examined ('C') it can be seen that not just at 1,500', but at all heights, the number of eggs far outstrips the number of sites available for them.

In the fortnight after the maximum numbers of eggs per stem, there was a fall in numbers as dramatic as the initial rise, and eggs had practically disappeared by the end of July. This was about the same time as the last eggs were recorded in 1956. Since egg-laying started earlier in 1957, the egg period extended over a longer period than in the previous year. (47, as opposed to 35 days).

Other stations seemed to go through the egg cycle rather faster, egg maxima usually being a week earlier than at the 1,500' station. Eggs disappeared upto a fortnight earlier too. (1,600' and 1,700').

2. Larval results. (See graph 2.)

It has been shown that, apart from the actual numbers involved, the general pattern of events in the egg stage was similar in the two years studied. This was not so with the larval stages.

In 1957, larvae first appeared on July 2cd., 16 days before they did so in 1956, and just three weeks after the first eggs were laid. Numbers even then (July 2cd.) were quite high (7.5 l.p.s.) so that the first hatchings would have taken place some time before this. No larvae appeared in the samples taken a week previously, on June 25th., however. During the next week numbers rose to their maximum of

10.8 l.p.s., on July 9th., after which there was a steady fall in numbers, until on, and after Aug. 21st., so few larvae were present in the field as to appear only irregularly in the samples of 20 stems. At some heights (1,600' and 1,650') no larvae were recorded after Sept. 5th., while the last trace (.15 l.p.s.) from 1,500' appeared on Sept. 25th.

Except for a few rudimentary ones, no larval cases appeared in the rush samples in 1957. However on the J. effusus areas of this transect an unusually high amount of C. alticolella activity was observed, and many of the fruiting heads were seen to bear larvae with cases. (See plate 2.) The actual significance of this is discussed later.

It seems then, that on the J. squarrosus at least, no final instar larvae were produced and that the fall in larval numbers after the maximum was not in any way effected by migration.

The reason as to why this reduction in numbers to virtual extinction should occur in 1957, and not in 1956 is partially explained by data shown in append. 1,(2)., and table 6., which give the number of rush capsules available in the two years. Table 5., gives the results for the whole transect in 1956.

Graph 3., shows the results from the 1,500' station
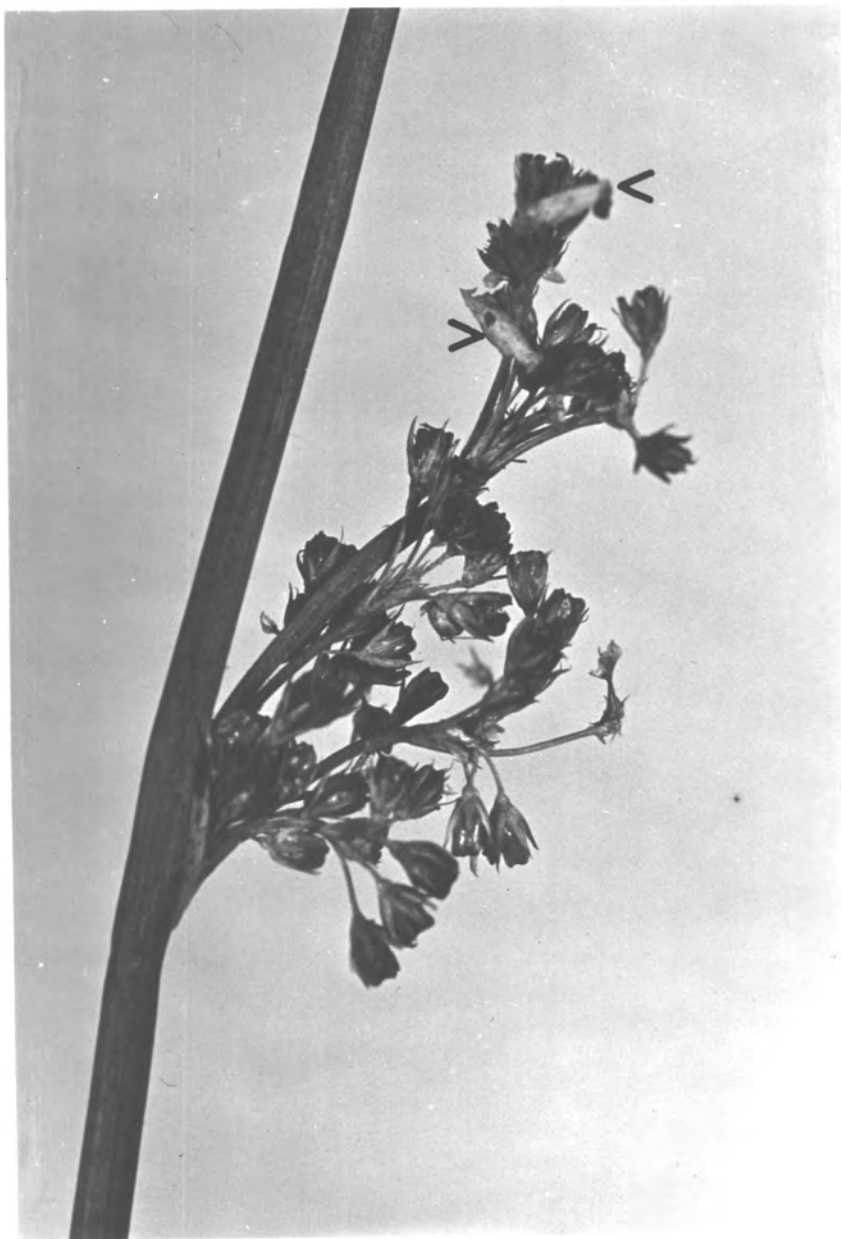
Plate. 2. Final instar larvae (marked 'V') feeding
on Juncus effusus.

Graph. 3. The vertical lines show the Standard Errors.

EASTERN TRANSECT

1,500 FEET

1956

1957

MEAN NUMBER OF RIPE CAPSULES PER STEM.

JUNE — JULY — AUG — SEPT — OCT — NOV
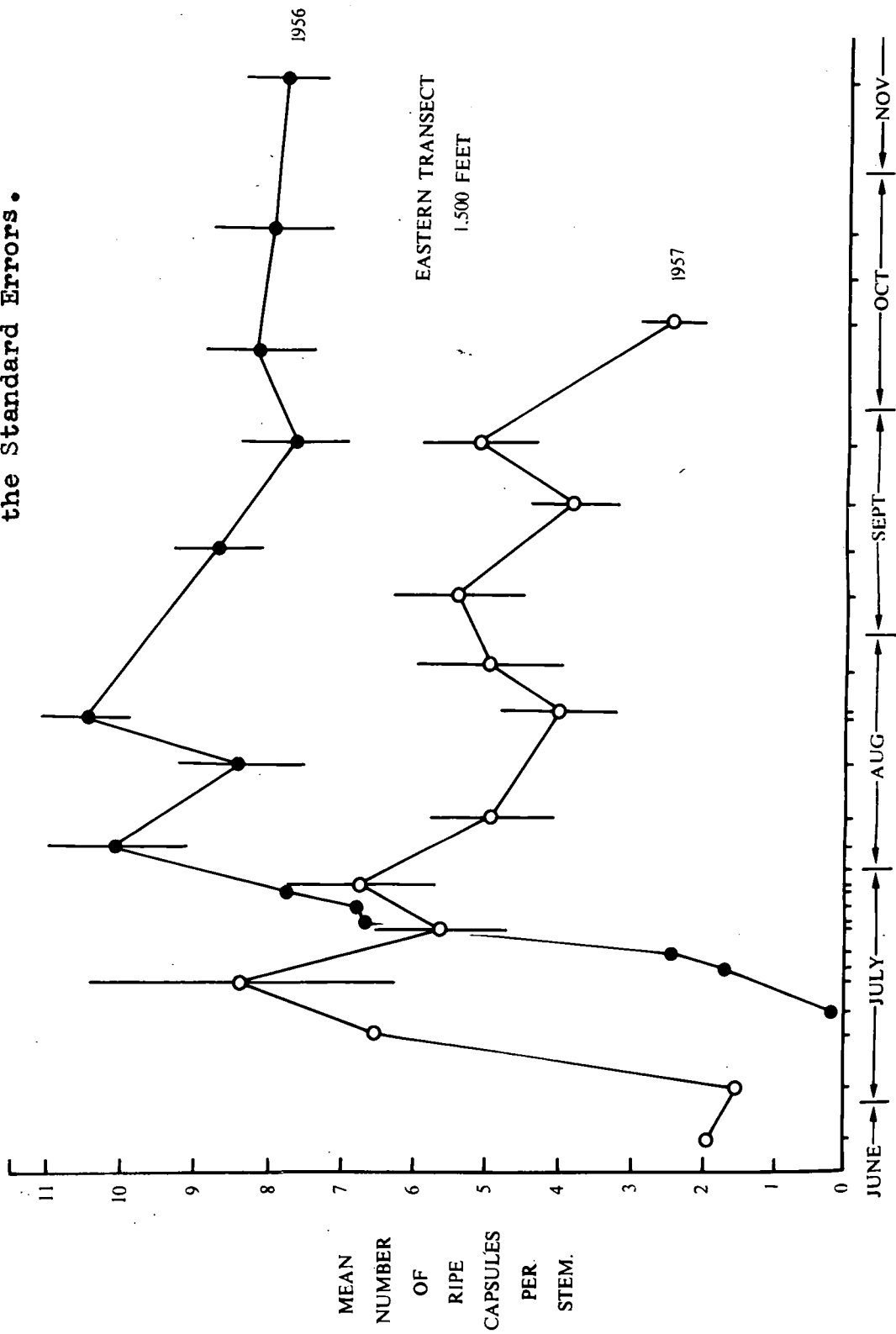
only, and in order to prevent undue complication, standard
errors have been included only after numbers had raeched their
maximum.

Table 5. E. transect, 1956.

The mean number of ripe capsules per stem of J. squar.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
July 20	2.5 ± .58	1.1 ± .43	.75 ± .42	.85 ± .53	.30 ± .16	.05 ± .049	-	-
July 26	6.8 ± .75	5.8 ± .94	3.9 ± .83	3.7 ± .68	4.3 ± .86	1.7 ± .40	.10 ± .068	.50 ± .40
Aug. 3	10.2 ± .93	12.5 ± .80	11.4 ± .63	8.4 ± .81	7.9 ± .97	7.1 ± .86	3.5 ± .70	2.8 ± .82
Aug. 20	10.6 ± .65	12.2 ± 1.2	6.8 ± .78	9.2 ± .76	8.8 ± .87	6.3 ± .83	5.5 ± .68	2.5 ± .59
Sept 11	6.8 ± .58	11.5 ± .92	8.9 ± 1.0	9.8 ± .84	9.6 ± 1.0	9.7 ± 1.1	4.2 ± .66	4.4 ± .63
Oct. 17	8.3 ± .71	9.6 ± .68	6.5 ± .75	9.0 ± .61	8.3 ± .71	8.8 ± .68	4.3 ± .79	3.6 ± .71
Nov. 12	7.9 ± .54	9.2 ± .73	5.3 ± .61	7.2 ± .73	7.1 ± .66	6.8 ± .59	4.6 ± .59	2.6 ± .46

The general order of events is the same in both years
except that the 1957 season started about three weeks earlier
than the previous year. As the ovaries begin to enlarge after
flowering and fertilisation, so the number of ripe capsules
increases in the rush samples, until a maximum is reached
about three weeks after their initial appearance. Numbers
tend to fall after this, probably due to mechanical removal
by wind, rain and sheep grazing. The most significant feature
of graph 3, however is that it shows that there were con-
sistently fewer capsules in 1957, than in 1956.

Table 6. E. transect, 1957.

The mean number of ripe capsules per stem.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
June 25	2.0 ± .48	.53 ± .41	.60 ± .29	2.0 ± .69	1.1 ± .38	1.0 ± .40	0	0
July 2	1.6 ± .35	1.2 ± .44	1.5 ± .69	4.3 ± .87	1.8 ± .43	2.3 ± .63	1.3 ± .35	0
July 9	6.6 ± 1.1	3.7 ± .70	2.8 ± .56	5.0 ± .82	3.1 ± .68	6.0 ± 1.0	2.3 ± .55	3.6 ± .88
July 16	8.4 ± 2.0	2.7 ± .88	1.9 ± .33	4.4 ± .78	5.0 ± 2.0	NOT SAMPLED ON THIS DATE		
July 23	5.7 ± .90	4.0 ± 1.2	2.0 ± .44	3.1 ± .56	2.1 ± .83	6.0 ± 1.1	1.8 ± .55	1.4 ± .64
July 29	6.8 ± .98	2.9 ± 1.1	2.0 ± .36	4.6 ± .96	2.6 ± .85	5.3 ± .88	.60 ± .21	2.0 ± .94
Aug. 7	5.0 ± .86	NOT SAMPLED ON THIS DATE						
Aug. 21	4.1 ± .79	-	1.4 ± .38	2.7 ± .76	1.8 ± .56	5.2 ± .95	3.3 ± .88	2.6 ± .67
Aug. 26	5.0 ± 1.0	NOT SAMPLED ON THIS DATE						
Sept 5	5.5 ± .93	-	1.6 ± .68	3.4 ± .93	-	8.3 ± .96	2.5 ± .72	4.6 ± 1.0
Sept 17	3.9 ± .61	-	1.2 ± .42	3.5 ± .67	-	7.3 ± 1.1	3.2 ± .73	2.2 ± .55
Sept 25	5.2 ± .77	NOT SAMPLED ON THIS DATE						
Oct. 11	2.55 ± .48	-	1.3 ± .44	2.1 ± .55	-	3.9 ± .76	1.4 ± .45	3.9 ± .72

Figures for the percentage of ripe capsules damaged by _Coleophora_ larvae have already been given (table 4, p.27). This shows that the highest figure for the whole transect was only 55-60% of the capsules damaged, while generally the figure was much lower than this. In other words, even when all the larvae had finished feeding, there was still a good deal of food left uneaten.

This was not so in 1957, when from the outset, all

capsules showed some degree of damage, and at all levels the maximum number of larvae exceeded the maximum number of ripe capsules available. The food supply was thus exhausted in 1957.

Early in the season, although there was a greater number of larvae than ripe capsules, many larvae had infected unripe capsules, many of which would never ripen. This meant that very few ripe capsules had more than one larva. As the season proceeded however, there tended to be a concentrating of larvae into those capsules remaining untouched. This caused a certain amount of crowding, and an attempt has been made to show this below.

Table 7. E. transect, 1957.

(a). The percentage of ripe capsules with two or more larvae.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
July 23.	18.0	7.0	0	0	0	13.0	5.0	17.0
July 29.	7.0	3.0	0	0	0	4.0	8.0	0
Aug. 7.	2.0	NOT SAMPLED						
Aug. 21.	0	0	5.0	2.0	0	4.0	0	0

(b). The percentage of larvae in "crowded" conditions.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
July 23.	39.0	23.0	0	0	0	45.0	19.0	32.0
July 29.	26.0	15.0	0	0	0	21.0	25.0	0
Aug. 7.	21.0	NOT SAMPLED						
Aug. 21.	0	0	100.0	66.6	0	35.0	0	0

Note.

1. 'Crowded' conditions are interpreted as those in which two or more larvae are present in the same capsule.

2. Where percentages have been underlined, the number of larvae in the sample was three or under.

Results from the 1,500' station show the phenomenon quite well. Thus, on July 25th., 18% of the capsules were supporting 40% of the larvae, while nearer the extinction point of the larvae, 20% of the larvae were concentrated into 2% of the ripe capsules.

Jordan estimated that each larva needs on the average the contents of about two seed capsules to reach maturity. The theoretical maximum of larvae then, that a rush head can support is equivalent to about 50% of its number of ripe capsules. Since this figure was consistently surpassed in 1957, it is obvious as to why the larvae became extinct.

Graph 4. has been prepared to give a direct comparison of numbers in the two years. Since there were such great differences in number, the egg and larval means have been plotted on a log scale.

Graph. 4.

EASTERN TRANSECT
1,500 FEET

LOG N+1
OF
MEAN
NUMBER
OF
EGGS
&
LARVÆ
PER
STEM.

2·0
·9
·8
·7
·6
·5
·4
·3
·2
·1
1·0
·9
·8
·7
·6
·5
·4
·3
·2
·1
0

JUNE — JULY — AUG — SEPT — OCT — NOV
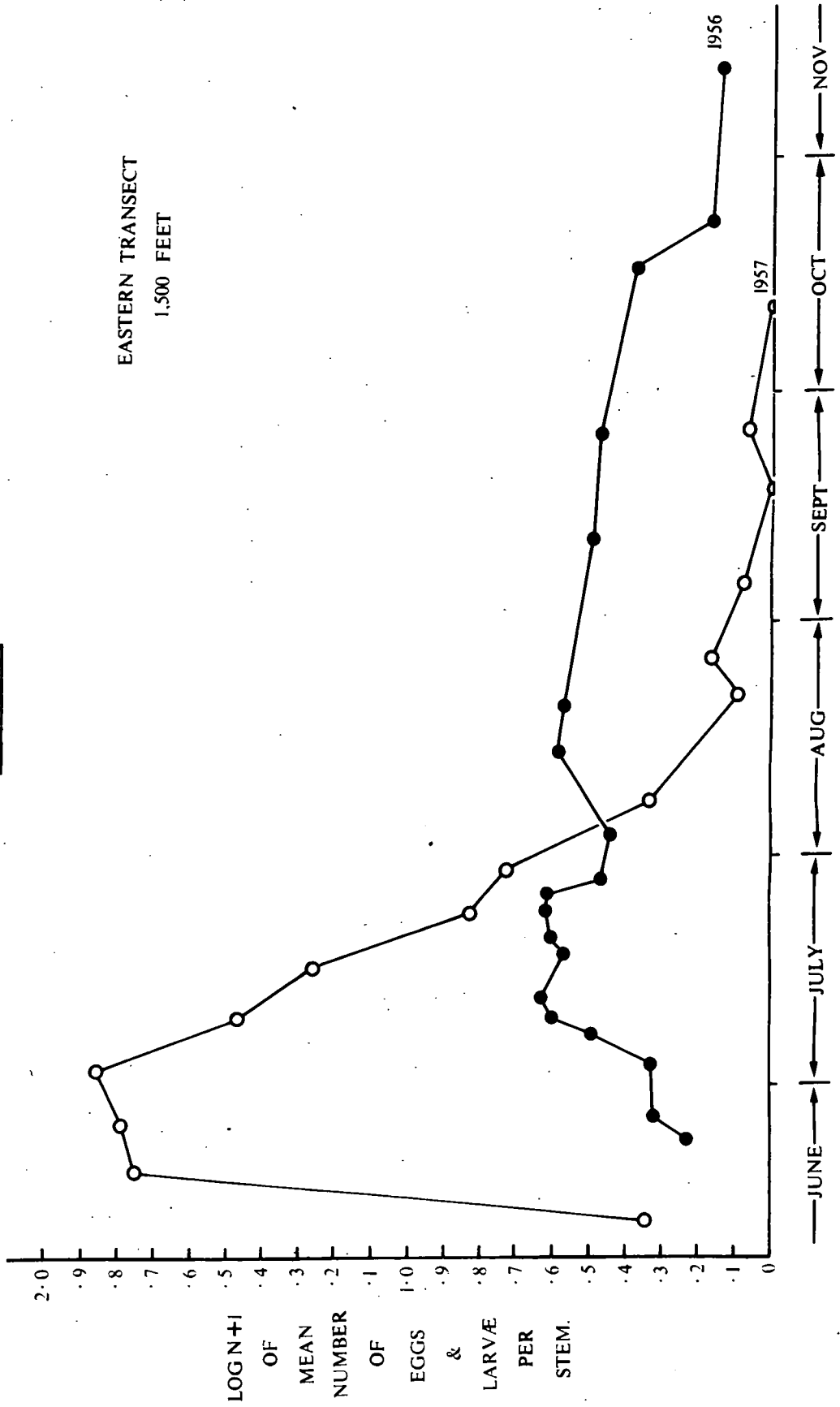
1956

1957

THE GENERAL SITUATION ON THE W. TRANSECT DURING 1956 & 1957.

Tables 8 and 9 summarise the results from the two years under consideration.

Table 8. W. transect, 1956.

The mean number of eggs (E) and larvae (L) per stem.

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500		T
June 21	-	-	1.8±.33	3.4±.64	.20±.18	.35±.18	.10±.068	-	-	-	E	20
July 11	.20±.13	1.3±.31	4.5±.59	12.7±.97	13.2±1.0	3.9±.67	1.0±.28	1.6±.34	.15±.11	.15±.11	E	
	.05±.049	-	.45±.23	1.1±.24	.05±.049	.20±.09	-	-	-	-	L	14
July 25	NOT SAMPLED			1.0±.26	NOT SAMPLED ON THIS DATE						E	
				7.5±.63							L	15
Aug.9	1.5±.35	1.9±.38	5.9±.78	10.5±.71	6.5±.80	3.6±.45	.50±.15	1.3±.26	-	.10±.068	L	12
Aug. 21	NOT SAMPLED			9.9±.62	NOT SAMPLED ON THIS DATE						L	14
Sept 4	NOT SAMPLED			4.9±.61	NOT SAMPLED ON THIS DATE						L	14
Sept 18	.95±.15	.90±.23	3.4±.55	4.9±.61	6.5±.70	2.6±.50	.35±.16	1.7±.30	-	.10±.068	L	21
Oct. 9	.15±.07	.60±.18	1.5±.43	1.4±.63	1.9±.45	1.8±.39	.55±.17	1.5±.32	.05±.049	-	L	15
Oct. 25	NOT SAMPLED			.85±.25	NOT SAMPLED ON THIS DATE						L	

'T'. The number of days between samples.

