Biological studies on certain species of British phalangida

Barry N. Heighton

Heighton, Barry N. (1964) Biological studies on certain species of British phalangida. Doctoral thesis, Durham University.

BIOLOGICAL STUDIES ON CERTAIN SPECIES OF BRITISH PHALANGIDA

BY

BARRY N. HEIGHTON, B.Sc. (DUNELM.)

Being
A thesis presented in Candidature for the
Degree of Doctor of Philosophy
in the
University of Durham, 1964.

BIOLOG[illegible] OF [illegible]

Abstract of a Thesis presented in candidature for the Degree of [illegible] Philosophy in the University of Durham, 1964, by Barry [illegible].

From 1957 to 1960 both field and laboratory studies were carried out on six British species of woodland harvest-spider, Lacinius ephippiatus (C. L. Koch), Mitopus morio (Fabr.), Nemastoma lugubre (Mull.), Odiellus palpinalis (Herbst), Oligolophus agrestis (Meade) and Oligolophus tridens (C. L. Koch.) The only comparable study is that of Todd (1949, Journal of Animal Ecology, 18, 209-29) whose findings were, in general, restricted to adult harvest-spiders: hence in the present study many of Todd's ideas were extended to juveniles.

Initially a method of determining the various life stages (instars), based on the femur length of the second walking leg, was found for each of the above species. Using this information the course of seasonal development of each species was followed in detail: it was also found that, while all instars of L. ephippiatus, N. lugubre, O. palpinalis and O. tridens were exclusively ground dwelling in habit, an extension of range from the ground layer into the shrub layer and tree canopy occurred in the penultimate and final instars of M. morio and O. agrestis. Most of the interstratal movement was restricted to the period between dusk and midnight.

To find the cause of the vertical migration these findings were compared with the results of laboratory studies on temperature and relative humidity preferenda, resistance to dessication and locomotor activity patterns, and with microclimate measurements made in the field. It became clear that, although very closely associated, seasonal migration should be considered separately from diel migration. The former was caused by endogenous factors probably associated with reproduction and not by any change in the physical conditions affecting the various instars. The latter was 'triggered' by the loss of light at dusk, but was not necessarily caused by the increase in the intensity of locomotor activity resulting from this loss.

CONTENTS

I INTRODUCTION 1

II DETERMINATION OF THE INSTARS OF SINGLE SPECIES 3

- 1. Material and methods. 4
- 2. Results. 8
  - (a) Identification of the species. 8
  - (b) Identification of the instars of single species. 11

III SEASONAL DEVELOPMENT: SEASONAL POPULATION DENSITY AND DRY WEIGHT CHANGES. 28

- 1. The study area. 28
- 2. Sampling method. 29
- 3. Seasonal development. 31
  - (a) Changes in the proportions of the various instars. 31
  - (b) The 'mean instar'. 36
  - (c) Growth rates: estimation of times of hatching and of final moult. 38
  - (d) Relationship between field temperatures, hatching periods and growth rates. 45
- 4. Seasonal changes in population density. 48
  - (a) Variability between samples. 48
  - (b) Seasonal density changes in the total harvest-spider population. 50
  - (c) Seasonal density changes in individual species populations. 52
  - (d) Comparison of population densities in 1958 and 1959. 61

(e) Relationship between moisture content of litter and mortality rates. 67

5. Seasonal changes in dry weight. 70

(a) Determination of mean dry weight per instar. 70

(i) Method. 70
(ii) Results. 70

(b) Seasonal dry weight changes in the total harvest-spider population. 73

(c) Seasonal dry weight changes in individual species populations. 73

6. Comparison of the densities and weights with the data of Todd (1949). 75

IVa BEHAVIOUR STUDIES: FIELD WORK. 77

1. The study area. 77

(a) General features. 77

(b) The flora. 78

(c) Micro-habitat classification. 79

2. Measurement of physical factors. 81

(a) Light. 81

(i) Method. 81
(ii) Results. 81

(b) Temperature and relative humidity. 83

(i) Method. 83
(ii) Results. 84

3. Sampling methods for the different field levels. 94

(a) Ground layer. 95

(b) Surface layer. 96

(c) Field layer. 97

(d) Shrub layer. 98

(e) Tree trunks. 99

(f) Tree branches. 103

4. Results. 105

A. Mitopus morio 107

(a) Ground layer. 107

(i) Comparison of catches of regions 1 and 2. 107
(ii) Numbers and instars. 110
(iii) Sex ratios. 110
(iv) Distribution of the catch over the 'day' and 'night' periods. 112

(b) Surface layer. 114

(i) Numbers and instars. 114
(ii) Sex ratios. 116
(iii) Distribution of the catch over the diel. 116

(c) Field layer. 119

(i) Numbers and instars. 119
(ii) Sex ratios. 119
(iii) Distribution of the catch over the diel. 121

(d) Shrub layer. 121

(i) Numbers and instars. 121
(ii) Sex ratios. 123
(iii) Distribution of the catch over the diel. 123

(e) Tree trunks. 124

(i) Numbers and instars. 124
(ii) Sex ratios. 125
(iii) Distribution of the catch over the diel. 126
(iv) Duplicated collections. 129

B. Oligolophus agrestis. 133

(a) Ground layer. 133

(i) Comparison of catches of regions 1 and 2. 133

(ii) Numbers and instars. 135
(iii) Sex ratios. 135
(iv) Distribution of the catch over the diel. 136

(b) Surface layer 136

(c) Field layer 136

(d) Shrub layer 137

(i) Numbers and instars. 137
(ii) Sex ratios. 139
(iii) Distribution of the catch over the diel. 140

(e) Tree trunks. 140

(i) Numbers and instars. 140
(ii) Sex ratios. 143
(iii) Distribution of the catch over the diel. 143
(iv) Duplicated collections. 144

C. Species other than M. morio and O. agrestis. 147

(i) Comparison of ground layer catches of regions 1 and 2. 147
(ii) Numbers. 154
(iii) Instars. 157
(iv) Sex ratios. 157

5. Discussion of field results. 160

A. Mitopus morio. 160

(a) Survey of events by time. 161

(b) Pitfall trap data 164

(i) Efficiency of trapping for different life stages. 164
(ii) Changes of activity with age. 166

(c) Vertical migration and the distribution of the species at different levels during the diel. 168

(d) Sex ratios. 169

(e) Site of the final moult. 173

B. Oligolophus agrestis. 175

(a) Survey of events by time. 175

(b) Vertical migration and the distribution of the species at different levels during the diel. 178

(c) Sex ratios. 179

C. Species other than <u>M. morio</u> and <u>O. agrestis</u>. 181

(a) Survey of events by time. 181

(b) The distribution of each species over 'day' and 'night' periods. 183

(c) Sex ratios. 186

IVb BEHAVIOUR STUDIES: LABORATORY INVESTIGATIONS. 188

1. Temperature and relative humidity preferenda. 188

2. Survival at different humidities and temperatures. 190

(a) Methods. 191

(b) Preliminary experiments. 192

(c) Results. 195

(i) Relationship between survival time and age at constant temperature and humidity. 195
(ii) Relationship between survival time and temperature at constant humidity. 203
(iii) Relationship between survival time and humidity at constant temperature. 206
(iv) Comparison of survival times of different species under the same conditions of temperature and humidity. 206

(d) Discussion. 208

3. Activity over the 24 hour period. 212

(a) The aktograph. 212

(b) Constructional details of the aktograph. 215

(i) The recording device. 215
(ii) The barograph. 220
(iii) The time marker 220
(iv) The phototransistor mount. 221
(v) The lamp. 221
(vi) The animal arena . 222

(vii) The time switch. 223
(viii) Preliminary experiments. 224

(c) Methods. 226

(d) Results. 229

(i) *Mitopus morio.* 229
(ii) *Lacinius ephippiatus.* 232
(iii) *Oligolophus tridens.* 235
(iv) *Oligolophus agrestis.* 237
(v) The na^ture of the diel rhythm in adult *M. morio.* 240

(e) Discussion. 244

4. Weight differences among adults of *Mitopus morio* and *Oligolophus agrestis.* 248

(a) Methods. 248

(b) Results of wet weights determinations. 249

(i) *Mitopus morio.* 249
(ii) *Oligolophus agrestis.* 253

(c) Results of egg counts. 255

(i) *Mitopus morio.* 255
(ii) *Oligolophus agrestis.* 255

(d) Discussion. 258

(i) Males. 258
(ii) Females. 259

V GENERAL DISCUSSION. 264

VI SUMMARY. 288

VII APPENDICES. 292

VIII REFERENCES. 303

IX ACKNOWLEDGEMENTS. 309

1 INTRODUCTION

1 INTRODUCTION

Todd (1949) outlined the seasonal development of nineteen of the twenty-one known species of British harvest-spider, noted a vertical migration in certain species from one microhabitat to another during the course of a single life history and correlated laboratory determined temperature and relative humidity preferenda of adults with the observed temperature and humidity conditions of their normal habitat.

The present study on six species of harvest-spider from the North of England is a re-examination and extension of Todd's ideas. Particular attention has been paid to:

1. The seasonal development of each of the species, *Lacinius ephippiatus* (C. L. Koch), *Mitopus morio* (Fabr.), *Nemastoma lugubre* (Mull.), *Odiellus palpinalis* (Herbst), *Oligolophus agrestis* (Meade) and *Oligolophus tridens* (C. L. Koch.).
2. Seasonal changes in population density and dry weight of all the species studied.
3. Vertical migration of the different life stages of *M. morio* and *O. agrestis*.
4. The relationship, for each life stage of *L. ephippiatus* *M. morio*, *O. agrestis* and *O. tridens*, between field

conditions and laboratory determined:

(a) Temperature and humidity preferenda.

(b) Survival times at different temperatures and humidities.

(c) 24 hourly patterns of locomotor activity.

No means of separating the different life stages (instars) of British harvest-spiders has been published: thus before any of the detailed studies outlined above could be made, it was necessary to find methods for identifying the different instars. This study forms the subject matter of Section II.

In the subsequent Sections, an account is given of field and laboratory studies carried out from 1958 to 1960 on the basis of the findings reported in Section II. The studies of both seasonal development (Section III) and field behaviour (Section IVa) were to have been carried out in Great High Wood, Durham, but because of impending tree felling operations the behaviour studies were made in Nannys Plantation, County Durham.

II DETERMINATION OF THE INSTARS OF SINGLE SPECIES

II DETERMINATION OF THE INSTARS OF SINGLE SPECIES

Several keys for the determination of the British species of harvest-spider were produced between 1890 and 1948, and that by Todd (1948) was used in the present study. No means of identifying the different instars of any of the British species has been published, and an account is now given of a method of instar determination for each of the following species:

Lacinius ephippiatus	Family PHALANGIIDAE Sub-family OLIGOLOPHINAE
Mitopus morio	
Odiellus palpinalis	
Oligolophus agrestis	
Oligolophus tridens	
Nemastoma lugubre	(Family NEMASTOMATIDAE)

1. Material and methods

Material was collected throughout 1958 and 1959 from Great High Wood, Durham (described in Section III) and from fields, hedgerows and woodland in the immediate vicinity of the University Science Laboratories, Durham City. In addition, specimens of the earliest juvenile stages were obtained from eggs produced by adults of known species kept in the laboratory according to Phillipson (1960 a).

Both laboratory and field specimens were preserved in 70% alcohol. Using Todd's (1948) key, juveniles of L. ephippiatus, M. lugubre and O. palpinalis could be readily identified. However, the earliest stages of M. morio, O. agrestis and O. tridens could not be identified with certainty, and before attempting to determine the instars of each species, it was necessary to find means by which to recognise the early stages of M. morio and the Oligolophus species. This was done by comparing specimens reared in the laboratory from eggs of known species with specimens obtained from the field.

The first attempt at determining instars was made on M. morio, of which approximately 100 specimens were examined in detail. Various measurements were made by means of a micrometer eyepiece previously calibrated against a scaled microscope slide. A separate record sheet (Fig. 1) was used for each specimen and the following features were examined:

Body length - the distance from the anterior edge of the cephalothorax to the tip of the abdomen (Fig. 2a).

'Eye distance' - the maximum width of the ocularium (Fig. 2b).

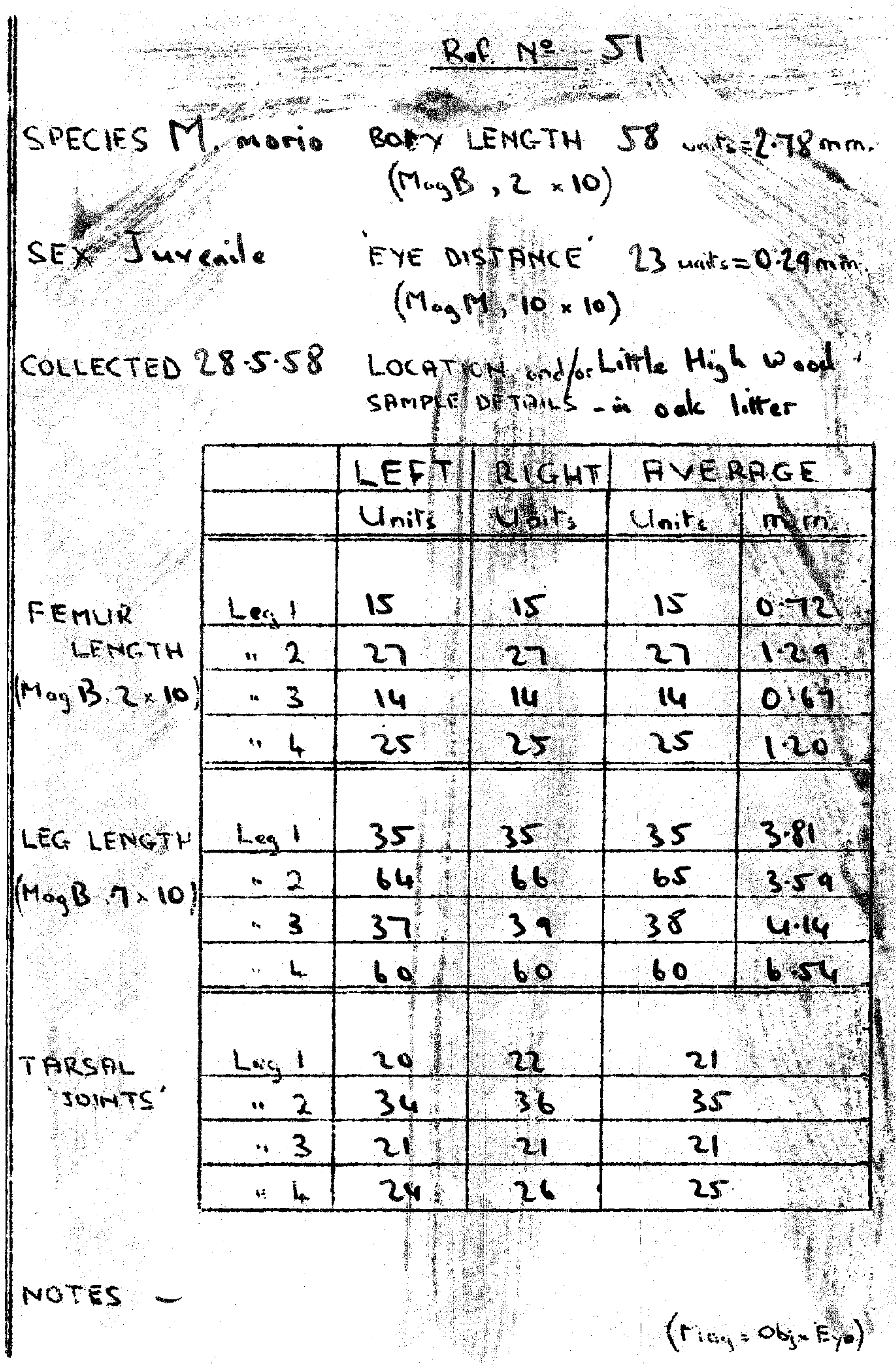
Femur length - the distance between the proximal and distal ends of the femur (Fig. 2c).

Leg length - the length of the leg from the proximal end of the trochanter to the tip of the tarsus (Fig. 2d).

Tarsal 'joints' - the number of segments in the tarsus (Fig. 2e).

Frequent loss of the ends of the tarsi made both leg length and tarsal 'joints' unsatisfactory characters. Body length and 'eye distance' were too greatly influenced by shrinkage and distortion on preservation to be of any value. Femur length was the most reliable character. The femur of the second walking leg was the easiest to position under the microscope for measurement, and for the main investigation of the instars of M. morio only this was examined.

On the basis of the work on M. morio, only the second femur was measured in the other species.



Ref. No. 51

SPECIES M. morio BODY LENGTH 58 units = 2·78 mm.
(Mag B, 2 × 10)

SEX Juvenile 'EYE DISTANCE' 23 units = 0·29 mm.
(Mag M, 10 × 10)

COLLECTED 28·5·58 LOCATION and/or SAMPLE DETAILS Little High Wood – in oak litter

		LEFT	RIGHT	AVERAGE	
		Units	Units	Units	mm.
FEMUR LENGTH (Mag B. 2 × 10)	Leg 1	15	15	15	0·72
	" 2	27	27	27	1·29
	" 3	14	14	14	0·67
	" 4	25	25	25	1·20
LEG LENGTH (Mag B .7 × 10)	Leg 1	35	35	35	3·81
	" 2	64	66	65	3·59
	" 3	37	39	38	4·14
	" 4	60	60	60	6·54
TARSAL 'JOINTS'	Leg 1	20	22	21	
	" 2	34	36	35	
	" 3	21	21	21	
	" 4	24	26	25	

NOTES –

(Mag = Obj × Eye)

Fig. 1. Record sheet for Mitopus morio.

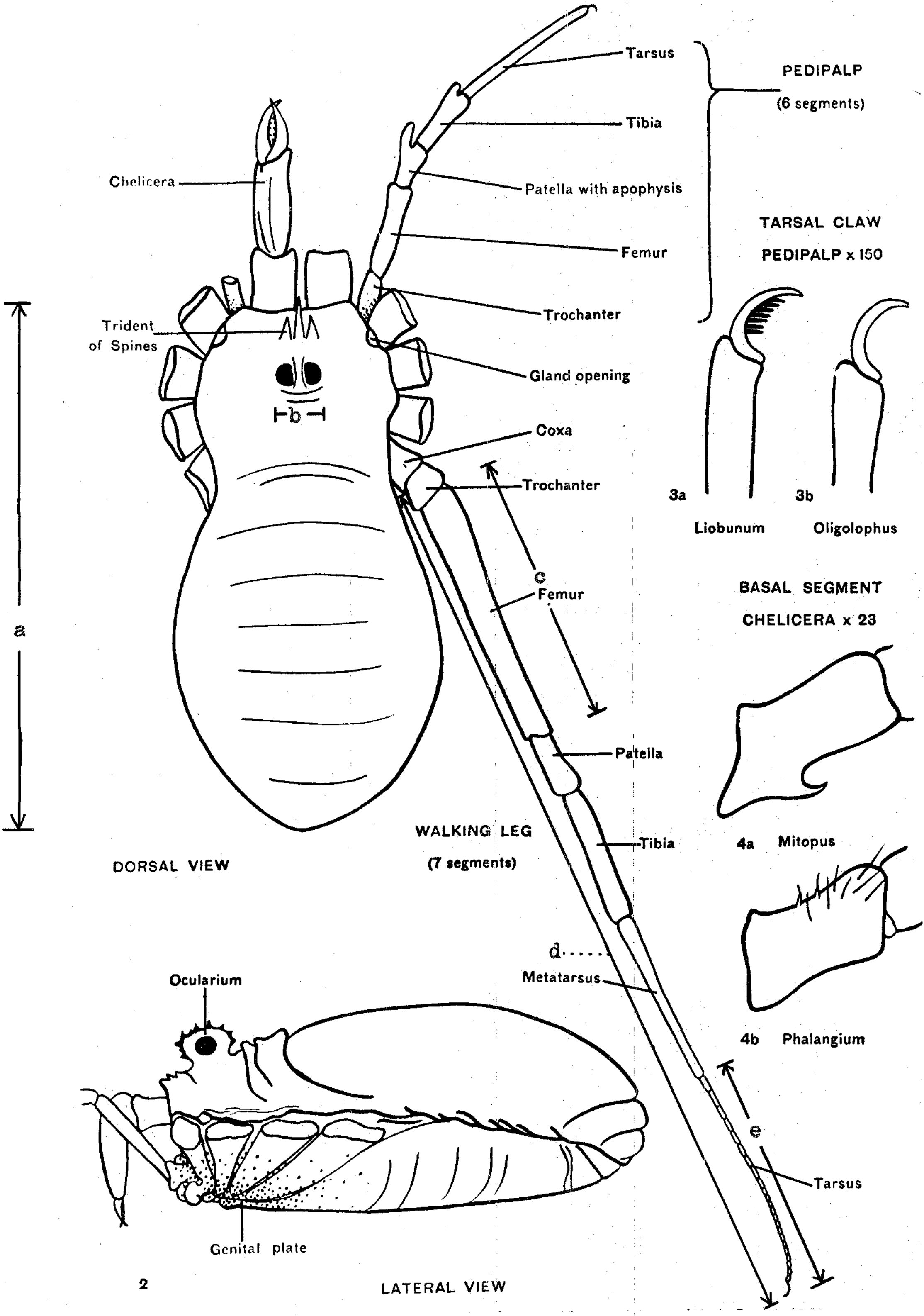


Fig. 2. Features used in the determination of instars.
a = Body length. b = 'Eye distance'. c = Femur length.
d = Leg length. e = Tarsal 'joints'. The figure is reproduced from Todd (1948).

2. Results.

(a) Identification of the species.

It was discovered later that each species of the Sub-family Oligolophinae examined had seven instars. However the first instar was so short-lived, that from the point of view of identification of field specimens it need not be taken into account.

That part of Todd's key which deals with the genera of the Sub-family Oligolophinae is reproduced below, and the relevance of each taxonomic character to the juvenile stages from the second instar onwards is given in parentheses.

1 (2) Femur of palp with conspicuous tubercles ventrally.................................... 3
(tubercles present in all juveniles of _Odiellus_ and _Lacinius_, ranging in number from two to four in the second instar to approximately twelve in the sixth instar).

2 (1) Femur of palp without conspicuous tubercles ventrally........................ 5
(tubercles absent in all juveniles of _Mitopus_ and _Oligolophus_).

3 (4) Coxa of leg 1 with conspicuous tubercles ventrally and without distal spur......... _Odiellus_

(tubercles present in all juveniles of *Odiellus*, ranging in number from one or two in the second instar to approximately twelve in the sixth instar: distal spur absent in all juveniles).

4 (3) Coxa of leg 1 without conspicuous tubercles ventrally and with distal spur...................................... *Lacinius*.

(tubercles absent in all *Lacinius* juveniles; distal spur always present, although very short in the second instar.)

5 (6) Fore edge of prosoma with trident well defined...................................... *Oligolophus*.

(Well defined trident present in third instar onwards; only a single well defined central spine present im the second instar.)

6 (5) Fore edge of prosoma with trident ill defined, represented by three small tubercles...................................... *Mitopus*

(Ill defined trident present in third instar *Mitopus* onwards; fore edge of prosoma completely devoid of tubercles in the second instar.)

Therefore to permit identification of second instar Mitopus and Oligolophus, stages 5 and 6 should be modified thus:

5 (6) Fore edge of prosoma with trident well defined, or, if a very small specimen, with femur length of second walking leg less than 0·8 mm and with a well defined single central spine.................... Oligolophus

6 (5) Fore edge of prosoma with trident ill defined, represented by three small tubercles, or, if a very small specimen, with femur length of second walking leg less than 0·8 mm and fore edge of prosoma completely devoid of tubercles or spines................................ Mitopus

In this study one species each of Odiellus, Lacinius and Mitopus and two species of Oligolophus were involved. The second, third and fourth instars of Oligolophus agrestis and Oligolophus tridens could not be satisfactorily separated by the characters given by Todd and a method which covers all instars is given below:

1 (2) Femur length of second walking leg greater than 1·2 mm 3

2 (1) Femur length of second walking leg less than 1.2.mm.......................... 5

3 (4) Genital plate rounded. Trident of spines in a straight line (Todd's Figs. 7b and 11c.) .... *O. tridens*

4 (3) Genital plate with notch or dark mark. Trident of spines with middle one in advance of others (Todd's Figs. 7a, 11a, 11b.)........................ *O. agrestis*

5 (6) Ocularium, in side view, with two rows of two to five tubercles or spines each borne on a slightly raised base. Reddish-brown body of stink gland clearly visible through dorsal body wall............................. *O. tridens*

6 (5) Ocularium, in side view, either without tubercles or spines or with two rows of up to four minute bristles not borne on a slightly raised base. Body of stink gland not visible through dorsal body wall..............*O. agrestis*

(b) Identification of the instars of single species

For each species, measurements of femur length of the second walking leg are shown as frequency distributions equally spaced to represent each instar (Figs. 3 to 8;

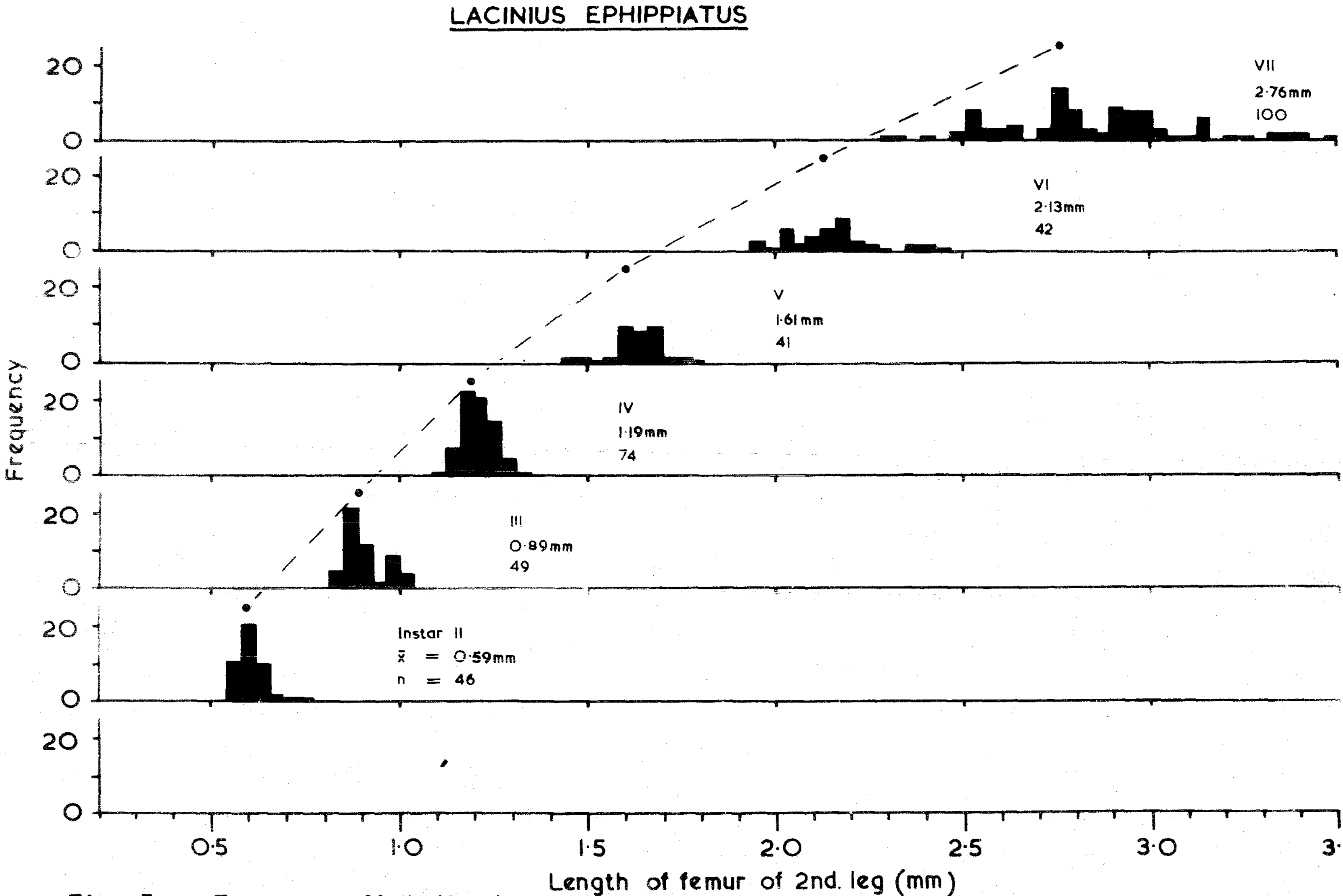


Fig. 3. Frequency distributions of second femur length. The small points represent mean length (x) per instar. The wider histogram bars for the seventh instar result from the use of a lower magnification.

MITOPUS MORIO

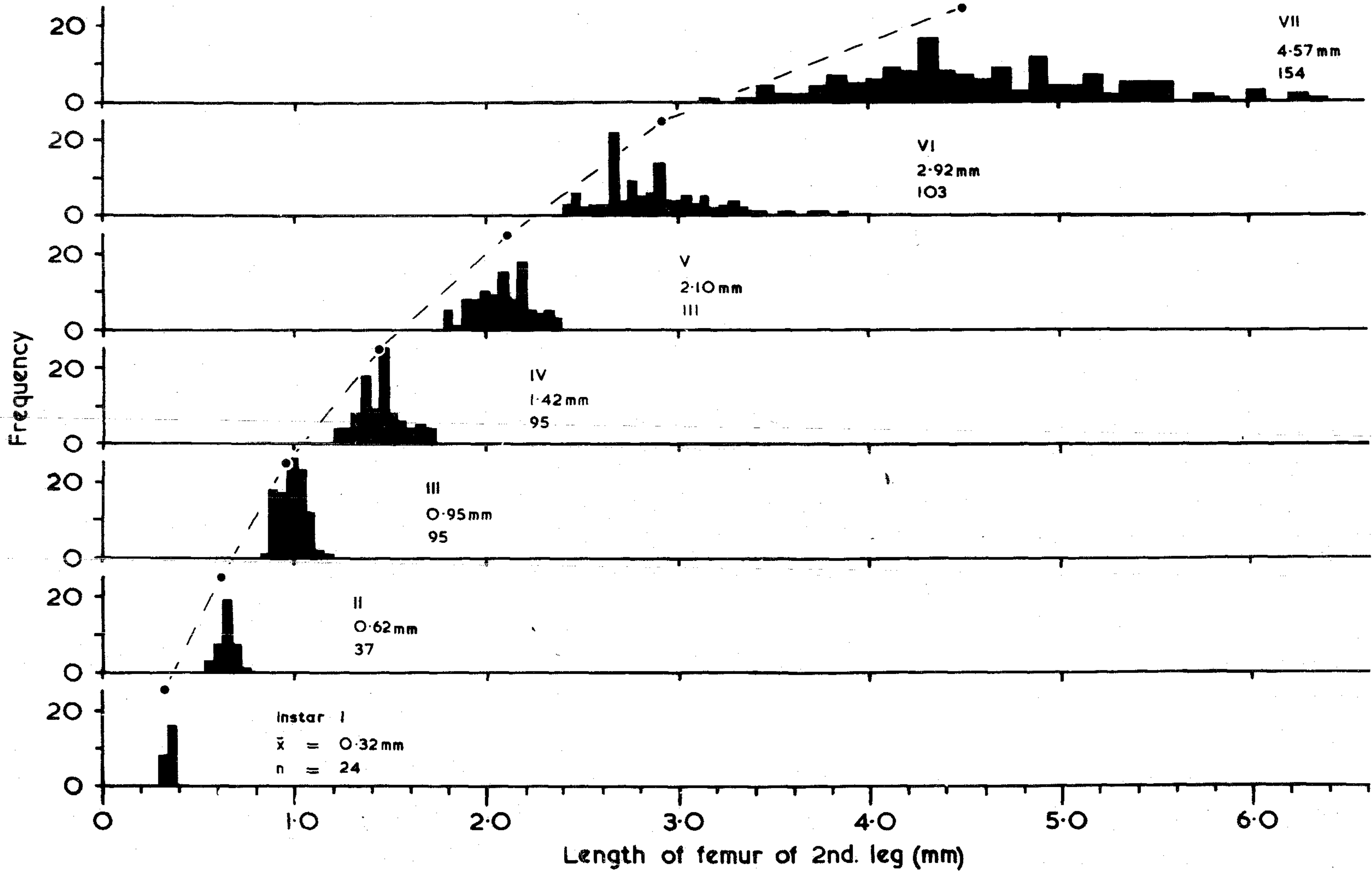


Fig. 4. Frequency distributions of second femur length. The small points represent mean length (x) per instar. The wider histogram bars for the seventh instar result from the use of a lower magnification.