Unlike tables 1 and 2, the earliest date mentioned in the tables of this section is not necessarily the first on which eggs appeared in the field. However the maximum height shown gives the upper limit of the Coleophora infestation, but not necessarily the upper limit to which ripe seed capsules were produced. In this latter respect, the tables for

the two transects are comparable.

Table 9. W. transect, 1957.

The mean number of eggs (E) and larvae (L) per stem.

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500		T
June 5	3.9±.72	5.6±.69	6.1±.97	1.2±.40	1.0±.24	5.8±.92	.80±.46	3.2±.73	-	-	E	12
June 19	13.5±1.7	15.6±1.9	21.8±2.3	18.0±2.6	9.9±1.6	22.5±3.5	18.8±3.0	12.8±2.1	5.4±.83	2.5±.42	E	13
	1.2±.38	1.0±.43	1.2±.30	-	-	.10±.068	-	.15±.08	-	-	L	
July 2	6.3±1.1	7.3±1.1	4.6±.87	11.2±2.0	11.6±2.1	10.3±1.6	13.4±1.9	4.4±.98	2.5±.71	2.5±.54	E	16
	17.6±1.7	17.9±1.5	23.5±2.0	12.5±1.1	7.0±1.0	14.1±1.5	7.6±.61	9.6±.87	2.9±.74	1.5±.41	L	
July 18	NOT SAMPLED			.45±.21	NOT SAMPLED ON THIS DATE						E	20
				12.8±1.80							L	
Aug. 7	4.7±.83	3.2±.66	4.2±.79	6.6±1.1	3.4±.76	4.5±.94	1.7±.43	3.0±.59	1.6±.51	2.7±.63	L	19
Aug. 26	2.1±.44	1.2±.40	2.2 ±.67	4.0±.77	-	1.5±.13	.75±.27	.90±.33	.75±.22	1.1±.37	L	

'T' The number of days between samples.

The tables are represented in figs. 7 and 8, the dis-
tance between each column being proportional to the time
between successive samplings. It may be pointed out that the
difference in scale between these two figures is not nearly
so great as between the comparable ones representing the E.
transect.

Although the 950' sample station was examined in more
detail than any of the other stations of this transect, it
was not sampled sufficiently to warrant the kind of detailed
analysis given to the 1,500' station of the E. transect.

-39-

Fig. 7.

WESTERN TRANSECT

1956

MEAN NUMBER OF EGGS & LARVAE PER STEM.

ALTITUDE

(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)

Fig. 8.

WESTERN TRANSECT

1957

(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)
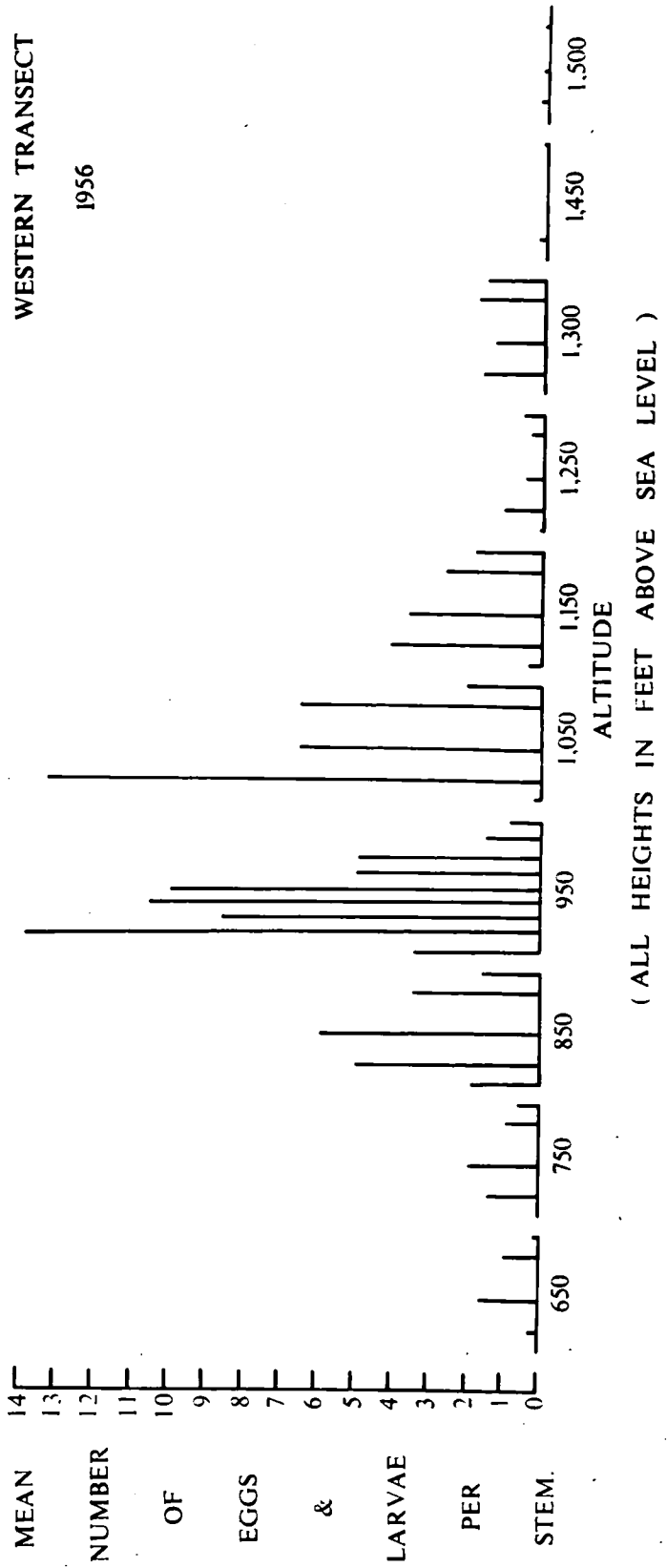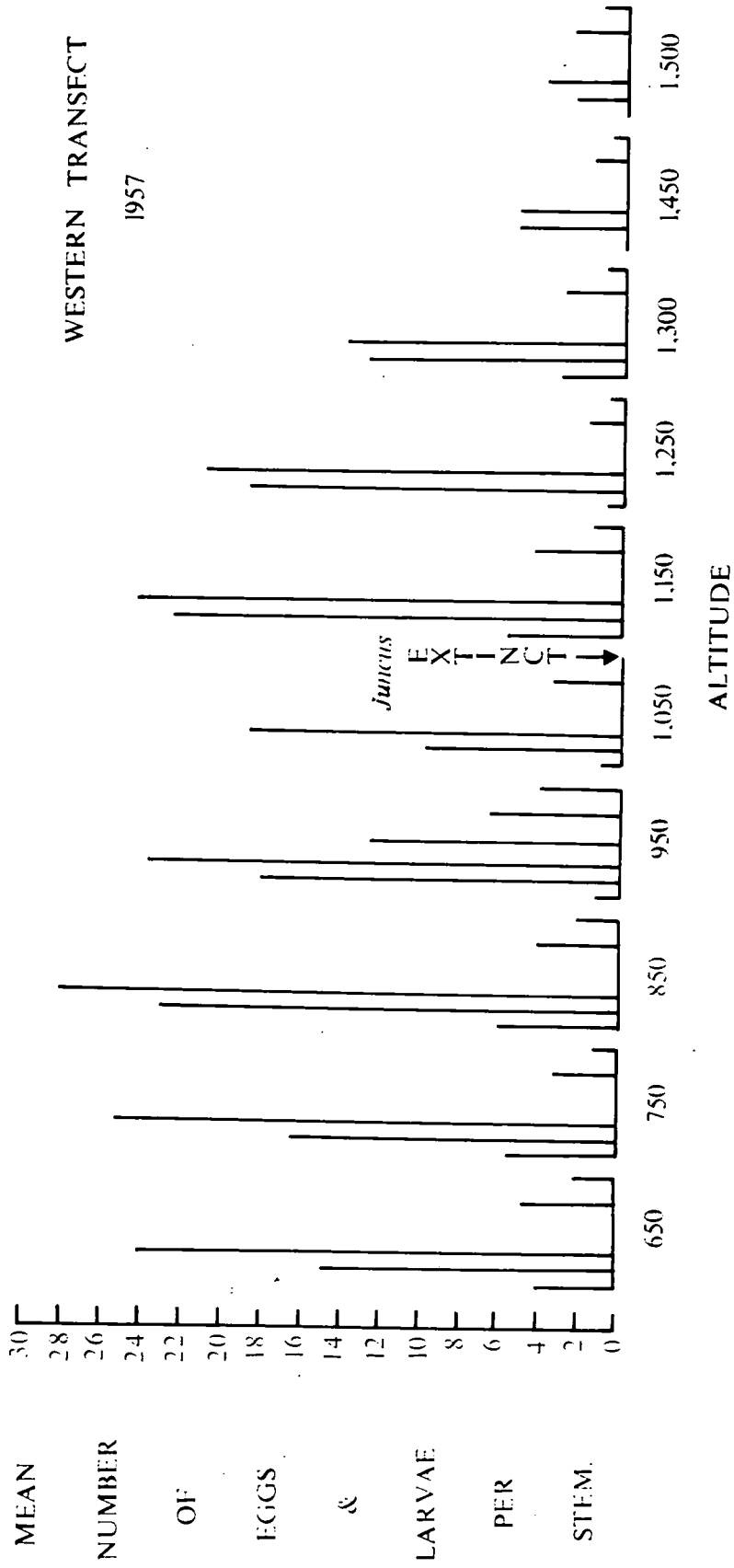
Instead, a general account of the Coleophora activity in each of the two years is given below.

All extra results from the 950' station are included in the tables and figures mentioned above, and not presented separately in an appendix.

THE W. TRANSECT, 1956.

At some stations (particularly 950') egg numbers were already quite high on the first date sampled (June 21st.) so that the first eggs were probably laid some time (perhaps a week or more) before this. No eggs at all were present at some other stations (the two lowest, and the three highest, of the transect) indicating that egg-laying commenced at different times at different altitudes. This contrasts with the E. transect, where the first eggs at all altitudes appeared within two or three days of each other.

Except for the 1,500' station, eggs from the E. transect first appeared in any numbers on June 26th., this being at least a week later than on the W. transect.

The rather long intervals between sampling dates prevents an estimation of the true egg maximum, but samples do indicate that the 950' and 1,050' stations probably yielded the highest numbers. Thus on July 11th., the combined egg and larval means were in the region of 13 per stem. This total is far above the maximum of just over three, from the east in 1956. Altitude for altitude however, the numbers from the 1,500' station, E. transect, are appreciably higher than from the 1,500' station, W. transect. In fact, it is only the 850' to 1,050' stations that have consistently higher

numbers than the highest readings from the E. transect.

Appendix lV. shows that at two stations (950' and 1,050')
the maximum numbers of eggs must have exceeded the number
of oviposition sites in 1956. This never occured on the E.
transect in this year.

The samples from July 11th., indicate the beginning
of the hatching season, since several stations show small
numbers of larvae for the first time. The first larvae from
the E. transect appeared between the 18th. and 20th.,July,
which serves to confirm the opinion that egg-laying began
at least a week earlier on the W, transect. The phenomenon
could however be explained by postulating that the eggs on
this transect took about a week less to hatch.

As shown in the table below, larvae with cases first
appeared in samples taken on Aug. 9th.

Table 10. W. transect, 1956.

The percentage of Coleophora larvae with cases

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
Aug. 9	6.0	8.0	4.0	6.0	-	2.0	-	4.0	-	-
Sept 18	68.0	94.0	65.0	64.0	51.0	54.0	56.0	52.0	-	100.0
Oct. 9	100.0	66.6	87.0	90.0	100.0	89.0	91.0	90.0	-	-

This date (Aug. 9th.) is approximately 30 days after
the beginning of hatching, and is in contrast with the 53

-42-

days taken by larvae from the E. transect (July 20th., to
Sept. 11th.) It seems then that larvae from the W. transect
are going through this stage of their life history faster
than those from the E. transect.

Long (1953), showed that certain lepidoptera under
crowded conditions in the laboratory went through the larval
stage more quickly than those in uncrowded conditions. The
present situation however is not analogous to that of Long,
as the table below shows.

Table 11. W. transect, 1956.

(a), The Percentage of Ripe Capsules with Two or More Larvae.									
650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
July 25	NOT SAMPLED		3.0	NOT SAMPLED ON THIS DATE					
Aug. 9	0	1.0	0	5.0	3.0	1.0	0	0	0	0
Aug. 21	NOT SAMPLED		3.0	NOT SAMPLED ON THIS DATE					
Sept 18	0	0	1.0	5.0	2.0	2.0	1.0	0.5	0	0
Oct. 9	0	0	1.0	2 .0	1.0	0.5	1.0	0.5	0	0

(b), The percentage of Larvae in "Crowded" conditions									
650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
July 25	NOT SAMPLED		11.0	NOT SAMPLED ON THIS DATE					
Aug. 9	0	10.5	0	13.0	11.0	8.0	0	0	0	0
Aug. 21	NOT SAMPLED		8.0	NOT SAMPLED ON THIS DATE					
Sept 18	0	0	9.0	2 3.0	8.0	15.0	28.5	8.0	0	0
Oct. 9	0	0 .	13.0	34.0	15.0	5.5	18.0	6.0	0	0

NOTE

Crowded conditions here are interpreted as those in which two or more larvae
are present in the same seed capsule

Thus it can be seen that, either the abbreviated larval

period occurs in both 'crowded' and uncrowded conditions
(950' and 650 'respectively) or does not occur in typically
'crowded' conditions (i.e. at 1,050' and 1,250').

On the last date when all sites were sampled (Oct. 9th)
numbers were down to quite a low level, although at some
stations (850' - 1,150') feeding had probably not then ceased.
A later sample from the 950' station (Oct. 25th.) showed that
even then there were still quite a few larvae on the rush
heads (.85 l.p.s.). Some of these larvae would of course
never leave the rush heads, and would overwinter there, a
phenomenon also noted on the E. transect, in 1956. This
situation was further complicated at the 850' and 950' stat-
ions where there were parasitised larvae, which would also
overwinter on the rush heads (see later).

The table below gives an account of the percentage of
Juncus capsules damaged in 1956.

Table 12. W. transect, 1956.

	650'	750'	850'	950'	1,050'	1,150'	1,250'	1,300'	1,450'	1,500'
July 11.	.4	0	10.0	18.0	0	3.0	0	0	0	0
Aug. 9.	10.0	13.0	40.0	73.0	54.0	25.0	6.0	12.0	0	2.0
Sept.18.	13.0	15.5	54.5	85.0	69.0	32.0	7.0	16.0	0	1.0
Oct. 9.	11.0	23.0	80.0	97.0	96.0	46.0	18.0	30.0	4.0	.6

It can be seen that the percentage damaged rose from

650' to 1,050', and then gradually fell to nil at, and above 1,500'. The 1,300' station had a consistently higher infestation than the station immediately below it (1,250'), but apart from this, the above pattern was maintained.

The food supply was never fully eaten out, although as much as 97% of the ripe capsules were consumed, and stations 850', 950', and 1,050' were obviously supporting their maximum number of larvae without actually reaching the extinction level.

THE W. TRANSECT, 1957.

It will be recalled that when the E. transect was sampled
on June 5th., of this year, no J. squarrosus flowering heads
were present. On the W. transect, not only were flowering
heads present, but also many stations had a high infestation
of eggs. In fact, the only stations that had no eggs were
the two highest (1,400' and 1,500'). In parallel with the E.
transect however, the first eggs this year (1957) must have
been laid some time before those of 1956.

Append. 1V. once again gives the relationship between
the numbers of sites available, and the number of eggs per
plant. At all stations, except the two highest, the number of
eggs per plant outstrips the number of sites available.

By June 19th'., the first larvae had appeared at some
stations in small numbers, so that this date is probably
near to the true beginning of the hatching period. The first
larvae on this transect in 1956, appeared on July 11th.,
confirming that the 1957 season was much earlier than the 1956
one .

As in 1956, sampling intervals were too large in 1957
to give a correct assessment of the maximum numbers of eggs
and larvae. It can be seen from fig. 8, that totals of 20
and more eggs and larvae per stem were recorded from all

stations upto 1,250' inclusive, with the exception of the 1,050' one. Above 1,250' numbers fell fairly regularly with increasing altitude. There was no regular pattern of rise and fall in numbers with altitude, as in the previous year (Compare figs. 7 and 8.)

Numbers fell quite appreciably between July 2cd. and Aug. 7th., though this fall was no doubt effected by migration, since on this latter date many of the larvae were seen to have cases. (see below)

Table 12a. W. transect, 1957.

The percentage of larvae with cases.

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
Aug. 7	62.0	51.0	40.0	14.0	15.0	43.0	25.0	20.0	9.0	7.0
Aug. 26	2 8.5	28.0	34.0	22.0	-	67.0	7.0	22.0	33.0	52.0

Although numbers at all altitudes were consistently higher than in 1956, there were not the huge differences in level that occured between the two years on the E. transect.

A certain ammount of crowding occured, as shown in table 13 (see over) and it was more extensive than in 1956, embracing all of the stations, except the highest one. It has been mentioned that many larvae produced cases, so it is quite likely that many larvae survived to overwinter, a point emphasised by the fact that it was as late as Aug. 25th.,

that all the ripe capsules were showing some signs of damage.

Table 13. W transect, 1957.

(a), The Percentage of Ripe Capsules with Two or More Larvae									
650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
July 2	9.0	14.0	33.0	11.0	3.0	9.0	24.0	6.0	0.5	0
July 18	NOT SAMPLED			17.0	NOT SAMPLED ON THIS DATE					

(b), The percentage of Larvae in "Crowded" conditions									
650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
July 2	22.0	31.0	53.0	22.0	10.0	21.0	5.0	16.0	3.0	0
July 18	NOT SAMPLED			34.0	NOT SAMPLED ON THIS DATE					

NOTE

Crowded conditions here are interpreted as those in which two or more larvae are present in the same seed capsule

No samples were taken after Aug. 26th., due to an outbreak of foot-and-mouth disease in the sampling area (see p. 17).

A certain number of parasitised larvae were found in 1957, but they will be dealt with in a later section.

THE UPPER LIMIT OF THE COLEOPHORA INFESTATION.

In the previous pages it has been mentioned several times that the upper limit (altitudinal) of the moth did not necessarily coincide with the upper limit of its food plant.

Jordan carefully considered this phenomenon and decided that the upper limit of C. alticolella was governed by the capacity of its host plant J. squarrosus, to set seed to a particular height. When his evidence (1952 - '54) is combined with that of the present study, this theory is well borne out.

Only results from the W. transect are presented below because they illustrate the phenomenon best.

YEAR.	UPPER LIMIT OF COLEOPHORA.
1952	c. 1,850'
1953	c. 1,850'
1954	c. 1,400'
1955	c. 1,400'
1956	c. 1,400' - 1,450'
1957	c. 1,500'

Both in 1952 and 1953, seeds were set to quite a high level (1,850') and this marked the upper limit of the moth. During 1954 however, no seed was set above 1,400', and the

moth consequently died out at stations above this height due to lack of sufficient food for the larvae. Jordan forecast that the upper limit of the moth in 1955 would be near to 1,400', even if seed was produced above this height.

This in fact did prove to be the case, and during the next three years seeds were set above the moths' upper limit but only gradually did the infestation move upwards. By 1957 it was quite well established at 1,500', but had not as yet reached the next sample station at 1,700'.

This slow upward dispersal is connected with the relatively inactive life of the adults, which move very little distance from the point of emergence.

It is now thought that this upward dispersion will continue until a year when once again seeds are set below the upper level of the previous year, as they were in 1954.

SOME RESULTS FROM 1955 AND 1958.

Although the 1956 and 1957 seasons have been extensively sampled, the present study was actually started in the autumn of 1955, and continued into 1958.

By the time the 1955 results were taken, all <u>Coleophora</u> activity had ceased, and the only measurable factor was the percentage of ripe capsules showing damage. It should be borne in mind that research had then only recently been started and hence sampling technique and methods of examining the material were not well developed.

So as to allow for direct comparison the only 1958 results presented below are for a similar period in the insects life history.

1. The E. transect.

Table 14. 1955.

The end of season estimates.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
A.	15.6 ± 1.25	13.8 ± .961	13.2 ± .948	13.2 ± .948	12.0 ± .671	17.2 ± .961	16.2 ± .937	17.4 ± 1.19
B	2.05 ± .604	1.2 ± .425	.95 ± .335	2.75 ± .693	1.35 ± .507	.15 ± .146	.90 ± .357	.60 ± .357
C	13.0	9.0	7.0	21.0	11.0	1.0	5.5	3.0
D	104.0 ± 5.2	88.0 ± 5.7	115.2 ± 6.8	105.6 ± 8.0	91.2 ± 5.9	91.2 ± 6.7	108.8 ± 8.0	88.0 ± 8.0

Note.

A. The mean number of ripe capsules per stem.

B. The mean number of damaged capsules per stem.

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C. The percentage of ripe capsules damaged.

D. The mean number of <u>Juncus</u> fruiting stems per square metre.

<u>Table 15. 1958.</u>

End of season estimates.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
A.	13.7	8.7	9.9	8.75	7.55	8.05	7.0	2.75
B	1.1	4.9	4.1	4.1	3.9	1.75	.25	0
C	15.0	56.0	42.0	47.0	52.0	22.0	3.0	0

<u>Note.</u>

A. The mean number of ripe capsules per stem

B. The mean number of damaged capsules per stem.

C. The percentage of ripe capsules damaged.

In order to emphasise their significance, sections 'C'
of the above tables have been presented in <u>fig. 9.</u>, together
with comparable figures from 1956 (see <u>table 4</u>, p. 27) and
1957 (when 100% of the capsules were damaged).

It can be seen that there was a general increase in
the percentage of ripe capsules showing damage from 1955 to
1957. The only station that does not follow this pattern is
the 1,850' one, but the numbers are so low from here, that
not much significance can be paid to the difference. It has
already been mentioned that no final instar larvae were pro-
duced from the <u>J. squarrosus</u> in 1957, and that an unusual
amount of <u>Coleophora</u> activity was observed on the <u>J. effusus</u>

Fig. 9.

PERCENTAGE OF RIPE CAPSULES DAMAGED

ALTITUDE
(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)
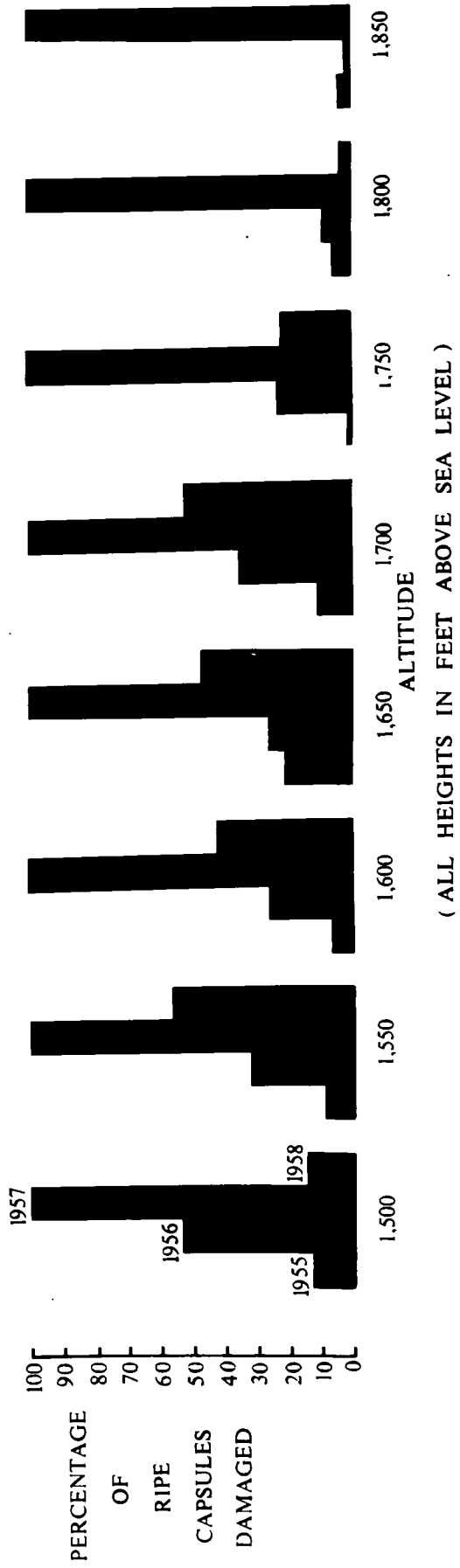
of the transect. Various reports indicate that this food plant was also utilised to an unusual extent by this species in 1957 in places as far apart as Derbyshire and the Lake District.

The recovery of quite a high infestation in 1958, after a marked depletion of the food supply in 1957, probably has its explanation in the moths' ability to utilise an alternative food plant.

It is possible (though it was not observed) that some egg-laying females in 1957, due to lack of suitable sites on the normal food plant, were forced to turn to J. effusus for oviposition sites. Larvae from these eggs plus larvae that had migrated there from the overcrowded J. squarrosus probably formed a resevoir of individuals in non-crowded conditions. These larvae would be able to complete their life cycle in the normal way and produce adults in the following year (1958).

The low reading for the 1,500' station, 1958, is perhaps due to the fact that so many larvae were produced in 1957 that much of the food from the J. effusus was eaten as well as that from the J. squarrosus.

Above 1,750' there is very little J. effusus on this transect, and hence no 'emergency' food supply. The moth

thus failed to re-establish itself at 1,850', and only just managed to do so at 1,800'.

2. The W. transect.

Table 16. 1955.

The end of season estimates.

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
A	11.7±1.0	15.5±1.8	10.5±.76	12.8±.88	16.0±1.1	14.4±.82	19.1±1.2	12.0±.71	19.0±1.2	19.5±.47
B	.90±.53	1.6±.53	5.2±.77	11.7±.85	8.1±1.2	11.6±.93	.75±.40	.85±.34	.15±.15	0
C	8.0	10.0	48.0	92.0	51.0	81.0	4.0	7.0	1.0	0
D	68.8±4.8	56.0±4.3	44.9±4.6	36.8±4.3	31.6±4.6	53.4±5.6	139.3±5.4	122.2±7.5	141.0±7.5	0

Note.

A. The mean number of ripe capsules per stem.

B. The mean number of damaged capsules per stem.

C. The percentage of ripe capsules damaged.

D. The mean number of Juncus fruiting heads per square metre.

No samples were taken in 1958, and so the three years data have been presented in graph 5. Except for the 1,150' station, the same trend of increasing percentage damage as was seen from the E. transect, occured. As mentioned previously the moth had not, in 1955, established itself at 1,500'.

-54-
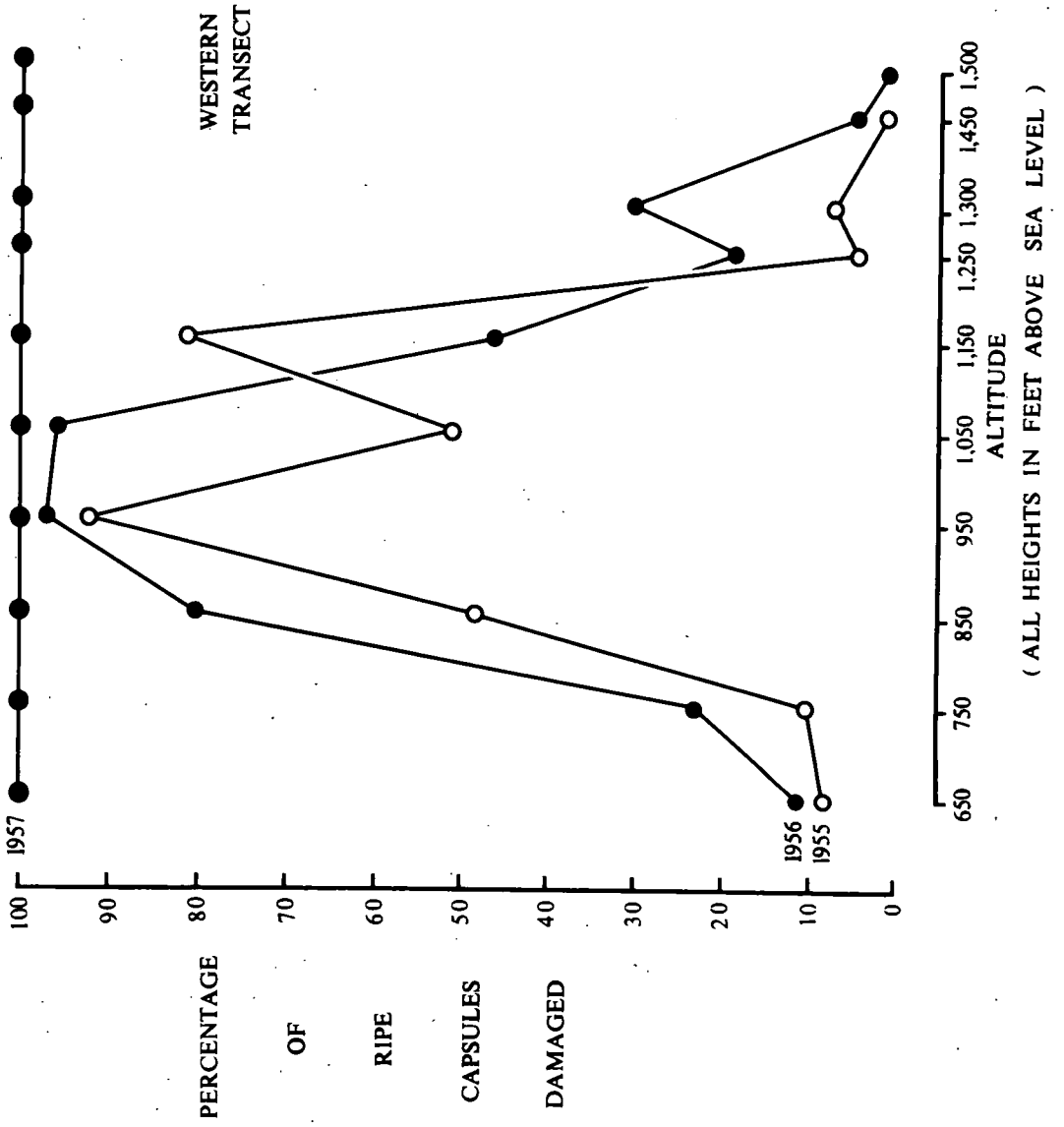
Graph. 5.

THE OVERWINTERING LARVAE.

It was originally decided to try and measure the number of larvae that overwinter from one _Coleophora_ season to another, and to estimate just how their numbers were depleted. The larvae during this stage are part of the surface litter fauna of the moorland, and so it was thought best to try a soil sampling technique.

A soil core sampler was used, of 5cm. diameter, a number of cores being taken randomly at each station. These peat cylinders were about 15cm. long, but only the top 5cm. and their vegetation were used in the extraction of the larvae. These units were placed in an oven at 60 ^{o}C., and baked for 36 hours. They were then cooled and powdered. The comminuted peat and plant remains were then put through a series of sieves, the fractions being saved from those whose mesh was known to be small enough to retain larvae.

By extensive macroscopic examination it was found possible to find any larvae present. By this method, one could discriminate between the current years larvae and cases containing the pupal remains of previous years, but not between the living and dead ones of the current year.

In order to get some idea of the efficiency of this method, several cores were taken from areas which lacked a

Coleophora infestation, and these were 'seeded' with numbers
unknown to the investigator. On examination the following
results were obtained from six cores.

Numbers put in.	Numbers extracted.
13	13
7	7
10	10
14	12
13	13
12	10
Total 69	Total 65

It can be seen that the method is quite an accurate
one, and so a field test was carried out during the winter
of 1955-6.

Forty cores from 1,500' yielded 21 larvae, of which only
five were from the current year. Even so this is approxim-
ately 64 per square metre. If the emergence trap data (see
p.12) is anything to go by, only about 16 of these per sq.m.
survived to emerge as adults in the spring of 1956.

However on practical grounds it was decided that this
method was too time consuming to be of much use to the pre-
sent study.

THE POPULATION STUDY. (PART 2).

INTRODUCTION.

Upto now <u>Coleophora</u> units have been considered only in terms of 'mean numbers per stem of <u>J. squarrosus</u>'. This method of expressing results is useful on a relative basis for comparing one year with another, or one sampling station with another, but does not give any indication of the absolute numbers of individuals to be found 'per unit area' of the study transects.

As a first stage in estimating this latter phenomenon, surveys were made of the density of rush flowering and fruiting heads 'per square metre'. This involved the use of a quadrat frame measuring 25cm. by 25cm., and thus enclosing an area of 1/16th., of a square metre. This frame was thrown down randomly over a specified area of more or less uniform <u>Juncus</u> cover, and each time it landed the number of flowering stems it enclosed was recorded. In order to give as accurate a result as possible, it was thrown down 64 times at each station. By multiplying these results by 16, it was possible to obtain the 'number of <u>Juncus</u> stems per square metre'.

The product of the above data and that from the previous section (on the egg and larval numbers 'per <u>Juncus</u> stem'),

gives an estimation of the 'number of Coleophora units per square metre'.

Greig-Smith (1952) points out that the use of quadrats thrown at random was originally developed, mainly by Scandanavian ecologists, in an attempt to obtain quantitative data on the abundance of species in plant communities. He concluded however that this method was not sufficient to determine the randomness or otherwise of the distribution of a species, and found the best method of analysis to be that using a grid of contiguous quadrats.

Kershaw and Tallis (1958) applied the above method to a field problem, and selected an area of J. squarrosus in N. Wales. They found that in an apparently uniform cover of Juncus, there was really a mosaic of patches of a mean diameter of 3.2m., in which the density, vigour and pattern of J. squarrosus varied.

In the present study, these complicating factors in the distribution of the host plant have been ignored, and in the following pages it has been assumed that the distribution of Juncus on the study area is more or less random.

Table 17.

The mean number of _Juncus_ heads per square metre.

(Quadrat data multiplied by 16)

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850	J
June 26	109.9±16.8	57.4±7.8	85.9±11.3	95.3±13.4	68.4±12.2	51.3±9.2	40.4±10.9	20.9±5.4	A
	134.7	77.2	108.8	110.4	89.9	65.9	61.3	29.6	B
July 19	159.6±10.4	96.9±8.9	131.6±10.6	125.4±11.6	111.0±12.1	80.4±9.4	62.2±9.8	38.2±8.8	C
Sept 19	167.6±9.2	118.7±8.3	156.9±10.1	122.4±8.1	117.4±11.0	105.9±11.1	98.4±12.6	32.6±7.2	D

The earliest quadrat survey (A) was done on June 26th.,
at a time when by no means all of the rush plants had, as
yet, produced flowering stems. Even those that were present
had only poorly developed florets, which were nevertheless
in a suitable state for oviposition.

By July 19th., (C), which was the main flowering period
numbers had increased at all stations, and a Students 't'
test, comparing this data with that from June 26th., showed
the difference to be highly significant, the .1% probability
level being exceeded. These two sets of results are shown
in graph 6.

The last date sampled (D), was Sept. 29th., which was
well into the fruiting season (see graph 3.). A 't' test
comparing these figures with those from July 19th., gave

Graph. 6. The vertical lines show the Standard Errors.

EASTERN TRANSECT

1956

JULY 19th

JUNE 26th

MEAN NUMBER OF FLOWERING HEADS PER SQUARE METRE
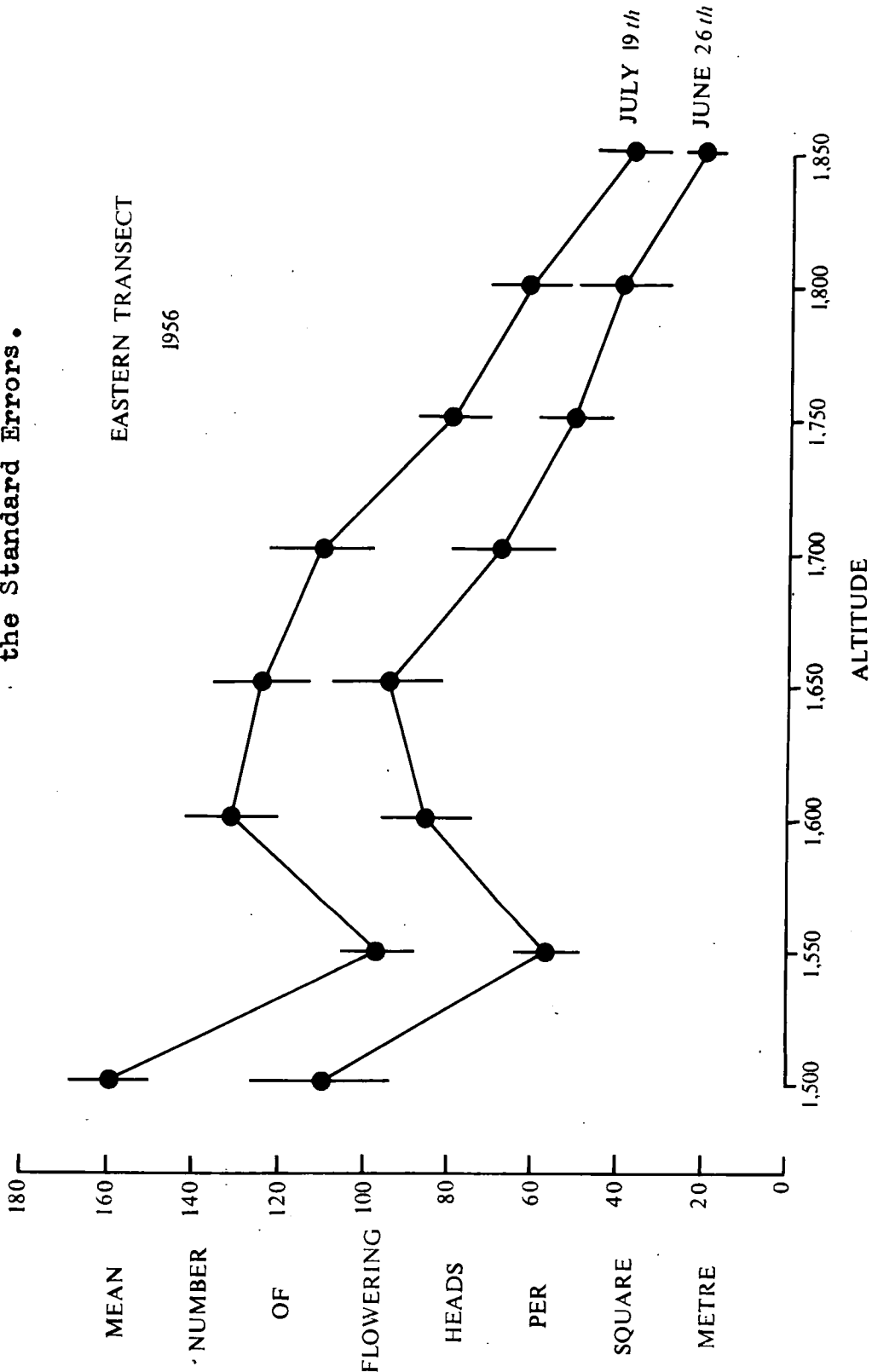
ALTITUDE

(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)

inconclusive results as to whether they were significantly different or not.

Graph 6., shows that the density falls with increasing altitude, except for the 1,550' station which has consistent-ly lower numbers than one would have expected. This may poss-ibly be connected with the fact that soil conditions there are by far the wettest of the whole transect, and at times the plants were standing in free water, a situation which occured at no other station.

It will be recalled that rush samples for eggs and larvae were taken at much smaller time intervals than the Juncus surveys (see table 1., p.19). Also, significant chan-ges in rush density took place between June 26th., and July 19th., while a set of samples for Coleophora numbers was taken on July 7th., mid-way between the two. To cover this intermediate period section 'B' has been added to table 17, the figures shown being simply an average from those of sections 'A' and 'C'. Sections 'C' and 'D' were not considered to differ significantly enough to justify similar treatment.

Table 18, (see over) shows the approximate numbers of eggs and larvae per square metre. These figures have been arrived at by multiplying data from table 1, with that from the relevant section of table 17. (see column 'J').

Table 18.E. transect, 1956.

The approximate numbers of eggs (E) and larvae (L) per square metre.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850		J
June 23	77.0	-	-	28.5	-	-	-	-	E	A
June 26	121.0	26.0	43.0	57.0	20.5	28.0	7.0	3.0	E	A
July 7	283.0	100.0	120.0	105.0	76.0	53.0	13.0	1.0	E	B
July 20	471.0	121.0	184.0	126.0	106.0	76.0	15.5	4.0	E	C
July 20	24.0	-	-	12.5	11.0	4.0	-	-	L	C
July 26	243.0	154.0	173.0	92.0	164.0	69.0	20.0	2.0	E	C
July 26	255.0	68.0	33.0	56.0	78.0	-	6.0	2.0	L	C
Aug. 3	287.0	102.0	125.0	88.0	95.0	48.0	6.0	2.0	L	C
Aug. 20	461.0	125.0	133.0	110.0	135.0	42.0	-	3.0	L	D
Sept. 11	352.0	184.0	157.0	177.0	129.0	63.0	20.0	2.0	L	D
Oct. 17	226.0	101.0	63.0	104.0	111.5	58.0	20.0	-	L	D
Nov. 12	59.0	65.0	63.0	24.0	45.0	32.0	20.0	-	L	D

Note.

'J' The appropriate section of <u>table 17.</u>, used in calculating the results.

THE E. TRANSECT, 1957.

In order to get a direct comparison with the 1956 season, the first rush density survey in 1957 was done on June 25th., just one day earlier than the previous year.

Table 19.

The mean number of Juncus heads per square metre.

(Quadrat data multiplied by 16)

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
June 25	9.25±2.2	.75±.42	2.25±2.2	4.5±1.3	.75±.42	6.75±1.8	5.25±2.0	1.5±1.3 A
	8.0	1.0	3.0	5.0	1.1	13.0	13.0	8.0
July 16	7.25±2.1	1.25±.53	3.5±1.1	4.25±1.5	1.75±1.05	6.5±1.5	11.25±2.9	1.0±.60 B
	4.5	1.0	3.0	3.0	1.5	8.0	18.0	.60

Note.