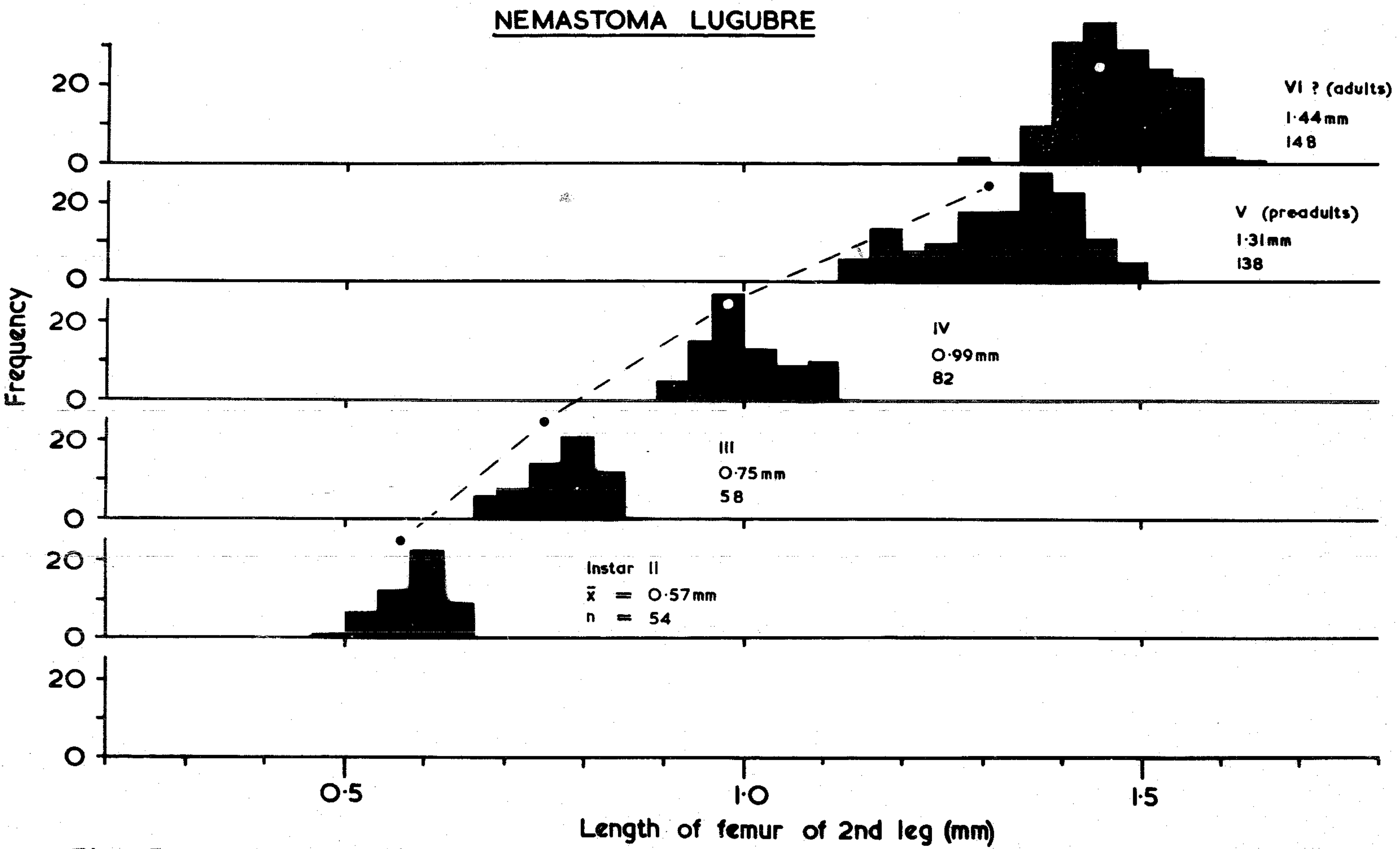


Fig. 5. Frequency distributions of second femur length. The small points represent mean length (x) per instar.

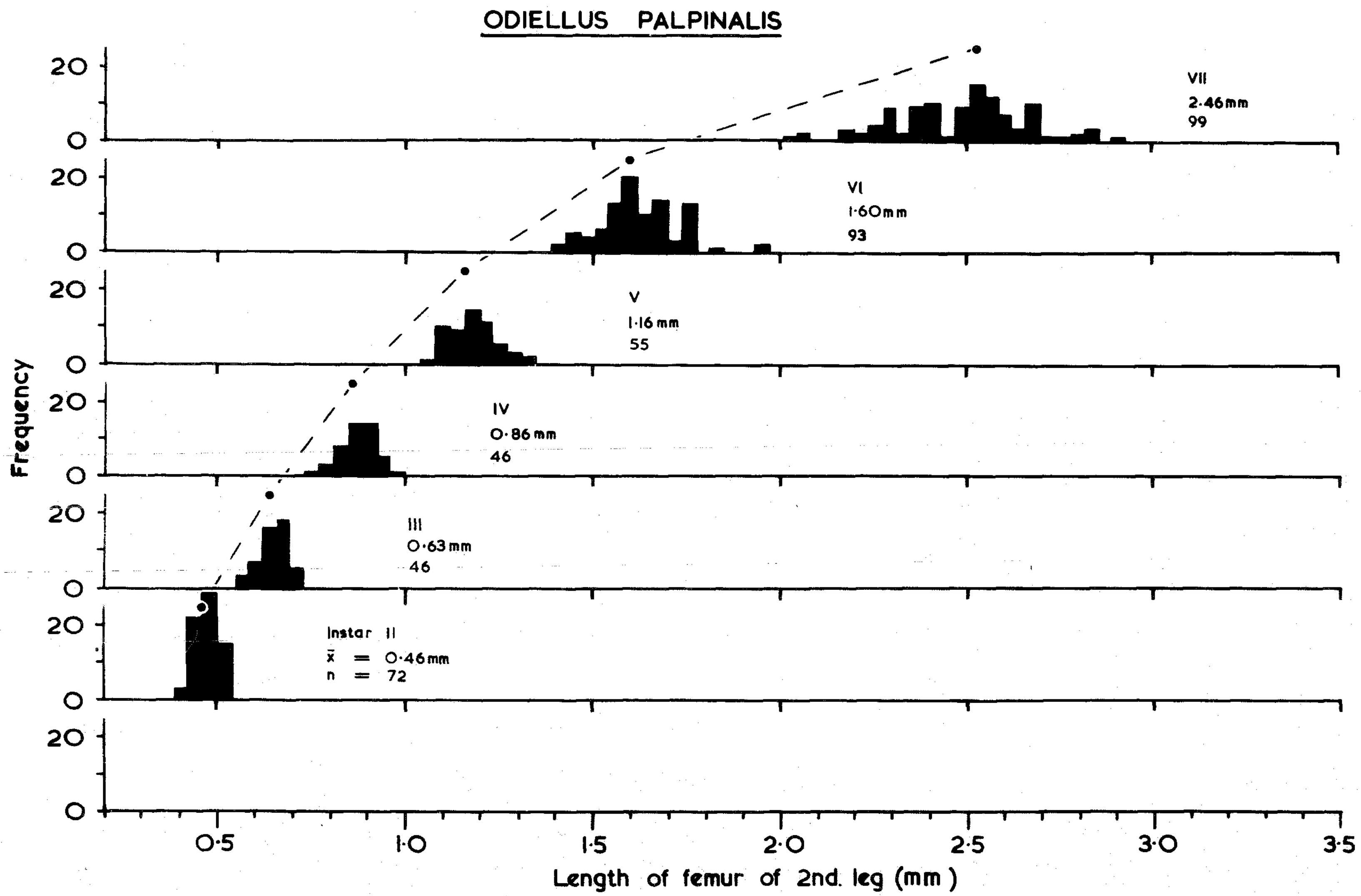


Fig. 6. Frequency distributions of second femur length. The small points represent mean length (x) per instar.

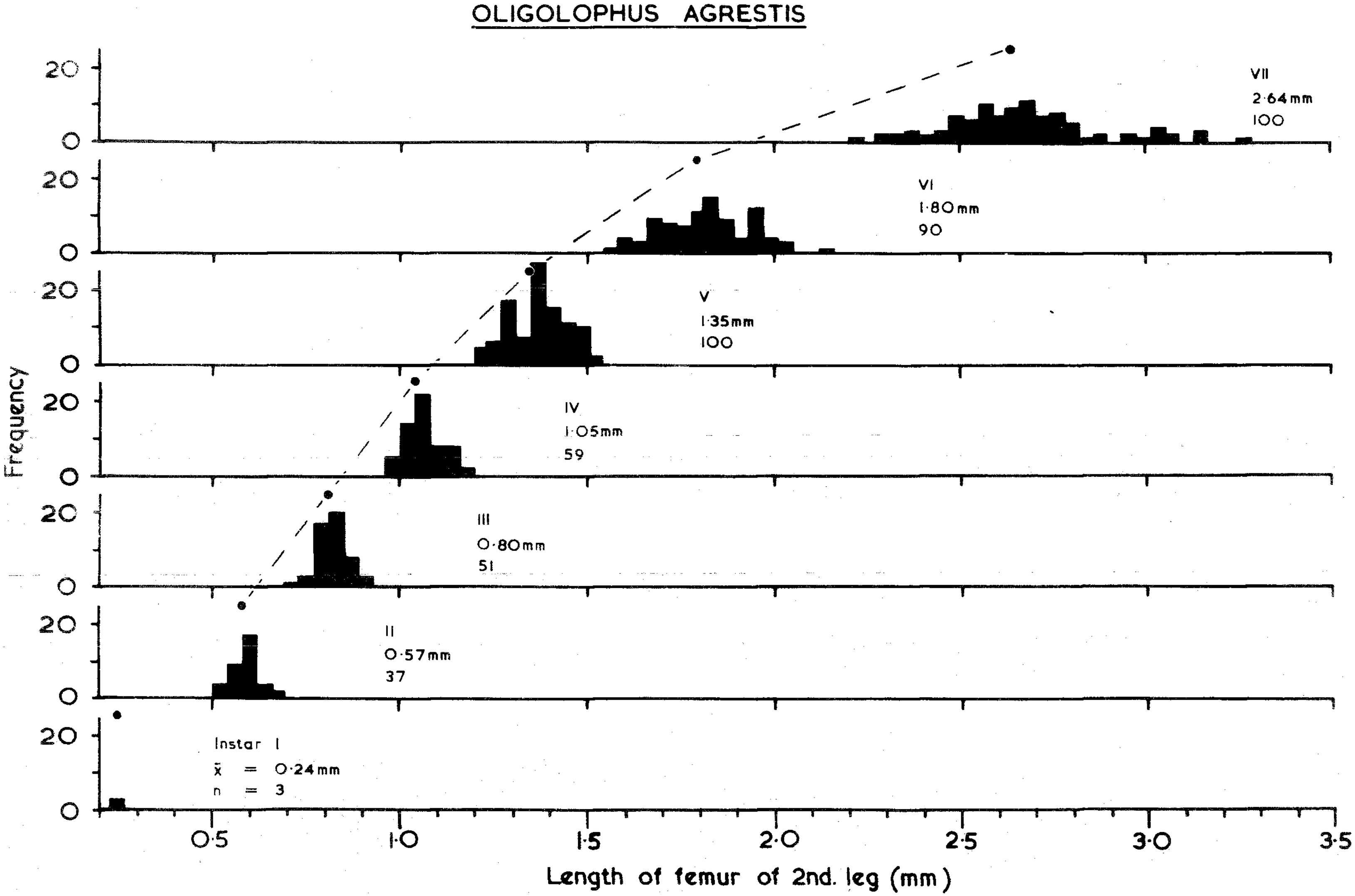


Fig. 7. Frequency distributions of second femur length. The small points represent mean length (x) per instar.

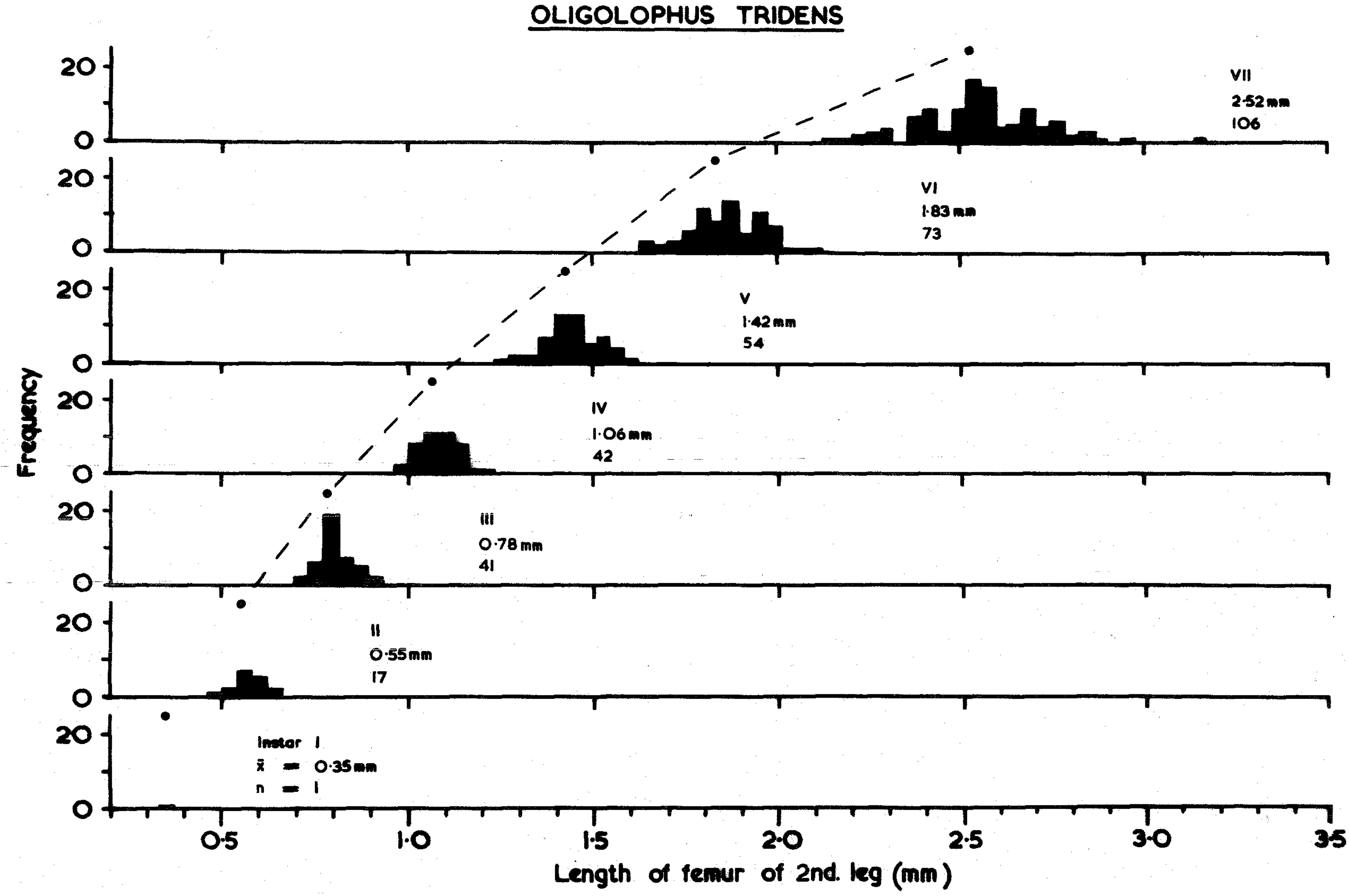


Fig. 8. Frequency distributions of second femur length. The small points represent mean length (x) per instar.

method after Ghent 1956). The upper and lower limits of femur length for each instar are given in Table 1. These limits were usually obvious from examination of the data. However, in cases of difficulty, the original specimens were re-examined, account being taken of features noted as characteristic of but not necessarily specific to a particular instar (for example body shape, body colour and number of tarsal segments) in deciding to which stage they should belong.

It can be seen from Figs. 3 to 8 that the range of femur length for the f^irst instar is only adequately represented in the case of *M.morio*. In no species was the instar (which is characterised by the possession of a distinct egg tooth on the fore edge of the prosome) ever found in the field, the only specimens available being those obtained from eggs which hatched in the laboratory.

Approximately fifty eggs of each species except *N. lugubre* were carefully observed during the hatching period. In *M. morio* the first instar remained clinging to the egg shell after emerging, and from this position moulted into the second instar within 10 to 30 minutes of hatching. In *L. ephippiatus*, *O. palpinalis*, *O. agrestis* and *O. tridens* the moult into the second instar nearly always occured during emergence from the egg shell, and only one first instar *O. tridens* and three first instar *O. agrestis* were obtained.

Table 1. Determination of instars by femur length of the second walking leg (length in mm). The upper figures for *Nemastoma lugubre* V refer to the preadults, the lower figures to the adults (See text for explanation).

	Instar II	III	IV	V	VI	VII
Lacinius ephippiatus	0.54 - 0.77	0.77 - 1.08	1.08 - 1.39	1.39 - 1.85	1.85 - 2.43	2.28
Mitopus morio	0.43 - 0.81	0.81 - 1.20	1.20 - 1.68	1.68 - 2.35	2.35 - 3.89	3.16
Nemastoma lugubre	0.46 - 0.66	0.66 - 0.85	0.85 - 1.12	1.12 - 1.47 1.27 - 1.62		
Odiellus palpinalis	0.39 - 0.54	0.54 - 0.73	0.73 - 1.00	1.00 - 1.35	1.35 - 1.97	1.97
Oligolophus agrestis	0.50 - 0.69	0.69- 0.96	0.96 - 1.19	1.19 - 1.54	1.54 - 2.16	2.16
Oligolophus tridens	0.46 - 0.69	0.69 - 0.93	0.93 - 1.23	1.23 - 1.63	1.63 - 2.12	2.12

In both *L. ephippiatus* (Fig. 3) and *M. morio* (Fig. 4) it can be seen that slight overlap of femur length of the preadult and adult instars occurs, but the instar of specimens within this range of overlap can be determined by examination of the genital operculum which is only open in the adult. Although any similar overlap between the earlier instars would be difficult to detect, a general check on the reliability of instar determination by this method was carried out on *O. agrestis*. The second femur length of individual specimens was noted before and after a moult, and the lengths were then compared with the frequency distribution of femur length for this species. A total of thirty specimens of the second to the fifth instar was lightly anaesthetised with ether vapour and the second femur measured. Each specimen was then kept in a separate container in the laboratory, was f^ed daily , then killed with ether vapour a few hours after a moult was seen to take place. The same femur was again measured.

The results are illustrated in Fig. 9. For each specimen examined, the femur lengths before and after the moult are shown, respectively, by the vertical lines to the left and right of each arrow. The limits of femur length per instar, based on the histogram, are indicated by the broken lines. Clearly, in most cases, the observed increase in femur length was in agreement with these limits.

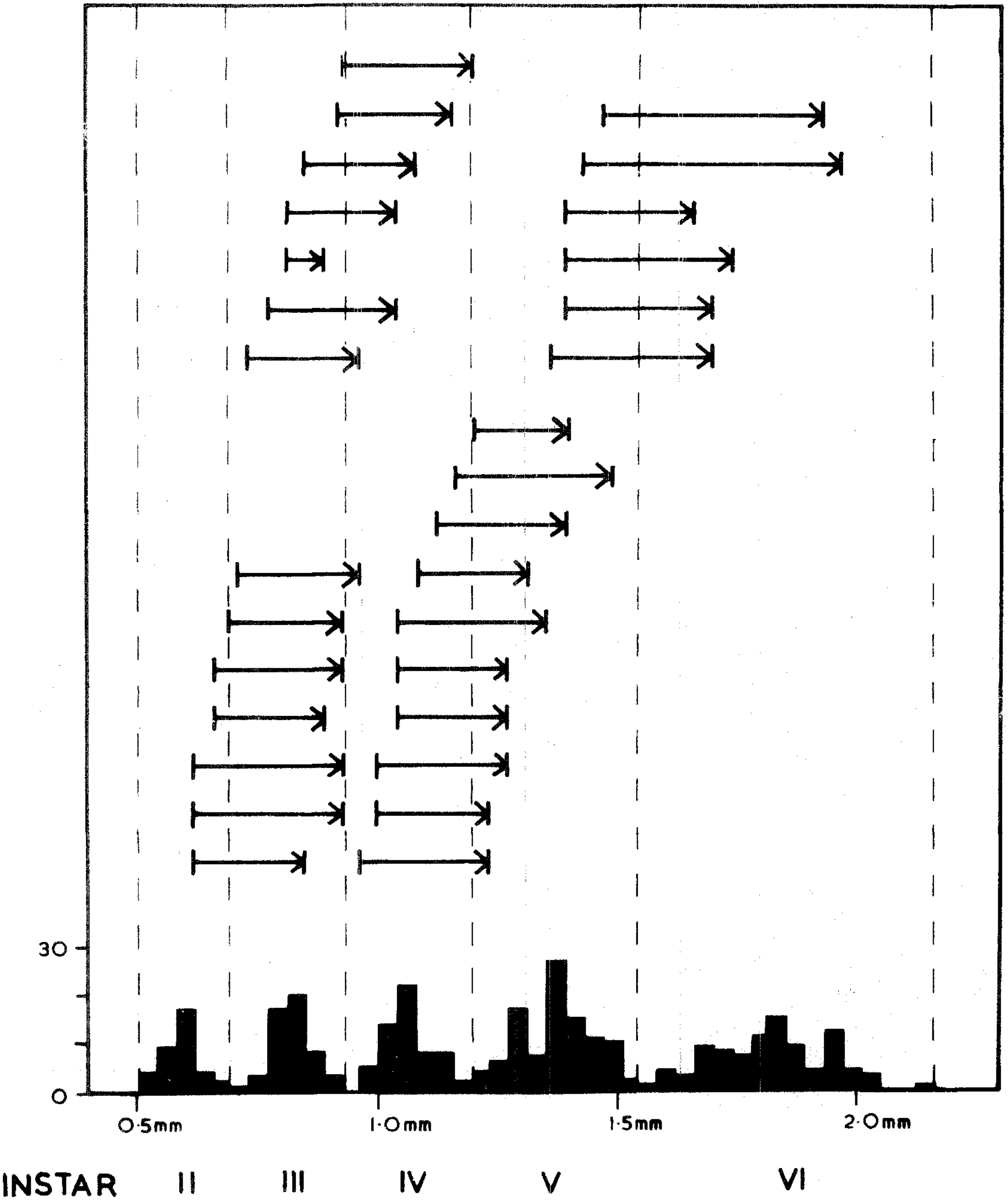


Fig. 9. Growth in second femur length in single specimens of Oligolophus agrestis. The vertical lines to the left and right of each arrow represent, respectively, femur length of an individual before and after a moult. The histogram is based on Fig. 7.

In Figs. 3 to 8 the mean second femur lengths per instar are shown by points placed at the same height above the x axes. A broken line is drawn through these points, but only in *M. morio* (Fig. 4) is it extended back to the mean for the first instar. From inspection of these lines it is clear that growth in femur length was exponential rather than linear in all species except *N. lugubre* (Fig. 5). This type of growth was confirmed by plotting femur length per instar on a logarithmic scale (Figs. 10, 11 and 12) when a straight line passed through nearly all points. However, it can be seen that in *M. morio* (Fig. 10) the rate of femur length increase between the first and second instar was greater than that occuring between subsequent instars. Thus, although first instar femur lengths could be estimated for the other species by extrapolation, it is questionable whether such estimates would be of any value.

The instars of *N. lugubre* (Fig. 5) could not be satisfactorily determined although a total of 480 specimens was examined. Eggs could not be obtained from adults kept in the laboratory, and attempts to rear specimens individually from one instar to the next all failed. If, as in the other species, the moult from the first to the second instar occurs during or immediately after emergence from the eggs, the first juvenile stages found in the field were probably the

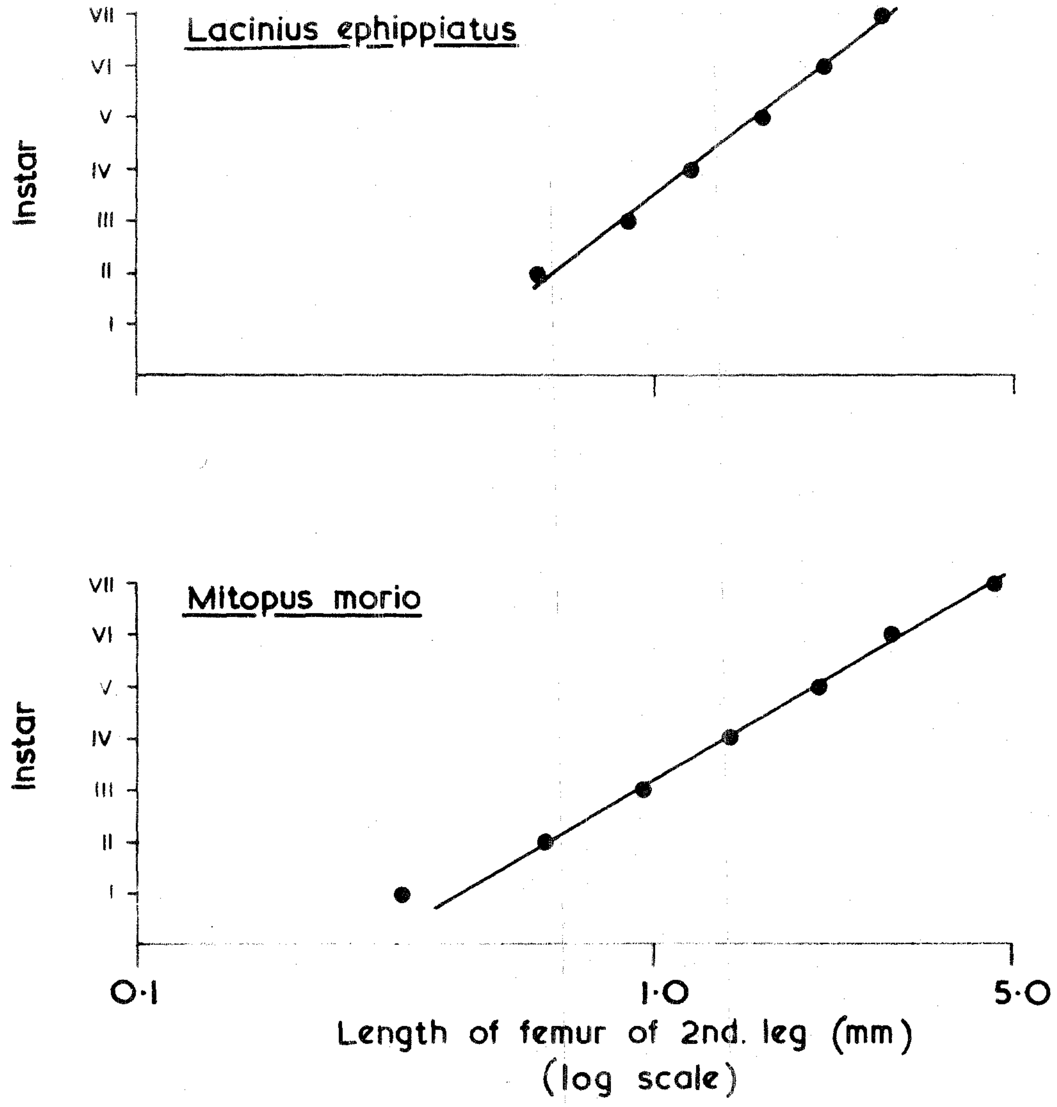


Fig. 10. Mean second femur length per instar. The lines through the points are drawn by inspection.

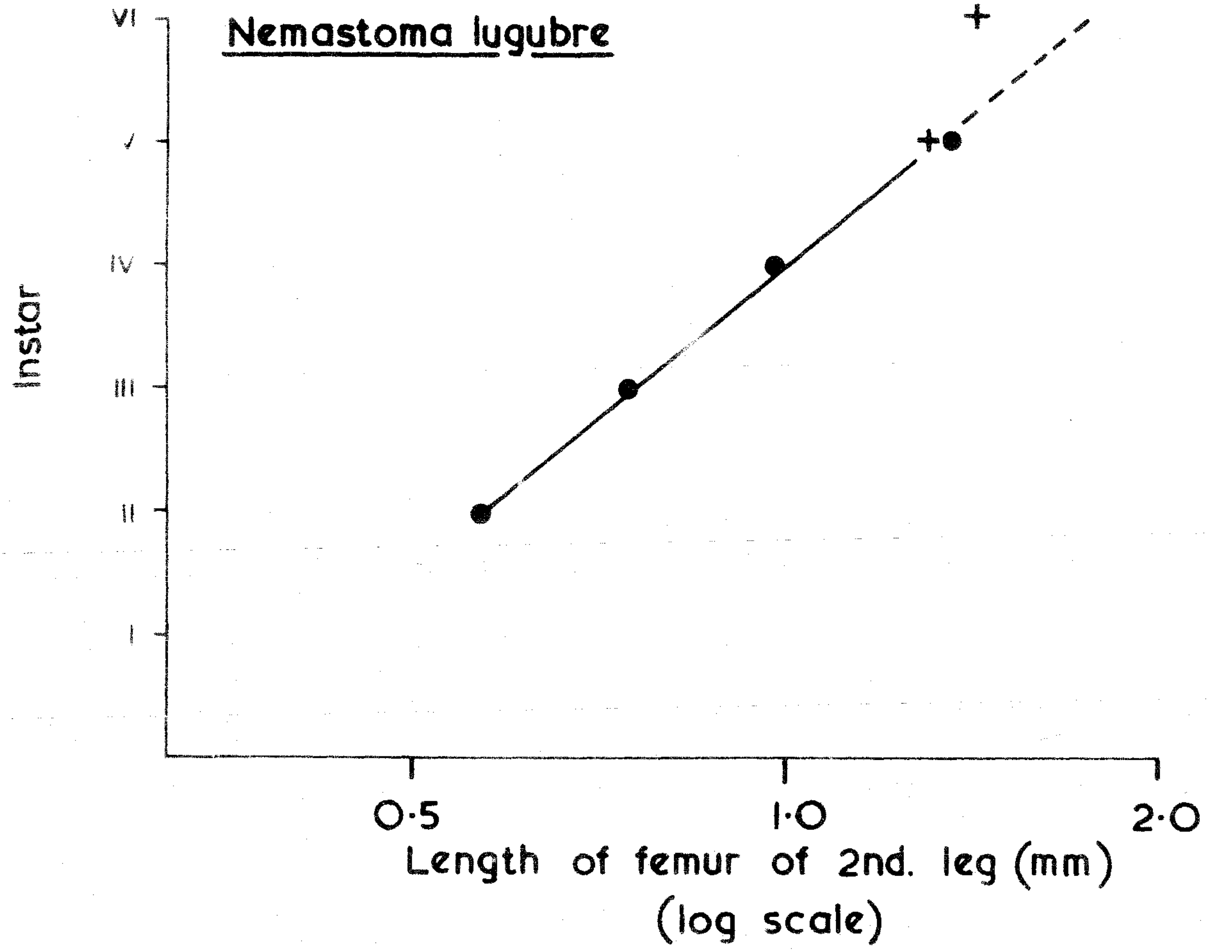


Fig. 11. Mean second femur length per instar. The uppercross represents mean length for adults (6th instar?), the lower cross that for preadult juveniles, the point beside the lower cross that for preadults and adults combined.

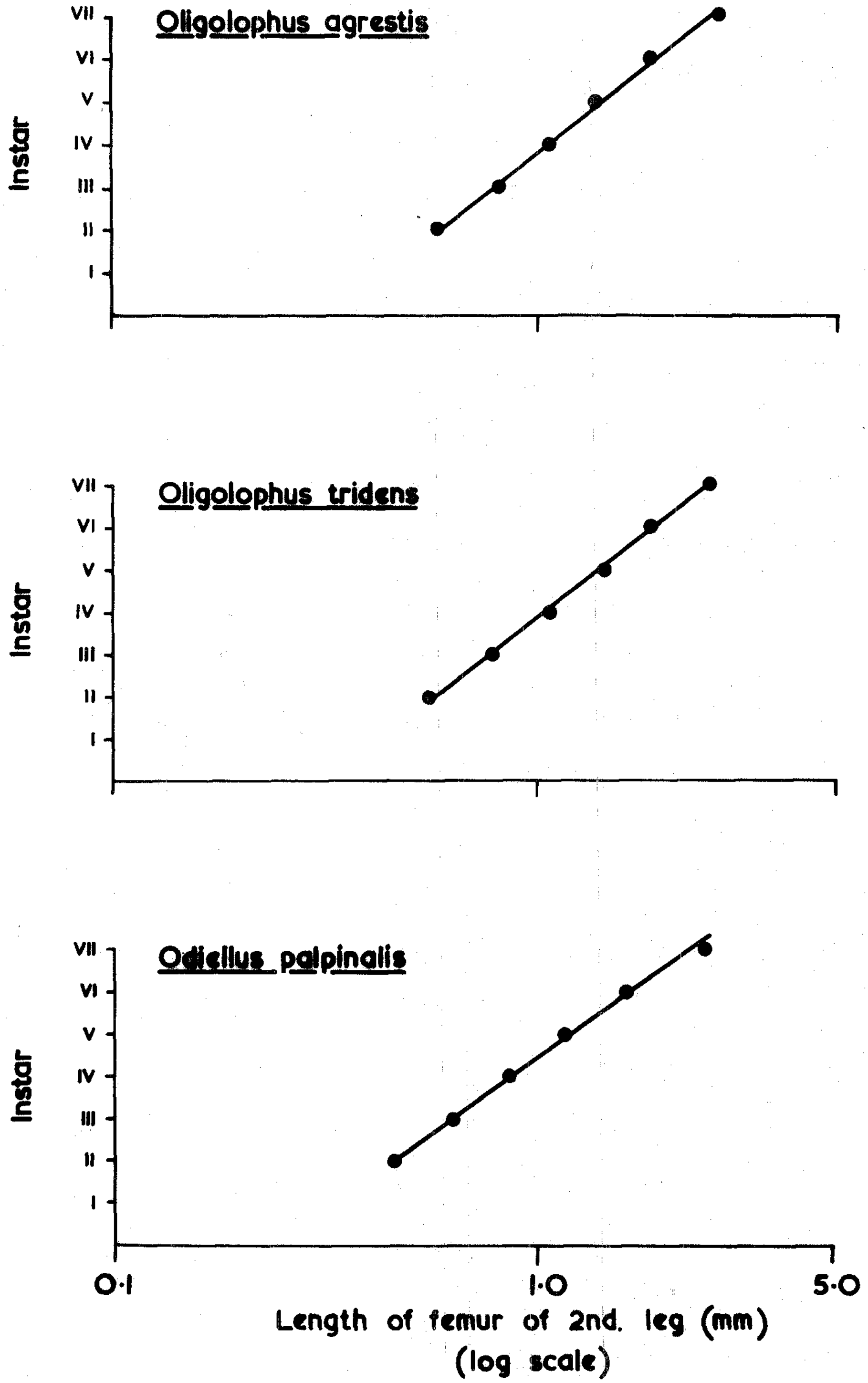


Fig. 12. Mean second femur length per instar. The lines through the points are drawn by inspection.

true second instar. Thus, in constructing Fig. 5, the smallest juveniles were considered to represent the second instars. (In a study of Nemastoma quadripunctatum, a species not found in Britain, Immel (1955) observed that the moult into the second instar occured within 30 minutes of emergence from the egg.)