In each case the current years result is presented above, and its value, as a percentage of the equivalent 1956 result, below.

The differences between the two years are obvious. Even the highest 1957 figures are only 13% of the 1956 ones (at 1,750' and 1,800') while the lowest density, at 1,700', is only 1% of the previous year.

It was thought at the time that the numbers were probably low because the season may not have been as advanced as in 1956, i.e. that many of the plants had not as yet produced flowering heads. However, the next survey, done on

July 16th., (again in <u>table 19</u>) showed that this was not the case. The density showed very little change at any height, except 1,800', and even there it was still only 18% of the 1956 figure of about the same time of the year. (Actually July 19th.) A Students 't' test, as might be imagined, showed that these two sets of figures were not significantly different. Both of these sets of figures are shown in <u>graph 7</u>.

Unlike 1956, there was no regular decrease in numbers with increasing altitude, although again, the 1,550' station had a low density. In fact sampling so depleted the numbers of plants that by early August no further samples could be taken. The situation at 1,700' was similar, though it was not until September that sampling had to be terminated.

These were the only two <u>Juncus</u> surveys done in 1957, but they do throw extra light on the 'abnormally' high infestations found on the rushes in that year, as discussed in the previous section.

During 1956 an egg-laying female had anything from about eight to eighty times more (depending on the station) plants on which to oviposit, than one in 1957. Only a reduced number of females and/or a reduced number of eggs laid per female, could have relieved this position in 1957. This condition was not fulfilled as is obvious from the amount of

Graph. 7. The vertical lines show the Standard Errors.

EASTERN TRANSECT

1957

MEAN NUMBER OF FLOWERING HEADS PER SQUARE METRE

ALTITUDE

(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)

JUNE 25 th

JULY 16 th
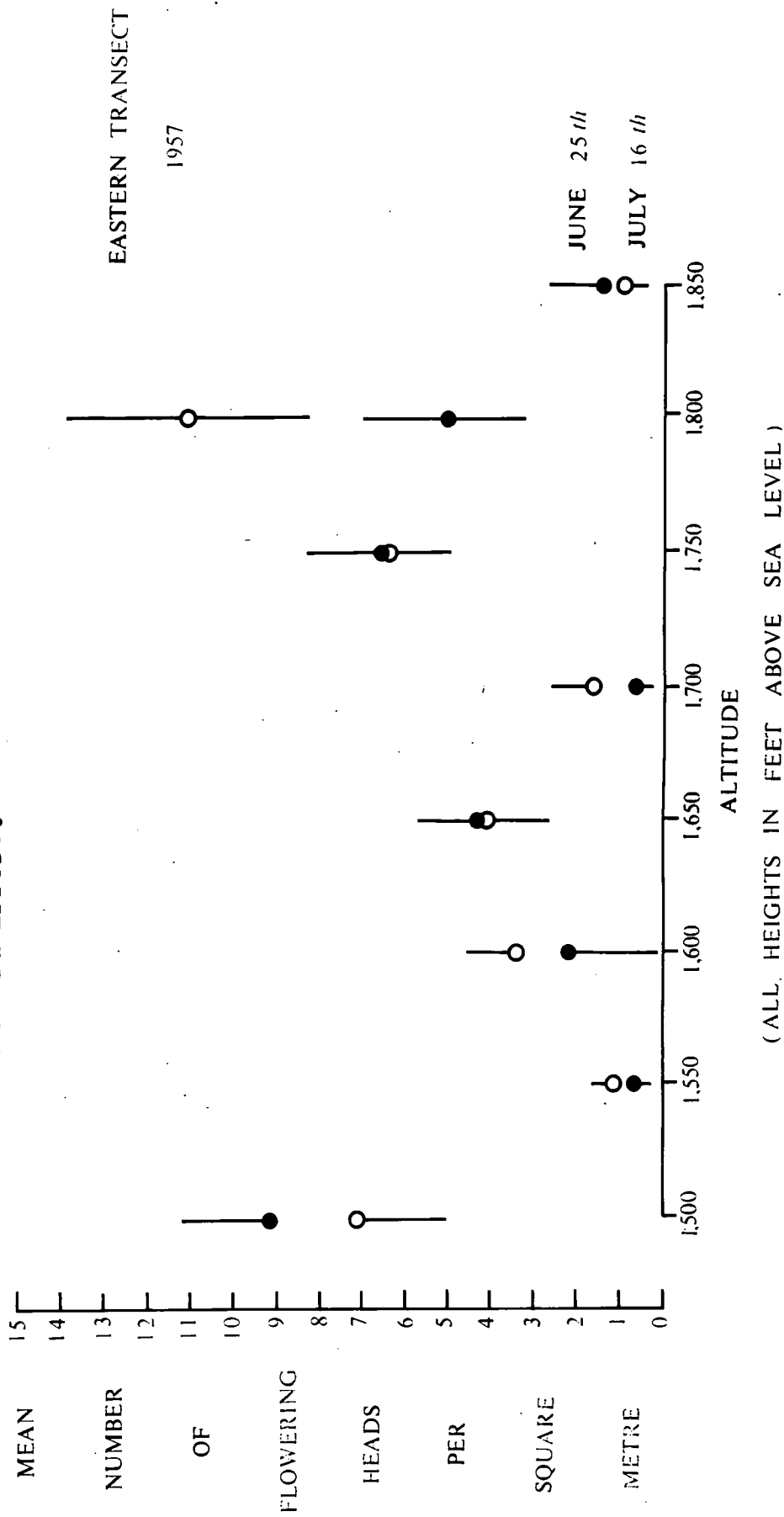
crowding that took place.

Even though there was probably a great deal of mortality in the egg stage in 1957, the crowded conditions were carried over into the larval stage too (see figures on crowding) a position further aggravated by the reduced number of ripe capsules per plant in that year. (See graph 3).

Table 20. E. transect, 1957.

The approximate number of eggs (E) and larvae (L) per square metre.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850		J
June 12	11.5	-	.60	-	-	-	-	-	E	A
June 19	520.0	51.0	75.0	131.0	22.0	204.0	50.0	19.0	E	A
June 25	554.0	37.0	108.0	271.0	28.0	275.0	97.0	21.0	E	A
July 2	577.0	32.0	89.0	131.0	19.5	171.0	82.0	12.5	E	A
	69.0	4.0	12.0	22.5	4.0	30.0	9.0	1.0	L	A
July 9	128.0	16.0	32.0	42.0	20.0	57.5	56.0	4.5	E	B
	78.0	10.0	19.0	33.5	10.0	49.0	52.0	3.0	L	B
July 16	52.0	7.5	14.0	13.0	4.0	NOT SAMPLED ON THIS DATE			E	B
	73.0	4.5	14.0	20.0	7.5				L	B
July 23	2.0	.10	0	1.0	0	2.0	2.0	.10	E	B
	41.0	3.0	3.0	2.5	1.0	25.0	12.0	1.5	L	B
July 29	.40	0	0	0	0	0	0	0	E	B
	31.5	2.0	2.0	3.0	.50	14.0	4.5	1.0	L	B
Aug. 7	9.0	NOT SAMPLED ON THIS DATE							L	B
Aug. 21	2.0	-	.45	1.0	.50	7.0	3.0	.10	L	B
Aug.26	4.0	NOT SAMPLED ON THIS DATE							L	B
Sept. 5	1.0	-	.45	0	-	3.0	.60	.60	L	B
Sept 17	0	-	0	0	-	1.0	.60	.10	L	B
Sept 25	1.0	NOT SAMPLED ON THIS DATE							L	B
Oct. 11	0	-	0	0	-	0	0	0	L	B

'J' The appropriate section of table 19., used in calculating the results.

The above table gives the results per square metre for 1957. The estimates for June 12th., and 19th., have been calculated assuming that the density of _Juncus_ then was the same as when the survey was done on June 25th., i.e. section 'A' of _table 19_ has been used. It will be recalled that very few rushes were present on June 12th.,and that the density would probably still be rising upto, and in some cases after June 25th.The figures shown for June 12th., and 19th., will thus be overestimates.

The period from June 23rd., to July 23rd., is well covered by the two density surveys, but after this latter date, section 'B' was also used in calculations, even though it was known that successive sampling was depleting the already low numbers of _Juncus_. Figures after _July 23rd._, will thus be overestimates too.

Figures from _tables 18 and 20._, are shown together in _fig. 10·_, and results from the 1,500' stations in the two years are shown separately in _graph 8_. In both of these cases it was not necessary to have to resort to using a logarithmic scale in order to present the two years results together as was used in _graph 4_.

It is obvious from the above, that in simply considering _Coleophora_ numbers in terms of their 'mean per stem', of

APPROXIMATE
NUMBER OF EGGS & LARVÆ PER SQUARE METRE

1957   1956

700 600 500 400 300 200 100 0 100 200 300 400 500 600 700

1,500

Juncus
EXTINCT

1,550

1,600

EASTERN

TRANSECT

1,650

Juncus
EXTINCT

1,700

Fig. 10. 'T' shows
a trace.

1,750

ALL HEIGHTS IN FEET

ABOVE SEA LEVEL

1,800

1,850

1957   1956

Graph . 8 .

EASTERN TRANSECT
1,500 FEET

APPROXIMATE NUMBER OF EGGS & LARVAE PER SQUARE METRE

700
50
600
50
500
50
400
50
300
50
200
50
100
50
25
0

JUNE — JULY — AUG — SEPT — OCT — NOV—
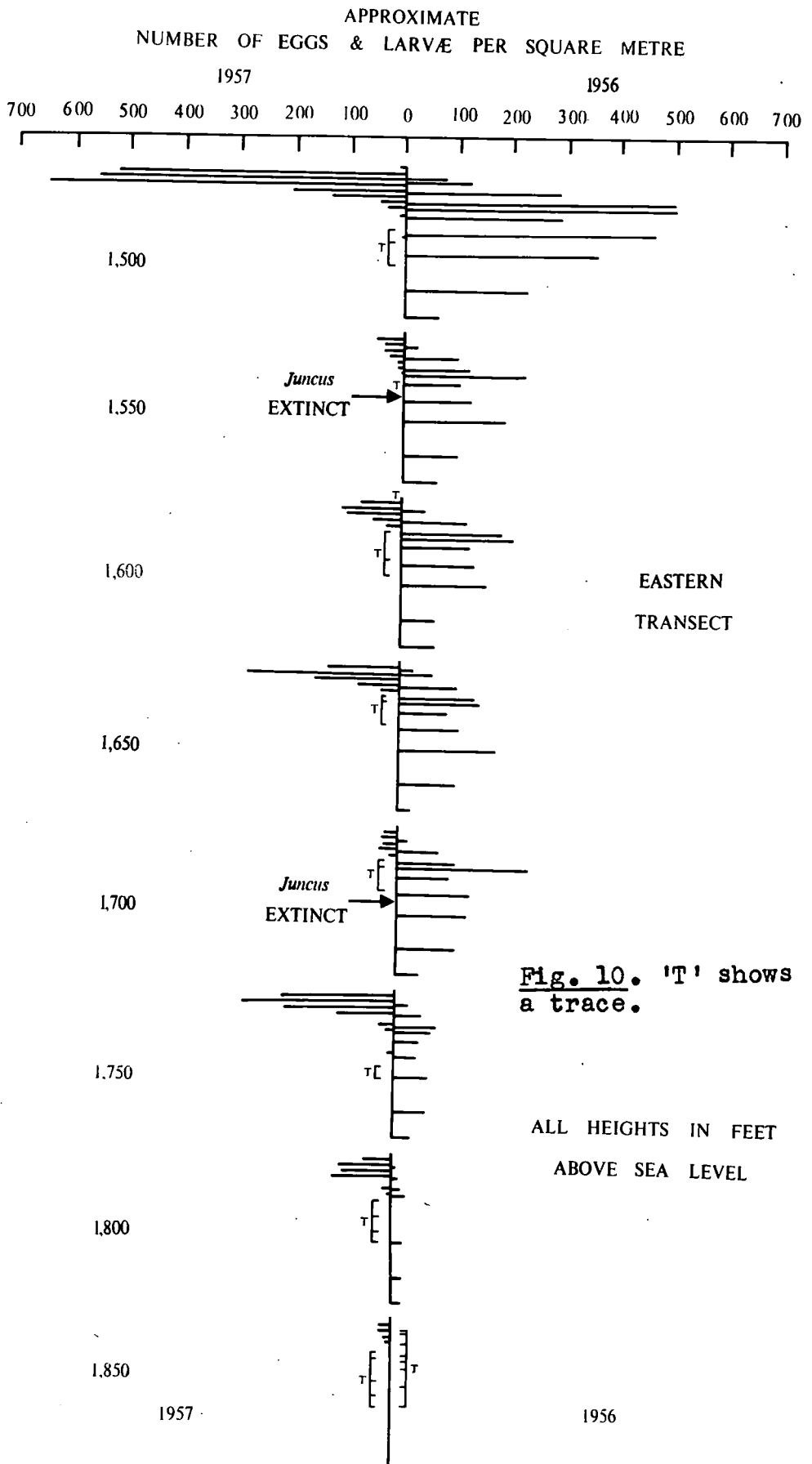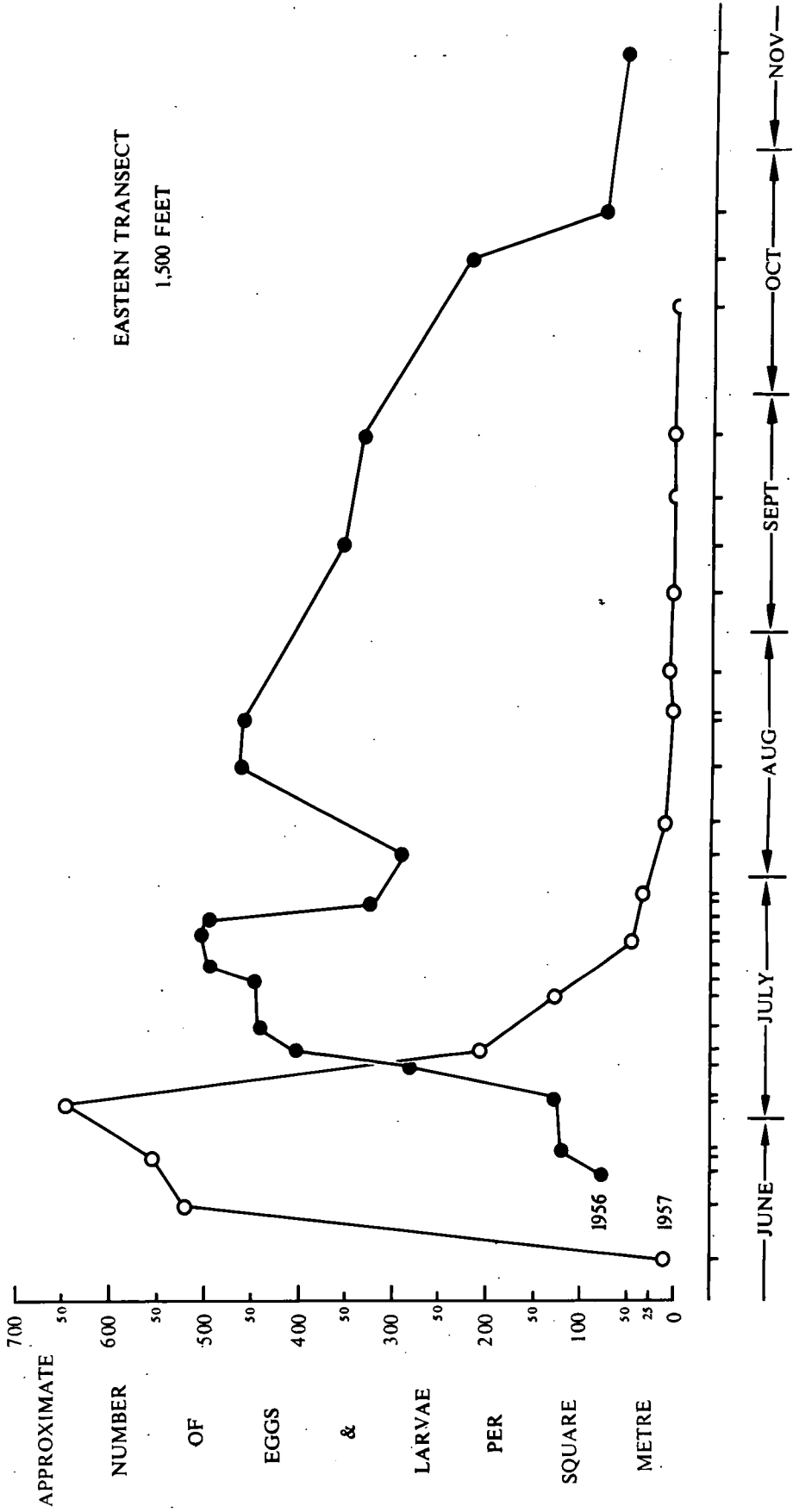
1956
1957

J. squarrosus, only a part of the complete situation was being studied. Thus during 1956 numbers per stem were low, but the density of the _Juncus_ itself was high, while during 1957 the opposite was true. Taking the two years together, in terms of numbers per unit area, there is much more overlap than one would have suspected if only figures from 'part 1', had been presented.

THE W. TRANSECT, 1956.

Table 21.

The mean number of _Juncus_ heads per square metre.
(Quadrat data multiplied by 16).

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
July 11	122.2± 10.4	28.0± 7.2	35.3± 8.4	53.9± 8.0	28.1± 6.5	128.1± 11.4	208.1± 10.1	161.4± 10.8	92.6± 9.3	-

It can be seen from the above table, that only one
density survey was done in 1956. No regular effect of alti-
tude is obvious, but the figures do show stations 750' to
1,050' have densities significantly less than the others. It
will be recalled that three of these stations (850' to 1,050')
had the highest concentrations of larvae of the whole trans-
ect, and this fact combined with a low density of the food
plant is the explanation for the high percentage of damaged
capsules. (This is well shown in graph 5).No quadrat data is
available for the 1,500' station as it was not appreciated
at the time of sampling that there was any Coleophora in-
festation at this height.

The quadrat data shows that the lowest density was at
1,050', with only 28 stems per square metre (p.s.m.), while
the highest (208 p.s.m.) was from the 1,250' station. On an
equivalent date (actually July 19th.) the lowest and high-

est figures respectively from the E. transect were 38 p.s.m.,
(1,850') and 159 p.s.m. (1,500').

Table 22.

The approximate number of eggs (E) and larvae (L) per
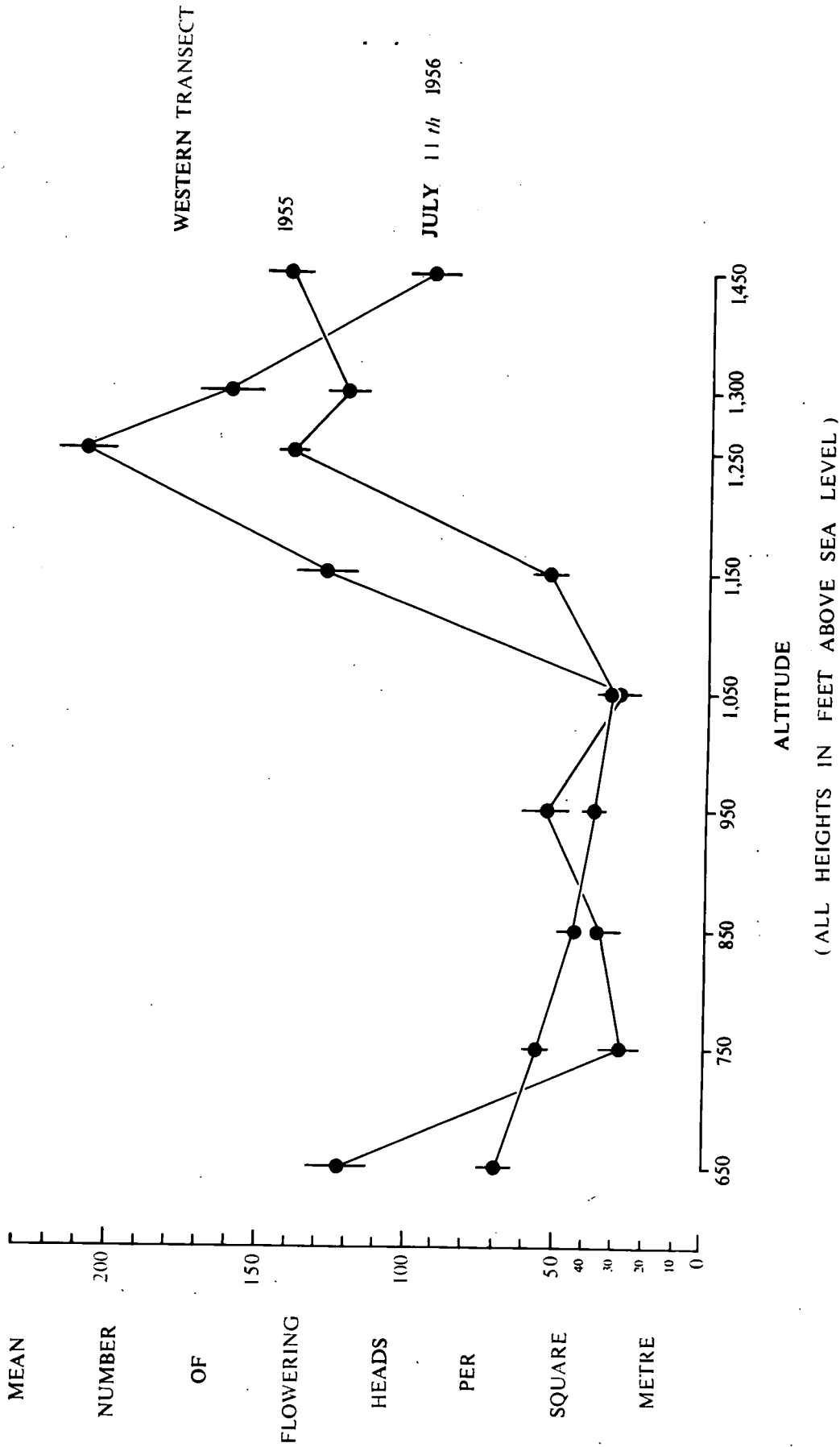square metre.

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500	
June 21	-	-	64.0	183.0	6.0	45.0	21.0	-	-	-	E
July 11	24.0	38.0	161.0	685.0	372.0	500.0	219.0	266.0	14.0	?	E
	6.0	-	16.0	62.0	1.0	26.0	-	-	-	-	L
Aug. 9	190.0	53.0	209.0	566.0	183.0	461.0	104.0	210.0	-	?	L
Sept. 18	116.0	26.0	120.0	267.0	183.0	333.0	73.0	282.0	-	?	L
Oct. 9	18.0	17.0	55.0	78.0	55.0	231.0	114.0	250.0	5.0	-	L

Only one set of Juncus data was available for calculat-
ing the results shown above, and thus estimations both before
and after the time of the survey must only be rough approx-
imations.

Results from July 11th., however have some significance,
and the figure from 950' of 747 units p.s.m., is not only the
highest of the transect, but also surpasses any figure from
the east, either in 1956 or 1957.

The quadrat data are also shown in graph 9., where they
are presented alongside results from the end of the 1955 sea-
son. They are thus not directly comparable, but they do never-
theless show similar trends. The figures for the 1955 part of
the graph are shown in table 16, p.54.

Graph. 9. The vertical lines
show the Standard Errors

WESTERN TRANSECT

1955

JULY 11 *th* 1956

MEAN
NUMBER
OF
FLOWERING
HEADS
PER
SQUARE
METRE

200

150

100

50
40
30
20
10
0

650   750   850   950   1,050   1,150   1,250   1,300   1,450

ALTITUDE

(ALL HEIGHTS IN FEET ABOVE SEA LEVEL)

THE W. TRANSECT, 1957.

Table 23.

The mean number of <u>Juncus</u> heads per square metre.

(Quadrat data multiplied by 16).

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500	
June 19	15.2±3.0	8.5±2.6	9.7±2.25	9.5±2.0	5.7±1.8	11.5±2.6	10.2±2.5	9.0±1.8	6.7±2.0	12.2±3.0	A
	12.0	30.0	28.5	18.5	21.0	8.5	5.0	5.5	7.0	-	
Aug. 7	8.5±1.9	6.2±1.6	8.25±2.1	2.0±.82	.50±.049	1.25±.16	8.5±2.0	6.0±1.6	2.0±.74	11.5±2.8	B

Note.

For June 19th., the current years result is presented above, and its value, as a percentage of the equivalent 1956 result, below.

It has already been stated that the 1957 season was somewhat earlier than the 1956 one, so that the first <u>Juncus</u> survey was done on June 19th., as opposed to July 11th., in 1956.

As only one set of results was obtained in 1956, and this 22 days later than in 1957, the percentages given in the above table are not quite analogous to those given in <u>table</u> 19, p51. Thus in the latter the sampling dates in the two years were only separated by a few days at the most. Since this period is one of rapid growth, and the discrepancy in sampling times so great, the real differences between the two

years may be less than the table would indicate.

Even so there is still a great deal of difference between the two years, though not so much as on the E. transect. The highest figure is only 30% of the 1956 one (750') and four stations are 8% or less (1,150'-1,450') of that year. An analysis of variance was done on these (June 19th.) figures showed that all of the samples were drawn from averages which were alike. This is well illustrated in graph 10., where there is much overlap amongst the standard errors. The general pattern shown in graph 9., for 1955 and 1956, is not seen in 1957, though as in those years the 1,050' station has the lowest numbers.

The second survey was done on Aug. 7th., and results show that numbers dropped at every station, so much so at 1,050' that sampling had to be discontinued shortly after this date. A Students 't' test comparing these figures with those of June 19th., showed them to be significantly different, though an analysis of variance no longer indicated that there was any similarity between the numbers of rushes at each station. Results are shown in section 'B' of table 23.

The above two surveys have been used in the same way as in previous sections to calculate the density of Coleophora per square metre, as given below.

Graph. 10. The vertical lines show
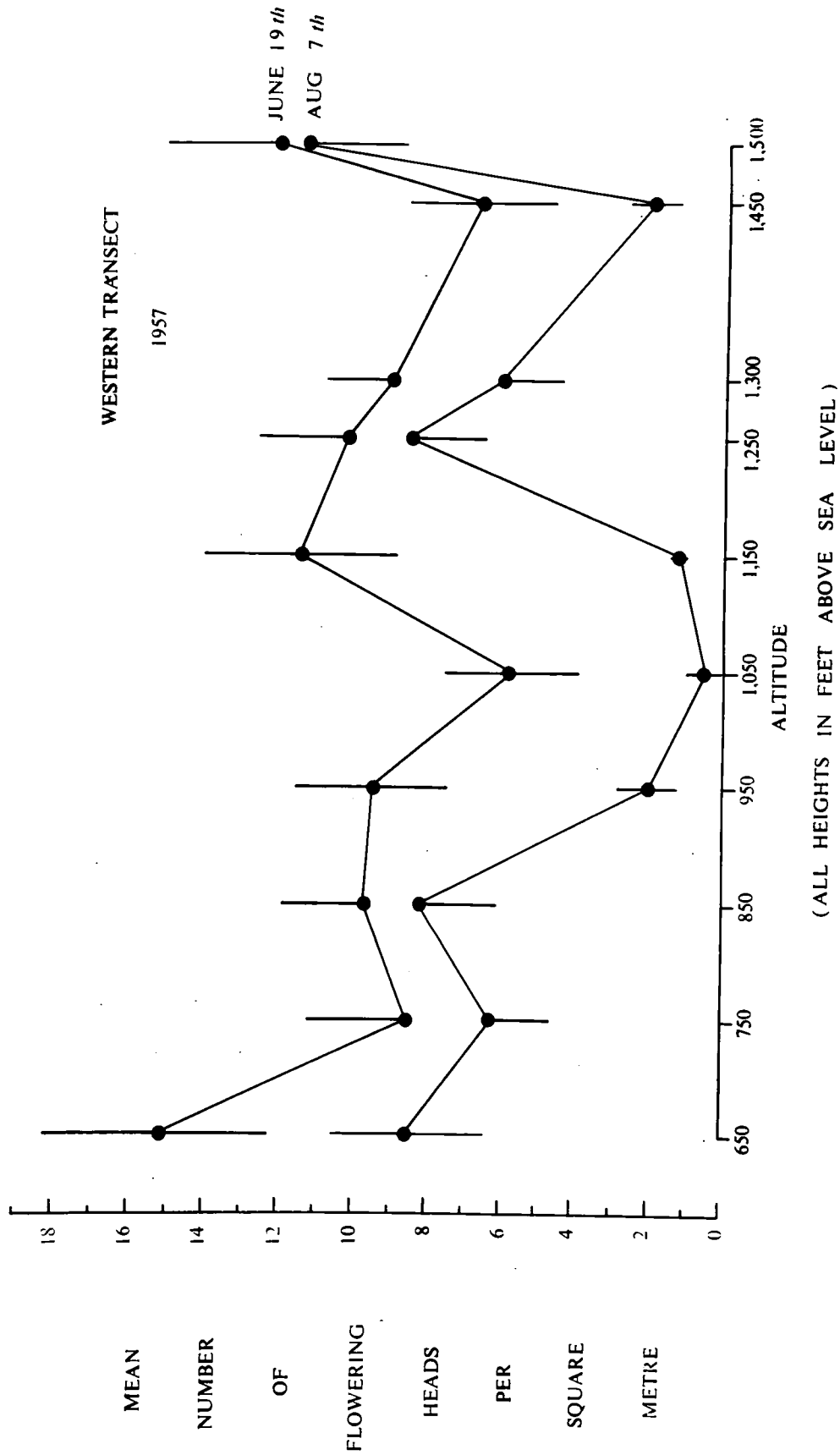the Standard Errors.

Table 24. 1957.

The approximate number of eggs (E) and larvae (L) per square metre.

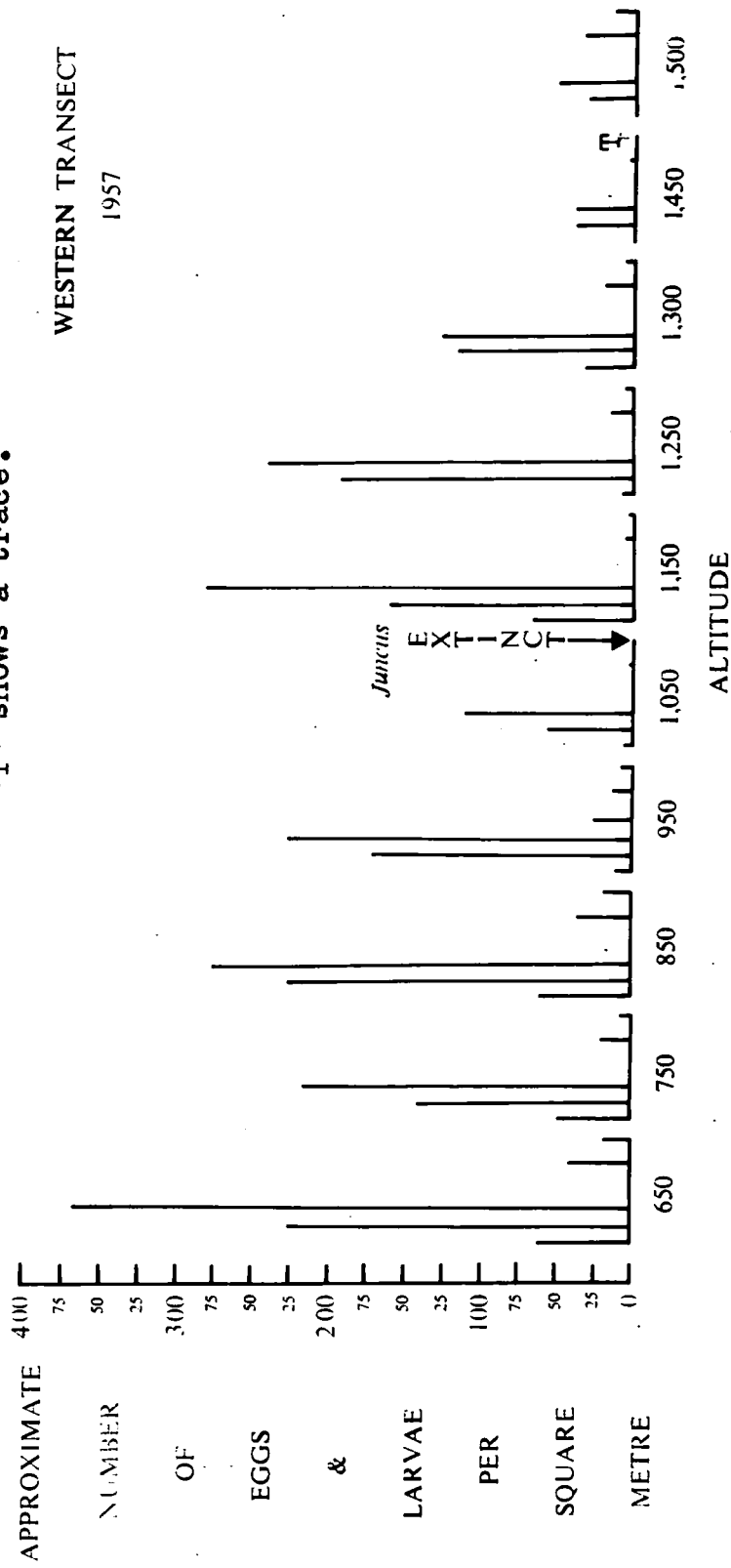|	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500		J
June 5	60.0	47.5	59.0	11.0	6.0	66.5	8.0	29.0	-	-	E	A
June 19	206.5	132.0	212.0	170.0	56.0	258.0	192.0	115.0	37.0	31.0	E	A
	19.0	8.0	12.0	-	-	1.0	-	1.0	-	-	L	A
July 2	97.0	62.0	45.0	106.0	68.0	118.0	137.0	40.0	17.0	31.0	E	A
	268.0	152.0	229.0	119.0	41.0	162.0	77.5	86.0	19.5	18.0	L	A
July 18	NOT SAMPLED			1.0	NOT SAMPLED ON THIS DATE						E	B
				24.0							L	B
Aug. 7	40.0	20.0	35.0	13.0	2.0	6.0	15.0	18.0	3.0	32.0	L	B
Aug. 26	18.0	7.0	18.0	8.0	-	2.0	6.0	5.0	1.5	13.0	L	B

'J' the appropriate section of table 23., used in calculating the results.

These results are shown in fig. 11, where it can be seen that maximum numbers have risen at the three lower, and the two upper stations, the moth now being well established at 1,500'. All of stations 950'-1,300', excepting 1,250', show a fall in maximum numbers. The maximum figure for the transect of 376 units p.s.m., (650', July 2cd.) is well below that of 1956. (747 ps.m., 950', July 11th.)

These figures show once again, how in considering only the numbers of the moth 'per stem', only a part of the complete situation is being studied.

Fig. 11.

'T' shows a trace.

WESTERN TRANSECT

1957

APPROXIMATE

NUMBER

OF

EGGS

&

LARVAE

PER

SQUARE

METRE

400
75
50
25
300
75
50
25
200
75
50
25
100
75
50
25
0

Juncus

E
X
T
I
N
C
T

ALTITUDE

650   750   850   950   1,050   1,150   1,250   1,300   1,450   1,500

THE PARASITE SURVEY.

INTRODUCTION.

It has been previously mentioned that the life history of C. alticolella is sometimes interrupted by hymenopterous parasites, and since these form a measurable cause of mortality some attention has been paid to their biology.

They are without exception larval parasites, and they usually attack the late third, or fourth instar larvae which are feeding on the Juncus seed capsules. Although it is usually case-bearing individuals that are parasitised, moth larvae with parasites feeding on them are sometimes found within seed capsules and with only a rudimentary case. In the main parasitised larvae overwinter on the rush stems and thus do not undergo the usual migration away from the food plant in the autumn.

Jordan (from 1952-54) recorded four species of hymen-opterous parasites :-

(1). ICHNEUMONIDAE   Ephialtes brevicornis Grav.

(2). BRACONIDAE   Bracon sp.

(3). CHALCIDOIDEA   A genus near Miotropis.

(4). PTEROMALIDAE   Unidentified males.

These were identified by J.F.Perkins and G.J.Kerrich

of the B.M. (Nat. Hist.) and were additions to the list already made by Thompson (1945), of the parasites of C. alticolella, then C. caespititiella:-

(5). ICHNEUMONIDAE   Gelis instabilis Forst.

(6). ICHNEUMONIDAE   Hemiteles sp.

(7). BRACONIDAE   Microbracon obscurator Nees.

(8). BRACONIDAE   Microbracon osculator Nees.

When the parasites bred from Coleophora larvae from the present study were examined it became evident that there were two new species present which were not covered by the above list. They were identified by the above specialists as:-

(9). PTEROMALIDAE   Habrocytus sp.

(10). EULOPHIDAE   Euderus sp.

Although only a few individuals of the Habrocytus sp. have been found, the Euderus sp. proved to be one of the commonest parasites on the W. transect during 1956-57.

Thus, todate, at least ten different species of parasite have been recorded from this one species of Coleophora, which goes some way towards refuting an idea that there is much host specificity in the parasitic hymenoptera. Morley and Rait-Smith (1933) came to this conclusion for the host-parasite relationships of the Lepidoptera in general. Their work shows that for 33 species of Coleophora examined, there

was a total of 46 hymenoptera parasitic on them, one of which (Hemiteles areator Panz.) having 8 separate hosts.

With one exception, very little is known of the detailed biology of any of the parasites met with in the present study, the exception being E. brevicornis. This latter has been studied by Stuart (1957) whose results are presented below together with relevant observations from the present work.

(1). Sex ratio.

(a) Morley (1908) stated that the females were common everywhere throughout northern and central Europe, but that the males were always uncommon.

(b) Thorpe (1930) during observations on the Pine-shoot moth (Rhyacionia buoliana) and its parasites found 86 males and only 6 females.

(C) Stuart, himself recorded a majority of males, and this is supported by the present observations, and those of Jordan.

(2). Hosts.

The literature showed that its hosts ranged over 8 families of Lepidoptera (including Coleophora frischella) and one family of Hymenoptera. Stuart offered female wasps certain species of New Zealand Coleophora (e.g. C spissicornis) but they were ignored. The most favourable host was

-74-

found to be the diamond-back moth, *Plutella maculipennis* Curt,.

(3). Field activity.

It was taken in the field from the end of June until the end of September, being commonest towards the end of August. This is consistent with the present observations, and the period mentioned is seen to bear a marked resemblance to the feeding period of the *Coleophora* larvae.

(4). Feeding habits.

The adults feed on the body fluids of the host, and it seems that although not essential, a meal does speed up the maturaion of eggs.

(5). Oviposition.

Eggs are laid 7-10 days after emergence, and when *Plutella* was the host, there was a definite preference for the prepupae, seemingly because the final instar larvae reacted violently to the ovipositor, and possibly that the cuticle of the pupa wastoo thick to allow for easy penetration.

In *C. alticolella* the final instars only are attacked and it is possible that the close confines of the case or the seed capsule prevent the reaction of the larvae being too violent.

Usually only one egg is laid per host, and if more were laid only one survived. Jordan considered that *Miotropis*

produced more than one individual per host, and in the present case dissection has shown that this is certainly so with Euderus sp.

(6). The larvae, etc.

There are three moults before pupation, and the adult may emerge 6-7 days later. The whole life history may be completed in 16 days at 20°C., and 60% R.H.

In the field of course, the life cycle is greatly protracted due to the overwintering phase from one Coleophora season to another. This period, unlike that of its host but similar to the other parasites studied, is not one of true diapause, since adults emerge after only a week or two when brought into laboratory conditions from the field.

Of the two new species, there are only two relevant references to the genus Euderus. Thompson (1945) recorded E. cushmani as a parasite of C. pruinella in the U.S.A., and Nickels et al. (1952) recorded E. acrobasis as a parasite of the overwinter-ing larvae of the Pecan Nut Casebearer.

Thompson also recorded five species of Habrocytus as parasitising seven different Coleophora spp. although again most of the examples were American.

Beacher (1950) considered hymenopterous parasites to have been the dominant factor in reducing the importance of

C. malivorella as an apple pest, and among the 15 species of
parasites which attacked the overwintering 3rd. instar larvae
were representatives of the genera, Ephialtes, Bracon, and
Habrocytus.

From the literature we now turn to consider the para-
sites in the present study.

The E. transect.

In 1953 Jordan recorded a few parasitised larvae in a
sample of 10 stems taken from his lowest station on this
transect (equivalent to the present 1,500'). These gave an
infestation of only about 1%, while in the other years ('52
and '54) only traces were found of E. brevicornis and the un-
identified pteromalidae.

The current investigation yeilded two specimens, bred
from a sample of 15 rush stems taken from 1500', in 1955.
They were the same two species as above, and although many
larvae were examined during the next two years no further
trace of parasitism was recorded.

The W. transect.

Jordans results for 1952-4 are summarised below, and
presented in fig. 12. They have been included to show how
they compare in species content and distribution with res-
ults from the present study.