N. lugubre juveniles of instars 2, 3, 4, and 5 are similar in general appearance, having a soft white-brown body which is relatively small compared to the length of the legs. The adults have a hard black body which is relatively large compared to the length of the legs. Mainly because of the striking difference between the appearance of the fifth instar juveniles and the adults, the latter were at first thought to represent a sixth instar. However, examination of Fig. 5 suggests this may not be the case: considerable overlap of second femur length occurs between the two stages, and if the broken line was extended to the last mean, it would represent a distinct departure from the previous rate of growth. The situation is clarified somewhat by examination of Fig. 11 in which the mean lengths are plotted on a logarithmic scale. The upper of the two crosses represents the mean femur length of the adults (sixth instar ?), the lower cross that of the fifth instar juveniles and the circle beside the lower cross that of fifth instar juveniles and adults combined.

Clearly, a straight line can be drawn through all the means if the pre-adult juveniles and the adults are considered to be the same instar. Also, assuming a similar rate of growth throughout the period of development, the mean length for a sixth instar would be far greater than that actually recorded for the adults.

Thus, from the evidence of femur length alone, it would seem that preadult fifth instar juveniles develop into adults without a moult, and field specimens can actually be found which are intermediate in colour between the white-brown of the juveniles and the black of the adults. However, other evidence suggests the existence of two instars within that now considered as the fifth; distinct structural differences occur between preadults and adults for which no intermediate stages were found. In addition it can be seen from Table 7 that while the body weight is approximately doubled between each instar from the second to the preadult fifth, it increases by a factor of about 5 between preadult and adult stages. Clearly, specimens must be reared in the laboratory in order to determine the precise number of instar in N. lugubre.

III SEASONAL DEVELOPMENT: SEASONAL POPULATION DENSITY AND DRY WEIGHT CHANGES

III SEASONAL DEVELOPMENT: SEASONAL POPULATION DENSITY AND DRY WEIGHT CHANGES

1. The study area.

The material for the investigation of seasonal development and seasonal population density and dry weight changes, was collected in Great High Wood, Durham. (National Grid Reference NZ 276407). This wood forms a narrow strip, about a mile long, within a broad loop of the River Wear. It is a mixed deciduous - coniferous wood, well established on ground which slopes down to the flood plain of the river. The region actually used was a wide gulley running in a west-east direction from the 300 ft. to the 200 ft. contour. The tree layer consisted of old beech trees (Fagus sylvatica L.) with a few relatively young pine trees (Pinus sylvestris L.). There was no shrub layer and the field layer was very sparse, consisting of large patches of ferns (Dryopteris austriaca (Jacq.) Woynar) on the south side of the gulley and a general covering of bluebells (Endymion nonscriptus (L.) Garcke) over the whole region. Throughout the year the ground was covered by a layer of beech litter ranging in depth from 2 cm to 5 cm on the high ground, to 15 cm or more on the gulley floor.

2. Sampling method.

Two sets of samples were taken each month from May 1958 to December 1959. Eight sampling stations, approximately 5 metres apart, were marked out along a line running from north to south across the gulley (Plate 1). Stations 1, 7 and 8 were in shallow litter on the high ground, 2, 3 and 4 in deeper litter among the ferns and 5 and 6 in the deep litter free from ferns on the floor of the gulley. On each sampling occasion, one quadrat (0·25 sq. m in 1958, 0·125 sq. m in 1959) was marked out at each station by placing a square wire frame on the ground. All animals moving on the surface within it were picked off, then the litter was removed for examination. The position from which samples were taken had been marked out with small sticks at the beginning of the study to avoid sampling the same area on more than one occasion.

Preliminary sorting of the litter showed that the early instars were seldom recovered from samples returned in large polythene bags to the laboratory for examination, whereas large numbers were obtained from similar samples sorted immediately in the field. This was presumably due to the fact that they were easily crushed and killed while being transported, and were subsequently overlooked

Plate 1. The study area in Great High Wood from the east.

during sorting, while larger specimens, of which similar numbers were recovered from both laboratory and field sorted samples, were easily seen even when crushed. Thus, samples were normally sorted in the field, and only in autumn, when it was clear that juveniles were no longer present, were they occasionally returned to the laboratory for sorting. The litter of both field and laboratory sorted samples was spread out on a large sheet of white oilcloth and carefully handsorted twice, all specimens being immediately placed in 70% alcohol. It was then spread out again and left undisturbed for at least 5 minutes, during which time any animals still remaining began to move and were picked off. It is believed that this method of removing harvest-spiders from litter was fairly efficient, as extremely careful sorting for a third and fourth time seldom produced more than one, or at the most two further specimens.

The preserved material was examined in the laboratory, and each specimen was classified according to its species, instar, and if adult, its sex.

3. Seasonal development.

(a) Changes in the proportions of the various instars.

The complete results of the sampling in Great High Wood are given in appendix A. For each species, the seasonal change in the proportions of the various instars present is shown graphically (Figs. 13 to 16). It is clear from these figures that two or three instars were generally present at any one time with the exception of the beginning and the end of the development period. The presence of third instars of *M. morio* and *L. ephippiatus* in the first samples of 1958 shows that hatching must have started some time before sampling began: in the remaining species in 1958 and in all species in 1959 the period of hatching is indicated to within the nearest two or three weeks.

Unfortunately the 1959 *N. lugubre* material was badly preserved, and the legs had become detached from almost every specimen. Instars were therefore determined by reference to body size and general appearance rather than to length of the second femur. As this method was probably unreliable, only the instars of the 1958 material (identified by second femur length) are illustrated in Fig. 14.

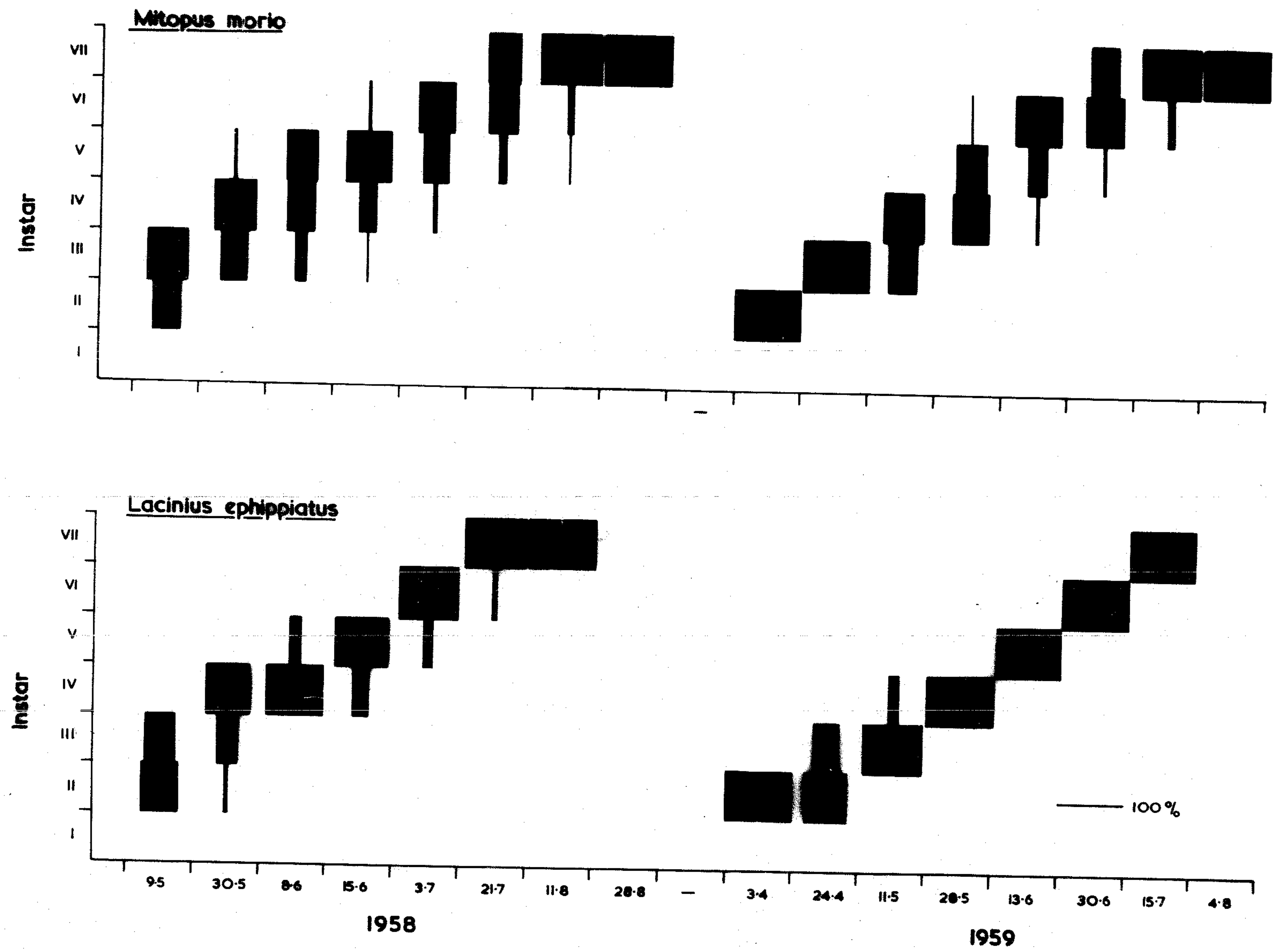


Fig. 13. The instar composition of each collection of M. morio and L. ephippiatus.

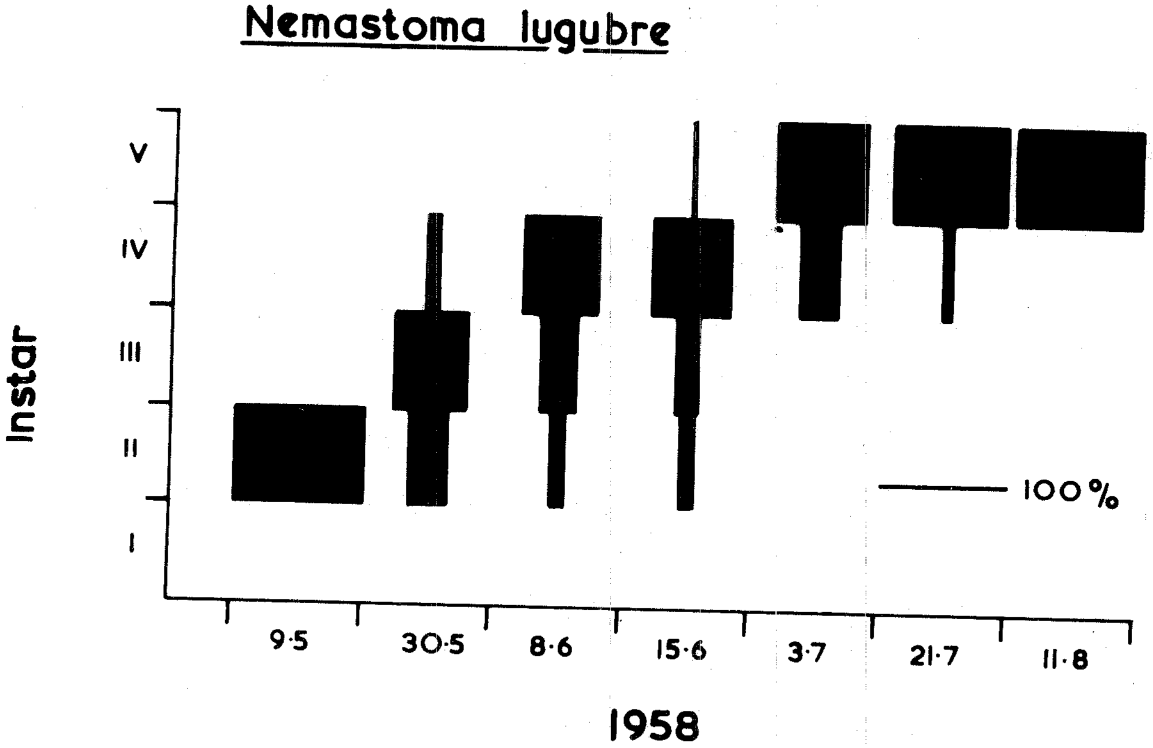


Fig. 14. The instar composition of each collection of N. lugubre.

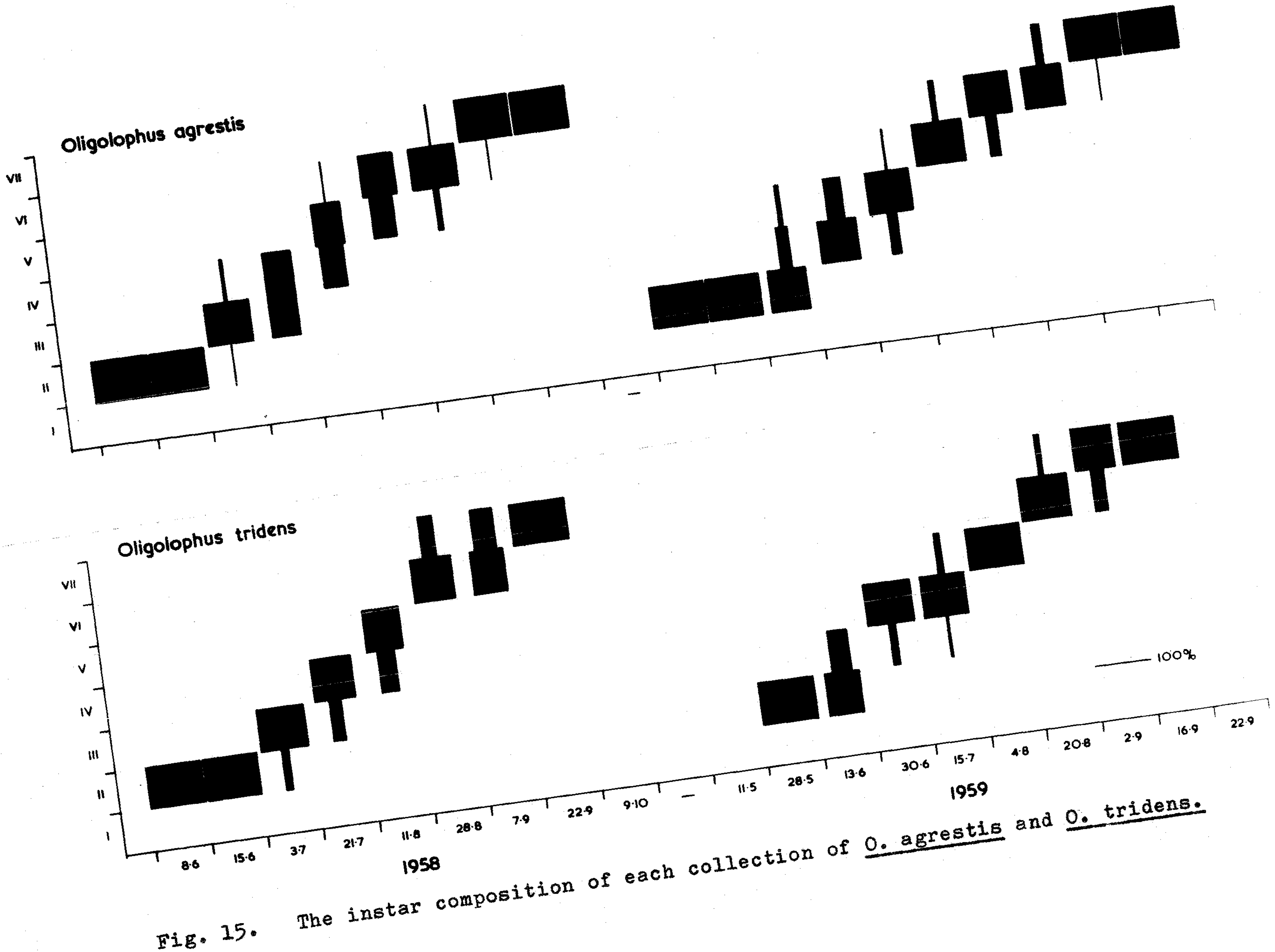


Fig. 15. The instar composition of each collection of O. agrestis and O. tridens.

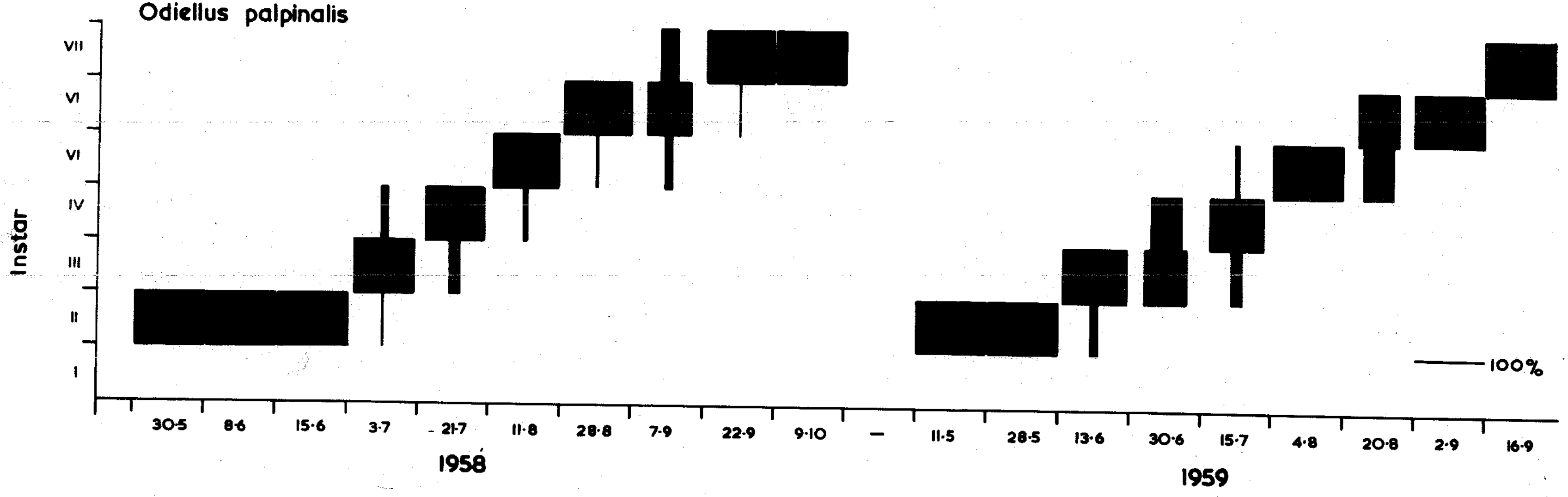


Fig. 16. The instar composition of each collection of O. palpinalis.

To show the nature of the overlap of generations known to occur in N. lugubre (Phillipson 1959), some of the data of Appendix A are reproduced in Table 2. This table shows that a few adults from 1957 persisted at least into July 1958, when the sudden increase of mature (black) adults from 10 on 21 July, to 54 and 88 on 11 and 28 August respectively indicates that the 1958 generation reached maturity in August. A similar overlap of adults of the 1958 and 1959 generations is also apparent. In constructing Fig. 14 adults of the 1957 generation were not considered.

(b) The 'mean instar'.

While Figs. 13 to 16 show the instar composition of each collection, the time interval of two to three weeks between sampling precludes any precise estimates of the times at which any one instar was most abundant in the population. This can be found however by a method based on that used by Gabbutt (1959). Knowing that each instar of Nemobius sylvestris (Orthoptera, Gryllidae) was recognisable on the basis of its head-width measurement, he calculated the 'mean head-width' of all individuals in each collection. By plotting these means against time, he was able to estimate when any particular instar was most abundant. In the present

Table 2. The instars of <u>Nemastoma lugubre</u> present in each collection from Great High Wood, 1958 and 1959.

	Instar II	III	IV	V (preadults)	V (adults)	
9. 5.58	17				6	1957 Generation
15. 5.58	12				2	
30. 5.58	17	31	6		10	
8. 6.58	5	12	26		17	
15. 6.58	6	10	30	3	12	
3. 7.58			13	31	5	
21. 7.58			3	33	10	
11. 8.58				8	54	1958 Generation
28. 8.58					88	
7 . 9.58					87	
22. 9.58					47	
9.10.58					43	
23.10.58					37	
5.11.58					47	
20.11.58					21	
5.12.58					13	
14.12.58					16	
19. 2.59					4	
13. 3.59					2	
3. 4.59	1				8	
24. 4.59					6	
11. 5.59	8	9			2	
28. 5.59	2	11	2		9	
13. 6.59	1	4	10	1	3	
30. 6.59			3	7	3	
15. 7.59			2	4	6	
4. 8.59				5	10	1959 Generation
20. 8.59					12	
2. 9.59					5	
16. 9.59					7	
22. 9.59					9	
11.10.59					-	
31.10.59					5	
11.11.59					1	
5.12.59					2	

study a 'mean instar' value was calculated for each collection of each species as shown by the following example: of the 78 *Mitopus morio* collected on 8 June 1958, 12 were in the third instar, 30 in the fourth, and 31 in the fifth, and the 'mean instar' value was:

$$\frac{(12 \times 3) + (30 \times 4) + (31 \times 5)}{12 + 30 + 31} = 4{\cdot}26$$

For reasons given earlier, the 1959 *N. lugubre* instar data are unreliable and were therefore not used. As movement of the final and penultimate instars of *M. morio* and *O. agrestis* away from the ground (described in Section IV a) would have influenced the means, it is believed that a reasonable approximation to the true mean instar value of each species population as a whole was given by including in the calculations all individuals taken from eight ferns within the study area.

(c) Growth rates: estimation of times of hatching and of final moult.

When the resulting mean instar values were plotted against time (Figs. 17 to 19) it was clear that a linear relationship existed: thus for each species a linear regression was calculated (Bailey 1959). Where the first samples comprised only second instar juveniles, the

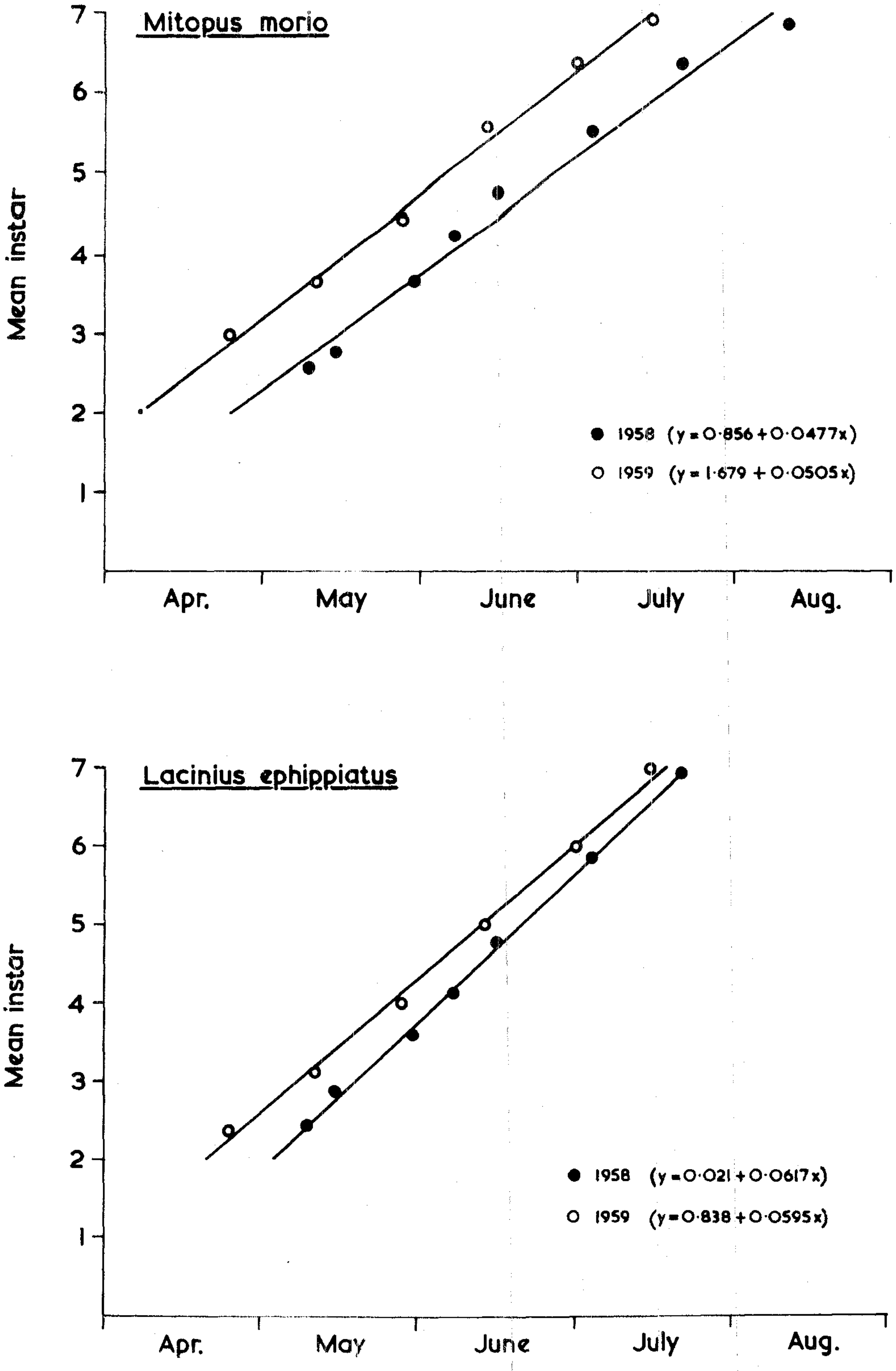


Fig. 17. Growth rates of M. morio and L. ephippiatus. Each line is plotted from the linear regression fitted to the mean instar data. The mean instar values are indicated by circles.

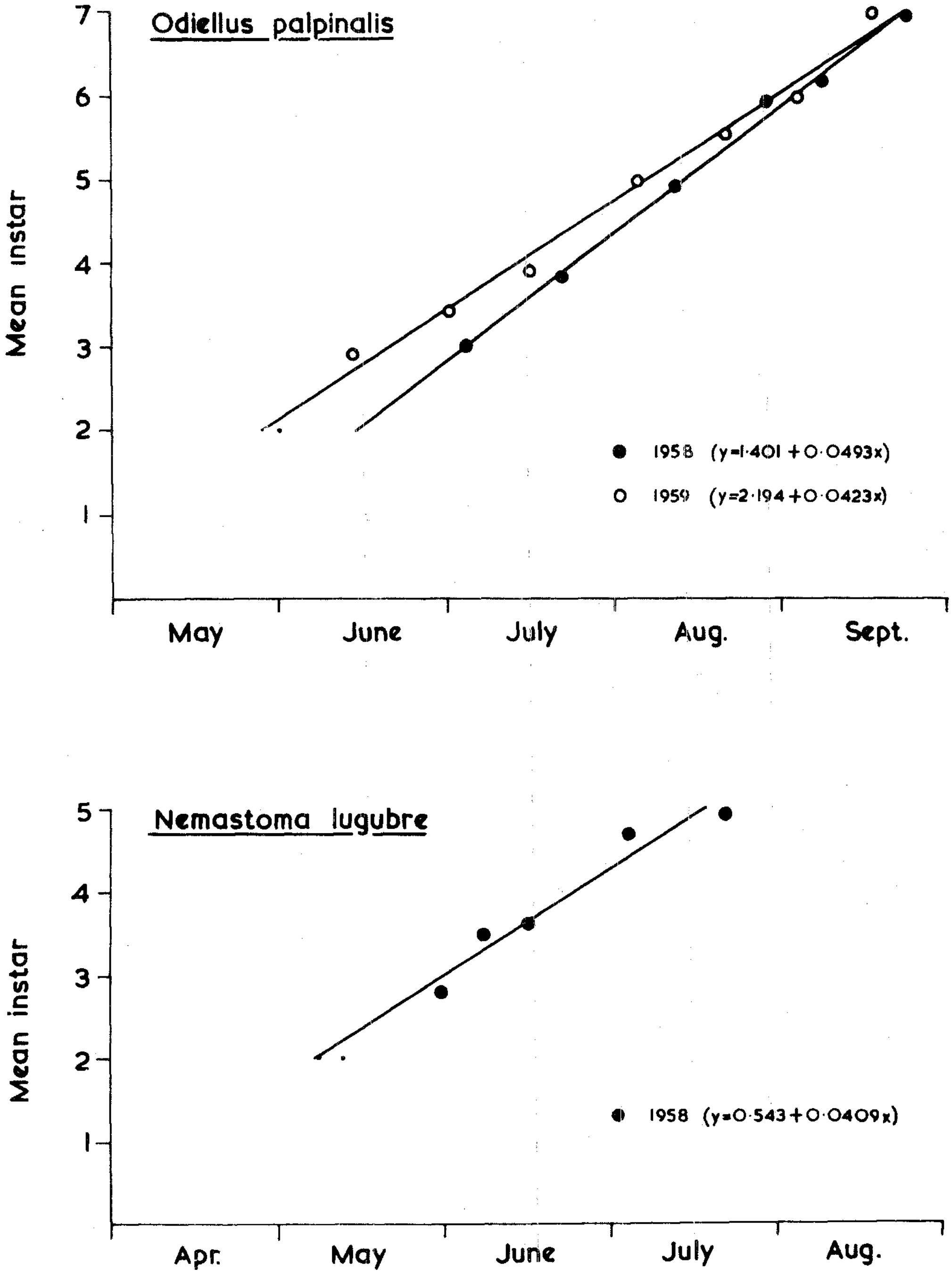


Fig. 18. Growth rates of O. palpinalis and N. lugubre. Each line is plotted from the linear regression fitted to the mean instar data. The mean instar values are indicated by circles.

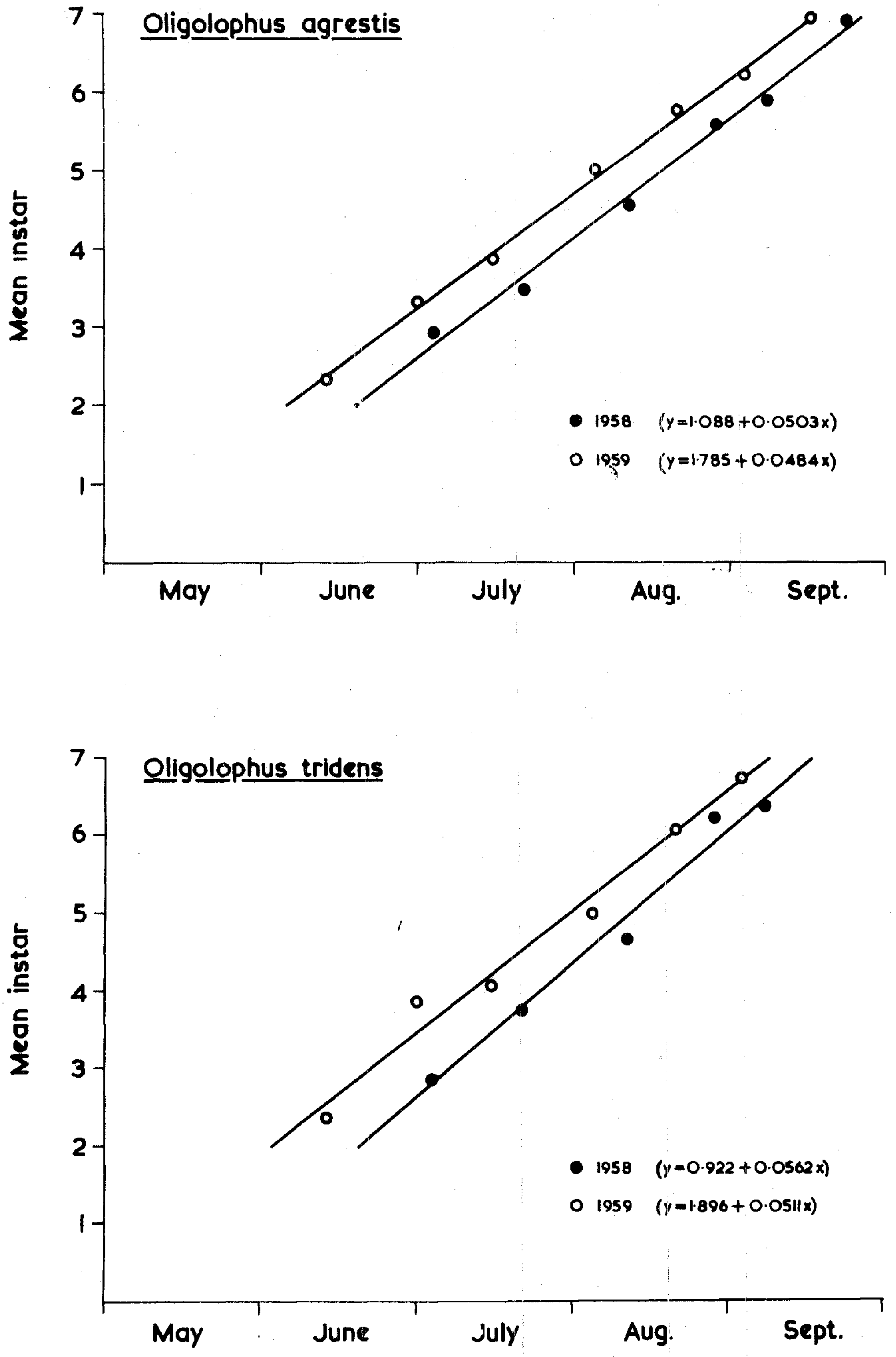


Fig. 19. Growth rates of O. agrestis and O. tridens. Each line is plotted from the linear regression fitted to the mean instar data. The mean instar values are indicated by circles.

corresponding mean instar values of 2·0 were not used in the calculations. These values are represented in Figs. 17 to 19 by small dots instead of circles.

Clearly some points deviate from linearity due, perhaps, to the effect of seasonal temperature fluctuations on growth rates, or to the use of relatively small samples in calculating the means. It is assumed however that in all species studied, the growth rates were linear throughout the developmental period, the coefficient of linear regression, b, providing a quantitative description of these rates. Therefore the equations can be used to estimate the time at which any one instar was most abundant, by substituting instar numbers for y and calculating the corresponding value of x (time). It was stated in Section II that in all species studied except N. lugubre, the moult into the second instar occured during or immediately after emergence from the egg; thus, a value of $y = 2$ was used to determine this time for the earliest instar found in the field, while a value of $y = 7$ was used for adults. In N. lugubre, the first specimens found in the field were considered to be the true second instar and the fully grown individuals, the true fifth. As a linear growth rate is assumed, the time spent in any one instar, other than the last, would be one third the length of the developmental period in N. lugubre and one fifth the length in the remaining species. By subtracting half this value from that of x for the earliest and the final instars, the average time of hatching and of the final moult are given. The results of all calculations are shown in Table 3. In determining actual dates, day 1 ($x = 1$) was taken as 1 April, so that, in Lacinius 1958 for example, when $y = 2$, x is 32·0 and the corresponding date is 2 May. It is clear that in all species, hatching and the final moult took place slightly earlier in 1959 than in 1958, although in O. palpinalis, the difference with respect to the last moult was relatively small. It can be seen from Figs. 17 to 19 that in this species alone was there any marked difference between the apparent growth rates in the two years, but as the 1959 calculations were based on so few individuals, this difference is unlikely to be of any significance.