Fig. 12. (After A.M. Jordan).
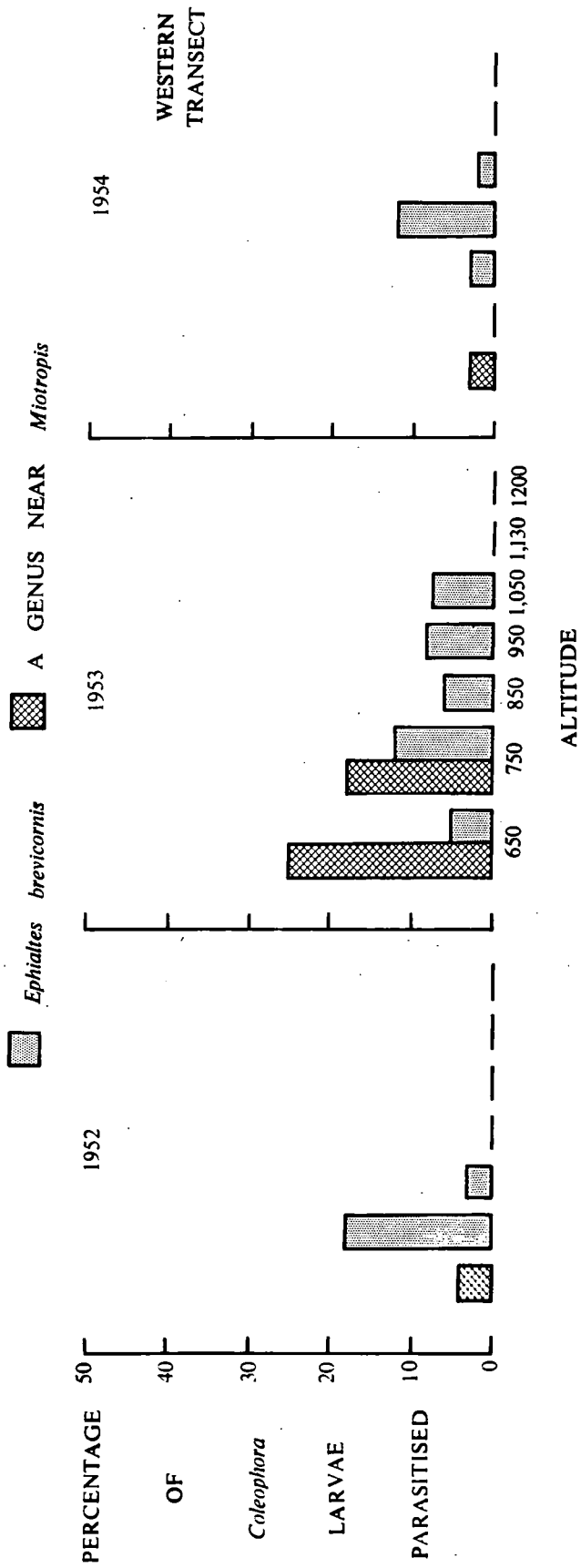
Table 25. (After A.M. Jordan)

The percentage of _Coleophora_ larvae with parasites.

	650	750	850	950	1,050	1,130
1952	4.0	18.0	3.0	0	0	0
1953	32.0	31.0	6.0	8.0	8.0	0
1954	3.0	0	3.0	12.0	2.0	0

Only _E. brevicornis_ and the genus near _Miotropis_ were considered by Jordan, and his figures for '53 and '54 were obtained by expressing the September-October numbers of parasites as a percentage of the August numbers of moth larvae.

The first survey of the current work was done in the early winter of 1955, at about the same time as the _Juncus_ survey shown in table 16., p.54. Only the 950' station was sampled and in all 36 stems were collected and brought back to laboratory conditions in Durham. The following wasps subsequently hatched out:-

E. brevicornis.	31 (22 males; 9 females)
Euderus sp.	25
Genus near _Miotropis._	3
Total	59 (from 36 stems)

This total gives a mean of about 1.7 parasites per stem, or about 60 per square metre. Even after subtracting overwintering mortality of the wasps from this figure the result may still not represent the number of adults available to

parasitise the moth larvae of the following, 1956, season.
This is because other host species may contribute extra adults
or in turn be utilised by those emerging from the Coleophora.

The extent to which the parasites emerging in 1956 were
successful has been examined in two different ways. First of
all during the normal sampling routine, those larvae which
showed signs of parasitism were noted, as follows:-

Table 26. 1956.

	850 '	950 '
Sept. 4th.	-	-
Sept. 18th.		
Total number of larvae.	68	99
Total number of parasites.	4	2
Percentage of larvae parasitised.	6%	2%
Mean number of parasites per stem.	0.2	0.1
October 9th.		
Total number of larvae.	31	29
Total number of parasites.	5	2
Percentage of larvae parasitised.	19%	7%
Mean number of parasites per stem.	0.25	0.1

Note.

(1). These are the only two stations with parasites.

(2). All numbers are from a total of 20 stems.

Although the first larvae appeared on Sept. 18th., oviposition probably occured at, or perhaps before, the beginning of that month, since it is quite possible that the minute eggs of the wasps could have been missed in the samples from Sept. 4th.

The rise in the percentage of parasitised larvae shown in the above table could be misleading since, whereas the number of parasites has remained constant between the two dates, the total number of larvae has fallen, due to normal pre-winter migration.

The October figure probably represents the full extent of the parasites pre-winter numbers. The season is then well advanced, climatic conditions would be worsening, and hosts rapidly becoming scarce.

The next estimation was done in the spring (April) of 1957. Fifty stems were taken from each station and brought back to Durham in order to hatch out any contained parasites. These samples were then examined at the beginning of July when it was considered that all of the parasites that were capable of emerging would have done so.

The results are presented below (see over) and are thus calculated from 50 stems, and not 20, as was used to obtain results in table 26.

Table 27. Spring, 1957.

Altitude.	Numbers & Species.	Total.	Mean/stem.
650'	1 Pteromalid.	1	.02
750'	1 Euderus; 1 Ephialtes.	2	.04
850'	27 Euderus; 1 Habrocytus.	28	.54
950'	2 Euderus; 1 Ephialtes.	3	.06
1,050'	1 Ephialtes.	1	.02

The larger number of Juncus stems has shown that there was a small parasite infestation at stations 650', 750' and 1,050' in addition to that already known at 850' and 950'.

Whereas table 26., gives only the number of larvae with parasites it does not show how many parasites there were to each larva. It is possible that the high number of adult wasps at 850', in table 27.,is attributable in part to the fact that a single Coleophora larva can successfully support more than one Euderus larva.

Since this survey was done as late as the April of 1957, these figures must represent the wasps which have been successful in surviving the winter. They also represent a part or whole, depending on whether alternative hosts are utilised or not, of the numbers available to attack the moth larvae which appeared in the late June of 1957.

The effect that the parasites had on the 1957 moth

larvae is shown below.

Table 28. 1957.

All numbers are from 20 stems unless stated otherwise.

August 7th.	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
A.	94.0	65.0	85.0	132.0	34.0	90.0	35.0	61.0	33.0	55.0
B.	13.0	7.0	21.0	18.0	0	2.0	0	0	0	0
C.	14.0	11.0	25.0	14.0	-	2.0	-	-	-	-
D.	.65	.35	1.05	.90	-	.10	-	-	-	-

August 26th.	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
A.	42.0	25.0	44.0	81.0	-	30.0	15.0	18.0	15.0	23.0
B.	28.0	13.0	16.0	41.0	-	5.0	0	0	0	0
C.	66.0	52.0	36.0	51.0	-	17.0	-	-	-	-
D.	1.4	.65	.80	2.05	-	.25	-	-	-	-

Note.

A. The total number of Coleophora larvae in the sample.

B. The total number of parasites in the sample.

C. The percentage of larvae parasitised.

D. The mean number of parasites per stem.

Figures for 1,050' (Aug. 7th.) are from a sample of 10 stems only.

The above figures were obtained from the normal course of rush sampling, and it can be seen that the first larvae appeared on Aug. 7th. It will be recalled that sampling had to be terminated after Aug 26th., and hence this is the only other set of results shown above. As to the exact time that

the parasites appeared in the field, nothing is known since the sampling intervals before Aug. 7th., were too large to determine it. It is known however that there were no parasite larvae at 950' on July 18th.

In most cases table 28. shows not only a rise in the percentage of larvae attacked (this, as has been shown can give a false impression) between the two dates, but also the number of parasites per stem increased. This latter is probably a reflection of a true rise in numbers in the field. At all stations there are higher numbers than at an equivalent time in 1956 (see table 26, p.79) though they appeared about a month earlier in 1957. There was also an established infestation at 1,150' for the first time since 1952 at least.

The next, and final sampling was done in the November of 1957. Once again it comprised of taking 50 stems from each station and breeding out the wasps.

It can be seen from the table presented below (over) that the numbers of parasites per stem had decreased at all levels, especially if as supposed, some larvae support more than one parasite.

It has already been mentioned that in this year the food supply of the moth larvae was greatly depleted at all stations. It is thus possible that many larvae only received

a fraction of their normal food requirements and such larvae probably were unsuitable to successfully maintain a parasite.

Table 29. 1957 (Nov.)

Altitude.	Numbers & Species.	Total.	Mean/stem.
650 '	21 Euderus; 2 Habrocytus; 3 Pteromalidae.	26	.52
750 '	9 Euderus; 4 Ephialtes; 2 Pteromalidae.	15	.30
850 '	18 Euderus.	18	.36
950 '	40 Euderus.	40	.80
1,050 '	Juncus extinct.	-	-
1,150 '	8 Euderus.	8	.16
1,250 '	1 Euderus.	1	.02

The species composition of tables 27 and 29, is shown in fig. 13.

Fig. 13.
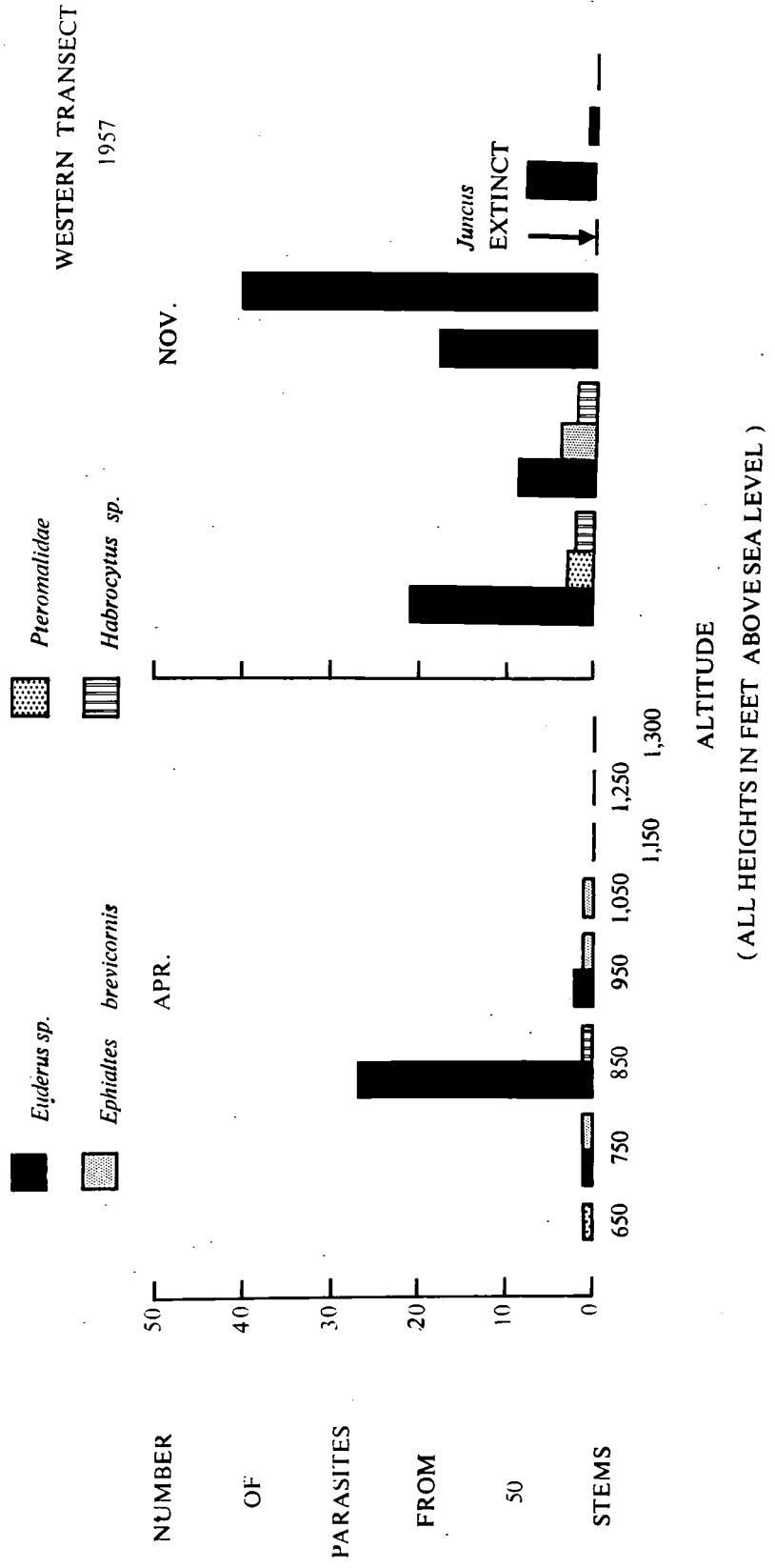
<u>FEEDING BIOLOGY</u>.

As has been mentioned, once a <u>Coleophora</u> larva has burrowed into a <u>Juncus</u> seed capsule it feeds solely on the contained seeds until it has completely 'eaten-out' the contents, it then moves away in search of another, undamaged one. Living on such a restricted diet has simplified the task of measuring various aspects of the moths feeding habits. The following proceedure has been adopted.

In the September of 1956, when the seed capsules were ripe, 20 stems were taken from each station of both transects. All of the ripe, undamaged capsules were then removed so that each station was represented by a large number of such capsules. From the latter, 8 groups, each containing six capsules were removed and then dried to a minimum constant weight at 100°C. After this process the seeds were easily removed from their capsules, and were then weighed again. The results are presented below, for the E. transect.

<u>Table 30. Sept. 1956.</u>

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
A.	1475.0	1365.0	1405.0	1206.0	1133.0	1033.0	413.0	145.0
B.	18.3± 1.2	21.5± 1.8	16.5 ± 1.4	18.2± .90	20.0 ± 1.5	16.5 ± 1.2	16.3 ± 1.1	13.2 ± 1.4
C.	4.4	4.9	3.9	3.6	3.8	2.8	1.1	.32

Section 'B' is also given in <u>graph 11</u>.

Graph. 11. The vertical lines show
the Standard Errors.
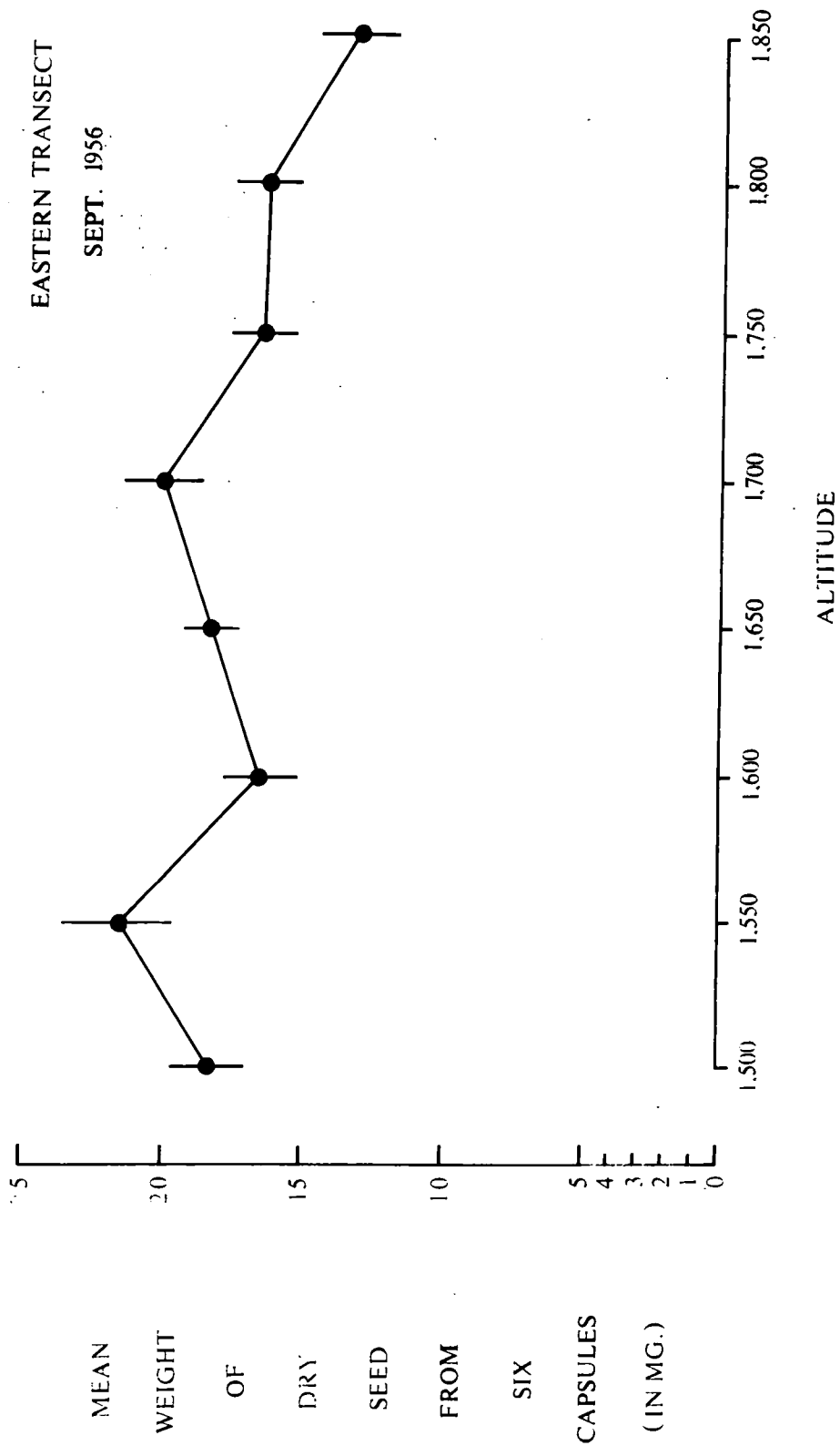
EASTERN TRANSECT

SEPT. 1956

ALTITUDE

MEAN
WEIGHT
OF
DRY
SEED
FROM
SIX
CAPSULES
(IN MG.)

<u>Note.</u>

A. The approximate number of ripe capsules per square metre.
(This is calculated from data given in <u>tables 5</u>, Sept. 11th.,
and 17., Sept. 19th.)

B. The mean dry weight of seed from six capsules, <u>in mg.</u>

C. The approximate weight of dry <u>Juncus</u> seed produced per
square metre, <u>in gm.</u>

An analysis of variance done on the figures shown in 'B'
showed that the seed weights were drawn from sources whose
averages differed from one another, though when the same test
was applied leaving out data from the 1,850' station, the
opposite was true, Similar results from the W. transect are
given below.

<u>Table 31, Sept. 1956.</u>

	650	750	850	950	1,050	1,150	1,250	1,300
A.	1265.0	279.0	366.0	528.0	348.0	1238.0	1394.0	1380.0
B.	30.0±.90	30.5±.90	25.0±1.1	23.0±1.2	27.0±1.7	25.0±1.5	21.0±1.8	24.0±2.0
C.	6.3	1.4	1.5	2.0	1.5	5.3	5.0	5.4

Section 'B' is also given in <u>graph 12</u>.

<u>Note.</u>

A. The approximate number of ripe capsules per square metre.
(This is calculated from data given in <u>table 21</u>., and <u>app-
endix 11</u>.)

Graph. 12. The vertical lines show
the Standard Errors.
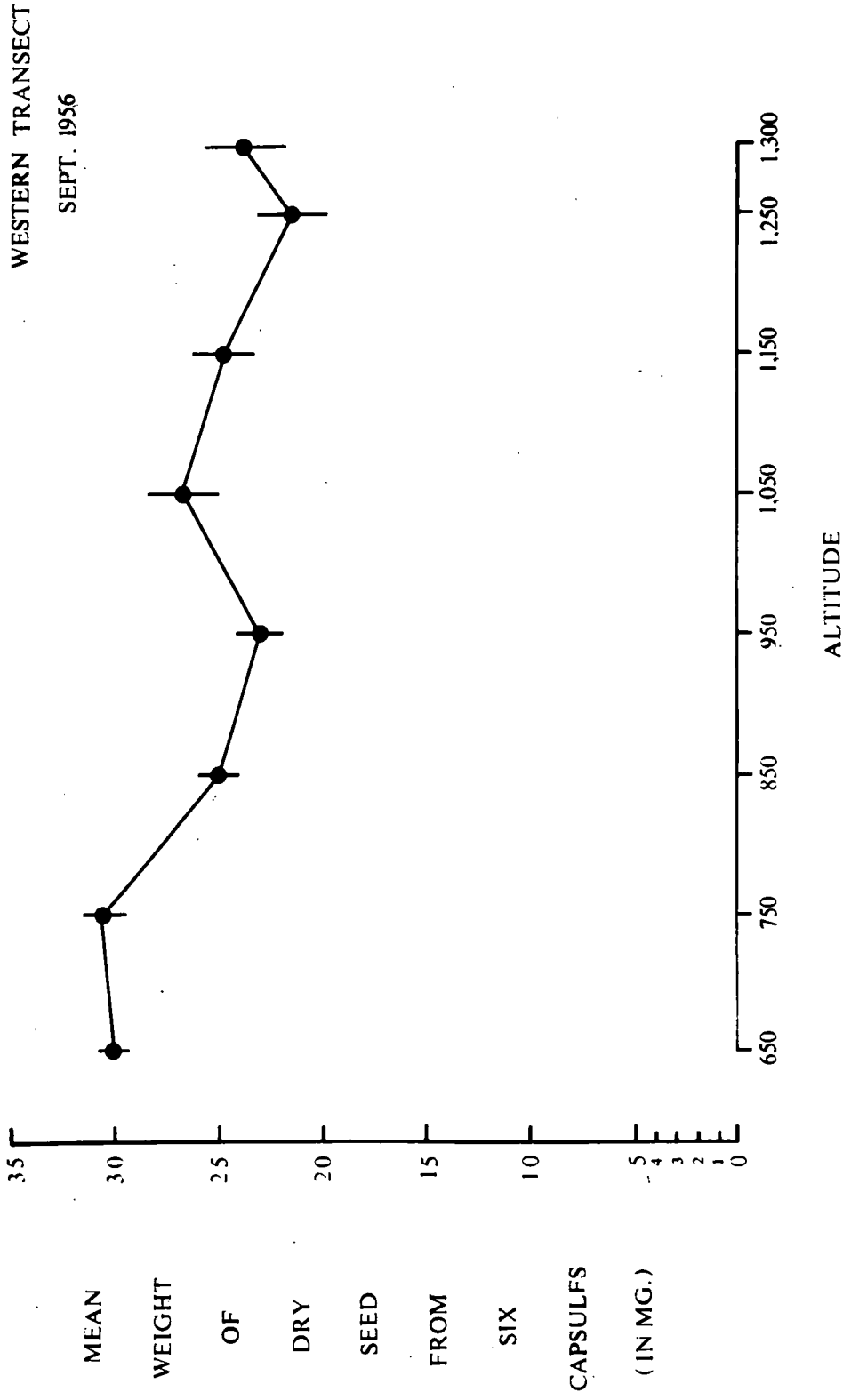
WESTERN TRANSECT

SEPT. 1956

MEAN

WEIGHT

OF

DRY

SEED

FROM

SIX

CAPSULFS

(IN MG.)

ALTITUDE

B. The mean dry weight of seed from six capsules, in mg.

C. The approximate weight of dry Juncus seed produced per square metre, in gm.

The above tables show how the dry seed estimates were used to calculate the actual seed production per unit area, by utilising data from part 11., of the population study (see pp.57-71). In table 31., section 'A' had to be calculated using data collected in July (see table 21) and hence will not be extremely accurate.

Bearing these limitations in mind certain comparisons can be made with data given by Pearsall and Gorham (1956). These authors were concerned with the production ecology of various perennial plants, and they expressed their results in Kg. per hectare, of dried material. Certain provisions were given, thus they took no account of that portion of a plant underground, and to quote, ".... were more concerned with the attempt to define the problems, than with the accurate analysis of any one of them".

In sampling they used contiguous quadrats covering 1/16th of sq.m., and chose areas of uniform vegetation with a single species dominant. From their figures it seems that. J. squarrosus (no location is given) produces about 6,900 Kg. per Ha., though this figure is only from a sample of five quadrats. In

the present study where only seed production was considered
the comparable figures were in the range of 3 to 49 Kg. per
Ha., on the E. transect, and a range of 14 to 63 Kg. per Ha.,
on the W. transect.

The above results of ripe seed production, whether
expressed in kg. per Ha., or gm. per sq.m., are an indication
of the amount of food available to the larvae per unit area
in 1956. Due to the extreme difficulty of finding undamaged
capsules in 1957, no such survey could be done in that year.

In order to find out how much of this food potential
was utilised in 1956, and to get an idea of how efficiently
it was utilised, a series of larval weighings was carried
out. Larvae were sampled as soon as a sufficient number of
them with recognisable cases appeared at a particular stat-
ion. Thirty larvae were taken at each station and divided
into five groups of six larvae each. These groups were dried
at 100°C., to a minimum constant weight.

Table 32. E. transect, 1956.

	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
A.	Oct.2	Sep.25	Oct.2	Oct.2	Oct.2	Oct.10	Oct.17	-
B.	7.5	5.6	5.6	5.8	5.6	5.0	6.4	-
C.	125.0	93.0	93.0	96.0	93.0	83.0	106.0	-

Note.

A. The sampling date.

B. The mean dry weight of six larvae, in mg.

C. The mean dry weight of 100 larvae, in mg.

Also:

(1). Larvae first appeared with cases on Sept. 25th., at 1,500', hence the high figures in 'B' and 'C'.

(2). Larvae first appeared with cases on Oct. 10th., at 1,800', hence the high figures in 'B' and 'C'.

(3). At 1,850' there were never sufficient larvae for the experiment to be carried out.

Table 33. W. transect, 1956.

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
A.	Sep.4	Sep.4	Sep.4	Sep.4	Sep.18	Sep.18	Sep.18	Sep.18	Oct.25	Oct.25
B.	8.3	9.0	8.0	7.2	7.0	6.2	5.8	5.4	5.7	6.5
C.	138.0	150.0	133.0	120.0	116.0	103.0	96.0	90.0	95.0	108.0

Note. As for table 32.

(In addition to information about larval weights, the above tables also show how larval cases appeared progressively later in the season with increasing altitude. Thus table 33 shows that larvae were present with cases at the lowest station (650') on Sept. 4th., while at the highest station (1,500') they did not appear until Oct. 25th.)

Since most of the larvae in the above two tables were at a similar stage in their life cycles, an analysis of variance was done on all of the figures shown in 'B' of both

tables, inall 17 items being involved. It showed that although at a glance there was some overlap in weights, both within and between the two transects, nevertheless the samples were drawn from sources whose value differed from one another.

As well as the straight estimations of seed production and larval biomass presented above, it is also possible to get a rough estimate of the quantity of seed utilised to produce a known weight of larvae. In the calculation presented below, the data have been taken from the 1,500' station of the E. transect in 1956. The assumption has been made that a capsule recorded as 'damaged' had in fact had its entire seed contents consumed by <u>Coleophora</u> larvae. Field observations show that this is probably a justifiable assumption.

<u>An attempt to estimate the amount of seed utilised to produce a known weight of larvae:</u>

The following data are available from the appropriate tables;

(1). <u>The mean dry weight of seed from 6 capsules.</u>   18.3mg.
      (see table 30,p.85. section B.)

(2). <u>The mean dry weight of 6 larvae.</u>   7.5mg.
      (see <u>table 32</u>,p.88. section B) Early Oct.

(3). <u>The mean number of rush heads per sq.m.</u>   167.6
      (see <u>table 17</u>,p.59. section D) Early Oct.

The following data are available by interpolating from the appropriate tables;

(4). The approx. number of damaged caps. per stem.   3.9
     (see appendix 1. section 3) Early Oct.

(5). The approx. number of larvae per sq.m.   300.0
     (see appendix 1. section 9) Early Oct.

The following data are available from the five sections given

above;

(6). The approx. number of damaged caps. per sq.m.   654.0
     (see sections 3 and 4 above)

(7). The approx. dry weight of larvae per sq.m.   375.0mg.
     (see sections 2 and 5 above)

Assuming that all of the seed in a damaged capsule has been

consumed by Coleophora larvae, the following estimate can

be made;

(8). The approx. dry weight of seed eaten per sq.m.   1995.0mg.
     (see sections 1 and 6 above) Upto Early Oct.

It can be concluded that upto the beginning of October

1956, 1995 mg. of seed were consumed per sq.m.,at the 1,500'

station, and that 375 mg. per sq.m., of larvae were produced.

These figures are in the ratio of 5:1.

Similar ratios have been worked out for other stations

where the sampling times did not entail interpolations which

would have been so approximate as to have been meaningless.

They are presented below (see over). Some of the ratios will

be overestimations, since the larval weighings were usually

done at the time of active case production, i.e. at or slight-

ly after the onset of migration. This means that the larvae

which have moved away from the rush heads will not appear in
the calculations. Nevertheless, the similarity of the results
from such a diverse selection of sites suggests that it does
in fact take about 3 to 6 times as much _Juncus_ seed to pro-
duce 1 unit of _Coleophora_ larvae, weight for weight.

Table 34. 1956.

Transect.	Altitude.	Ratio.	Period.
Eastern	1,550'	4:1	Late Sept.
"	1,800'	5:1	Mid Oct.
Western	1,050'	4.5:1	Early Sept.
"	1,150'	6:1	Early Sept.
"	1,250'	5:1	Early Sept.
"	1,300'	3.5:1	Early Sept.

DISCUSSION.

Before discussing the present study with reference to
the current (late 1958- early 1959) published thoughts on the
biology of insect numbers, it was thought relevant to include
here a brief summary of the results and conclusions drawn
from them, as presented in the previous pages.

On both transects, and at all stations, the density of
J. squarrosus per unit area was much higher in 1956 than in
1957. On the E. transect in the former year, the maximum num-
bers of Coleophora were about 3 per stem, while on the W.
transect, it was about four times this figure. Only three
out of all the stations studied in 1956, had more than 60%
of their ripe capsules damaged, and all of these were on the
W. transect (850', 950' and 1,050'). Two of these stations
were the only areas from which hymenopterous parasites were
recorded in this year (850' and 950').

In 1957 the rush density, even at its maximum was no
more than a few percent of the previous years at any station,
the highest percentage recorded being about 30%. Conversely
the numbers of eggs and larvae per stem were significantly
higher in 1957, being twenty-five to thirty times more (70
eggs plus larvae per stem) at certain stations on the E. tra-
nsect. The rise in numbers was not so dramatic on the W.

transect, and the maximum reading for all of the stations
was only half of that from the East, quoted above. At all
stations, on both transects every available ripe seed caps-
ule was damaged and, unlike 1956, no larvae were seen to pro-
duce the case characteristic of the later instars. Once again
parasites were only recorded from the W. transect, in 1957,
but their range had been extended, and was now from stations
650' to 1,250' inclusive.

Where it was in proximity to the J. squarrosus, another
rush, J. effusus, was widely utilised in 1957 as an alter-
native food supply for the moth larvae. (see plate 2)

So much for the facts to date. The following section
of the discussion is concerned with the origins and evolution
of the various theories put forward today on the subject of
the natural 'control' of animal (mainly insect) numbers.

Although the term 'population dynamics' was probably
first used by Elton (1933) and was meant to embrace the study
of rates of increase, fluctuations, and the relationships
of animal numbers to the environment, it was by no means the
first time that such problems had been either realised or
tackled.

We are not so much concerned here with the now class-
ical type of socialogical study of Malthus, who even in 1798

recognised "... a persistent force resisting depopulation".
More relevant are the early entomological studies on animal
numbers, among which is the well known paper by Howard and
Fiske (1911) on the Gypsy moth. Here they discussed the nat-
ural causes of mortality in insect populations, and came to
the conclusion that this mortality was divisable into two
large categories, 'catastrophic' and 'facultative'. They de-
fined a catastrophic factor as one which killed a constant
proportion of the population irrespective of the populations
density, while a facultative one killed an increasing prop-
ortion of the population as the density of that population
increased.

These two authors could never have forecast the real
division that their classification has lead to in contemp-
orary biological writing, a situation summed up (cynically!)
by Milne (1957) thus: "Today the student of animal population
dynamics is confronted with an ever growing literature which
is a disheartening jumble of insufficient facts, alleged
facts, ill defined terminology, and conflicting theories.

Further investigation shows that the present situat-
ion evolved from the simple analysis of Howard and Fiske,
and that it was complicated by a parallel line of develop-
ment, in the so called 'mathematical model' field of biology.

Malthus had shown that if the resources of food and space of a population were unlimited, the population was capable of increasing indefinately, the curve representing the growth of the population in absolute numbers being the exponential curve of a geometric progression. He also recognised that in nature, food and space are definitely not unlimited, and hence drew attention to the fact that a discrepancy develops between the population and, say, the available food. This fact was elaborated by Verhulst (1838) who developed an equation describing the course of population increase in proportion to population density. When plotted this equation was of the sigmoid type with upper and lower asymptotes, in fact, the familiar 'logistic' curve of today.

It was not until sometime later that Pearl and Read (1920) 'rediscovered' the curve, and as in earlier times it was applied to the growth of a human population, this time of the U.S.A. Lotka (1925) further extended this problem to include the growth of two different species living together in the same space, and independently, Volterra (1931) covered the same ground.

With this mathematical basis established there followed a spate of laboratory experiments to test the fitness

or otherwise of these models, and also the interpretation of mortality factors in the light of Howard and Fiskes' classification.

The pioneering work in this field was done by Pearl and Parker (1922) when they set up experimental populations of Drosophila with varying initial adult densities and used yeast as the food source.

It turned out that as the population density increased the number of offspring decreased. In other words they demonstrated an inverse relationship between crowding and productivity. This work lead to a series of other papers (see various editions of Pearl, 1925) and Pearl became convinced that the logistic curve was applicable to his fruit-fly populations. He found that as his cultures became more crowded competition occurred between the flies in them, this being mainly for food (and perhaps oviposition space) and resulting eventually in a lowered fecundity.

In his recent review, Sang (1950) has shown that Pearls' work contained a number of errors, simply because he had not dealt with all of the complexities of the Drosophila cultures. One of Sangs main criticisms was that Pearl in fact had not been dealing with a single species, but instead with a predator and prey confined together in the

same limited space. The reason for this of course, is that the yeast itself is a population capable of reproduction. Hence, Pearls work was more of a special case than a general one and thus does not fall into the kind that is directly applicable to the logistic formula.

Gause (1934) however, realised the importance of studying a simple, single species situation, thus: "We must therefore begin by analysing the laws of growth of homogeneous groups consisting of individuals of one and the same species and the competition between individuals in such homogeneous groups". This author was more careful in his experiments and used Paramecium cultures fed on standard amounts of Bacillus pyocyaneus each day. The culture conditions of the bacteria were so controlled as to prevent any multiplication. It was in this respect that he avoided Pearls mistake of using a food supply capable of multiplication.

Gause thus created a situation of 'constant' environment, but with 'limited' space, and thus one directly applicable to the logistic equation. When the estimations of the numbers of Paramecium each day were plotted they were found to fit fairly well into the sigmoid logistic curve.

The more modern studies however have been concerned with animals of more complex life cycles than protozoa, but

uncomplicated by the food problem of Pearl. The insect type which fits best into this category is the grain-beetle, and much work has been done on a variety of species.

Two notable studies, are those of Park et al. (1941) who used three species (Tribolium confusum, Gnathoceros cornutus, and Trogoderma versicolor), and Birch (1953b.) who used Calandra oryzae. Probably the most significant feature of these and many other workers, was that they extended the length of their cultures in time, after the initial rise in numbers to an upper asymptote. The general result was that in the later
                                          insects
stages of the experiments the density of the∧failed to stay steady around an asymptote, as is required if they were to confirm to the logistic theory.. Instead a series of fluctuating curves was produced . It should be added here that Richards (1932) working on a pure strain of the yeast Saccharomyces cerevisiae, kept his cultures going for as long as 1,200 hours. He found that the asymptote was reached after about 200 hours, and that it was maintained steadily , with a minimum amount of fluctuation until the experiment was terminated.

This latter situation seems to fit into the more modern idea that, whereas the logistic theory fails to account for some of the information provided by studies on animals with

complex life cycles, it does confirm more closely to the data from simpler situations. Nevertheless, even with such animals as grain-beetles, the logistic curve can usually be fitted to at least a part of the first phase of a populations' growth period.

As stressed by Gause (see above) attention must be paid to animals of the same species, but there is also another situation in which animals interfere with one another, i.e. when contact occurs between animals of different species populations. Typical examples are the type of relationship found between a host and its parasite, or a predator and its prey. A consideration of this field takes us back again to Howard and Fiskes work, and its subsequent results.

~~Thompson~~ Smith (1935) recognised the distinction made by these two workers, in their classification of mortality factors, but gave them different names. The term 'catastrophic' became 'general' or 'independent', and the term 'facultative' became 'individualised' or 'dependent'. Broadly, he considered that the first group contained the physiochemical aspects of the environment, and the second, the predaceous and parasitic organisms.

This classification was then examined by Smith (1935) from the point of view of the host-parasite relationship and

he made yet another change in the terminology. Under the heading 'density independent' he included those factors which destroyed a constant percentage of organisms no matter what the density of the population. This term is thus analogous to the ' catastrophic' group of Howard and Fiske, and the 'general' of Thompson. The second group he created was the 'density dependent' one, which included those factors that destroy a percentage that increases with increasing population density, or roughly equivalent to 'facultative' and 'individualised' of the above authors.

Along with these Smith actually recognised a third group of factors, on which he laid only a little emphasis. These were of the type that destroyed a percentage of a population which decreased with increasing density, or increased with decreasing density. To this group he gave no name.

If Smith failed to name this category, subsequent authors have certainly made up for it, and it is apoint which well illustrates the confusion that has occurred over the definition of various words.

To include Smiths third group Allee (see Allee et al., 1949) suggested that density dependent factors should be split into 'direct' and 'inverse', it being under the latter that he included the un-named group. Solomon (1949) simply called it 'inverse', but more recently (1958) in a re-classification

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of all mortality factors, he has extended the term to become 'inversely density related'.

Varley (1953) sums up Haldane (1953) and gives his own views on the problem thus: "It is unfortunate that in his lucid article on the regulation of animal populations, Haldane has perversely applied the term 'density dependent factor' to this third group (i.e. of Smith) and used the term 'negative density dependent' factor' for what, by the original definition to which we prefer to hold, is simply a density dependent factor".

Perhaps the most complex analysis of mortality factors was that of Nicholson (1954) who, in his own words was concerned with a "Classification of requisites and of their properties in relation to response to density change, and the influence they have upon population density". Under this classification, Smiths' third category would come under the heading, 'density disturbing'.

However, to return from sematics to the mixed species problem. Lotka and Volterra had concluded from their mathematical background that a biological system composed of two species dependent on one another, would exhibit regular, periodic fluctuations in the relative and absolute abundance of each species. Once again experimental work in this field goes

back to Gause (1934a., and 1935) who used several species of micro-organisms as his research material. His work was confined to the predator-prey relationship, rather than to the parasitic one, and, in certain cases he was able to demonstrate the regular oscillations predicted by Lotka and Volterra.

It is from laboratory studies on the host-parasite relationship however that most controversy has arisen, and in particular from the works of Nicholson (1933) and Nicholson and Bailey (1935)

The earlier (1933) paper was published before Smith had coined the phrase 'density dependent', so this term does not appear until later. In this paper, Nicholson argued thus: the fact that there is a relationship between the population densities of animals and their environmental conditions can only be explained in terms of balance, and for this balance to be achieved "..... it is essential that a controlling factor should act more severely against an average individual when the density of the animals is high, and less severely when the density is low, in other words the action of the controlling factor must be governed by the density of the population controlled".

Nicholson went on to say that competition was the only factor which could be governed in this way ".... generally

competition between animals seeking the things they require for existence, or competition between natural enemies that hunt for them", The paper published with Bailey (as the mathematician) in 1935 gives the mathematical basis for the conclusions reached in 1933.

Many authors have subsequently accepted this balance concept (see examples given in Lack, 1954) and Varley (1947) applied it to a natural population in the field. He claimed to have vindicated Nicholson, and to have shown that there was natural control, in the knapweed gall-fly, Urophora jaceana of balance. Milne (1957) severely criticised this conclusion however, and it is true to say that Nicholson himself in later work does not give much prominence to Varleys work. Indeed Nicholson has shown his dislike of the use of field experiments in population biology. Thus in 1957, when defending the use of laboratory experiments (on the blowfly, Lucilia cuprina) in explaining natural phenomena, he says, "An inherent difficulty with field studies is that the observable events in natural populations consist largely of end results, and the situation in the field is generally so complex that it is difficult to identify with certainty the underlying causes of many of the observable facts".

In his 1954 paper, Nicholson recognised several cat-

egories of animals in relation to their feeding biology, but
laid particular stress on three of them. The first of these
was the 'scramble' type, the rate of whose food supply was
determined by factors other than the activities of the animals
themselves, and he included his blowflies in this group. The
second, or 'contest' type lays claim to a supply of requisites
(food, space etc.) sufficient to maintain themselves, and to
ensure the production of offspring. This relation is epitomised
in the territorial behaviour of certain birds. The third imp-
ortant category embraced those animals that not only control
the depletion of their requisites, but also determine its
quantity. This type includes the predator-prey, and host-
parasite relationships.

Using evidence from all of these three groups (but
particularly from the 'scramble' type) Nicholson concluded
in his 1957 work that, " ..... automatic compensatory mechan-
isms exist which permit the populations to adapt themselves
to widely different circumstances, by density induced reac-
tions".

Views contrary to those of Nicholson go back to even
before his first paper in 1933. Thompson (1929, summarised
in his review of 1956) expressed the idea that " ..... the
natural control of organisms is primarily attributable, not

to any complex cosmic mechanisms, or regulatory factors, but rather to the intrinsic limitations of the organisms themselves".

In 1939, in an expansion of the equations of Lotka and Volterra, he re-affirmed his earlier concept, and distinctly contradicted certain of Nicholsons (1933 and '35) tennets, particularly that which suggests that parasites hunt at random for their hosts. (The latter fact forms the basis of much of Baileys mathematics) When Thompson had talked about the limitations of organisms, he was really emphasising the role of the environment, as well as the fact that he did not believe that populations were self governing systems. In 1956 he expanded his theories of natural control in a more philosophical way, which in his own words ".... verges on the metaphysical". His theory went thus: "When we recognise the specific intrinsic limitations of organisms, we have in my opinion, arrived at the absolutely fundamental explanation of control: that is to say, the fundamental explanation of the fact that no organism increases without limit".

In their book, Andrewartha and Birch (1954) have probably brought together the most impressive array of arguments against Nicholson and his associates. Right at the beginning (p. 18) they express their dislike of an environment divided

into'factors', thus, ".... we do not know of any experimental or observational evidence which would indicate that any component of the environment characteristically destroys a constant proportion of the population, irrespectively of its density. If then no 'factor' is 'density independent' why single out some in particular and call them 'density dependent'?" Or again (p. 19) "We conclude that 'density independent factors' do not exist; and that there is no need to attach any special importance to 'density dependent factors!.when discussing the way environment may influence the distribution and abundance of animals in nature".