Of the two 'spring species', Mitopus morio hatched between one and two weeks earlier than Lacinius ephippiatus in both years. However, of the two species, its developmental period was by far the largest, so that, despite its earlier emergence, it still reached maturity later than L. ephippiatus.

Of the three 'summer species', Odiellus palpinalis emerged about a week earlier than both Oligolophus agrestis and Oligolophus tridens which hatched within one or two

Table 3. Information calculated from the regression equations shown in Figs. 17 to 19.

Species	Year	Average date of hatching	Average date of final moult	Growing period (days)	Intervals between adjacent instars (days)
Lacinius ephippiatus	1958	2 May	22 July	80.9	16.2
	1959	19 April	12 July	84.0	16.8
Mitopus morio	1958	24 April	7 Aug	104.7	20.9
	1959	6 April	14 July	99.1	19.8
Nemastoma lugubre	1958	6 May	18 July	73.2	24.4
Odiellus palpinalis	1958	12 June	22 Sept	101.5	20.3
	1959	27 May	21 Sept	118.1	23.6
Oligolophus agrestis	1958	18 June	25 Sept	99.5	19.9
	1959	4 June	16 Sept	103.5	20.7
Oligolophus tridens	1958	19 June	16 Sept	88.9	17.8
	1959	2 June	8 Sept	97.9	19.6

days of each other. However, O. tridens had the shortest period of development, so that in both years it reached maturity earlier than the other two species.

In view of the uncertainty about the number of instars in M. lugubre (see Section II) the length of the developmental period cannot be estimated with any reliability, but on the assumption that four exist, the calculated period is 73·2 days, a figure considerably lower than that of any other species.

(d) Relationship between field temperatures, hatching periods and growth rates.

Figure 20 shows the average monthly air temperatures at the Durham University Observatory, situated three quarters of a mile from Great High Wood. This figure shows that the 1959 temperatures were consistently higher than those of 1958, a difference which was probably the major factor contributing to the earlier emergence of all species in 1959. However, it might also have been expected that the 1959 growth rates would have been slightly greater than those of 1958, but with the exception of M. morio the reverse occured, the growing period being slightly longer in 1959. Either the growth rates, as determined from the mean instar values, are too coarse a measure to

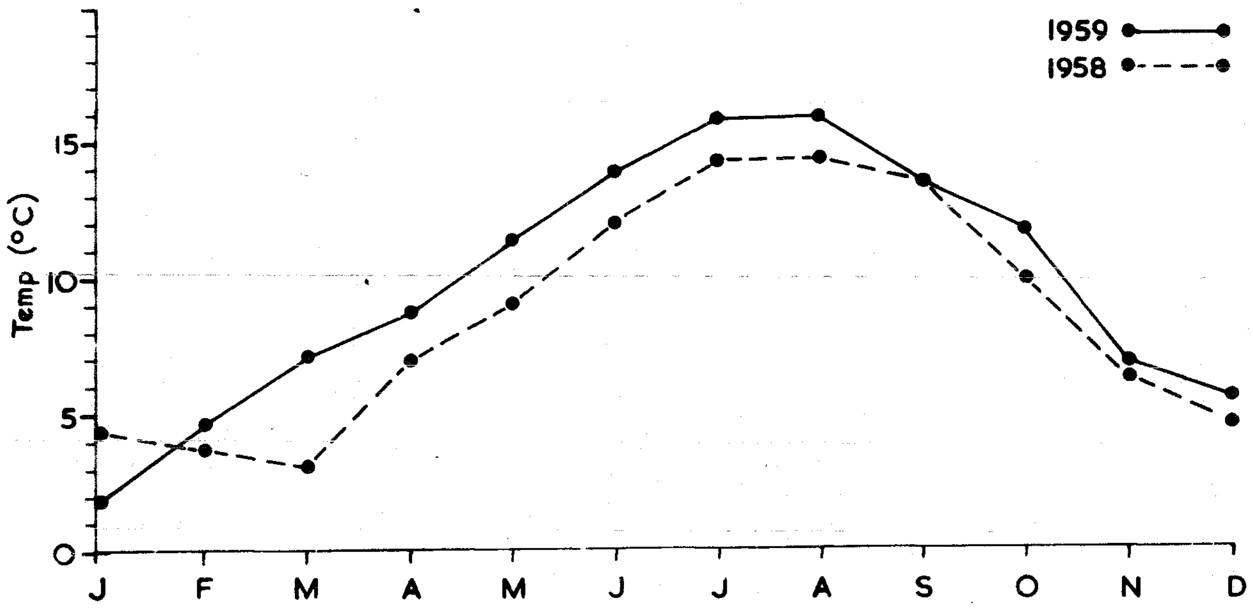


Fig. 20. Air temperatures recorded at the Durham University Observatory. Each point represents the average of the mean maximum and mean minimum monthly air temperatures.

show what would necessarily be relatively minor differences, or temperature differences within the limits illustrated by Fig. 20 would have had virtually no effect on the overall rate of growth. The former is the more likely explanation, but clearly, only carefully controlled laboratory experiments could decide the issue.

4. Seasonal changes in population density.

(a) Variability between samples.

In all the species studied except N. lugubre there was very little variation between the numbers obtained from each of the eight quadrats on any one occasion, and consequently, only the totals are given in Appendix A. The distribution of N. lugubre in 1958 however, was less uniform, the numbers from the quadrats on the floor of the gulley tending to be greater than from those on either side. This is illustrated by Fig. 21 which shows the total number of animals per quadrat per month. As the numbers in quadrats 5 and 6 tended to increase up to September, it is possible that individuals actually moved from the higher ground to the floor during the late spring and summer. In view of the high humidity requirements of this species (Todd 1949) this would not be surprising, as the water content of the deep litter on the gulley floor was always noticeably greater than that of the thinner litter layer found elsewhere.

To examine the variability between apparently identical samples, a detailed examination of one square metre of litter was carried out on 4 June 1960. A square in the region of station 5 was divided into sixteen smaller

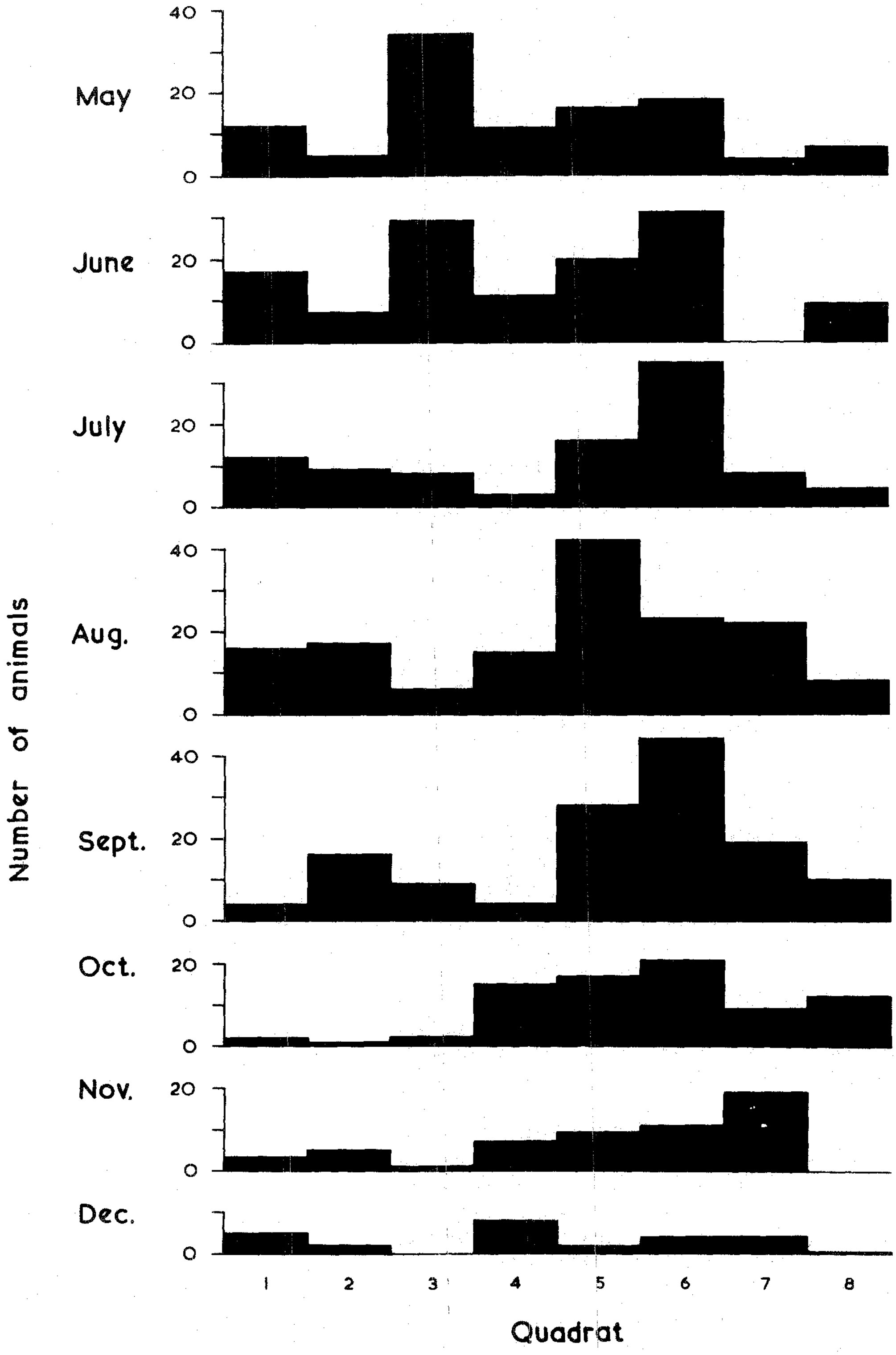


Fig. 21. Total number of Nemastoma lugubre per quadrat per month in 1958.

quadrats, each 25 cm square, and the litter from each was sorted separately. The results are given in Table 4. It can be seen from this table that each species was distributed fairly uniformly over the sixteen quadrats, although the numbers were generally too low to examine the variability statistically. However a χ^2 test carried out on the combined totals from each quadrat showed the absence of any significant heterogeneity ($P>0{\cdot}05$)

Thus, with the exception of N. lugubre, the distribution of each of the species studied, is likely to have beem fairly uniform throughout the litter of the study area, and the data of appendix A presumably give a reasonable approximation to the true population density. These data were therefore used as the basis for the construction of Figs. 22 to 28 in which changes in population density per square metre are represented by the lines joining the solid circles, and changes in dry weight per square metre by the lines joining the open circles. Although shown together on each graph, densities and weights are described separately.

(b) Seasonal density changes in the total harvest-spider population.

Seasonal changes in the combined numbers of all six species of harvest-spider found within the study area are

Table 4. The numbers of harvest-spiders from each of 16 similar quadrats from Great High Wood, 4 June, 1960.

Quadrat	*Lacinius ephippiatus*	*Mitopus morio*	*Nemastoma lugubre*	*Odiellus palpinalis*	*Oligolophus agrestis*	*Oligolophus tridens*	Totals	X^2
1	3	3	6	5	4	1	22	0.02
2	0	1	8	1	7	1	18	0.51
3	1	4	0	6	8	3	22	0.02
4	0	9	4	6	1	6	26	1.04
5	1	3	1	9	7	3	24	0.34
6	2	3	2	2	4	0	13	3.23
7	0	4	2	5	7	3	21	0
8	1	3	1	3	8	2	18	0.51
9	0	2	1	3	5	1	12	4.05
10	1	1	2	6	9	0	19	0.25
11	1	5	0	11	7	7	31	4.41
12	2	6	1	4	12	3	28	2.11
13	1	5	4	3	9	1	23	0.13
14	0	3	4	3	6	3	19	0.25
15	0	8	2	3	5	2	20	0.08
16	1	4	3	6	9	2	25	0.64
Totals	14	64	41	76	108	38	341	17.59

$\sum X^2 = 17.59$ $P > 0.05$

illustrated in Fig. 22. It can be seen from this that the maximum 1958 density of approximately 130 animals per square metre was recorded in early July, the maximum 1959 density of approximately 170 animals per square metre in mid-June.

(c) Seasonal density changes in individual species populations.

The results for individual species are illustrated in Figs. 23 to 28. A small vertical arrow shows the first sample from which juveniles were completely absent, the whole population by then being adult. In general, the changes in population density followed a similar trend in allspecies in both 1958 and 1959. Following the first appearance of each species, the numbers increased rapidly, reaching a maximum while the samples still comprised second and third instar juveniles. There was more variability following this peak, but in general the numbers declined steadily throughout the rest of the season.

The study in Great High Wood was confined to the ground layer population, no attempt having been made to investigate the nature of any vertical migration. However, assuming the behaviour of animals in this study area to have been similar to that described for Nannys Plantation (Section IVa), L. ephippiatus, N. lugubre, O. palpinalis and O. tridens

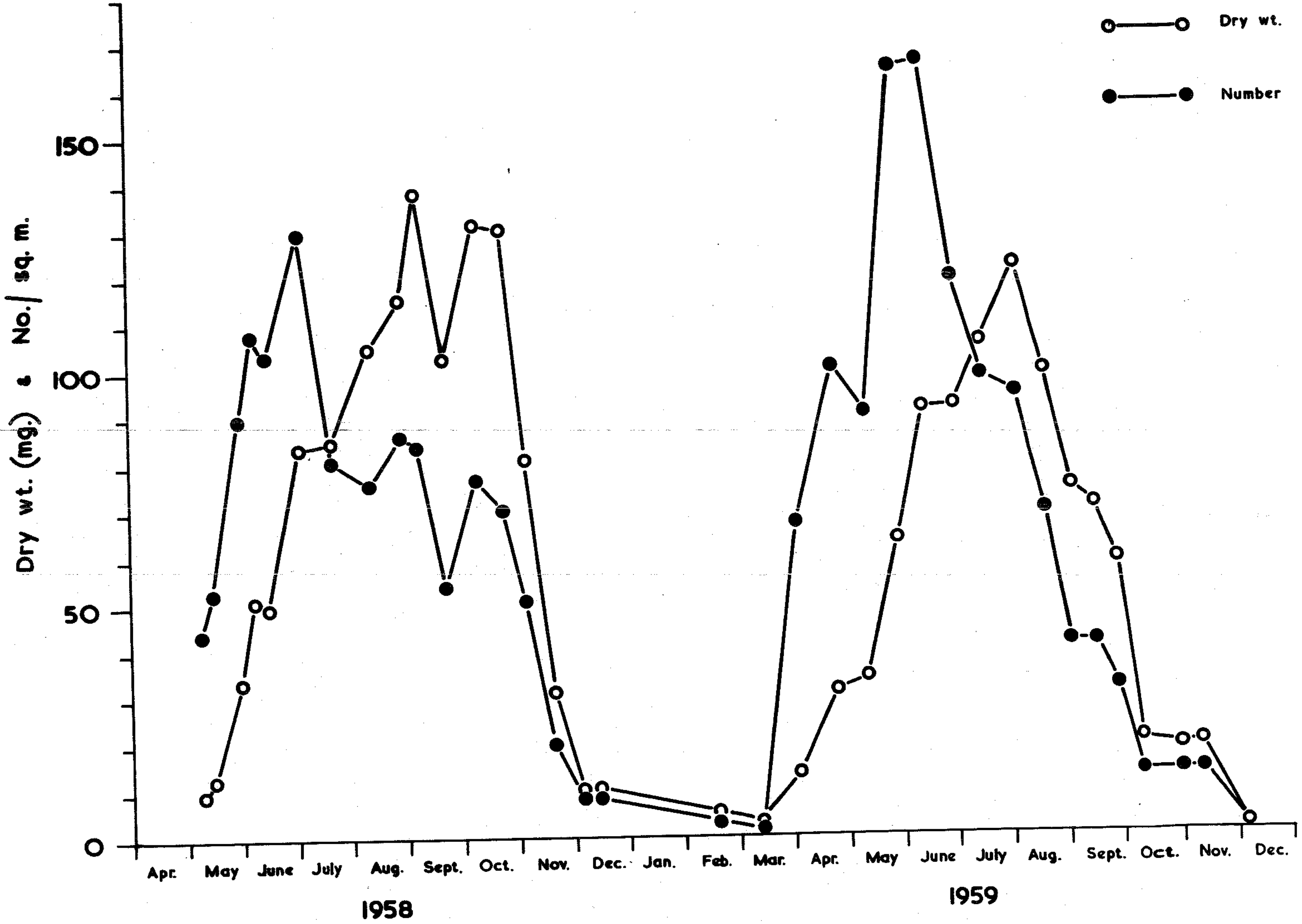


Fig. 22. Seasonal changes in population density and dry weight of the total harvest-spider population.

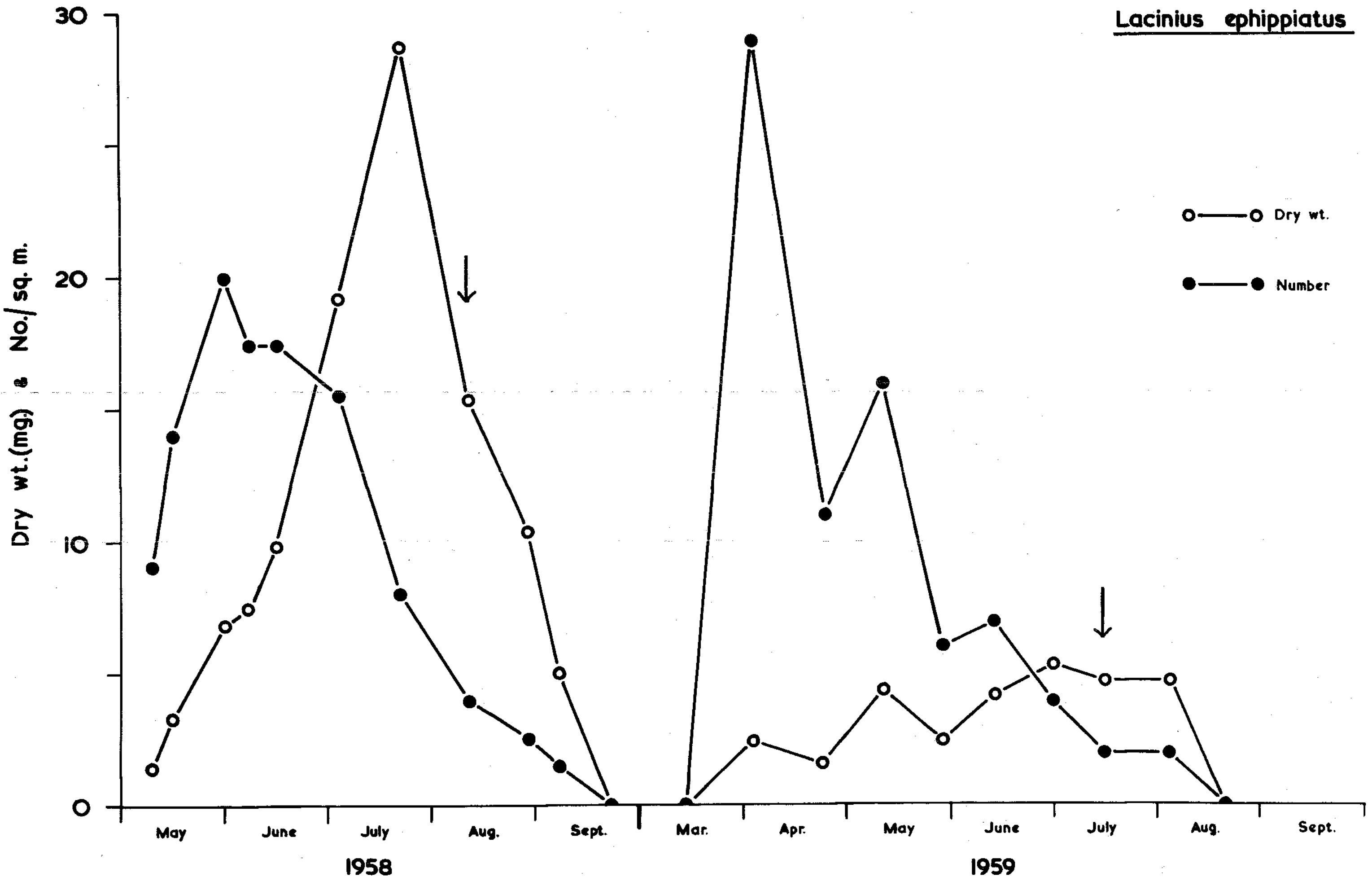


Fig. 23. Seasonal changes in population density and dry weight. The vertical arrows indicate the first samples containing only adults.

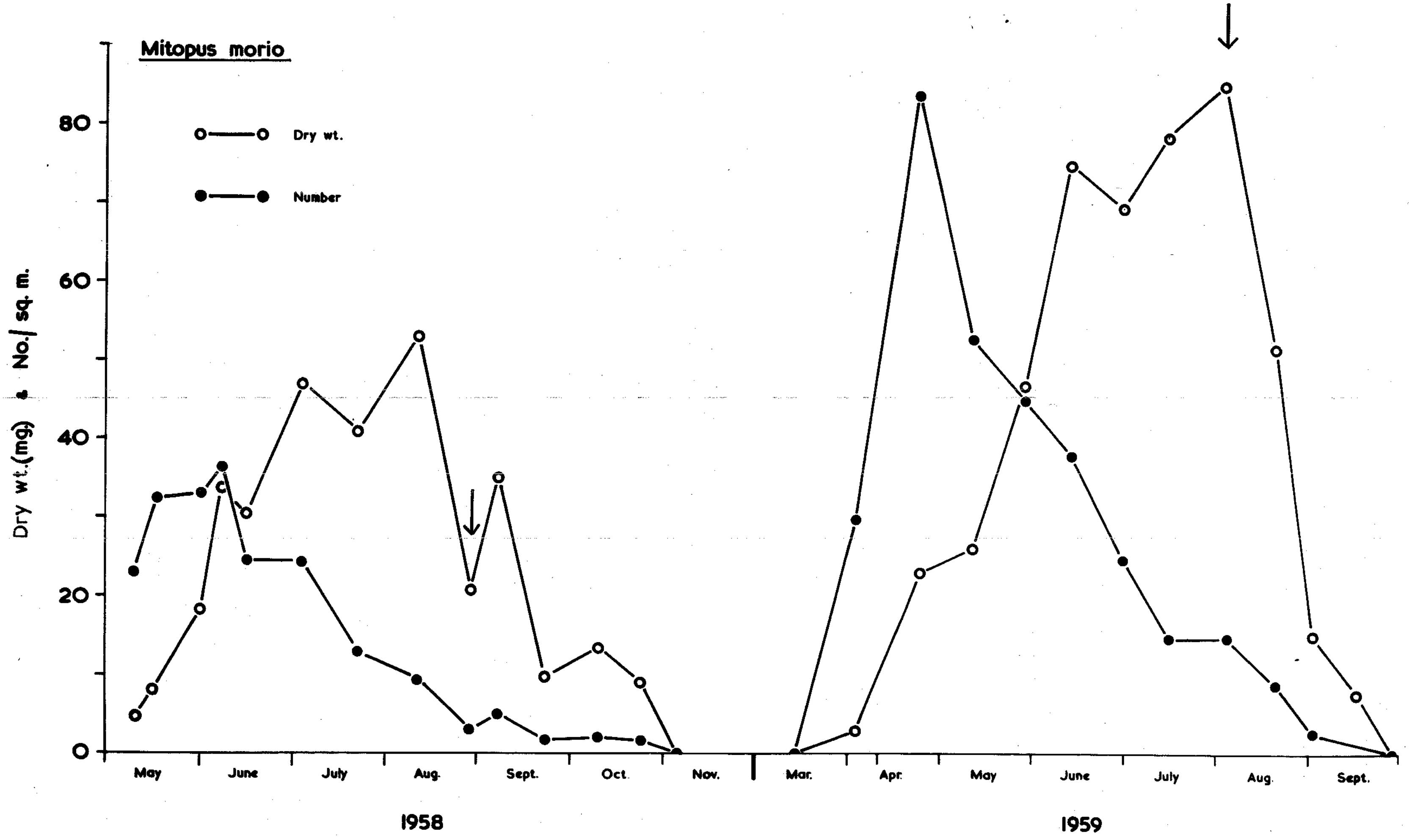


Fig. 24. Seasonal changes in population density and dry weight. The vertical arrows indicate the first samples containing only adults.

Nemastoma lugubre

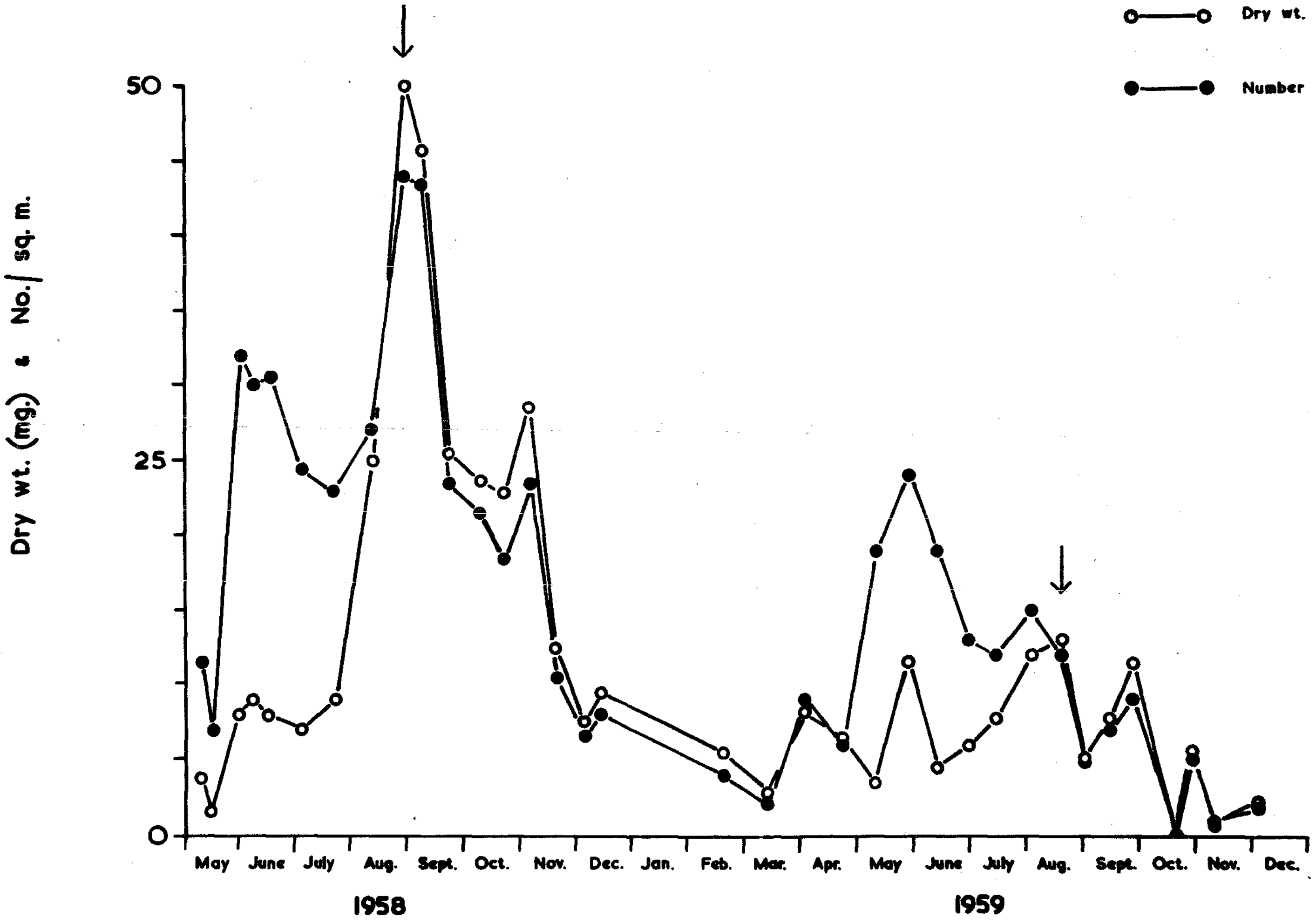


Fig. 25. Seasonal changes in population density and dry weight. The vertical arrows indicate the first samples containing only adults.

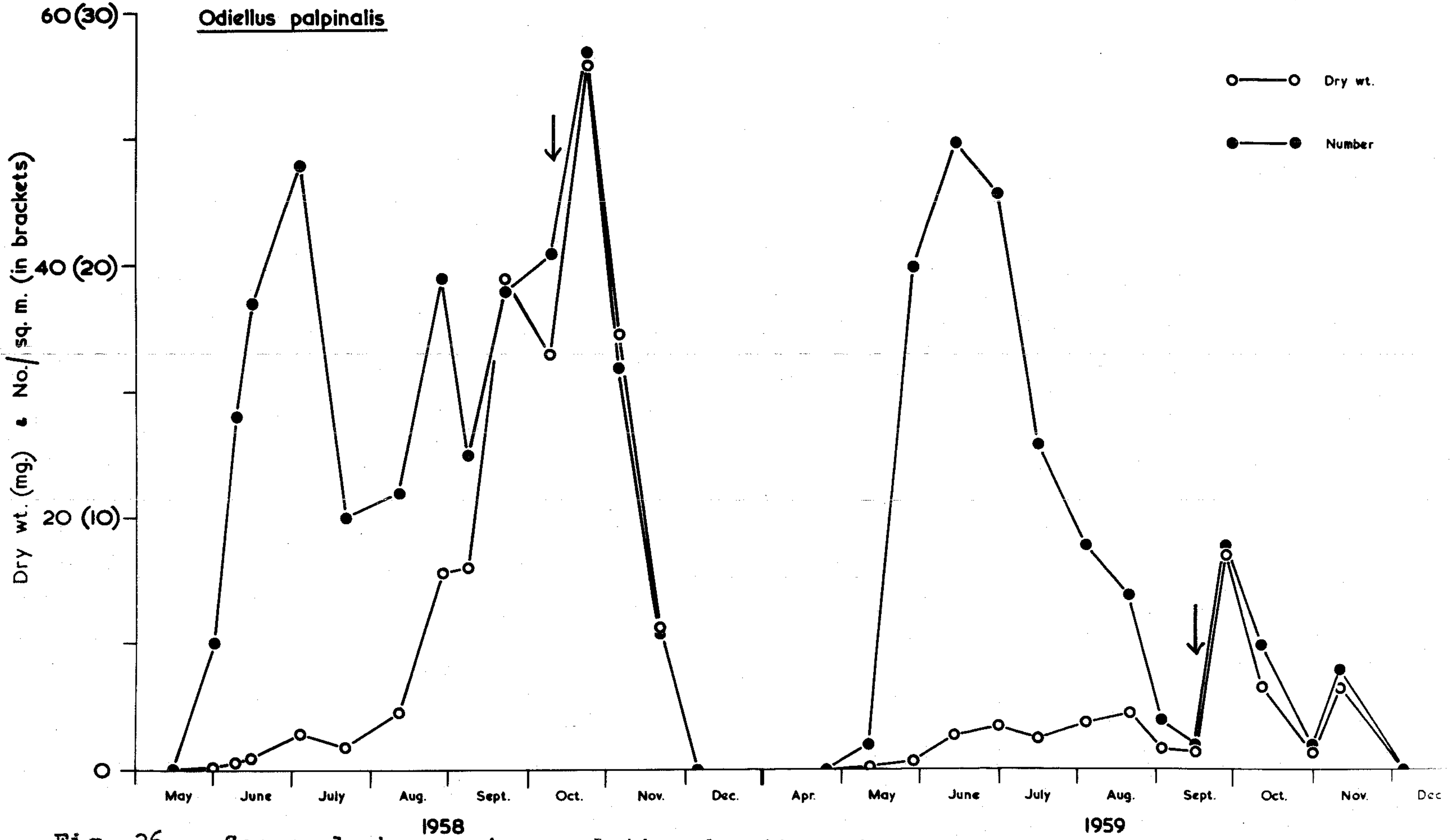


Fig. 26. Seasonal changes in population density and dry weight. The vertical arrows indicate the first samples containing only adults.

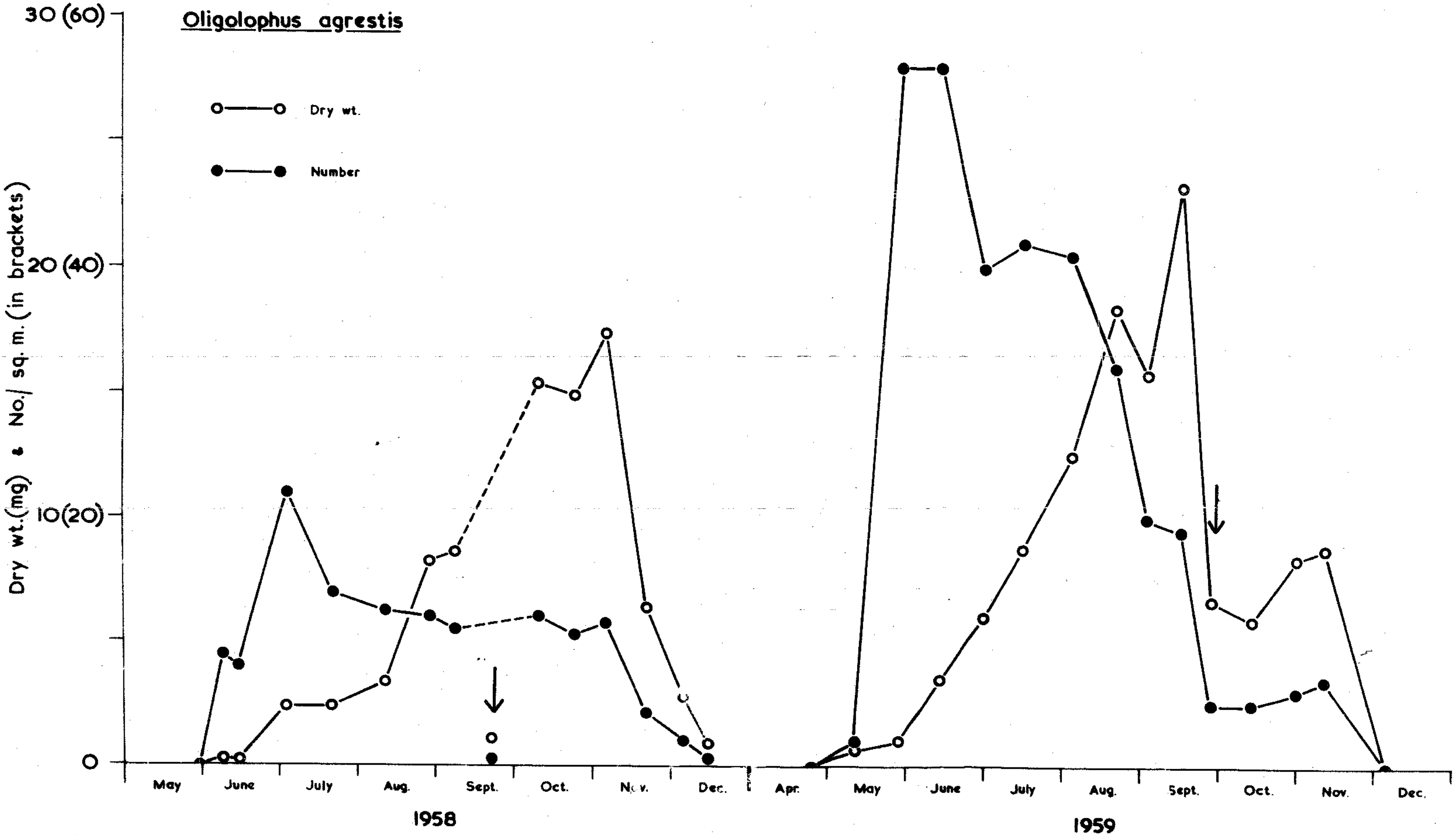


Fig. 27. Seasonal changes in population density and dry weight. The vertical arrows indicate the first samples containing only adults.

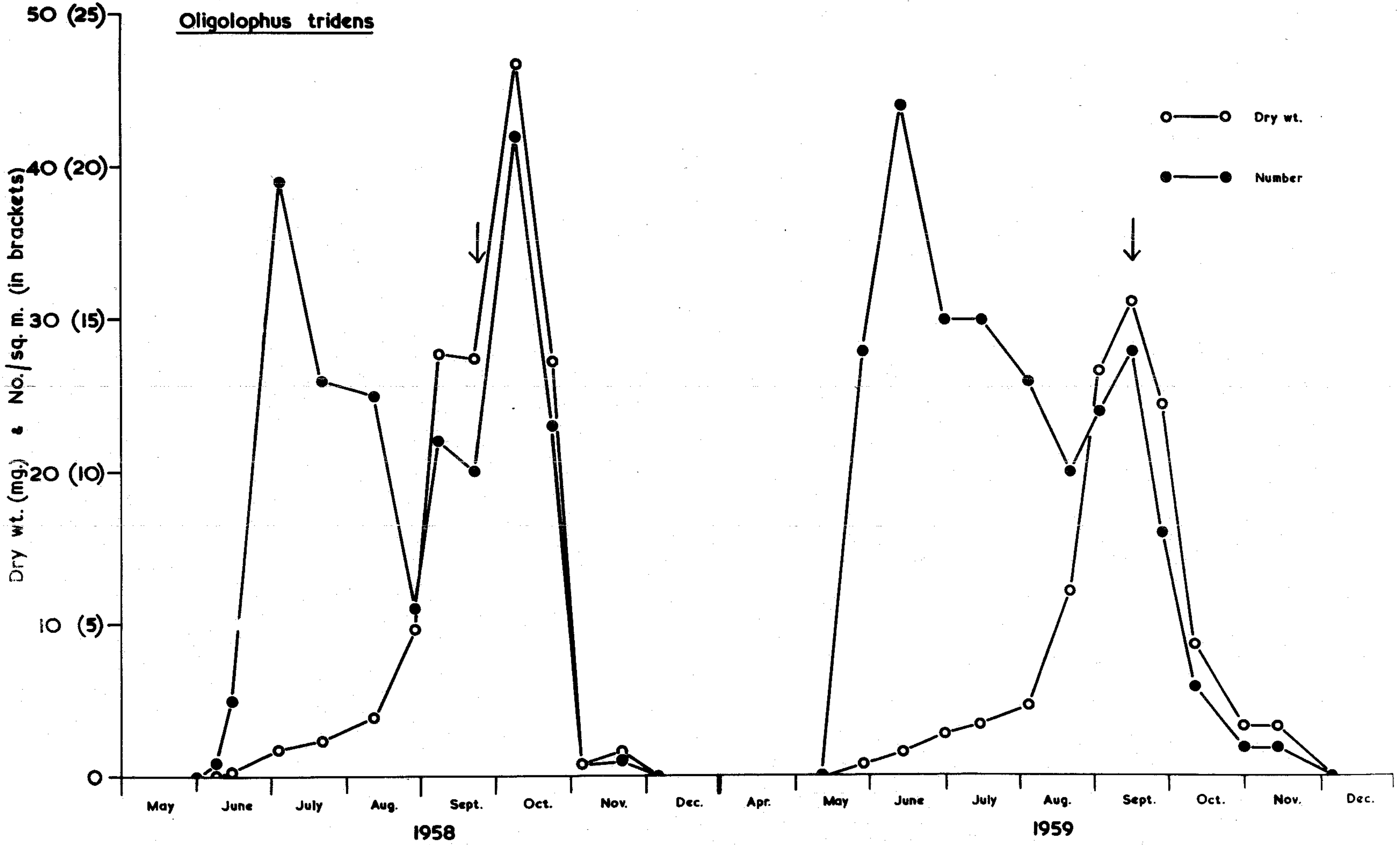


Fig. 28. Seasonal changes in population density and dry weight. The vertical arrows indicate the first samples containing only adults.

would have been exclusively ground dwelling in habit, while *M. morio* and *O. agrestis* would have begun to move above the ground layer in the penultimate instar. The seasonal decline in numbers in the ground dwelling species would therefore directly reflect the effect of mortality on each species population, while the decline in *M. morio* and *O. agrestis* would also reflect losses due to vertical migration.

Several deviations from the general trend were apparent. Some, for example the low number of *O.agrestis* in late June 1958, were perhaps simply due to chance, but a more satisfactory explanation must be offered for others. Smaller harvest-spiders often stuck to the leaves of damp litter, as a result of which some were perhaps overlooked during sorting. However, this explanation alone cannot account for the sudden but temporary drop in numbers in the summer months of 1958 in *O. palpinalis*, *O.agrestis* and *O. tridens*: the lowest densities did not coincide in time, occuring in the three species respectively on 21 July, 22 September and 28 August. The temporary loss of *O. agrestis* from the ground layer could be attributed to vertical migration, but in the assumed absence of any such migration in the other two species, no sound explanation can be put forward.

It is believed that the efficiency of sampling was fairly high, there being no apparent difficulty in picking out even the earliest instars from the leaf litter. Nevertheless, in both years, the numbers of O. palpinalis and O. tridens rose sharply soon after the whole population had reached maturity, suggesting that the order of sampling efficiency was slightly higher for adults then for juveniles.

(d) Comparison of population densities in 1958 and 1959.

Clearly differences exist between the graphs of 1958 and 1959 and to enable reliable conclusions to be drawn, for each species the population densities over the two years were compared by the x^2 test. The total area sampled on each occasion was reduced from 2 sq. m. in 1958 to 1 sq. m in 1959, and it is apparently statistically unsound to compare the densities directly by simply doubling the figures of 1959 or halving those of 1958. Therefore the original data were used in a formula provided by Dr. O. W. Kurth (Department of Mathematics, University of Durham) which takes into account the change of sample size. This has the form:

$$x^2 = \frac{(k_1 - k_2)^2}{2\,(k_1 + k_2)}$$

where k_1 and k_2 are the totals from the eight quadrats in 1958 and 1959 respectively.

It has already been shown that in all the species studied except N. lugubre, the course of the life history in 1959 was approximately two weeks in advance of that of 1958, and the results were arranged so that comparisons were made between the densities at corresponding stages of the life history rather than at similar times of the year. For example, the totals of 30 May 1958 were not compared with the totals of 28 May 1959, but with those of 11 May 1959. Because of this, no dates are shown in table 5, but the first figure in each column represents the density at the start of the life history, the last, that towards the end of the life history.

Using the basic equation, two series of tests were carried out (Table 5), the results of both being taken into account in the subsequent description. Test I examines the possibility that the differences between the individual totals, k_1 and k_2, are greater than would be expected by chance alone. Test II, while operating quite independently of the single terms, does the same for the grand totals Σk_1 and Σk_2.

In both migratory species, the overall 1959 densities were significantly greater than those of 1958 (test II, $P<0 \cdot 001$).

Table 5 Comparison of 1958 and 1959 population densities for all species collected in Great High Wood (see text for explanation).

	k_1(1958)	k_2(1959)	χ^2	Level of significance (P)
Lacinius ephippiatus - test 1	18	11	0·27	ns
	40	16	0·57	ns
	35	6	6·45	<0·05
	35	7	5·25	<0·05
	31	4	7·55	<0·01
	24	4	4·57	<0·05
Lacinius ephippiatus - test II	183	48	16·38	<0·001
Mitopus morio - test 1	47	84	55·89	<0·001
	66	53	6·72	<0·01
	73	45	1·22	ns
	49	38	4·19	<0·05
	44	25	0·01	ns
	26	15	0·19	ns
	6	15	13·71	<0·001
	20	13	0·54	ns
Mitopus morio - test II	336	288	46·15	<0·001

Table 5 Continued.

	k_1(1958)	k_2(1959)	χ^2	Level of significance (P)
Nemastoma lugubre - test 1	22	6	1·78	ns
	64	19	4·07	<0·05
	60	24	0·86	ns
	61	19	3·31	ns
	49	13	4·27	<0·05
	46	12	4·17	<0·05
	88	15	16·33	<0·001
	87	12	20·04	<0·001
	90	12	21·35	<0·001
	118	6	45·31	<0·001
Nemastoma lugubre - test II	685	138	101·63	<0·001
Odiellus palpinalis - test I	38	21	0·14	ns
	37	25	1·36	ns
	48	23	0·03	ns
	20	13	0·54	ns
	39	9	4·59	<0·05
	63	9	14·06	<0·001
	98	6	35·56	<0·001
	43	5	11·34	<0·001
Odiellus palpinalis - Test II	386	111	27·06	<0·001

Table 5 continued.

	k_1 (1958)	k_2 (1959)	X^2	Level of significance (P)
Oligolophus agrestis - test I	18	58	63·18	<0·001
	16	56	64·00	<0·001
	44	40	7·71	<0·01
	28	42	22·40	<0·001
	24	41	25·88	<0·001
	22	32	16·33	<0·001
	25	39	21·94	<0·001
	56	18	2·70	ns
Oligolophus agrestis - test II	233	326	157·03	<0·001
Oligolophus tridens - test I	12	36	37·50	<0·001
	39	15	0·75	ns
	26	15	0·15	ms
	11	13	2·52	ns
	22	10	0·06	ns
	20	12	0·25	ns
	42	14	1·75	ns
	25	5	3·75	ns
Oligolophus tridens - test II	197	120	2·92	ns

The results of test I show that in O. agrestis, other than at the end of the season, the 1959 densities were consistently and significantly greater than those of 1958, this difference probably having arisen initially from a relatively greater 'hatch' in the second year. In M. morio the results of test I similarly suggest that the number hatching in 1959 was greater than that of the previous year, but as the first two samples of 1958 appear to have been influenced by human error, the magnitude of this difference is probably exaggerated. The subsequent population density levels were slightly, although not usually significantly greater in 1959.

Of the four non-migrating species, the overall density of O. tridens was about the same in both years (test II, $P > 0{\cdot}05$), while the other three were relatively less abundant in 1959 (test II, $P < 0{\cdot}001$). The results of test 1 show that, apart from O. tridens, the densities were very similar at the start of the life history, indicating a similar hatch in both years, but the subsequent mortality among juveniles of the 1959 generations of L. ephippiatus, O. palpinalis and N. lugubre would seem to have been so heavy that relatively few survived through to maturity.

(e) Relationship between moisture content of litter and mortality rates.

In the above comparison of population densities over both years, those of 1959 were the highest of the two in the migratory species and lowest of the two in the purely ground dwelling species, and it is thought that much of this difference would have been associated with the unusually dry summer of 1959. It can be seen from Fig. 29 that the monthly rainfall in that year was generally less than that of 1958, and the full effect of this difference on the moisture content of the litter was especially noticeable from May to September. During this period in 1958 the litter was always quite damp other than at the surface, but in 1959, as a result of the implied long intervals between rainfall (Table 6), it was frequently dust dry even where deepest along the floor of the gulley.

If the degree of resistance to water loss is an important factor in determining the vertical distribution of a species, the two migratory species might be expected to have been better adapted towards this end, and hence to surviving the dry summer of 1959 than were the four non-migratory species. Laboratory experiments described later showed that the survival time (and by implication, resistance to water loss) at any one humidity was greatest

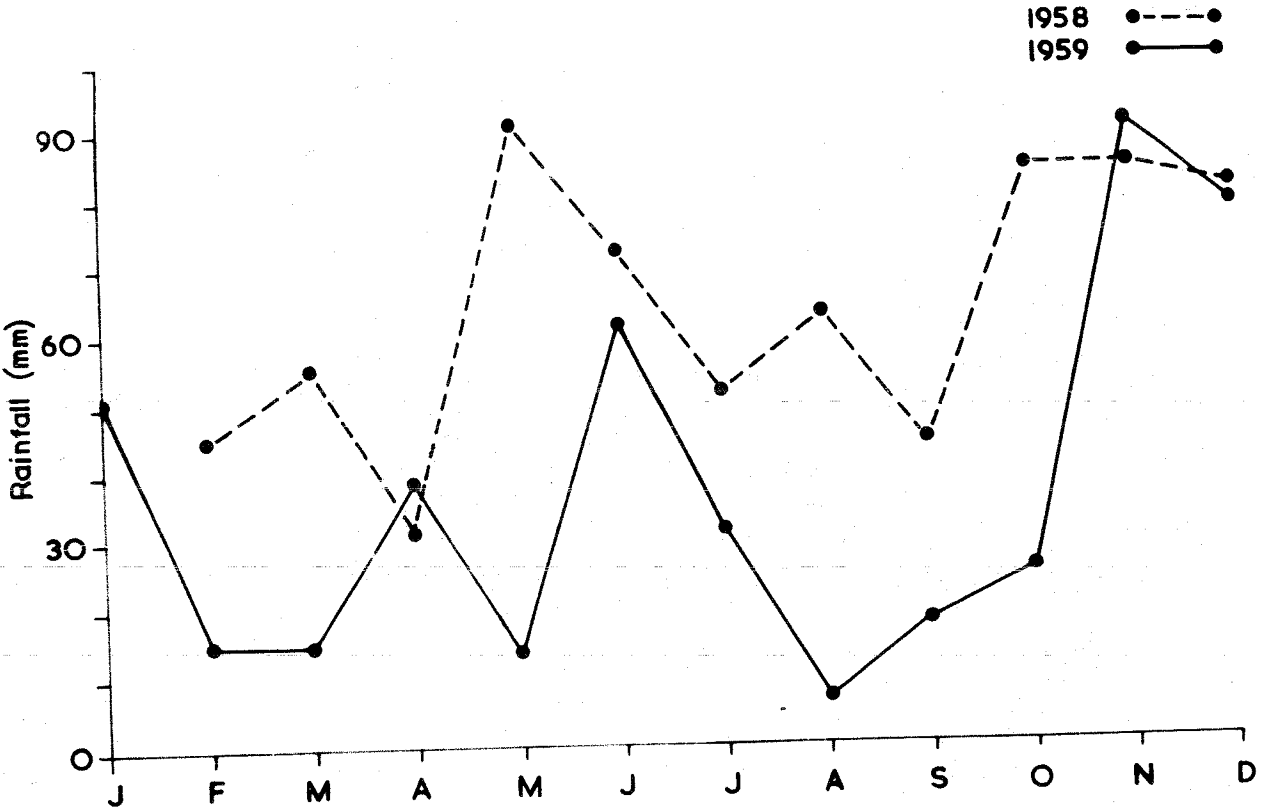


Fig. 29. Total rainfall per month recorded at the Durham University Observatory.

in *O. agrestis*, slightly less in *M. morio* and *O. tridens* and least in *L. ephippiatus* (*O. palpinalis* was not tested).

Table 6 Number of days of rainfall per month recorded at the Durham University Observatory.

Month	1958	1959
Jan	13	17
Feb	No record	6
Mar	19	14
Apr	15	13
May	19	7
June	19	13
July	21	8
Aug	20	4
Sept	16	5
Oct	12	15
Nov	15	20
Dec	20	28

It therefore seems probable that the drier conditions of 1959 produced a level of juvenile mortality which was highest in the three exclusively ground dwelling species, least in the two migratory species and intermediate between the two extremes in *O. tridens* which is not completely restricted to the ground layer.

5. Seasonal changes in dry weight.

(a) Determination of mean dry weight per instar.

(i) Method.

The data of Appendix A in conjunction with the mean dry weight of each instar, were used to estimate the total dry weight of each species per square metre on each sampling occasion. In M. morio dry weights were determined by weighing all specimens separately: ten individuals of the second, third and fourth instars and ten of each sex for the remaining instars were weighed after having been dried for 7 days in an electric oven maintained at 90° to 95° C. In the case of the remaining species, specimens were not weighed individually, but in groups of ten per instar. The sexes were treated separately only in the adults, but whenever identification was possible, each sample of juveniles consisted of five males and five females.

(ii) Results.

The mean dry weight of all instars except the first, of all six species examined are given in Table 7. As only M. morio specimens were weighed separately, standard errors of the means could only be calculated for this species.

The results for M. morio are also illustrated graphically in Fig. 30, where the logarithm of mean weight is plotted against instar. The solid circles represent the mean

Table 7. Mean dry weight (mg) of the instars of six species of harvest-spider. The figure in parentheses for Nemastoma lugubre V refers to the preadult juveniles, the other figures to the adults of each sex.

Instar	Mitopus morio	Lacinius ephippiatus	Oligolophus agrestis	Oligolophus tridens	Odiellus Palpinalis	Nemastoma lugubre	
II	0.1032 ± 0.0071	0.0830	0.0284	0.0646	0.0346	0.0248	
III	0.2758 ± 0.0433	0.2539	0.1173	0.0946	0.1169	0.0448	
IV	0.6681 ± 0.0362	0.4000	0.2242	0.2051	0.1860	0.1188	
V male	0.9130 ± 0.0795	0.6046	0.2992	0.3666	0.4132	(0.2232)	0.8000
V female	1.9717 ± 0.2369						1.3800
VI male	2.1192 ± 0.1588	1.3333	0.6850	1.1500	0.8100	-	
VI female	3.6935 ± 0.3175						
VII male	5.1819 ± 0.4777	2.37	1.06	1.90	1.33	-	
VII female	7.8035 ± 0.7409	5.31	1.74	3.43	2.60	-	

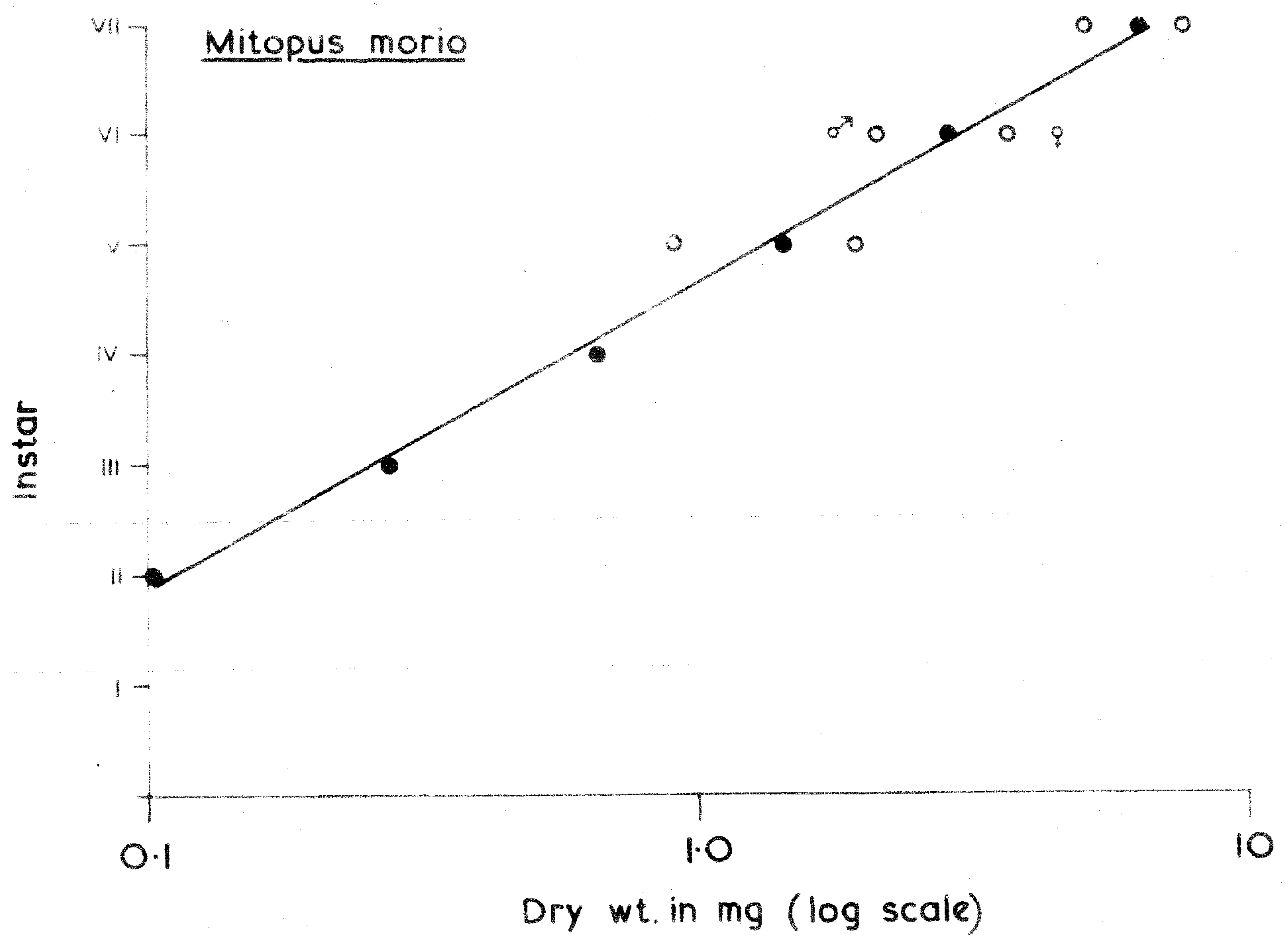


Fig. 30. Increase of mean dry weight with age. The open circles to the left and right of the line represent, respectively, the weight of males and females separately. The solid circles represent the mean weight of the sexes combined.

weight based on all the weighed individuals of each instar, the open circles, in the case of the fifth, sixth and seventh instars, the mean weight of each sex. The existence of a straight line relationship between log. mean weight and instar is clear.

(b) Seasonal dry weight changes in the total harvest-spider population.

The combined dry weights per square metre of all six species of harvest-spider studied are represented by the open circles in figure 22. This figure shows that in both years, the maximum dry weight was found about two months after the maximum population density.

(c) Seasonal dry weight changes in individual species populations.

As with the density changes, those of dry weight were generally very similar among the species, rising steadily to reach a maximum around the time of the final moult, several months after the initial population density peak.

In M. morio (Fig. 24), although it has been shown that the population density in 1959 was not generally significantly greater than that of 1958, the contribution of late juveniles and adults towards the total dry weight was such that throughout the summer of 1959 the dry weights were considerably greater than those of the previous year.

In *O. tridens* (Fig. 28), changes in dry weight and density were very similar in both years, but in the three other ground dwelling species, *L. ephippiatus* (Fig. 23), *O. palpinalis* (Fig. 26) and *N. lugubre* (Fig. 25) the relatively higher 1959 juvenile mortality rates are clearly emphasised by the dry weight figures: at the time when maturity was reached in 1959 (*L. ephippiatus* and *N. lugubre* July - August, *O. palpinalis* September - October) these weights were only a fraction of those of the previous year.

6. Comparison of the densities and weights with the data of Todd (1949)

It is of interest to compare the numbers and weights in the present study with those of Todd (1949) based on material collected in Oxfordshire.

Of the species common to both studies, the maximum numbers obtained in Durham were generally greater than those recorded by Todd, either from a similar habitat (habitat II - beech wood) or from any of the fourteen different habitats examined. For example, the maximum density of M. morio recorded in Oxfordshire was 13 per sq. m (habitat 4, June 1946) whereas in the Durham Study, the maximum densities in 1958 and 1959 respectively, were 36·5 and 45·0 per sq. m (Todds figure are not clearly stated to represent the density per sq. m, although examination of the text suggests this to be the case).

The maximum density recorded by Todd of all species of harvest-spider in the ground layer samples, was 49 per sq m (June 1946) whereas the corresponding maxima of 130 (3 July 1958) and 167 per sq m (13 June 1959) in the present study were approximately three times greater.

This difference is obviously reflected by corresponding weight differences, but as dry weights were used in this study and wet weights in the Oxford study, no direct comparison with Todd's maximum biomass figure is possible. However, Phillipson (1962) has given the mean live weight of several instars of M. morio and O. tridens, and by using his data, the relationship between live and dry weights can be examined. On 7 September 1958 when the highest dry weight (138·1 mg) of either year was found, the collection comprised only adults of the three 'spring species' but both penultimate and final instars of the three 'summer species'. Comparison of the live and dry weights of adult M. morio, a spring species, shows the dry weight to have been only 20·8 % of the total live weight, while in the case of the penultimate and final instars of O. tridens, a summer species, this proportion was, on average, 18·9%. Assuming therefore, the proportion to have been approximately 20% in all species, by multiplying the maximum dry weight figure by 5, the maximum biomass in terms of live weight per sq m would seem to have been approximately 690 mg. This is over three times greater than the corresponding figure of 213 mg per sq m given by Todd.

IVa BEHAVIOUR STUDIES: FIELD WORK

IVa. BEHAVIOUR STUDIES: FIELD WORK

1. The study area.

(a) General features.

The field behaviour studies were carried out in Nanny's Plantation, a small area of mixed deciduous - coniferous woodland situated some 7 miles to the east of Durham City (National Grid Reference NZ 390386). The wood, which forms a square with an area of about 80 acres, lies on clay which slopes gently downwards from south to north. It was planted about a century ago, and for the last twenty years was so badly neglected that the original drainage system has completely broken down. As a result, a thick layer of raw acid humus has accumulated, ranging in pH from 4.40 at the higher (southern) side to 4.32 at the lower (northern) side. Largely because of the poor drainage and high acidity the flora of the whole area was impoverished, and from a forestry point of view the plantation, in 1959, was in a very bad condition. However in being left undisturbed for so long the flora and fauna would presumably change only slightly from one year to the next, and the area was therefore quite suitable for the present work.

(b) The flora.

The area chosen for study was a 100 x 50 metre rectangle near the centre of the plantation (Plate 2). The flora was essentially similar throughout, although the relative abundence of the species differed slightly between the northern and southern halves (subsequently referred to as regions 1 and 2).

The tree layer comprised both deciduous and coniferous trees which, in general, were well separated giving a fairly open canopy. Oak (*Quercus petraea* (Mattuschka) Liebl.) and ash (*Fraxinus excelsior* L.) predominated in region 2, pine (*Pinus sylvestris* L.), larch (*Larix decidua* Mill.), beech (*Fagus sylvatica* L.) and oak in region 1. Small birch trees (*Betula pubescens* Ehrh. with a little *B. verrucosa* Ehrh.), many of them dead or dying, occurred equally throughout both regions. Many small patches of birch scrub bushes about 1.5 m tall, and fewer large groups of ferns (*Dryopteris austriaca* (Jacq.) Woynar and *D. filix-mas* (L.) Schott in equal amounts with a little *Athyrium filix - femina* (L.) Roth) were scattered at random over both regions. Long straggling stems of bramble (*Rubus fruticosus* L.) occurred uniformly but sparsely throughout the whole area.

Plate 2. Part of the study area in Nannys Plantation seen from the north.

Three grasses, *Anthoxanthum odoratum* L., *Dechampsia flexuosa* (L.) Trin. and *D. caespitosa* (L.) Beauv. were co-dominant in region 1, and although present in similar proportions in region 2, this region was being invaded by *Holcus mollis* L., patches of which were clearly spreading outwards and replacing the other grasses.

The remaining components of the flora occurred only occasionally or rarely: they were *Agrostis tenuis* Sibth., *Blechnum spicant* (L.) Roth., *Epilobium augustifolium* (L.) Scop., *Galium hercynicum* Weigel, *Holcus lanatus* L., *Luzula multiflora* (Retz.) Lej., *Oxalis acetosella* L., *Potentilla erecta* (L.) Räusch. and *Viola riviniana* Rchb.

(c) Microhabitat classification.

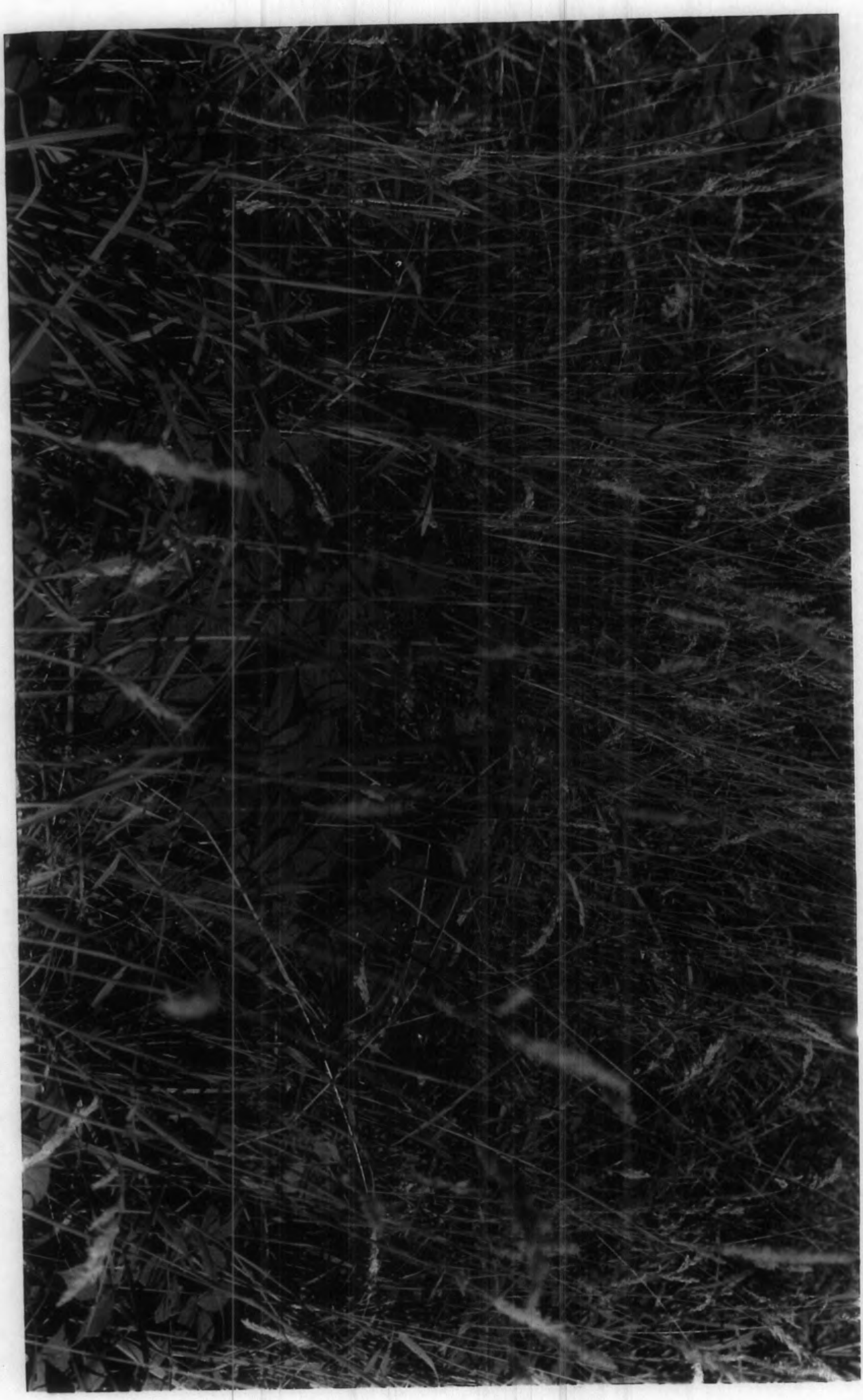
A slight modification at the microhabitat classification described by Todd (1949) and Elton and Miller (1954) was followed in the present study. The vegetation was considered to form six distinct vertical layers:

The ground layer - the leaf litter and ground surface vegetation.

The surface layer - the bramble leaves approximately 10 cm above the ground surface (Plate 3).

The field layer - the tall grasses (Plate 3).

Plate 3. The vegetation of the surface layer (brambles) and the field layer (tall grasses).