Whereas Nicholson (1957) found it necessary to defend the extrapolation of laboratory results to explain natural phenomena, Andrewartha and Birch have condemned it. They gave two main reasons, the first being that laboratory conditions are very idealised, and so different from natural situations, and the secondthat, "One would not expect to come across a limiting density in any finite number of observations."

As for such terms as 'balance', 'steady state' and 'control', these authors relegate them to nothing more than, "..... steming from the dogma of density dependent factors". Theycontend that their theory is not concerned with such "allegorical properties of populations", but with actual

numbers of animals, as seen and counted in nature.

The basis of their theory is an outline of the three ways by which the numbers of animals in a natural population may be limited: (1). Due to a shortage of such necessities as food or a place to live in. (2). Due to any of these necessities being inaccessible (i.e. relative to an animals ability to find them). (3). Due to, "Shortage of time when the rate of increase (called 'r') is positive". Andrewartha and Birch hazard that in nature, the first cause is probably the least, and the third cause, the most important in the limitation of animal numbers,

Some workers feel however that they cannot entirely agree with either of these opposing schools of thought on the regulation of animal numbers. In 1957 Milne outlined his 'compromise' theory, and then (1957a.) modified and supplemented it, stressing its limited applicability to insect populations. His objection to Nicholsons theory was that this author grouped the predator-prey and host-parasite relationships under 'density dependent' factors, and to Andrewartha and Birch, that they ignored the whole concept of 'density dependence' and hence deprived their theory of fulness.

Milne contended that the only true density dependent factor was competition within a species population (for food

space etc.) while the other of Nicholsons examples of this type he re-named 'imperfectly' density dependent. He then goes on to suggest that such interspecies competition is relatively rare in nature, so that "Control of increase for most of the time, if not almost endlessly, is a matter of the <u>combined</u> action of factors which are imperfectly density dependent, and factors which are density independent, <u>each supplying the lack of the other</u>". (Underlined words are his italics).

Solomon (1958) challenged this concept of 'imperfect' density dependence, on the grounds that the intensity of intraspecific competition can be different for the same population number.... hence it is not solely effected by numbers .... hence it is not perfectly density dependent. Milne (1958) rejected this deduction and contended that when intensity of competition is different for the same population number it is simply a reflection of differences in environmental capacity.

In the same paper, Milne challenged the need for re-classifying the category of the lag-response found in the host-parasite relationships. Varley (1953) had concluded that such a relationship should be called 'delayed density dependent'and Solomon had followed this (1957) and had suggested the term 'alternately density related'. Milne reasoned that because enemy reproduction was not immediate, the delay in

action simply contributes to the general 'imperfections' of this group of Nicholsons density dependent factors. The editor of 'Nature' terminated the correspondence at this point.

This review of the literature was opened with a rather dispairing commentary on the present state of population theory, but it is ended here with a much more constructive one by Huffaker (1957).

"In the study of population dynamics, the real ramifications which we are attempting to explain are indeed manifold, <u>yet those of purely sematic origin</u> (my underlining) contribute almost as much to the confusion.

It is obvious that workers' spheres of activity, and as a result, their relative emphasis of certain aspects have been major sources of differences..... There is greater agreement between them than is generally believed concerning the functional operations in the changes in abundance of any specific example. There are broad claims concerning the importance of, or the role of, certain factors which if interpreted according to a common understanding of certain words would not arouse such vehement differences of opinion. Also a claprification of direct and indirect causes and the recognition that there is more than one way to classify processes in population dynamics open an avenue to common understanding".

So much for the literature, and now for an analysis of the Coleophora study in the light of it.

It was considered relevant to discuss only the numbers of the egg and larval stages here, in the light of the relative amount of information gathered on the various stages of the moths life cycle. For a similar reason, many of the examples called upon to illustrate particular points have been drawn from the E. transect.

Coleophora eggs are laid in the angle between two developing florets of J. squarrosus for preference, though occasionally other sites are utilised.

The fact that there was a great deal of crowding of eggs in 1957 has already been discussed (pp. 30-31) the reason suggested being that the number of eggs laid per plant far outstripped the number of sites available. It is though unlikely that a female moth would lay eggs at a site already exploited, and where eggs have been found together there are indications that they were laid by one and the same female in one act of oviposition. If this was generally the case in 1957, it seems likely that in that year there would have been competition between egg-laying females for suitable sites. Thus the greater the number of females, the more intense the search for unoccupied sites, and the greater likelihood of an egg being laid

in an unsuitable place. Eggs in such postions would of course be more liable to removal by rainwash, or more exposed to predators, and the amount of mortality so caused would be directly related to the ratio of the 'number of egg-laying females to the number of oviposition sites available'. Such a situation did not occur in 1956.

The egg stage is followed by hatching, when the newly emerged larvae move away from the egg site in search of ripe capsules, their food source. This is potentially a vunerable period, since after leaving the sheltered egg site, they are exposing themselves to predators, and mechanical damage. Once they are established in a capsule however, and if they remain there alone, they lead a relatively sheltered existence until their final instar, when a case is produced, and the search for undamaged capsules intensified.

It has already been suggested (p.28) that at least for the 1,500' station in 1956, only a little mortality occurred in this transitional period, there being very little discrepancy between the maximum egg and the maximum larval numbers. This could be misleading of course, and simply a product of the sampling method, in line with Nicholsons criticisms of field estimations (see p. 104).

However this was not the case in 1957, when there were

great differences between the egg and larval maxima at each station, and it seems that mortality was taking place of the type mentioned in pp. 111-112, and applicable to the type of conditions prevailing in this year.

Jordan (1958) showed that on the average, a final instar larva visits just over two ripe capsules. This means that, ideally each rush stem can support a number of larvae, equal to just less than half of the number of its ripe capsules. Thus the amount of food available (in the form of ripe undamaged capsules) to the larvae is independent of the number of larvae themselves. Nicholson (see previous pages) put such animals in the 'scramble' category, and prophesied that, "with gross crowding, such scrambling leads to much wastage of the governing requisite, so that with excessive numbers of animals there is either excessive mortality, or the fertility may be temporarily reduced below the replacement rate".

It has already been shown that nowhere in 1956 (except at 950' and 1,050', W. transect) was the food supply totally exploited. In fact at a majority of stations, on both transects, more than 50% of the available ripe capsules remained untouched.

In 1957 however a drastic reduction in the amount of available food took place, due of course to the failure of

the J. squarrosus to produce as many flowering heads per unit area as they had done in 1956. This failure had the effect of concentrating the larvae on the individual rush heads, and hence on the capsules themselves. Nicholsons' tenet of 'gross crowding' was thus fulfilled. This reduction in the amount of available food lead to a situation where every capsule at every station on both transects showed damage, hence, "leads to a wastage of the governing requisites".

On the E. transect at least, Nicholsons' final conclusion "with excessive numbers there is ...... excessive mortality", was borne out by the fact that no larvae at any station, on the J. squarrosus survived long enough to reach the final instars and produce cases.

On the W. transect, larvae with cases were observed, but here the reduction of food supply in proportion to the number of larvae present in 1957 was not so great as in the East. Since sampling had to be concluded prematurely, the results from the W. transect are not conclusive.

It seems then, on the E. transect at least, in 1957 some larval mortality occurred which was due to intraspecific competition for a limited resource.... food. In Nicholsons' nomenclature, food was thus acting in a 'density governing' way, and in Milnes' in a 'perfectly density dependent' way since he

regarded intraspecific competition as the only true example of this factor. It is interesting to note that even Andrewartha and Birch (1954, p. 497) concede that, "When there is an absolute shortage of food, i.e. when all the food in the area has been consumed and there is not enough to go around, the numbers of animals (my underlining) may be of major importance". They do stress however that this is rather unusual over broad areas, though it may happen temporily in small local units of a larger population.

At one stage then in 1957, a mortality factor was probably in operation which both satisfied Nicholsons concept of the necessity of density governing factors in natural populations, and is also conceded possible, though as a rare and special case, by Andrewartha and Birch.

But what of 1956 when no such 'factor' was illustrated in either theegg or larval stage, when in fact, no requisite seemed to be in short supply? In other words, it is a situation typical of the kind used by Andrewartha and Birch to illustrate that requisites (food, space etc.) are not depleted because an animals numbers are suppressed by physical factors which act independently of the populations size.

Reynoldson (1957) described how Nørgaard (1956) in a ten year study of the spider, Theridion saxatile, ascribed

population fluctuations to destructive weather conditions only, which acted independently of the populations size. Reynoldson himself concluded that the numbers of his Enchytraeids were kept down by prevailing 'physical' conditions, and Milne (see Andrewartha and Birch, 1954) failed to detect any density dependent factors in his *Ixodes* populations.

This might seem at first to be contrary to Nicholsons ideas, but a closer examination of his more recent writings (1957 and 1958) showed that this was not the case. In his 1957 work he says, "I would like to stress that my investigations and theoretical considerations based upon them do not imply that density governing reaction should operate upon a population at all times. Populations may be progressively reduced over a period by adverse external factors (as in 1956?) without there being any compensatory reaction during that period. In spite of this itis necessary and inevitable that density induced reaction should limit populations in relation to the prevailing environmental conditions from time to time at least." Or again when discussing this paper with Reynoldson, "It must at times happen that the ability of the animals to multiply is exactly counteracted by the inherent resistance of the environment, particularly near the limits of possible distribution of a species. Under such conditions a local populat-

ion might persist for many generations at numerical levels too low to induce any significant depletion of the environment."

Once again there is seen to be a broad measure of agreement between the so called 'opposing schools of thought' on the population problem. Nicholsons latter point (above) introduces the problem of 'fringe' or 'marginal' populations, which he obviously considers to be a special case, and hence is willing to make concessions accordingly. Reynoldson (1957) also emphasises the role of environmental resistance in this type of population.

When one considers the great dependence of Coleophora on J. squarrosus it is evident that it comes close to being a marginal population, especially when it is so sensitive to the kind of change that took place in 1957. Thus in this year, it was only saved from total extinction by its ability to utilise an alternative, and closely allied species (J. effusus) as a food source. The fact too, that its upper, altitudinal, limit (see p. 49) is so sensitive to the upper limit of seed setting of its host plant, serves to emphasise its marginal aspect.

Finally, a word on the parasites of Coleophora. Nicholson (1957) conceded that, if a parasite is not completely specific, its density will not react so violently to changes in its host density. Such a reduction in intensity of reaction may result

in changing a system, from one of growing oscillations, to one of damped oscillations. How different and less complicated is even this situation from that of the moth and its hymenopterous parasites on the W. transect. Not only do several species attack one host, but probably none of them are specific, not all of them have their life cycles synchronous with their host, and some even produce more than one offspring per host. There is thus little hope of discovering oscillations or lag-oscillations in this study, even if it were persued for many years to come.

S U M M A R Y

S U M M A R Y

1. A population study on the moth <u>Coleophora alticolella</u>
has been carried out on the North Pennine moorlands in the
vicinity of the Moor House National Nature Reserve. (N.R.80)

2. The life history of the moth is given when it is assoc-
iated with its food plant in the area, <u>Juncus squarrosus</u>.

3. The present specific name of the moth was determined by
Bradley (1955), having previously been known as <u>C. caespitit-
iella</u>.

4. Two transects were chosen for study and the vertical in-
terval between the sampling stations fixed by an altimeter.
The transects are described, with respect to their topogr-
aphy, vegetation and soil.

5. An attempt was made to estimate the numbers of emerging
adults in the spring, using an emergence trap which is des-
cribed. An account is given of certain microclimatological
work on conditions inside of these traps, and conditions were
found to differ from those outside.

6. A major part of the work was confined to assessing the
numbers of moth eggs and larvae during 1956 and 1957, alth-
ough sampling was actually started in 1955 and continued
into 1958.

7. The sampling method used was to randomly select twenty stems from each station, at regular intervals throughout the known months of the insects life history. A list of the sampling dates is given.

8. The E. transect was the more frequently sampled of the two, and on it the 1,500' station was more extensively sampled than any other.

9. The rush samples were examined for eggs and larvae, whose 'mean numbers per stem' was worked out.

10. The E. transect was the first to be considered, and the numbers below (see 11 and 12) are from the 1,500' station.

11. In 1956, the first eggs appearedon June 23rd., while in 1957 they were earlier. June 12th. The maximum number of eggs per stem was about 3.3 in 1956, while in 1957 it was 62.4.

12. In 1957, the first larvae appeared on July 2cd., 16 days before they did so in 1956. The larval maximum in this latter year was about 2.9 per stem, while in 1957, it was 10.9.

13. The onset of migration (larval) in 1956 was determined both by examining the time that larval cases were produced and by examining the percentage of ripe capsules which showed damage. The onset of migration is heralded by a sharp rise in the latter.

14. All of the stations on the E. transect in both years are

also considered. The great differences in the number of eggs and larvae per stem (as noted at 1,500') between the two years are seen to occur at all heights. There is also a marked effect of altitude on moth numbers on the transect and in both 1956 and 1957, the uppermost station, 1,850' had the lowest readings.

15. The reasons as to why there should be these differences between the two years are investigated. It was found that the mean number of ripe capsules per stem was less in 1957 than in 1956, and that in the former year a greater percentage was eaten per stem. There was some evidence that crowding of the larvae took place in 1957.

16. The W. transect is next considered. This runs from 650' upto 1,500', and in 1956 the middle stations (c. 950') had the highest numbers. In 1957 numbers were very high at all stations, but there was not the great difference between the two years that there was on the E. transect.

17. The upper (altitudinal) limit of the moth during the last six years is examined, and the conclusion drawn that Jordan was correct in assuming that this upper limit was determined by the ability of the host plant to set seed to a particular height, in a particular year.

18. By the time that the 1955 results were taken, all Col-

<u>eophora</u> activity had ceased, and the only measurable factor was the percentage of ripe capsules showing damage at the end of the season. Figures are given for this together with similar ones from '56, '57, and '58.

19. A method of sampling the overwintering fourth instar larvae is described. Such larvae are part of the litter fauna and a soil sampling method was employed.

20. By using a quadrat frame of known area (1/16th sq.m.) a a survey was made at selected times of the year, of the density of <u>J. squarrosus</u> at all of the sampling stations in both of the years. Results are presented in terms of 'flowering heads per square metre'.

21. Between the two years there was a common pattern of events discernable from both transects. Thus in 1956 the density of rushes was high, e.g. at 1,500', E. transect there were in July about 110 heads per square metre. At the same station at the same time of the year in 1957, the figure was 9 per sq.m.

22. These orders of magnitude in the differences of density were common at all stations, the 1956 figures being always several times the 1957 ones. This was true of both transects and is put forward as the explanation of the major differences in moth numbers 'per stem' that occurred between '56 and '57.

23. Except for the 1,550' station the E. transect showed a

regular reduction in rush density with increasing altitude in 1956. This was not so with the W. transect in that year, or with either transect in 1957.

24. Using the _Juncus_ survey data, the numbers of _Coleophora_ eggs and larvae per square metre have been calculated. On the E. transect at 1,500' the maximum numbers in the two years were similar being just under 500 p.s.m. in '56, and just over 600 p.s.m. in '57.

25. There were greater differences between the two years on the W. transect. Thus at 950', there were 700 p.s.m. in 1956, while in '57, there were only about 200 p.s.m.

26. The late instar larvae of _Coleophora_ are attacked by hymenopterous parasites which have only been recorded from the W. transect. Four species were recorded in the present study, two of which were not recorded by Jordan. Of these, _Euderus_ sp. was by far the commonest of all species both in 1956 and '57.

27. By undertaking a series of weighings of both the moth larvae and the seed on which it feeds, it was found possible to estimate the weight of seed consumed, and to show how this was related to the weight of larvae produced. It was found that it took about 5 times as much seed to produce 1 unit of larvae, weight for weight.

28. Finally the extensive literature on population dynamics is reviewed to show how the present day theories of population control have been gradually evolved. The results of the present work are then examined in the light of these theories and various conclusions drawn as to what categories certain mortality factors may be placed in.

A P P E N D I C E S

APPENDIX 1. E. TRANSECT, 1,500'. 1956.

DATE	1	2	3	4	5	6	7	8	9	J	T
June 23	14.6±.60	-	-	-	.70±.31	-	-	77.0	-	A	
June 26	13.5±.84	-	-	-	1.1±.29	-	-	121.0	-	A	3
July 3	12.3±.60	-	-	-	1.15±.31	-	-	126.0	-	A	7
July 7	16.2±.88	-	-	-	2.1±.39	-	-	283.0	-	B	4
July 9	-	-	-	-	3.0±.60	-	-	404.0	-	B	2
July 12	-	.10±.07	-	-	3.3±.61	-	-	444.0	-	B	3
July 18	-	1.75±.32	.10±.07	6.0	2.7±.35	.10±.07	-	430.0	16.0	C	6
July 20	16.4±1.0	2.5±.58	.15±.07	6.0	2.95±.55	.15±.07	-	471.0	24.0	C	2
July 24	-	6.75±.83	1.35±.31	22.0	1.8±.37	1.35±.31	-	287.0	215.0	C	4
July 26	-	6.8±.75	1.55±.27	23.0	1.45±.32	1.6±.33	-	243.0	255.0	C	2
July 28	-	7.8±1.2	1.5±.28	19.0	.50±.17	1.5±.28	-	80.0	239.0	C	2
Aug. 3	-	10.2±.93	1.8±.25	18.0	-	1.8±.25	-	-	287.0	C	6
Aug. 14	-	8.4±.81	2.8±.50	33.0	-	2.9±.55	-	-	463.0	C	11
Aug. 20	-	10.6±.65	2.6±.28	25.0	-	2.75±.29	-	-	461.0	D	6
Sept. 11	-	8.8±.58	2.6±.30	24.0	-	2.1±.28	14.0	-	352.0	D	22
Sept 25	-	7.75±.71	3.0±.61	39.0	-	2.0±.36	65.0	-	336.0	D	14
Oct. 17	-	8.3±.71	4.8±.75	58.0	-	1.35±.28	100.0	-	226.0	D	22
Oct. 23	-	8.1±.80	4.95±.88	60.0	-	.45±.10	100.0	-	75.0	D	6
Nov. 12	-	7.95±.54	4.2±.42	53.0	-	.35±.13	100.0	-	59.0	D	20

1. The mean number of undifferentiated florets per stem of J. squarrosus.
2. The mean number of ripe capsules per stem of J. squarrosus.
3. The mean number of damaged capsules per stem of J. squarrosus.
4. The percentage of ripe capsules damaged.
5. The mean number of Coleophora eggs per stem of J. squarrosus.
6. The mean number of Coleophora larvae per stem of J. squarrosus.
7. The percentage of larvae with cases.
8. The mean number of eggs per square metre.
9. The mean number of larvae per square metre.
'J'. The appropriate section of table 17, used in calculating results per square metre.
'T'. The time interval between samplings.

APPENDIX. 11.

W. transect, 1956.

The mean number of ripe capsules per stem.

	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
July. 11	11.6± .71	11.9± 1.0	4.6 ± 1.0	5.8 ± .61	.95 ± .33	5.0 ± .93	.40 ± .20	2.5 ± .50	0	0
Aug. 9	15.5± .95	14.1± .24	16.1± 1.2	13.3± .90	11.8 ± 1.1	13.5 ± .81	8.7 ± 1.0	10.6 ± .92	5.9 ± .67	5.3 ± .73
Sept. 18	10.3± .75	9.9 ± .99	10.3± 1.1	9.3 ± .94	12.3 ± .90	10.0 ± .95	6.7 ± .95	8.5 ± .68	?	8.0 ± .84
Oct. 9	10.1± .71	11.2± 1.0	9.9 ± 1.0	11.4± .92	12.5 ± .91	10.7 ± .91	8.1 ± .81	9.9 ± 1.1	4.1 ± .80	8.3 ± .87

APPENDIX 111.

1956.	1,500	1,550	1,600	1,650	1,700	1,750	1,800	1,850
A.	16.2	16.5	15.8	16.1	17.5	18.1	14.6	12.8
B.	8	8	7-8	8	8-9	9	7-8	6-7
C.	2.9	1.3	1.4	1.0	1.4	.95	.25	.10
1957.								
A.	21.5	17.1	15.0	15.1	13.0	18.5	14.7	12.5
B.	10-11	8-9	7-8	7-8	6-7	9-10	7-8	6-7
C.	62.4	67.8	48.0	60.0	36.9	40.7	18.4	14.3

NOTES.

A. The maximum number of florets per stem during the egg season.

B. The approximate number of oviposition sites per stem.

C. The maximum number of eggs per stem.

APPENDIX IV.

1956.	650	750	850	950	1,050	1,150	1,250	1,300	1,450	1,500
A.	17.4	14.8	16.4	15.8	14.7	12.3	14.2	14.4	15.0	13.4
B.	8-9	7-8	8	7-8	7-8	6	7	7	7-8	6-7
C.	1.5	1.9	5.9	12.7	13.2	4.1	1.0	1.6	.15	.15
1957.										
A.	22.9	21.8	19.4	19.2	20.1	23.4	18.4	19.8	17.5	19.9
B.	11-12	10-11	9-10	9-10	10	11-12	9	9-10	8-9	9-10
C.	23.9	25.2	28.1	23.7	18.6	24.4	21.0	14.0	5.4	4.0

NOTES.

A. The maximum number of florets per stem during the egg season.

B. The approximate number of oviposition sites per stem.

C. The maximum number of Coleophora units per stem.

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