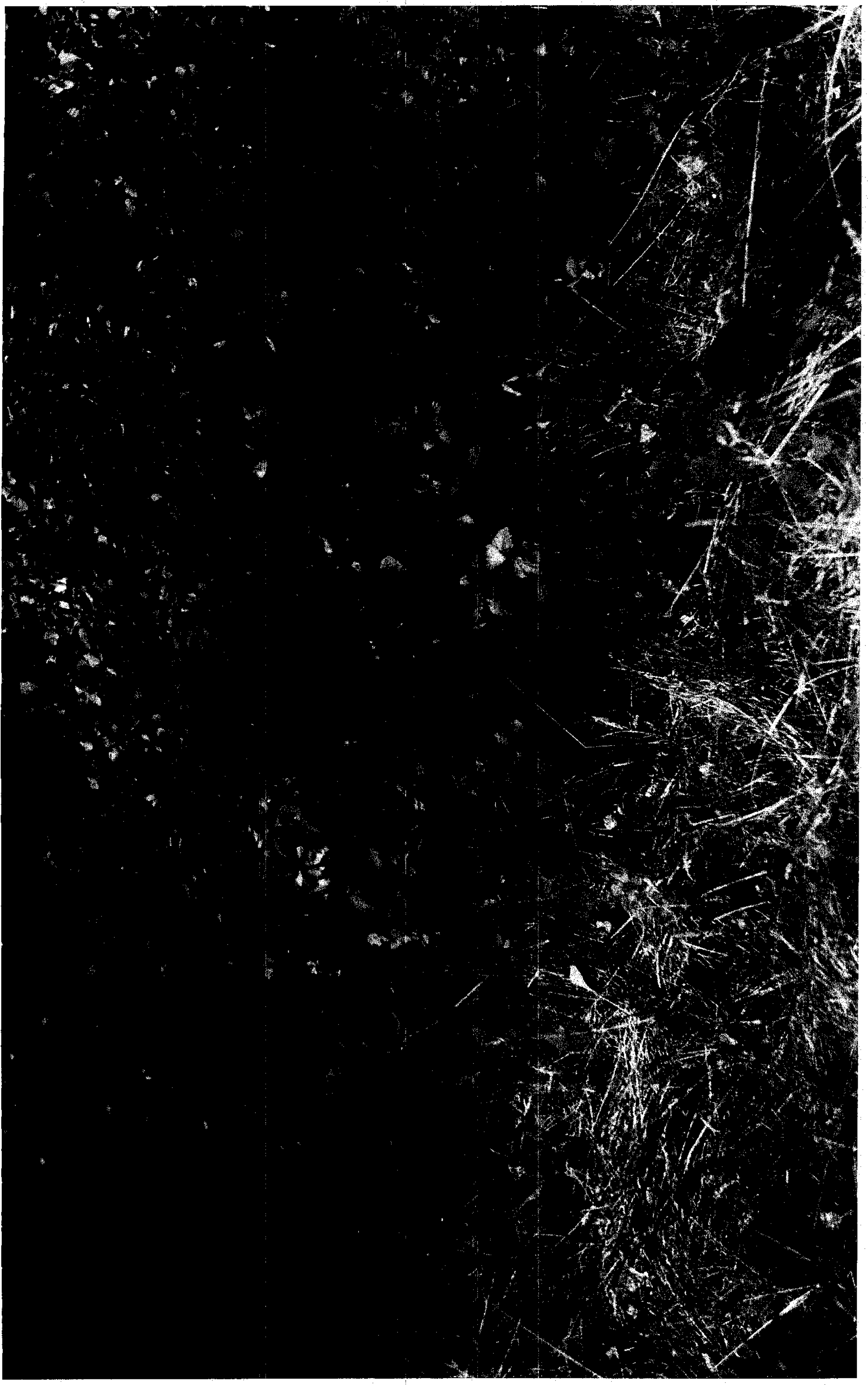


The shrub layer - the birch scrub bushes (Plate 4).

The tree trunks - the trunks of ash, beech, birch and oak trees.

The tree branches - low leafy branches of beech, birch and oak trees.

Plate 4. Birch scrub bushes of the shrub layer.



2. Measurement of physical factors.

In order to assess the effect of physical factors on behaviour, readings of light intensity, temperature and relative humidity were taken whenever sampling was carried out.

(a) Light

(i) Method.

Incident light readings were taken on a Weston Master 11 photo-electric exposure meter by pointing it upwards to a part of the sky well away from the sun.

(ii) Results.

Sampling was carried out during six half-hour periods in each 24 hour day-night cycle, these periods being chosen in relation to light intensity (Table 8). This Table shows the range of light values recorded at the start of corresponding periods from June to October. Because of the progressive time (GMT) change over the five months, only the period numbers are used in subsequent description.

Table 8. Light values and times at the start of each period.

Period number	The part of the day-night cycle	Range of light values (candles per sq ft)	Time in mid-June (GMT)	Time in mid-October (GMT)
1	Midday	400 - 800	1200h	1200h
2	Just after sunset	6.5 - 25	2100h	1715h
3	Just after dusk	0	2145h	1800h
4	Midnight	0	2400h	2400h
5	Just after dawn	6.5 - 25	0315h	0615h
6	Just after sunrise	100 - 400	0400h	0700h

(b) Temperature and relative humidity.

(i) Method

Temperature readings were made by using ordinary 'full immersion' type mercury thermometers.

Relative humidities were recorded by the use of cobalt chloride and cobalt thiocyanate papers, the former to cover the range 40% to 70% R.H., the latter the range 70% to 100% R.H. (Solomon 1945 and 1957). The papers were cut up into 2·5 x 1 cm strips and each strip was suspended by a hook of wire from the cork of a 5 x 2·5 cm glass specimen tube from which the bottom had been removed. After exposure, the papers were rapidly transfered to liquid paraffin and the relative humidity to which they had been exposed was determined by comparison with a set of standards. Solomon pointed out that the papers should be exposed for two hours in order to obtain a truly accurate reading, but it was found that provided they had been previously stored at 70% R.H. they gave a reading to within 1% or 2% R.H. after only fifteen minutes exposure. In practise therefore, although the papers were placed in position in the field about two hours before the start of each period, under continuously changing conditions the humidity reading given would have represented that prevailing about a quarter of an hour before fixation. For the present purpose, this is considered to have been the same as that occuring at the time of sampling.

Both thermometers and humidity papers were used in the same position throughout the season. They were sited as follows:

1. Inserted just below the surface of the litter (the ground layer).
2. Resting on bramble leaves just above the surface of the litter (the surface layer).
3. Suspended from the branch of a birch scrub bush, approximately 1 metre above the surface (the shrub layer).
4. Suspended from a low branch of a beech tree, about 2 metres above the surface (the tree layer).

During the hours of sunlight, care was taken to ensure that only shade temperatures and humidities were recorded at positions 2, 3, and 4. At each of these positions two glass tubes were fixed together, one with cobalt chloride paper, the other with cobalt thiocyanate paper, in order to cover the whole range of humidities likely to be encountered.

(ii) Results.

Temperature and relative humidity readings were taken at each of the above levels on each sampling occasion. The results are given in Table 9, and those of 16 and 25 June, and 27 August, being particularly relevant to subsequent discussion, are illustrated graphically (Fig. 31). In this Figure the results for the shrub layer are not

Table 9. Temperatures and relative humidities in the study area in Nanny's Plantation.

Date	Period number	Percentage relative humidity				Temperature (°C)			
		Ground layer	Surface layer	Shrub layer	Tree branches	Ground layer	Surface layer	Shrub layer	Tree Branches
16.6.59	1	97	65	61	64	11.5	20.5	19.0	18.5
	2	97	72	74	76	11.0	14.0	15.0	15.0
	3	97	82	79	82	10.0	9.5	11.5	11.5
	4	98	95	93	90	10.0	8.5	11.0	10.5
	5	96	97	93	90	9.5	10.5	11.5	11.5
	6	95	95	86	86	9.5	11.5	12.5	13.0
25.6.59	1	93	73	67	75	13.0	23.0	20.0	16.5
	2	93	88	87	91	12.5	15.0	15.5	14.5
	3	97	96	97	96	10.5	11.5	11.0	12.0
	4	100	100	100	100	10.5	10.5	11.0	11.5
	5	100	100	100	100	10.5	11.0	11.5	11.5
	6	100	100	100	100	11.0	12.5	12.5	12.5
7.7.59	1	84	63	59	55	13.5	25.5	22.0	23.0
	2	87	86	78	66	13.5	17.5	19.0	19.5
	3	94	92	90	83	13.0	14.0	15.0	16.0
	4	96	95	92	87	12.0	13.5	14.0	14.5
	5	96	96	96	91	12.0	12.5	13.0	14.0
	6	96	93	81	77	12.5	16.0	19.0	18.5

Table 9. Temperatures and relative humidities in the study area in Nanny's Plantation.

Date	Period number	Percentage relative humidity				Temperature (°C)			
		Ground layer	Surface layer	Shrub layer	Tree Branches	Ground layer	Surface layer	Shrub layer	Tree Branches
13.7.59	1	85	75	74	66	12.0	16.0	15.5	15.5
	2	86	78	77	77	11.5	11.0	11.5	12.0
	3	89	82	79	81	11.0	9.0	9.0	9.5
	4	99	94	87	84	9.5	7.0	6.5	7.5
	5	100	97	95	90	9.5	5.5	5.5	6.5
	6	100	98	84	84	10.0	9.5	10.0	10.5
24.7.59	1	81	59	56	57	13.0	23.0	22.5	21.5
	2	87	88	87	85	13.0	14.5	14.5	15.0
	3	95	96	95	94	12.5	11.0	12.5	13.0
	4	100	100	100	100	12.0	10.5	11.5	11.5
	5	100	100	100	97	11.5	10.0	11.0	11.0
	6	100	96	87	84	12.0	17.0	18.0	17.5
31.7.59	1	84	83	82	79	12.0	17.0	16.0	15.0
	2	92	92	91	90	12.0	11.5	12.0	12.5
	3	100	98	98	98	11.5	8.5	9.0	9.5
	4	100	100	100	100	11.0	8.0	8.5	9.0
	5	100	96	100	94	11.0	10.5	11.0	11.0
	6	98	91	95	87	11.0	12.0	12.0	12.0

Table 9. Temperatures and relative humidities in the study area in Nanny's Plantation.

Date	Period number	Percentage relative humidity				Temperature (°C)			
		Ground layer	Surface layer	Shrub layer	Tree branches	Ground layer	Surface layer	Shrub layer	Tree branches
7.8.59	1	95	87	79	78	12.5	18.0	18.5	18.0
	2	95	95	98	98	12.5	14.5	14.0	15.0
	3	100	100	98	98	12.5	13.0	13.5	14.0
	4	100	100	100	100	12.0	10.0	10.5	10.5
	5	100	100	100	100	11.5	11.5	11.5	11.5
	6	100	100	100	100	12.0	14.0	13.5	13.5
16.8.59	1	89	65	65	64	12.5	20.0	22.5	22.5
	2	95	89	84	83	12.5	14.0	15.0	15.0
	3	100	100	100	96	12.0	11.0	12.5	13.0
	4	100	100	100	100	11.5	9.0	10.9	10.0
	5	100	100	100	100	11.0	8.0	9.0	9.5
	6	98	97	94	96	11.5	14.5	17.0	17.0
27.8.59	1	89	70	65	64	13.0	20.0	20.0	19.5
	2	90	82	81	81	13.0	15.5	16.0	16.5
	3	93	90	89	88	12.5	13.0	14.0	14.5
	4	100	94	92	92	12.5	12.0	12.0	12.0
	5	100	96	93	93	12.5	10.5	10.5	11.0
	6	93	93	93	85	12.5	13.0	12.5	12.5

Table 9. Temperatures and relative humidities in the sutdy area in Nanny's Plantation.

Date	Period number	Percentage relative humidity				Temperature (°C)			
		Ground layer	Surface layer	Shrub layer	Tree branches	Ground layer	Surface layer	Shrub layer	Tree branches
5.9.59	1	79	78	73	73	12.5	21.0	20.0	18.5
	2	84	89	89	89	11.5	11.0	11.0	12.5
	3	93	96	96	96	11.5	10.5	11.0	11.0
	4	100	100	100	100	11.0	9.0	8.5	9.5
	5	100	100	100	100	10.5	7.0	7.5	8.5
	6	100	92	90	88	10.5	12.0	12.0	13.5
16.9.59	1	Humidity papers contaminated				11.0	16.0	15.5	15.0
	2	" " "				11.0	12.5	13.0	13.5
	4	100	100	100	100	11.0	12.5	12.5	12.5
	6	100	100	100	100	11.0	14.5	14.0	14.0
25.9.59	1	72	68	66	66	11.5	12.5	13.0	13.0
	2	100	100	100	100	11.0	5.5	5.5	7.0
	4	100	100	100	100	10.5	4.4	4.5	5.5
	6	100	100	100	100	10.0	8.0	10.0	10.5
9.10.59	1	100	97	98	98	11.0	14.5	15.5	15.0
	2	100	100	100	100	11.0	13.0	13.0	13.0
	4	100	100	100	100	10.5	11.0	12.0	12.5
	6	100	100	100	100	11.0	12.5	12.5	13.0

Table 9 Continued.

Temperatures and relative humidities in the study area in Nanny's Plantation.

Date	Period number	Percentage relative humidity				Temperature (^{o}C)			
		Ground layer	Surface layer	Shrub layer	Tree branches	Ground layer	Surface layer	Shrub layer	Tree branches
20.10.59	1	90	87	83	83	10.0	10.5	11.5	12.0
	2	92	87	83	83	10.0	6.5	7.5	9.0
	4	100	97	95	96	9.5	6.5	7.0	7.5
	6	100	96	93	93	10.0	12.0	11.5	11.5
3.11.59	1	100	90	85	82	9.0	10.0	10.5	10.5
	6	100	100	100	100	8.0	5.0	5.0	5.0

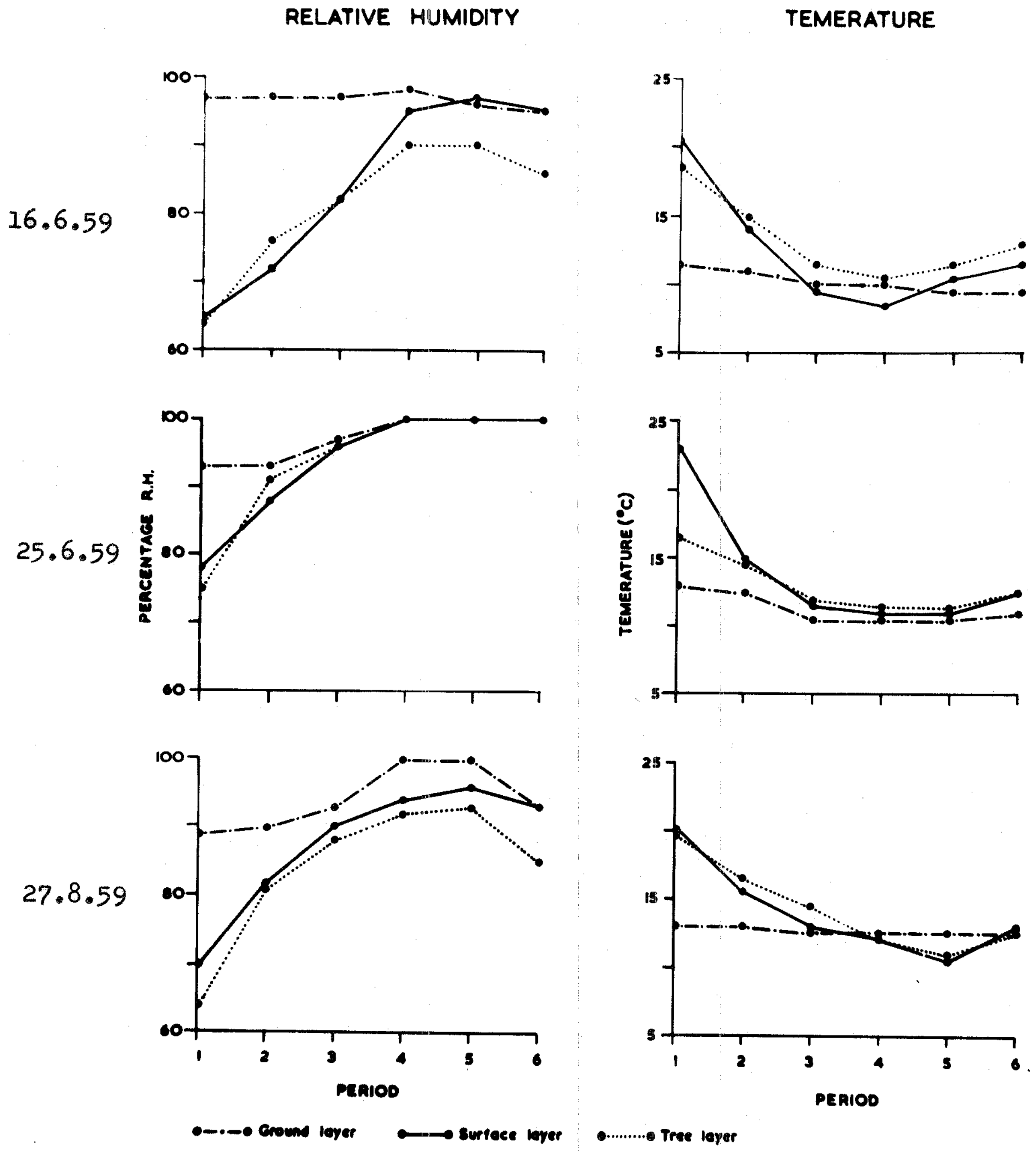


Fig. 31. Temperature and relative humidity at each period of the diel in Nannys Plantation.

illustrated, these being almost the same as those for the tree layer.

It can be seen that the greatest changes of temperature and humidity were recorded around sunset (period 2) and sunrise (period 6) rather than at the times following the disappearance and reappearance of light (periods 3 and 5 respectively). Nevertheless, as a result of the lag in cooling and warming following sunset and sunrise, conditions continued to change steadily in one direction throughout the night and early morning and only began to change in the reverse direction after sunrise. Thus, the lowest temperatures and highest humidities were frequently recorded just after dawn (period 5) rather than during the hours of darkness. (Two exceptions to the general trend were apperent: on 25 June and 7 August the relative humidity at all levels was still 100% R.H. at period 6, due, on both occasions, to the presence of heavy early morning mist).

Over any one 24 hour period, the smallest fluctuations of temperature and humidity occured in the ground layer, the greatest in the surface or shrub layers. This is illustrated by Table 10 which shows the range between the mean maximum and mean minimum temperatures and humidities calculated from the readings over the period 16 June to 5 September.

Table 10. The average range of the 24 hourly temperature and relative humidity fluctuations.

		Mean maximum	Mean minimum	Difference between mean max. and mean min.
Temperature (°C)	Ground layer	12.5	10.9	1.6
	Surface layer	20.4	9.1	11.3
	Shrub layer	19.6	9.7	9.9
	Tree layer	18.8	10.2	8.6
Relative humidity (% R.H.)	Ground layer	99.6	87.4	12.2
	Surface layer	98.7	71.8	26.9
	Shrub layer	97.7	68.1	29.6
	Tree layer	96.4	67.5	28.9

The relative stability of the ground layer temperatures (average range of 1.6°C) was frequently responsible for an inversion in the order of field temperatures during the 24 hours: it can be seen from Table 9 that air temperatures at midday were always considerably higher than those of the ground, while during the night or early morning air temperatures usually fell slightly below those of the ground.

At the other extreme, 24 hourly temperatures were least stable in the surface layer (average range of 11.3°C) and it was here that the highest day and lowest night temperatures were generally found. The surface layer therefore probably represented the 'outer active surface' described by Geiger (1951); that is, the surface at which most of the sun's energy is absorbed and from which most of it is radiated.

Unlike the order of temperature, that of relative humidity remained fairly similar at each of the six periods during the 24 hours, the highest being recorded in the ground layer, the lowest among the tree branches.

3. Sampling methods for the different field levels.

A preliminary survey carried out in 1958 indicated that the density of harvest-spiders in the study area was never very large, and as the investigation had to be carried out single handed, the resulting field work programme was necessarily a compromise between the needs for large numbers and for frequent sampling.

Particular attention was paid to vertical migration in Mitopus morio and Oligolophus agrestis. The programme involved samplimg each of the six vegetational levels described above at each of the six periods during a single 24 hour day - night cycle (Table 8). This was carried out two or three times a month from the time of the first sign of vertical migration in June 1959 until the end of the year.

As each level was sampled by a different method, the actual numbers from each were not directly comparable. It was felt however that the pattern of vertical migration would be satisfactorily indicated by comparing the relative changes, with time, in the numbers of harvest-spiders at the various levels.

All animals were transferred, soon after capture, to specimen tubes containing 70% alcohol together with previously written labels giving the date, time (G.M.T.) and sample details. The tubes were returned to the laboratory for examination.

(a) Ground layer.

Pitfall trapping was the obvious method by which regular and frequent samples of harvest-spiders could be obtained from the ground layer. Several types of simple pitfall traps were tested. At first the bottoms of dried milk tins were smeared with a thin layer of 'Stiktite' and sunk in the ground with the rims at ground surface level. However, leaves and other debris made it difficult to pick off animals from the grease. The same tins were then used with 3 cm of water in the bottom, but although this method gave large captures, harvest-spiders were also seen to climb up the walls and escape. Finally glass jars 10.5 cm across by 8.5 cm deep were used. Their inside walls were polished with a dry cloth to reduce the chance of escape. Several types of liquid were tried, including dilute formalin, dilute alcohol and phenyl - mercuric -acetate solution, but the best was found to be a weak solution of a detergent. This was odourless and thus had obvious advantages over the other solutions Harvest-spiders were seen to sink below the surface immediately after falling into it, and were dead within about five minutes.

Accordingly, fifty pitfall traps containing detergent solution were set out in the field. Half were placed in the upper part of the study area (region 2), half in the lower part (region 1). Both sets were arranged in five rows of five, the jars in each row being 5 metres apart, the rows 10 metres apart. The jars of the fourth and fifth rows in region 1 were among ferns and leaf litter. Those of the first three rows in region 1 and of all rows in region 2 were among grass.

It would have taken too much time to record the numbers caught in individual traps. and only the totals from regions 1 and 2 were noted separately. Each trap was emptied by swirling the liquid and its contents round the jar then rapidly pouring through a fine silk gauze, the liquid being collected for re-use. At first this was done six times a day, but the difficulty of locating and emptying fifty jars during the hours of darkness made it necessary to reduce the frequency of this operation. The catch was therefore taken over two 12 hour periods: the 'night' period extending from 2000 h to 0800 h G.M.T. and including both crepuscular periods, and the 'day' period, extending f^rom 0800 h to 2000 h G.M.T. which was in continuous day -light throug^hout.

(b) Surface layer

This layer was sampled by picking off all harvest-spiders seen during a standard ten minute search of the bramble leaves. Searches during the night were made using the light from a 6 volt car headlight. Although this light caused harvest-spiders to 'freeze', they were still so conspicuous that nocturnal searching was unlikely to have been less efficient than searching during the day.

(c) Field layer

The tall grass was sampled by the use of a sweepnet. A standard fifty sweeps with a 90 cm diameter net was made at each of the six periods. The path to be taken at each was decided in advance to avoid covering the same ground twice.

The distribution of the tall grass over the study area was rather patchy. To test for any associated uneveness in the distribution of harvest-spiders, five samples (each of fifty sweeps) were taken in different parts of the study area.between 1200 h and 1300 h G.M.T. on 25 June 1958. Only *Mitopus morio* was found and the results are given in Table II.

Table 11. Comparison of the numbers of *Mitopus morio* from five similar field layer samples.

Sample number	Total. *M. morio*
1	8
2	14
3	18
4	8
5	12

$\chi^2 = 5.32$ $P > 0.05$

A χ^2 test carried out on the totals gave a value of $P > 0.05$

showing the absence of any significant heterogeneity.

(d) Shrub layer.

The shrub layer was sampled by beating groups of ten bushes per sample over a large white sheet. Within the study area the bushes were confined to patches, each patch comprising ten to twenty bushes. It was hoped that the distribution of harvest-spiders among these patches would be fairly uniform so that any 24 hourly vertical migration could be detected simply by beating bushes from a different group at each of the six periods. To test for such uniformity, ten bushes from each of six different groups of scrub bushes (labelled A to F) were beaten between 1200 h and 1300 h G.M.T. on 25 June and 5 July 1958. The results, given im Table 12, show that although the numbers were rather small, no obvious lack of uniformity was detected by the X^2 test ($P > 0.05$)

Table 12. Comparison of the numbers of *Mitopus morio* from six similar shrub layer samples.

Group of bushes	25 June	5 July
A	11	5
B	8	9
C	3	7
D	7	4
E	3	3
F	4	5
X^2	8.64	4.27
P	>0.05	>0.05

The 1959 field studies were carried out on the assumption that at any one time the number of harvest-spiders in each group of ten bushes would be fairly similar. In 1960 it became apparent that adults of *Platybunus triangularis* (Herbst) were abundant in the shrub layer, and in the hope of gaining support for the above assumption all sixty bushes were beaten between 1200 h and 1300 h G.M.T. on 3 June, the numbers from each bush being recorded separately. A total of 106 specimens was collected and it can be seen from Table 13 that these were distributed fairly uniformly over the whole area.

Table 13. The numbers of *Platybunus triangularis* from each of sixty similar bushes.

Group of bushes	Bush 1	2	3	4	5	6	7	8	9	10	Totals
A	1	3	2	3	1	3	1	2	0	3	19
B	1	1	1	3	1	1	2	2	1	2	15
C	1	3	2	1	3	3	1	2	3	3	21
D	1	2	1	2	3	6	0	2	0	1	18
E	0	2	1	1	3	1	1	1	2	3	15
F	2	0	1	1	0	7	0	1	4	0	16

$\chi^2 = 1.69$

$P > 0.05$.

(c) Tree trunks.

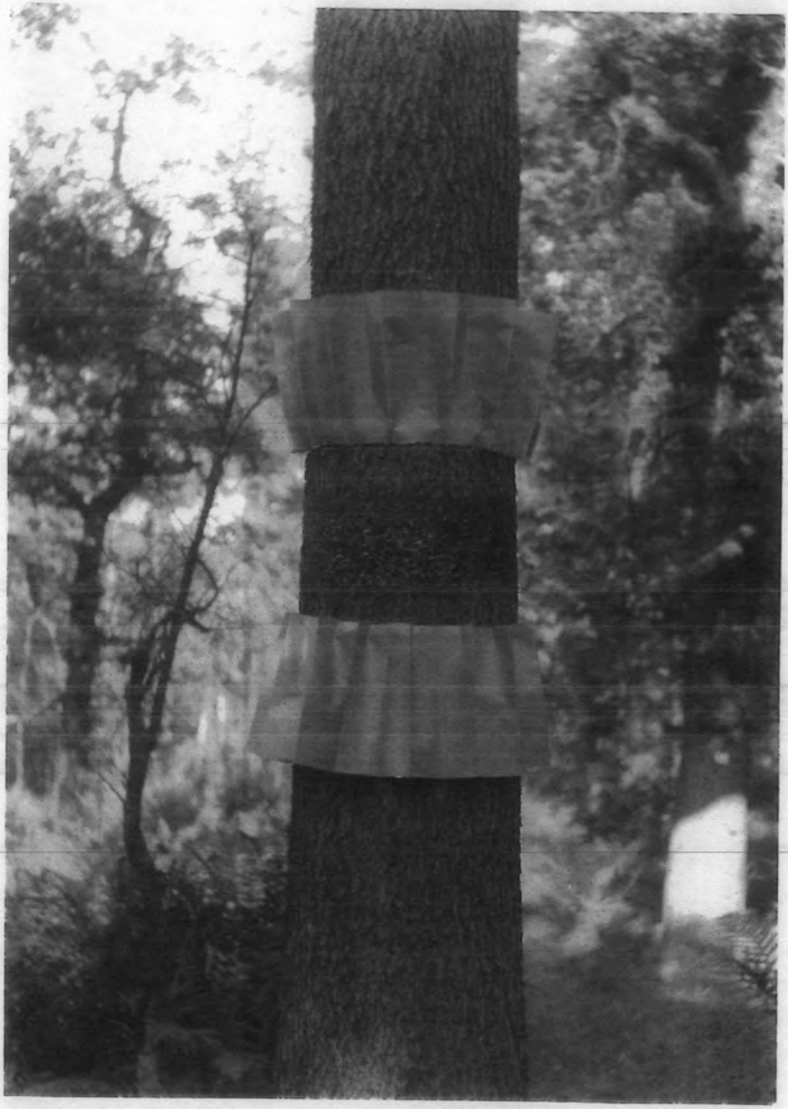
To investigate the nature of the movement of harvest-spiders between the ground and the tree canopy, it was decided to trap separately animals moving up and down the tree trunks. For convenience, several trapping methods were tested on the trees in Great High Wood rather than on those of the Nanny's Plantation study area.

In the first method a ring of 'Stiktite' about 30 cm deep was smeared round the trunks of five large beech trees at a height of 1·5 metres from the ground. It was thought that animals would move onto the grease and become trapped – those descending at the upper edge, those ascending at the lower edge of the grease. However, by the use of a red light for observation during the night, a strong avoidance reaction to 'Stiktite' was noted. The majority of animals (Mitopus morio and Oligolophus agrestis) halted on reaching the edge of the grease, over which they slowly 'waved' their second legs for a short time before moving away from it. They remained on the trunk, a few centimetres away from the grease, throughout the night, but around dawn returned either into the canopy or onto the ground.

Several other methods were tried and the one finally chosen is illustrated in Plate 5. Brown paper strips 20 cm wide were folded as shown, each fold being stapled together at one edge. By means of drawing pins the papers were fastened to the trunk with the stapled edge nearest the grease, one paper above and one below it. It was hoped that animals would walk under the paper placed in their path, and rather than turn round would remain between the paper and the trunk until dawn, when, by a combination of thigmotactic and negative phototactic responses, they would become effectively trapped. They could then be

Plate 5. The tree trunk grease and paper traps.

During sampling periods papers were fixed above and below the 'Stiktite' (right photograph). Between sampling periods they were removed and the 'Stiktite' was covered over (left photograph).



picked off by removing the papers during the day. Five large beech trees were chosen in Great High Wood and collections were made on 14 and 28 August 1958 after papers and grease had been in position for two days and nights on each occasion. By this time *M. morio* was rapidly disappearing from the field, but the total numbers of *M. morio* and *O. agrestis* trapped under the papers showed that the method was quite successful. The results are given in Table 14, the numbers trapped on the grease itself being shown in parentheses. Of a total of 285 harvest-spiders caught on 14 August only 7 were trapped on the grease, while on 28 August all 50 were caught under the papers.

This trapping method was employed in the 1959 field work in Nanny's Plantation. Twenty trees of similar girth were chosen and numbered individually. Grease bands were placed on the trunks of ten of these, the other ten were left untouched (Table 15). For the main study, trapping was carried out for a single 24 hour period about three times a month. The papers were put on the trees at 0800 h G.M.T., examined at about 2000 h the same day and again at 0800 h the following morning. The catch was therefore taken over two 12 hour periods, one including the hours of darkness, the other in continuous daylight. In between trapping, the folded papers were removed and an unfolded strip of brown paper placed over the grease to allow unrestricted movement on the trunks.

Table 14. The numbers of *Mitopus morio* and *Oligolophus agrestis* collected from the paper traps on each of five tree trunks. The numbers caught on the grease itself are shown in parentheses.

	Tree number	14 August		28 August	
		Mitopus morio	*Oligolophus agrestis*	*Mitopus morio*	*Oligolophus agrestis*
Lower papers	1	1	18	0	0
	2	1	28	1	1
	3	0	61 (1)	0	0
	4	1	68	0	3
	5	4 (2)	15	4	0
Upper papers	1	2	7 (1)	1	6
	2	1	13	1	6
	3	2	45 (1)	0	7
	4	1 (1)	10	2	17
	5	0	0 (1)	1	0
	Totals	13 (3)	265 (4)	10	40

Table 15. The species and girth of the trunk of each tree used for sampling in Nannys Plantation.

Greased trees			Ungreased trees		
Tree number	Species	Girth (cm)	Tree number	Species	Girth (cm)
1	Ash	142	2	Oak	142
3	Oak	156	4	Oak	165
5	Oak	140	6	Oak	107
7	Ash	164	8	Oak	146
9	Ash	128	10	Oak	171
11	Oak	110	12	Oak	98
13	Ash	139	14	Oak	170
15	Oak	180	16	Oak	141
17	Oak	141	18	Ash	192
19	Oak	164	20	Oak	119

In addition to the actual collections the number of animals on the trunks of both greased and ungreased trees was noted at each of the six periods during the 24 hour day - night cycle, using a red light for observation during darkness.

(f) Tree branches.

It was believed that 24 hourly changes in the numbers of harvest-spiders in the tree canopy would be indicated by beating ten low branches at each of the six periods. However, it proved almost impossible to locate and beat suitable branches during the hours of darkness and it was decided that the branches would be excluded from the main field programme. Sampling was simply carried out at midday, twice a month, during 1958 and 1959. The results, given in Table 16, show that at least at this time of day, *Mitopus morio* and *Oligolophus agrestis* were virtually absent from the lower branches in 1959.

Table 16. The numbers of *Mitopus morio* and *Oligolophus agrestis* from ten low tree branches. Each number is the total from two samples.

	Mitopus morio		*Oligolophus agrestis*	
	1958	1959	1958	1959
1-15 June	0	0	0	0
16-30 June	0	4	0	0
1-15 July	4	3	0	0
16-31 July	13	2	0	0
1-15 Aug	7	0	2	0
16-31 Aug	7	1	42	6
1-15 Sept	12	0	26	3
16-30 Sept	1	0	0	0
1-15 Oct	0	0	9	6
16-31 Oct	0	0	3	0
1-15 Nov	0	0	1	0
16-30 Nov	0	0	0	0

4. Results.

From the beginning of March 1959 up to the first week in June, both pitfall traps and grease/paper traps on the tree trunks were in position. These were examined by day and night generally once a week. At the same time collections were made by hand from the ground layer, the surface vegetation, the scrub bushes and overhanging tree branches. From these collections, made before the main sampling programme was started, the following purely qualitative information was obtained.

Platybunus triangularis and *Nemastoma lugubre* were present in the ground layer throughout, but in fairly small numbers. *Mitopus morio* and *Lacinius ephippiatus* first appeared, in the ground layer, in late March and early April followed by *Oligolophus agrestis*, *Oligolophus tridens* and *Odiellus palpinalis* in late May. Of all these species only *M. morio* was found above the ground layer before June, juveniles occasionally being seen on the litter surface. For example, on several rather damp nights in May fourth and fifth instar juveniles were seen 'sitting' on the surface of beech litter, while on two hot dry days in the same month large numbers of fifth instars were seen 'running' around on the litter surface in full sunlight. However, these cases were exceptional, and in general, juvenile *M. morio* were not found on or above the surface in March, April and May.

The first record of any species of harvest-spider occurring above the surface layer was made on 3 June when two sixth instar M. morio were found under the lower papers on the tree trunks. The first complete set of samples was taken a week later.

The results for each of the migratory species, M. morio and O. agrestis, are presented separately: the results for the ground dwelling species, L. ephippiatus, N. lugubre, O. palpinalis and O. tridens are then given together. Only nineteen specimens of P. triangularis were found from June to December 1959 and the results for this species are not given.

A. *Mitopus morio*

(a) Ground layer

(i) Comparison of catches of regions 1 and 2.

The results of the *M. morio* pitfall collections are shown in Table 17. The sexes of adults are given separately. Juveniles were not sexed and the instars are shown in parentheses.

Because of the floristic differences between the two regions and the possibility of associated differences in the distribution of *M. morio*, the two sets of results were first compared with respect to the annual totals, the distribution of the total catch over the 'day' and 'night' periods and the individual 24 hour collections.

Throughout the whole season totals of 238 and 205 *M. morio* were collected from regions 1 and 2 respectively. Comparison of these totals by the χ^2 test gave a value of $P > 0.05$ showing the difference was not greater than would be expected by chance alone.

The 'day' and 'night' totals from each region are shown as a 2 x 2 contingency table (Table 18). With $P > 0.05$, the difference was of no significance.

In Table 19 the individual totals are arranged as an r x c contingency table (Bailey 1959 Chapter 7). The first two lines represent the numbers of *M. morio*

Date	Region 1						Region 2						Totals from both regions		
	Day			Night			Day			Night					
	Juvenile	A.M	A.F	Juvenile	A.M	A.F	Juvenile	A.M	A.F	Juvenile	A.M	A.F	Day	Night	Day and night
11.6	2(5)4(6)	0	0	4(5)10(6)	0	0	5(5)11(6)	0	0	7(5)21(6)	0	0	22	42	64
16.6	1(5)6(6)	0	0	12(6)	0	0	1(5)11(6)	0	0	20(6)	0	1	19	33	52
25.6	2(6)	0	1	1(5)22(6)	0	8	5(6)	0	0	13(6)	0	11	8	55	63
7.7	3(6)	1	7	8(6)	10	22	1(6)	1	1	3(6)	5	34	14	82	96
13.7	0	2	0	2(6)	9	11	2(6)	1	4	1(6)	3	10	9	36	45
24.7	0	5	8	0	11	12	0	4	2	0	0	1	19	24	43
31.7	0	1	2	0	5	6	0	4	2	0	2	3	9	16	25
16.8	0	1	0	0	4	2	0	2	1	0	0	0	4	6	10
27.8	0	0	0	0	8	6	0	0	0	0	0	4	0	18	18
5.9	0	2	2	0	0	1	0	1	0	0	1	0	5	2	7
16.9	0	0	2	0	0	1	0	1	0	0	1	0	3	2	5
25.9	0	0	0	0	0	3	0	0	1	0	1	0	1	4	5
9.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 17. The numbers of <u>Mitopus morio</u> in the ground layer collections. The instars of juveniles are shown in parentheses. Adult male and Adult female are shown as A.M. and A.F. respectively.

collected from the twenty-five jars in regions 1 and 2 respectively, while the third line shows the combined totals from all fifty jars. The collections of 7 August to 9 November were all rather small and were grouped together.

Table 18. The distribution of the <u>Mitopus morio</u> ground layer totals over 'day' and 'night' in regions 1 and 2.

	Region 1	Region 2	Totals
Day	52	62	114
Night	186	143	329
Totals	238	205	443

$X^2 = 3.63 \quad P > 0.05$

Table 19 The 24 hour totals of <u>Mitopus morio</u> from the ground layer in regions 1 and 2.

	11.6	16.6	25.6	7.7	13.7	24.7	31.7	7.8 to 9.10	Totals
egion 1	20	19	34	51	24	36	14	40	238
egion 2	44	33	29	45	21	7	11	15	205
otals	64	52	63	96	45	43	25	55	443
X^2	6.03	2.84	0	0.01	0	7.20	0.03	3.74	19.85

$\sum X^2 = 19.85 \quad 7 \text{ d.f.} \quad P < 0.01$

Although $\sum X^2$ is 19.85 and the corresponding value of $P < 0.01$, on only one occasion was the difference between regions of clear statistical significance (24 July, $X^2 = 7.20$, $P < 0.01$). However on this occasion several of the jars in region 2 had been broken by tree felling operations, presumably accounting for the unusually low number of M. morio taken in this region. Therefore, allowing for this, it is assumed that the relative 24 hour catches from each region showed no more than chance variations from each other throughout the season.

As the above tests demonstrated the absence of any real difference between the catches of the two regions, for the purpose of this study only the combined totals from the fifty jars were considered. These are shown in the last three columns of Table 17 and are illustrated in Fig. 32 a.

(ii) Numbers and instars.

The totals collected increased from 64 on 11 June to reach the maximum of 96 on 7 July. This was followed by a sharp decrease to 45 on 13 July, after which time the numbers fell steadily until the species had died out by the beginning of October.

The first two June samples contained large numbers of the penultimate instar, and this persisted in progressively smaller proportions until the middle of July, after which time only adults were found.

(iii) Sex ratios.

For all samples in which the total number of adults

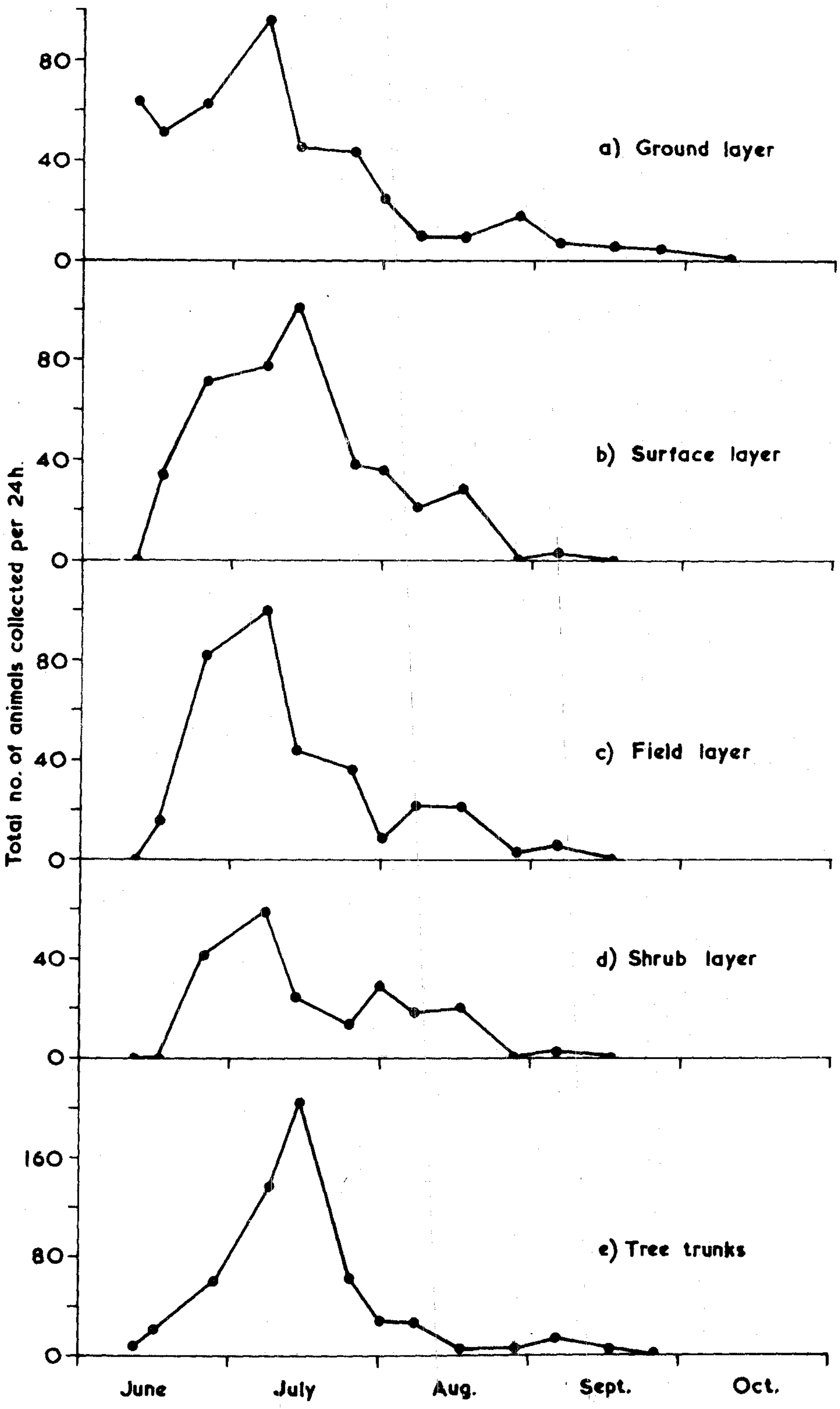


Fig. 32. Seasonal changes in the numbers of Mitopus morio taken, per diel, at each level of the field.

was not less than ten, the significance of any deviation from an assumed sex ratio of 1 was examined by the X^2 test. The results of this test are given in Table 20.

Table 20 The relative proportions of each sex in the ground layer collections of Mitopus morio.

Date	Adult males	Adult Females	X^2	P
25.6	0	20	20.0	< 0.001
7.7	17	64	27.42	< 0.001
13.7	15	25	2.50	ns
24.7	20	23	0.38	ns
31.7	12	13	0.04	ns
7.8	4	6	0.40	ns
16.8	7	3	1.60	ns
27.8	8	10	0.22	ns

Females first appeared in large numbers on 25 June, but no males were found until 7 July. On this occasion, with 17 males and 64 females, the departure from a sex ratio of 1 was highly significant ($P < 0.001$). There were still slightly more females than males on 13 July, but on this and all subsequent dates all departures of the ratios from 1 were accounted for by chance alone ($P > 0.05$).

(iv) Distribution of the catch over the 'day' and 'night' periods.

The 12 hour totals from the fifty traps are illustrated in Fig. 33a. In this figure solid lines represent the 'night' captures, broken lines the 'day' captures. The

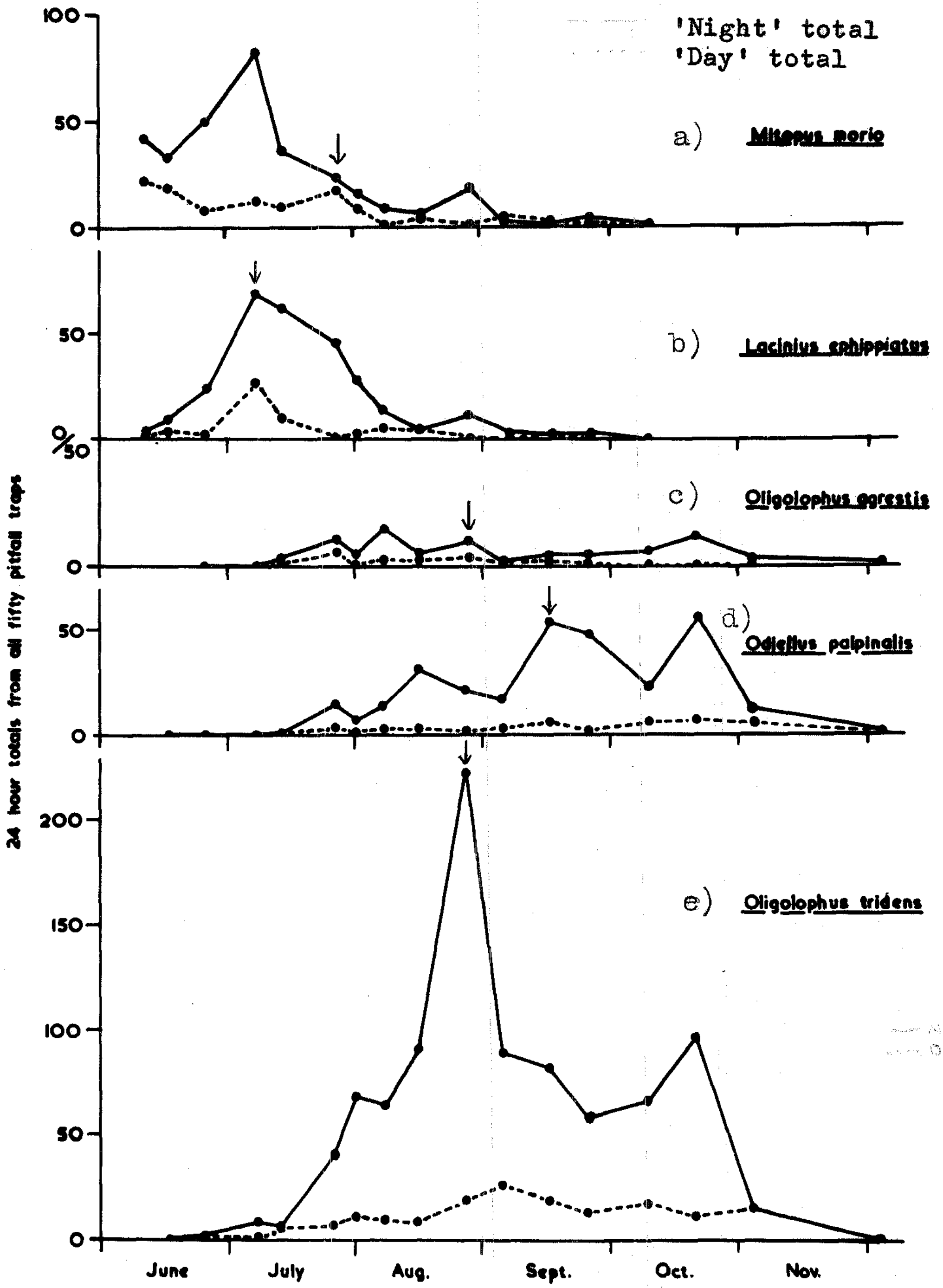


Fig. 33. Seasonal changes in the 'day' and 'night' ground layer totals. The vertical arrows indicate the first samples containing only adults.

small vertical arrow indicates the first sample comprising adults only. On the first two sampling occasions, with mainly juveniles present, the 'night' totals were approximately twice those of the corresponding 'day' period, but on the following two occasions, when first females and then males appeared in relatively large numbers, the nocturnal catches were between six and seven times greater than those of the day. This proportion fell to four on 13 July, after which time (with one exception) there was relatively little difference between the two sets of results.

(b) Surface layer.

(i) Numbers and instars.

The detailed results of the ten minute searches of the surface vegetation are shown in Table 21 and the totals collected on each date are illustrated in Fig. 32 b.

M. morio was completely absent from the surface vegetation on 11 June. 34 specimens were collected on 16 June, approximately two-thirds of them being sixth instar juveniles, the rest adult females. Adult males first appeared a week later, then the numbers increased to the maximum of 102 on 13 July. Following a sharp drop to 38 on 24 July, the numbers remained similar on the next three

Period	1			2			3			4			5			6			
Date	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	Totals
11.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16.6	0	0	0	1 (6)	0	0	5 (6)	0	9	16 (6)	0	2	1 (6)	0	0	0	0	0	34
25.6	4 (6)	1	3	1 (6)	0	2	3 (6)	13	7	1 (6)	15	6	0	4	4	0	3	4	71
7.7	0	2	6	0	5	4	0	2	5	0	18	5	0	16	7	1 (6)	3	3	77
13.7	1 (6)	18	7	0	10	7	0	9	4	0	16	8	0	10	4	0	5	3	102
24.7	0	0	1	0	6	2	0	4	1	0	4	1	0	10	1	0	6	2	38
31.7	0	2	0	0	1	0	0	4	0	0	11	0	0	8	2	0	8	0	36
7.8	0	2	1	0	2	0	0	0	1	0	4	1	0	6	0	0	3	1	21
16.8	0	1	1	0	1	0	0	0	0	0	6	1	0	12	2	0	3	2	29
27.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.9	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	3
16.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 21. The numbers of Mitopus morio in the surface layer collections. The instars of juveniles are shown in parentheses.

occasions, after which time the species was virtually absent from the surface vegetation.

(ii) Sex ratios.

Table 22 shows the results of the examination of the sex ratios for any deviation from 1.

Table 22 The relative proportions of each sex in surface layer collections of <u>Mitopus morio</u>.

Date	Adults males	Adult females	χ^2	P
16.6	0	11	11.	<0.001
25.6	36	26	1.6.	ns
7.7	46	30	3.37	ns
13.7	68	33	11.90	<0.001
24.7	30	8	12.74	<0.001
31.7	34	2	28.44	<0.001
7.8	17	4	8.05	<0.01
16.8	23	6	9.96	<0.01

Males outnumbered females on all occasions other than 16 June, and throughout most of July and August the deviation from an assumed ratio of 1 was statistically significant.

(iii) Distribution of the catch over the diel.

The spread of the catch between the six samples taken during each 24 hour period is illustrated by a series of graphs (Fig. 34a). Precise comparisons between nocturnal anddiurnal catches are best made by comparing the mean catch per 'night' sample with the mean catch per 'day'

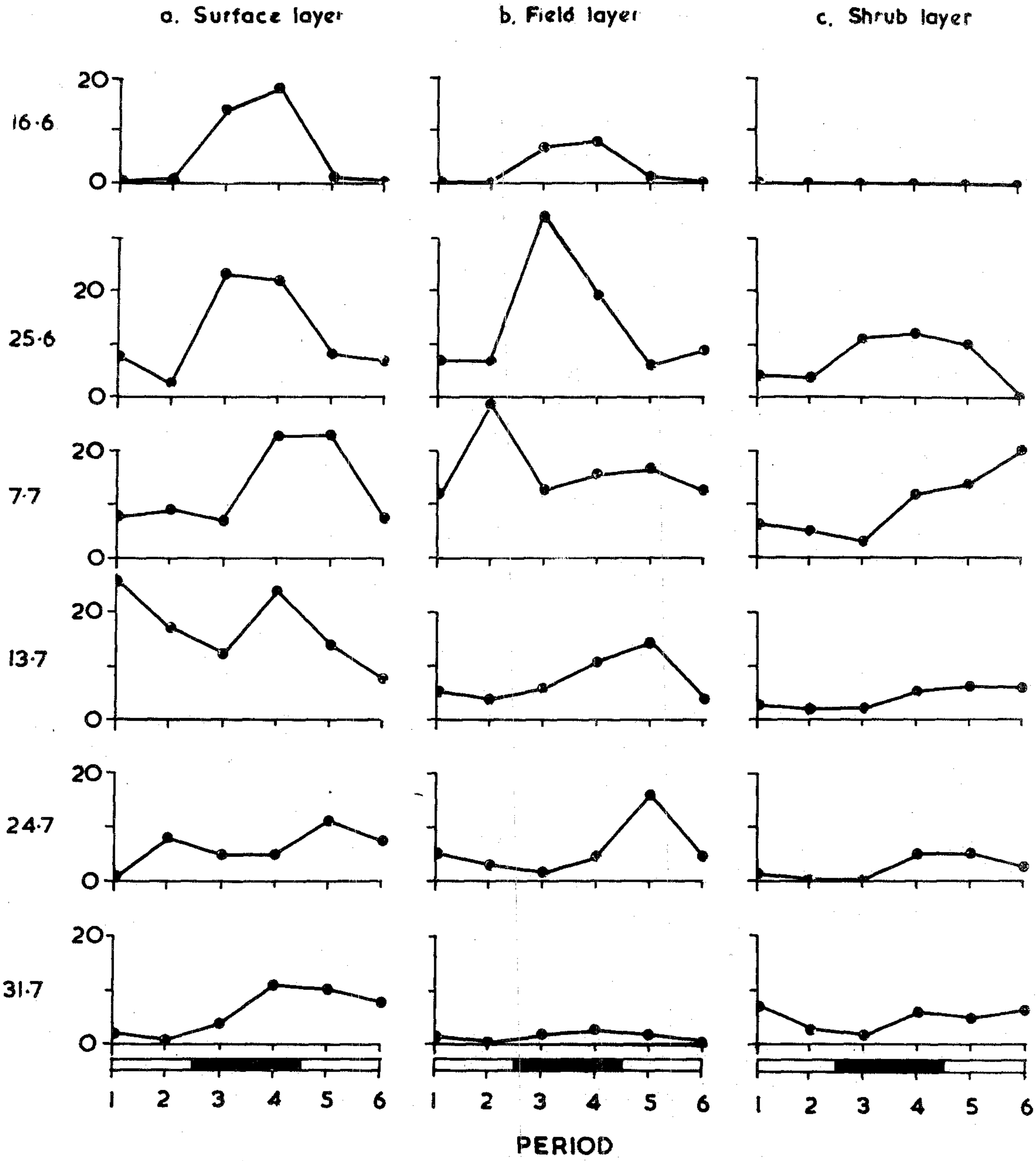


Fig. 34. The numbers of Mitopus morio taken at each of the six periods of the diel. The solid black lines represent the periods of darkness.

sample (Table 23). The mean 'day' catch was obtained by dividing the total for periods 1, 2, 5 and 6 by four, the mean 'night' catch by dividing the total from periods 3 and 4 by two.

Table 23. The relationship between mean catch per 'day' and per 'night' sample in Mitopus morio from the surface layer.

Date	'Day' mean	'Night' mean	Ratio $\frac{\text{'Night' mean}}{\text{'Day' mean}}$
16.6	0.5	16.0	32.0
25.6	5.7	22.5	3.9
7.7	11.7	15.0	1.3
13.7	16.2	18.5	1.1
24.7	7.0	5.0	0.7
31.7	5.2	7.5	1.4
7.8	3.2	3.0	0.9
16.8	5.5	3.5	0.6

In mid June, when the majority was still in the sixth instar, the presence of M. morio on the surface was much restricted to the hours of darkness, the day mean being 0.5 the night mean 16.0. By 25 June, when the majority had reached maturity, a larger number remained on the surface during the day, the day mean being 5.7, the night mean 22.5. Although some movement onto the surface occured between dusk and midnight on 7 July (Fig 34a), a large number was still there after dawn and the night mean was only slightly larger than that of the day. Throughout the rest of July there was no consistent trend in the pattern of distribution and the day and night means were always very similar.

(c) Field layer

(i) Numbers and instars.

Results of the collections from the tall grass are given in Table 24 and the totals are illustrated in Fig. 32c.

No M. morio were found on 11 June. 16 specimens, including both sixth instar juveniles and adult males, were collected on 16 June. Adult females appeared a week later. The maximum number of 100 was recorded on 7 July, after which time the species became progressively less abundant and had disappeared from the layer by mid-September.

(ii) Sex ratios.

The results of the x^2 tests on the sex ratios are given in Table 25.

Table 25. The relative proportions of each sex in the field layer collections of Mitopus morio.

Date	Adult males	Adult Females	x^2	P
25.6	24	45	6.38	<0.02
7.7	49	51	0.04	ns
13.7	24	20	0.36	ns
24.7	17	19	0.11	ns
31.7	6	3	1.00	ns
7.8	13	8	1.19	ns
16.8	11	10	0.05	ns

Table 24. The numbers of *Mitopus morio* in the field layer collections. The instars of juveniles are shown in parentheses.

Period	1			2			3			4			5			6			
Date	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	Totals
11.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16.6	0	0	0	0	0	0	5 (6)	2	0	3 (6)	5	0	1 (6)	0	0	0	0	0	16
25.6	4 (6)	1	2	3 (6)	2	2	4 (6)	8	22	1 (6)	9	9	0	4	2	1 (6)	0	8	82
7.7	0	8	4	0	18	11	0	1	12	0	7	9	0	6	11	0	9	4	100
13.7	0	4	1	0	2	2	0	3	3	0	6	5	0	7	7	0	2	2	44
24.7	0	2	3	0	1	2	0	1	1	0	2	3	0	9	7	0	2	3	36
31.7	0	1	0	0	0	0	0	2	0	0	1	2	0	1	1	0	1	0	9
7.8	0	0	1	0	3	2	0	2	0	0	2	2	0	2	2	0	4	21	21
16.8	0	4	1	0	1	4	0	1	0	0	1	3	0	4	1	0	0	1	21
27.8	0	0	0	0	0	0	0	0	1	0	0	2	0	1	1	0	0	0	3
5.9	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	5
16.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Apart from the higher proportion of females on 25 June, all deviations from an assumed ratio of 1 were accounted for by chance alone.

(iii) Distribution of the catch over the diel.

The 'day' and 'night' mean captures are shown in Table 26 and the individual totals are illustrated in Fig. 34 b.

Table 26. The relationship between mean catch per 'day' and per 'night' sample in Mitopus morio from the field layer.

Date	'Day' mean	'Night' mean	Ratio $\frac{\text{'Night' mean}}{\text{'Day' mean}}$
16.6	0.2	7.5	37.5
25.6	7.2	26.5	3.7
7.7	17.7	14.5	0.8
13.7	6.7	8.5	1.3
24.7	7.2	3.5	0.5
31.7	1.0	2.5	2.5
7.8	3.7	3.0	0.8
16.8	4.0	2.5	0.6

In general the sequence of events was so similar to that seen in the surface layer collections that further description is unnecessary.

(d) Shrub layer.

(i) Numbers and instars.

The results for the shrub layer collections are given in Table 27 and the totals are illustrated in Fig.32d.

Table 27. The numbers of *Mitopus morio* in the shrub layer collections. The instars of the juveniles are shown in parentheses.

Period	1			2			3			4			5			6			
Date	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	Total
11.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25.6	2 (6)	1	1	4	0	0	7 (6)	2	2	8 (6)	1	3	7 (6)	2	1	0	0	0	41
7.7	0	6	0	0	3	2	0	1	2	0	7	5	0	7	6	0	6	14	59
13.7	0	3	0	0	2	0	0	0	2	0	5	0	0	6	0	0	3	3	24
24.7	0	0	1	0	0	0	0	0	0	0	2	3	0	4	1	0	0	3	14
31.7	0	6	1	0	2	1	0	1	1	0	4	2	0	3	2	0	4	2	29
7.8	0	3	1	0	1	0	0	0	1	0	4	2	0	2	1	0	2	1	18
16.8	0	2	3	0	4	1	0	1	2	0	1	1	0	1	2	0	1	1	20
27.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.9	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2
16.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The species did not appear at this level until 25 June when approximately two-thirds of the collection consisted of sixth instar juveniles, the remainder of adults of both sexes. The numbers rose to a maximum of 59 on 7 July, then decreased until the species was absent from the bushes by mid-September.

(ii) Sex ratios.

The results of the χ^2 tests on the sex ratios are given in Table 28.

Table 28. The relative proportions of each sex in the shrub layer collections of Mitopus morio.

Date	Adult males	Adult females	χ^2	P
25.6	6	7	0.07	ns
7.7	30	29	0.17	ns
13.7	19	5	8.17	<0.01
24.7	6	8	0.28	ns
31.7	20	9	4.17	<0.05
7.8	12	6	2.0	ns
16.8	10	10	0	ns

The numbers of each sex were generally fairly similar and only on 13 July was the deviation from a ratio of 1 clearly of statistical significance.

(iii) Distribution of the catch over the diel.

Apart from the absence of specimens on 16 June, the 'night' and 'day' mean ratios (Table 29) followed a similar pattern to that already described for the other levels.

Table 29. The relationship between mean catch per 'day' and per 'night' sample in <u>Mitopus morio</u> from the shrub layer.

Date	'Day' mean	'Night' mean	Ratio 'Night' mean / 'Day' mean
16.6	0	0	-
25.6	4.5	12.5	2.5
7.7	11.0	7.5	0.7
13.7	4.2	3.5	0.8
24.7	2.2	2.5	1.1
31.7	5.2	4.0	0.8
7.8	2.7	3.5	1.3
16.8	3.7	2.5	0.7

(e) Tree trunks

(i) Numbers and instars.

The totals from the ten trees are shown in Table 30 and are illustrated graphically in Fig. 32e.

Table 30 The numbers of <u>Mitopus morio</u> in collections from the tree trunks. All juveniles (shown in Table as juv.) are sixth instars. No further specimens were found after 16 September.

Date	Lower papers				Upper papers			
	Juv	Adult male	Adult female	Totals	Juv	Adult male	Adult female	Totals
11.6	6	0	0	6	0	0	0	0
16.6	5	1	13	19	0	0	1	1
25.6	2	24	31	57	0	1	2	3
7.7	0	87	33	120	0	3	12	15
13.7	0	107	23	130	0	31	42	73
24.7	0	30	12	42	0	9	11	20
31.7	0	18	5	23	0	5	0	5
7.8	0	16	2	18	0	7	0	7
16.8	0	1	3	4	0	0	1	1
27.8	0	1	0	1	0	1	1	2
5.9	0	6	1	7	0	5	0	5
16.9	0	4	0	4	0	0	0	0

The first complete collection was made on 11 June when six penultimate instar M. morio were found, all under the lower papers. Very few juveniles were found after this time, the main migration being carried out by adults. The numbers ascending the tree trunks increased rapidly upto the maximum of 130 on 13 July, then subsequently decreased fairly rapidly. The totals caught moving down the trunks were never very large, and even the maximum of 73 recorded on 13 July was still only approximately a half of the corresponding ascending total.

(ii) Sex ratios.

The results of the X^2 tests on the sex ratios are given in Table 31.

Table 31 The relative proportions of each sex in the tree trunk collections of Mitopus morio.

	Date	Adult male	Adult female	X^2	P
Lower Papers	16.6	1	13	10.28	<0.01
	25.6	24	31	0.89	ns
	7.7	87	33	24.30	<0.001
	13.7	107	23	54.28	<0.001
	24.7	30	12	7.71	<0.01
	31.7	18	5	7.35	<0.01
	7.8	16	2	10.89	<0.001
Upper papers	7.7	3	12	5.40	<0.05
	13.7	31	42	1.66	ns
	24.7	9	11	0.20	ns

In mid June mainly females ascended the trees, but towards the end of the month males became more abundant and from

7 July onwards were found in significantly greater numbers than females.

There was no convincing evidence of any deviation from a sex ratio of 1 among adults descending the tree trunks, although females tended to outnumber males.

(iii) Distribution of the catch over the diel.

Unlike any of the previous collections, no *M. morio* were ever found during the hours of daylight, the migration being exclusively nocturnal. However a more detailed picture of the movement of this species was obtained by noting the numbers on the tree trunks at each of the six periods during the diel. (A 6 volt lantern with a red filter was used for observation by night). Both the ten greased and ten ungreased trunks were examined and the direction of movement of every specimen was recorded. No attempt was made to include any animals actually underneath the papers on the greased trees.

Some of the results (given in Appendix B) are illustrated by a series of graphs (Fig. 35). The same pattern is seen in all the graphs, those of 7 July being fairly typical. On this occasion the number ascending the ungreased trunks reached a maximum of 23 just after dusk (period 3) and by midnight (period 4) had fallen to 6. None were seen either before dusk (period 2) or after dawn (period 5). On the greased trees the maximum was recorded somewhat later,

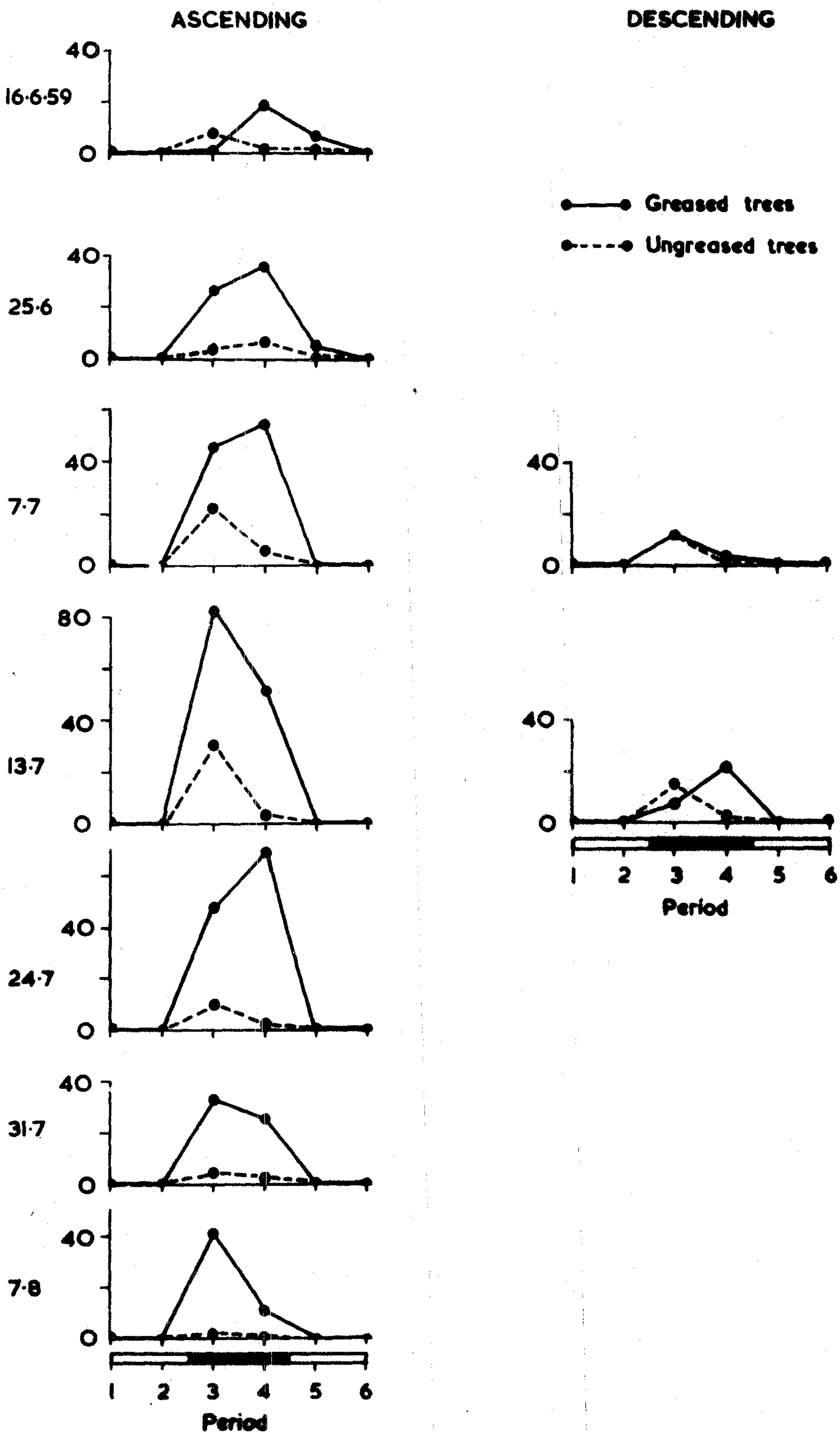


Fig. 35. The numbers of adult <u>Mitopus morio</u> ascending and descending the tree trunks. The solid black lines represent the periods of darkness.

but this merely reflected the progressive build up of numbers during the night due to the obstruction. It did not represent the period of greatest movement on the trunks. Very few M. morio were seen descending the trunks and only the results of 7 and 13 July are illustrated, only these being sufficiently large to indicate the general trend. On both these occasions the greatest activity was recorded at period 3, the peak at period 4 on the greased trees again reflecting the build up of numbers due to the obstruction. These results indicate that migration onto the tree trunks took place mainly in the period between dusk and midnight, but observation showed that the main movement occured over an even more limited period of time. A large ash tree (tree number 1) was observed on several nights. Just before the light had completely disappeared many M. morio appeared almost simultaneously near the base of the trunk. They ran quickly up the tree, only stopping a few times before passing out of sight. At the same time a few M. morio moved from the lower tree branches onto the trunk and quickly descended to the ground. Further specimens were seen moving in both directions throughout the night, especially in the period upto midnight, but never in such large numbers as those observed initially. No similar large scale migration was seen around dawn.

The direction of movement of any one specimen could not be changed. Individuals were picked off the trunks and placed on other trunks or on sticks placed in the ground, but in every single case the previous direction of movement was continued unchanged. Even when pushed or turned round to face the opposite direction, they always turned back and resumed the original direction of movement.

(iv) Duplicated collections.

From general observation during June and early July, it became increasingly apparent that there was very little variation from one night to the next in the numbers of M. morio moving on the tree trunks. To investigate this in more detail, and at the same time obtain some indication of the reliability of the main collections, after 7 July a further collection was made over the 24 hours immediately following each sampling period. Differences associated with changing weather conditions were kept to a minimum by only sampling when the weather seemed likely to remain similar over both periods. The numbers from individual trees were recorded so that confidence limits of the mean number per tree could be calculated. Both sets of means, with 95% confidence limits, are illustrated in Fig. 36. Clearly there was a greater similarity between mean captures on adjacent than on non-adjacent nights.

It has been shown that the nocturnal migration via

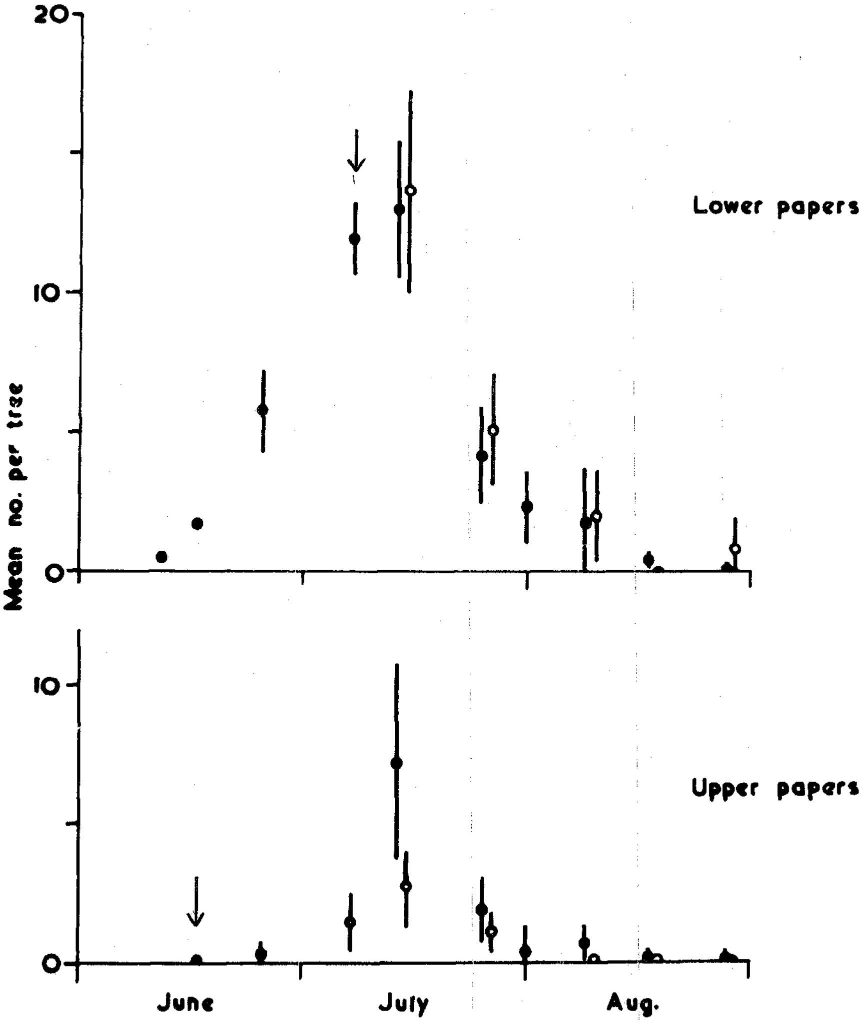


Fig. 36. Duplicated means of the numbers of Mitopus morio per tree trunk. (See text for explanation). The vertical arrows indicate the first samples containing only adults.

the trunks took place mainly before midnight, and it is therefore unlikely that individuals which moved into the canopy returned to the ground later the same night. As access to the canopy of the greased trees had been cut off, M. morio descending the first night had been there at least 24 hours, those descending the second night at least 48 hours. Although there is no direct evidence which could indicate the length of time spent by an individual among the tree foliage, this will therefore be at least 24 hours.

The overall similarity between adjacent means suggests that Fig. 36 adequately represents the true pattern of vertical migration. Assuming this to be true the graph was considered as a running mean, and values for the days on which sampling was not carried out were obtained by interpolation. By addition of the estimated and actual means over the period from the start of June to the end of August, it appeared that a total of approximately 743 M.morio ascended each tree, while only about 183 made the return journey by the same route.

This apparent loss of individuals was either a real one, resulting perhaps from predation by other components of the canopy fauna, or it was simply the result of a direct return to the ground made by dropping from, or being blown or shaken from the foliage. The latter possibility was tested by attempting to catch M. morio on greased paper as they fell to the ground. Ten horizontal trays were placed below the trees in the study area. Each tray consisted of a 45 cm square of hardboard. This was fixed through the centre to a vertical wooden support 2 m long, which was driven about 0.5 m into the ground. The top of the tray was covered by a sheet of brown paper smeared with 'Sticktite', and the support was also greased to cut off access to the tray from below.

These trays were left in the field almos^t continuously from mid - June until the end of November, the greased paper being renewed once a month. Vast numbers of Araneids and adult Diptera were trapped, yet over the whole period only three *M. morio* were caught. Despite the relatively small total surface area of the trays, this nevertheless suggests that any return to the ground by this route was of little importance.

The discrepancy between ascending and descending totals must therefore represent a real loss of *M. morio* from the canopy, rather than a simple return to the ground.

B. Oligolophus agrestis.

(a) Ground layer.

(i) Comparison of catches of regions 1 and 2.

The results for the pitfall trap collections are given in Table 32. As with *M. morio*, the catches of *Oligolophus agrestis* from the two regions were first compared.

Throughout the whole year only 94 and 35 animals were collected from the traps in regions 1 and 2 respectively. The difference between these totals was greater than would be expected by chance alone ($P < 0.01$) indicating that catches from the traps in region 1 were the greater of the two sets. It can be seen from Table 32 that the numbers of adults from the two regions were fairly similar, and the difference was due almost entirely to the large number of juveniles found in region 1.

Comparison, by the χ^2 test, of the distribution of the 'day' and 'night' catches of the two regions (Table 33) showed the absence of any significant difference ($P > 0.05$).

Table 33. The distribution of the *Oligolophus agrestis* ground layer totals over 'day' and 'night' in regions 1 and 2.

	Region 1	Region 2	Totals
'Day'	15	11	26
'Night'	79	24	103
Totals	94	35	129

$\chi^2 = 2.89$ $P > 0.05$

Table 32. The numbers of *Oligolophus agrestis* in the ground layer collections. The instars of juveniles are shown in parentheses.

Date	Region 1						Region 2						Totals		
	Day			Night			Day			Night			Day	Night	Total
	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF			
16.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25.6	0	0	0	1(4)	0	0	0	0	0	1(4)	0	0	0	2	2
7.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13.7	2(5)	0	0	1(4)1(5)	0	0	0	0	0	1(5)	0	0	2	3	5
24.7	3(5)5(6)	0	0	4(4)7(5)2(6)	0	0	0	0	0	0	0	0	8	13	21
31.7	0	0	0	3(5)2(6)	0	0	0	0	0	1(5)	0	0	0	6	6
7.8	0	0	0	18(6)	0	0	4(6)	0	0	0	0	0	4	18	22
16.8	1(6)	0	2	5(6)	0	1	0	0	0	0	0	0	3	6	9
27.8	0	2	0	0	4	3	0	0	2	0	1	4	4	12	16
5.9	0	0	0	0	0	1	0	0	0	0	0	2	0	3	3
16.9	0	0	0	0	2	3	0	3	0	0	1	0	3	6	9
25.9	0	0	0	0	1	2	0	1	0	0	1	1	1	5	6
9.10	0	0	0	0	1	7	0	0	0	0	0	0	0	8	8
20.10	0	0	0	0	1	5	0	0	0	0	2	7	0	15	15
3.11	0	0	0	0	1	1	0	0	1	0	1	1	1	4	5
14.12	0	0	0	0	1	1	0	0	0	0	0	0	0	2	2

Because of the relative scarcity of *O. agrestis* in the ground layer, only the combined totals from the fifty traps were considered.

(ii) Numbers and instars.

The totals given in Table 32 are illustrated in Fig. 33c. The pitfall traps were set out in the field from March 1959, and *O. agrestis* first appeared in them on 25 June. The numbers remained similar throughout most of the year and, although not shown in Table 32, a few were still present at the end of January of the following year.

Presumably because of the relative inefficiency of the pitfall traps with respect to the earlier instars (see discussion), second and third instar juveniles were never caught in them. Of the later stages, the total catch of the fourth instar was 7, of the fifth instar 18 and of the sixth instar 37. Adults first appeared in the traps on 16 August.

(iii) Sex ratios.

Because of the small numbers, samples of adults were combined in pairs in order to test for any deviation from a sex ratio of 1. The results of X^2 tests on these totals are given in Table 34.

Table 34 The relative proportions of each sex in the ground layer collections of <u>Oligolophus agrestis</u>.

Date	Adult male	Adult female	X^2	P
16.8 and 27.8	7	12	1.31	ns
5.9 and 16.9	6	6		ns
25.9 and 9.10	4	10	2.57	ns
20.10 and 3.11	5	15	5.0	< 0.05

Clearly, except when the species was beginning to die off, any departures from a ratio of 1 can be accounted for by chance alone.

(iv) Distribution of the catch over the diel.

The separate 'day' and 'night' totals are illustrated in Fig. 33c. Despite the low numbers, the nocturnal catches were always larger than those of the day.

(b) Surface layer.

Over the whole season only four specimens of <u>O. agrestis</u> were found during the ten minute searches of the surface vegetation. Of these, one adult female was collected at 1200 h G.M.T. on 5 September and three adult females at 1200 h on 20 October. Clearly neither juveniles nor adults normally occured at this level.

(c) Field layer

A few more specimens, all adults, were collected from the tall grasses from August to October (Table 35), but the only conclusion which can safely be drawn from these results is that the species did not normally occur at this level of the field.

Table 35. The numbers of Oligolophus agrestis in the field layer collections. Occasions on which none were taken are not shown.
M = Adult male. F = Adult female.

Period	1		2		3		4		5		6	
Date	M	F	M	F	M	F	M	F	M	F	M	F
27.8	0	1	0	0	0	1	1	2	0	0	0	0
5.9	0	1	1	0	1	2	0	3	0	1	0	1
16.9	0	0	0	0	0	0	1	2	0	0	2	1
9.10	0	1	0	0	0	0	0	0	0	0	0	1
20.10	0	0	0	0	0	0	0	2	0	0	0	0

(d) Shrub Layer.

(i) Numbers and instars.

The results for the shrub layer collection are given in Table 36. The last few collections were incomplete. On 16 and 25 September slight drizzle during the night caused animals to stick to the leaves when the bushes were shaken. On the remaining occasions sampling was not carried out at periods 3 and 5.

The first appearance of O. agrestis in this layer was made by two fifth instar juveniles on 24 July. From the end of July to the middle of August, only sixth instar juveniles

Table 36. The numbers of *Oligolophus agrestis* in the shrub layer collections. The instars of juveniles are shown in parentheses. The species was absent from all shrub layer collections before 24 July.

Period	1			2			3			4			5			6			
Date	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	juv	AM	AF	Totals
24.7	0	0	0	0	0	0	0	0	0	0	0	0	1 (5)	0	0	1 (5)	0	0	2
31.7	0	0	0	1 (6)	0	0	1 (6)	0	0	9 (6)	0	0	0	0	0	10 (6)	0	0	21
7.8	0	0	0	0	0	0	0	0	0	12 (6)	0	0	0	0	0	0	0	0	12
16.8	4 (6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
27.8	0	3	1	0	0	1	0	10	12	0	5	11	0	1	0	0	0	1	45
5.9	0	7	1	0	7	4	0	26	5	0	12	3	0	10	1	0	10	4	90
16.9	0	16	4	-	-	-	-	-	-	-	-	-	-	-	-	0	14	6	40
25.9	0	7	4	-	-	-	-	-	-	-	-	-	-	-	-	0	8	5	24
9.10	0	3	4	0	3	3	-	-	-	0	0	5	-	-	-	0	5	4	27
20.10	0	0	3	0	0	2	-	-	-	0	1	6	-	-	-	0	4	4	20
3.11	0	0	0	0	0	0	-	-	-	0	0	0	-	-	-	0	0	0	0
4.12	0	0	0	0	0	0	-	-	-	0	0	0	-	-	-	0	0	0	0

were collected. Adults appeared towards the end of August and although the total of 90 on 5 September was the highest recorded, inspection of Table 36 suggests that the real maximum probably occured about two weeks later. The limited data available suggests that the decline in numbers began towards the end of September. By 3 November, when the bushes were almost devoid of foliage, the species had completely disappeared from the shrub layer.

(ii) Sex ratios.

The results of the tests for any deviation from a sex ratio of 1 are given in Table 37.

Table 37. The proportions of each sex in the shrub layer collections of <u>Oligolophus agrestis</u>.

Date	Adult male	Adult female	χ^2	P
27.8	19	26	1.09	ns
5.9	72	18	32.40	<0.001
16.9	30	10	10.0	<0.01
25.9	15	9	1.50	ns
9.10	11	16	0.92	ns
20.10	5	15	5.0	<0.05

In the first two September samples the relatively large numbers of males represented a significant departure from an assumed sex ratio of 1, but otherwise the deviations were probably due to chance alone.

(iii) Distribution of the catch over the diel.

The distribution of O. agrestis throughout each 24 hour period is treated in the same manner as for M. morio. Some of the results are illustrated in Fig. 37 and the 'day' and 'night' mean captures are shown in Table 38.

Table 38. The relationship between mean catch per 'day' and per 'night' sample in Oligolophus agrestis from the shrub layer.

Date	'Day' mean	'Night' mean	Ratio $\frac{\text{'Night' mean}}{\text{'Day' mean}}$
24.7	0.5	0	-
31.7	2.7	5.0	-
7.8	0	6.0	-
16.8	1.0	0	-
27.8	1.75	19.0	10.8
5.9	11.0	23.0	2.1

In the collections upto 16 August the numbers were too small to indicate any particular pattern of movement. In the following collections, which comprised only adults, the totals were slightly larger, the 'night' means exceeded those of the 'day', and the graphs (Fig. 37) suggest that a migration up into the bushes occured during the night, followed by a movement down again in the early morning.

(e) Tree trunks.

(i) Numbers and instars.

The numbers of O. agrestis trapped on the tree trunks

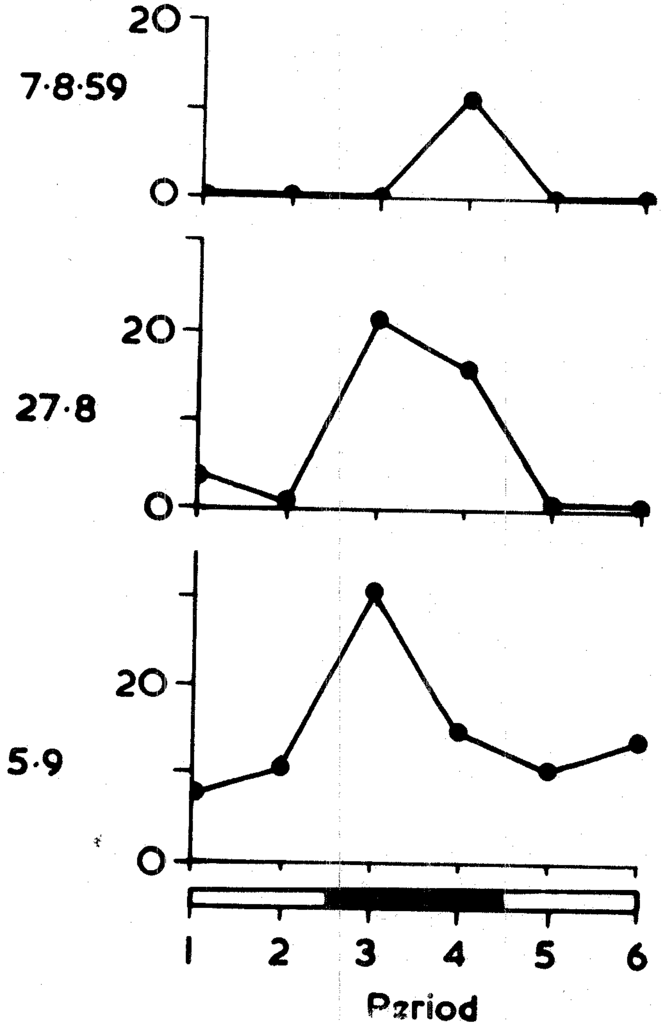


Fig. 37. The numbers of Oligolophus agrestis taken in the shrub layer at each of the six periods of the diel. The solid black lines represent the periods of darkness.

are given in Table 39. Although the trunks had been examined at frequent intervals since March, the first movement of this species onto them was recorded on 13 July, when two sixth instar juveniles were found under the lower papers. A week later 62 juveniles ascended, and this was followed by an increase to 197 on 31 July. Only 11 ascended on 7 August, after which time juveniles were replaced by adults

Table 39. The numbers of Oligolophus agrestis in collections from the tree trunks. All juveniles (shown in Table as juv.) were sixth instars. The species was absent from all collections made before 13 July.

	Lower papers				Upper papers			
Date	Juv	Adult males	Adult females	Totals	Juv	Adult males	Adult females	Totals
13.7	2	0	0	2	0	0	0	0
24.7	62	0	0	62	2	0	0	2
31.7	197	0	0	197	9	0	0	9
7.8	11	0	0	11	6	0	0	6
16.8	0	1	10	11	0	0	1	1
27.8	0	6	30	36	0	0	0	0
5.9	0	0	9	9	0	4	6	10
16.9	0	1	14	15	0	0	1	1
25.9	0	0	19	19	0	1	22	23
9.10	0	29	43	72	0	10	12	22
20.10	0	7	26	33	0	0	1	1
3.11	0	0	0	0	0	0	0	0
4.12	0	0	0	0	0	0	0	0

The numbers of adults moving upwards ranged between 9 and 36 during the next six weeks, but then rose quite suddenly to 72 on 9 October before falling to 33 on 20 October.

In general, very few O. agrestis were trapped under the upper papers, but the relatively higher catches of 25 September and 9 October are believed to represent a real peak in the numbers returning from the canopy to the ground.

(ii) Sex ratios.

It can be seen from Table 40 that more females than males were present in every collection of adults from both upper and lower papers, and on nearly every occasion the deviation from an assumed sex ratio of 1 was statistically significant.

Table 40. The proportions of each sex in the tree trunk collections of *Oligolophus agrestis*.

Date	Adult male	Adult Female	X^2	P
16.8	1	10	7.36	<0.01
27.8	6	30	16.0	<0.001
16.9	1	14	11.27	<0.001
25.9	0	19	19.0	<0.001
9.10	29	43	2.72	ns
30.10	7	26	10.94	<0.001

Only on 9 October, when there was an increase in the number of males moving in both directions, was the difference of no significance.

(iii) Distribution of the catch over the diel.

It had been intended to record details of the movement of *O. agrestis* on the trunks at intervals throughout the night as was done with *M. morio*, but because of the difficulty of seeing individuals against the background of the tree trunks, this could not be effectively carried out. However, as a result of general observation, it is believed migration occured mainly in the period between dusk and midnight.

(iv) Duplicated collections.

To assess the reliability of the main collections, these were duplicated as in *M. morio*, and the duplicated means, with 95% confidence limits, are shown together (Fig. 38). On the upper figure, the similarity between the two means on 9 and 10 October confirms the existence of a real peak in the numbers ascending the trees in mid-October. Although it was not possible to obtain a duplicate collection on 1 August, a very high level of activity was noted during the preceeding three nights, and this peak is quite representative of the general situation at that time. The numbers descending the trees were generally small and fairly similar on both nights, but the unusually high 'duplicate' means of 28 August and 10 October cannot be explained.

As in *M. morio*, the majority of *O. agrestis* which

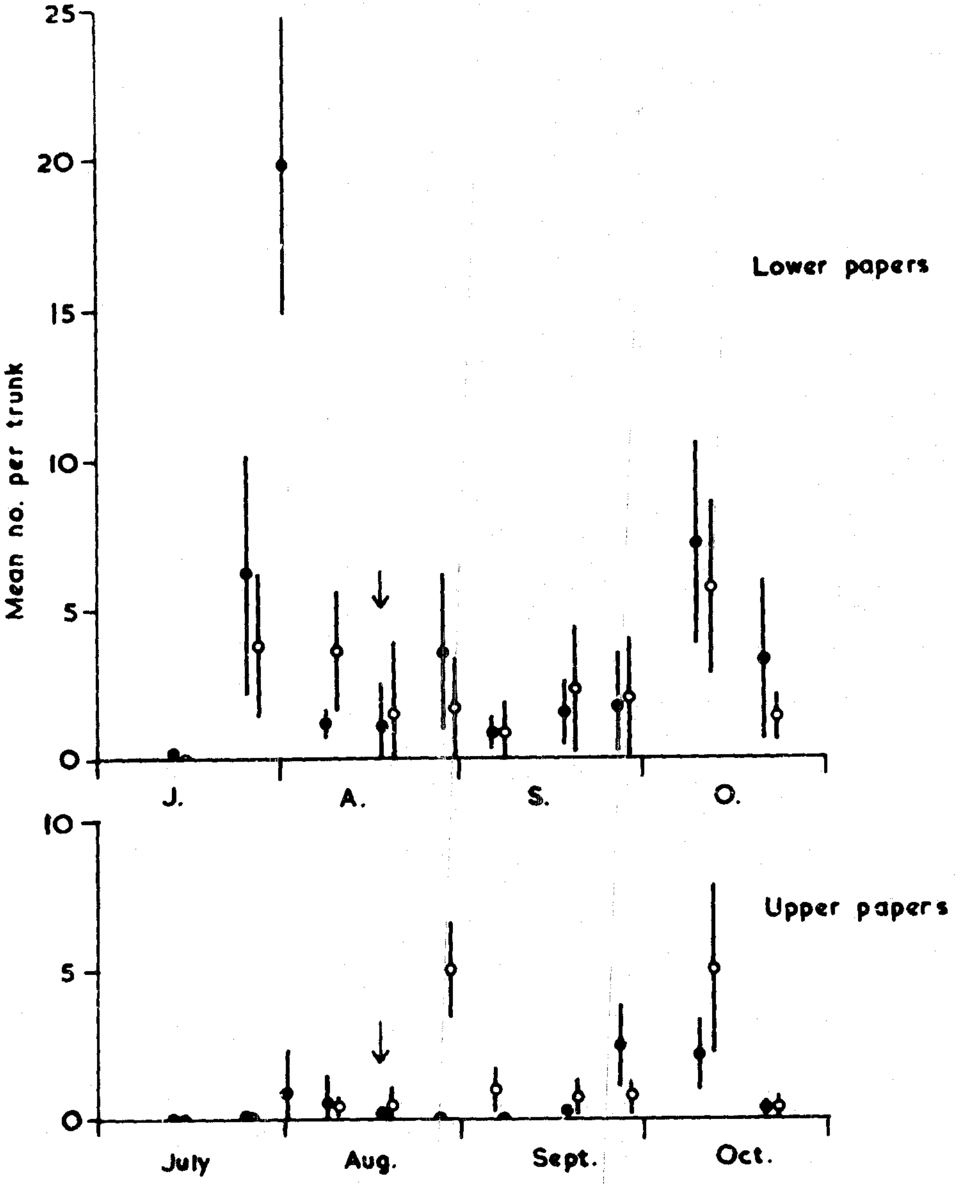


Fig. 38. Duplicated means of the numbers of Oligolophus agrestis per tree trunk. (See text for explanation). The vertical arrows indicate the first samples containing only adults.

ascended via the trunks apparently failed to return to the ground by a similar route. Only two females were found on the surface of the sticky traps placed below the trees, and there is therefore little chance that a full scale return to the ground was made by simply falling from the tree canopy.

C. Species other than *M. morio* and *O. agrestis*.

(i) Comparison of ground layer catches of regions 1 and 2.

The results of the pitfall trap collections of *Lacinius ephippiatus*, *Odiellus palpinalis*, *Oligolophus tridens* and *Nemastoma lugubre* are given, respectively, in Tables 41, 42, 43 and 44. As with *M. morio* the catches from regions 1 and 2 were first compared.

In *L. ephippiatus*, there was clearly no significance in the difference between the seasonal totals of 169 and 173 from regions 1 and 2 respectively. The individual 24 hour collections differed from each other (Table 45 $\sum\chi^2 = 31.37$, $P < 0.001$), although most of the difference was due to the low number collected from region 2 on 24 July, presumably due to the tree felling operations mentioned earlier.

Table 45. The 24 hour totals of *Lacinius ephippiatus* from the ground layer in regions 1 and 2.

	16.6	25.6	7.7	13.7	24.7	31.7	7.8	16.8 to 25.9	Totals
Region 1	6	13	25	33	41	17	15	19	169
Region 2	7	13	70	43	4	14	6	6	163
Totals	13	26	95	76	45	31	21	25	332
χ^2	0.05	0	11.24	0.83	14.31	0.09	1.73	3.12	31.37

$\sum\chi^2 = 31.37$, $P < 0.001$

41. The numbers of <u>Lacinius ephippiatus</u> in the ground layer collections. The instars of juveniles are shown in parentheses.

Region 1						Region 2						Totals from both regions		
Day			Night			Day			Night					
venile	Adult male	Adult female	Juvenile	Adult male	Adult female	Juvenile	Adult male	Adult female	Juvenile	Adult male	Adult female	Day	Night	Day and night
0	0	0	3(5)	0	0	0	0	0	0	0	0	0	3	3
)1(6)	0	0	3(5)1(6)	0	0	1(4)1(5)	0	0	4(6)	0	1	4	9	13
)	0	0	11(6)	0	0	0	0	0	13(6)	0	0	2	24	26
0	2	3	0	3	17	0	4	18	0	7	41	27	68	95
0	1	2	0	11	19	0	3	9	0	15	16	15	61	76
0	0	0	0	29	12	0	0	0	0	3	1	0	45	45
0	0	0	0	12	5	0	0	3	0	7	4	3	28	31
0	1	2	0	7	5	0	1	1	0	2	2	5	16	21
0	1	1	0	2	1	0	1	1	0	0	0	4	3	7
0	0	0	0	9	1	0	0	0	0	1	1	0	12	12
)	0	0	0	2	0	0	0	0	0	1	0	0	3	3
)	0	0	0	1	0	0	1	0	0	0	0	1	1	2
)	0	0	0	1	0	0	0	0	0	0	0	0	1	1
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0

42. The numbers of <u>Odiellus palpinalis</u> in the ground layer collections. The instars of juveniles are shown in parentheses.

(Table 42 Contd,)

Region 1						Region 2						Totals from both regions		
Day			Night			Day			Night					
Juvenile	Adult male	Adult female	Juvenile	Adult male	Adult female	Juvenile	A.M.	A.F.	Juvenile	A.M.	A.F.	Day	Night	Day and night
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1(4)	0	0	0	1	1
1(4)	0	0	0	0	0	0	0	0	1(4)	0	0	1	1	2
0	0	0	1(4)	0	0	0	0	0	0	0	0	0	1	1
3(5)	0	0	7(5)1(6)	0	0	1(5)	0	0	8(5)	0	0	4	16	20
1(6)	0	0	3(5)	0	0	1(4)	0	0	1(5)1(6)	0	0	2	5	7
1(6)	0	0	5(5)6(6)	0	0	0	1	1	1(5)3(6)	0	0	3	15	18
4(6)	0	0	28(6)	0	0	0	0	0	4(6)	0	0	4	32	36
0	0	0	4(6)	0	3	0	0	1	13(6)	0	2	1	22	23
0	0	0	2(6)	1	8	0	0	3	1(6)	0	6	3	18	21
0	1	4	0	11	21	0	0	2	0	5	18	7	55	62
0	0	2	0	3	20	0	0	1	0	6	19	3	48	51
0	0	1	0	5	9	0	0	7	0	2	8	8	24	32
0	0	0	0	9	12	0	3	3	0	11	26	6	58	64
0	0	0	0	2	2	0	3	0	0	6	3	4	13	17
0	1	0	0	2	0	0	0	0	0	0	0	1	2	3

The numbers of *Oligolophus tridens* in the ground layer collections. The instars of juveniles are shown in parentheses.

Region 1						Region 2						Totals fro both regio		
Day			Night			Day			Night					
venile	Adult male	Adult female	Juvenile	Adult male	Adult female	Juvenile	Adult male	Adult female	Juvenile	Adult male	Adult female	Day	Night	Day and nig
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1(4)	0	0	1(4)	0	0	1	1	2
0	0	0	0	0	0	1(5)	0	0	6(4)2(5)	0	0	1	8	9
0	0	0	1(5)	0	0	1(5)	0	0	3(5)	0	0	2	4	6
(6)	0	0	5(5)11(6)	0	0	5(6)	0	0	4(5)20(6)	0	0	6	40	46
(5)1(6)	0	0	27(6)	0	0	8(6)	0	0	41(6)	0	0	10	68	78
(6)	0	0	29(6)	1	2	0	1	2	29(6)	0	2	9	63	72
0	0	0	6(6)	0	27	0	1	6	4(6)	7	46	8	90	98
0	0	1	0	17	40	0	0	17	0	39	146	18	242	260
0	0	3	0	15	35	0	4	18	0	13	24	25	87	112
0	3	3	0	14	25	0	2	10	0	14	28	18	81	99
0	0	1	0	3	8	0	2	9	0	17	29	12	57	69
0	1	1	0	10	15	0	3	10	0	13	27	15	65	80
0	2	1	0	18	10	0	4	3	0	43	24	10	95	105
0	2	0	0	2	0	0	15	0	0	10	5	17	17	34
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The numbers of Nemastoma lugubre in the ground layer collections. The instars of juveniles are shown in parentheses.

Table 44 Contd.

Region 1						Region 2						Totals from both regions		
Day			Night			Day			Night					
ile	Adult male	Adult female	Juvenile	Adult male	Adult female	Juvenile	Adult male	Adult female	Juvenile	Adult male	Adult female	Day	Night	Day and night
	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	1(5)	0	0	0	0	0	1(5)	0	0	0	2	2
	0	0	2(4)	0	0	0	0	0	0	0	0	1	2	3
	0	1	1(3)3(4)	0	2	1(5)	0	0	1(3)1(5)	1	3	2	12	14
	0	0	0	2	1	0	0	0	0	1	2	0	6	6
	0	0	0	0	1	0	0	0	0	0	2	0	3	3
	0	0	0	1	0	0	0	0	0	1	5	0	7	7
	0	0	0	1	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	2	0	2	2
	0	0	0	1	1	0	0	1	0	0	2	1	4	5
	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	1	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The difference between the distribution of the total catch over the 'day' and 'night' periods was highly significant (Table 46, $P < 0.001$) and the $\frac{\text{total 'night' captures}}{\text{total 'day' captures}}$ ratios of 8.6 and 2.7 for regions 1 and 2 respectively show that this was due to the species being apparently more nocturnal in region 1.

Table 46. The distribution of the *Lacinius ephippiatus* ground layer totals over 'day' and 'night in regions 1 and 2.

	Region 1	Region 2	Totals
'Day'	18	44	62
'Night'	155	119	274
Totals	173	163	336

$\chi^2 = 11.63$ $P < 0.001$

In *O. palpinalis* there was clearly no difference between the seasonal totals of 183 and 173 from the two regions and although the species was more strongly nocturnal in region 1, the difference was not significant (Table 47 $P > 0.05$). In the comparisons between the individual

Table 47. The distribution of the *Odiellus palpinalis* ground layer totals over 'day' and 'night' in regions 1 and 2.

	Region 1	Region 2	Totals
'Day'	20	27	47
'Night'	163	146	309
Totals	183	173	356

$\chi^2 = 1.31$ $P > 0.05$

catches (Table 48), the difference between the observed and expected value was only clearly significant on 16 August ($x^2 = 9.65$, $P < 0.01$), and in general, there was no obvious and consistent difference between the two regions.

Table 48. The 24 hour totals of Odiellus palpinalis from the ground layer in regions 1 and 2.

	7.7 to 31.7	7.8	16.8	27.8	5.9	16.9	25.9	9.10	20.10	3.11 + 4.12	Totals
Region 1	17	12	32	7	11	37	25	15	21	8	185
Region 2	14	6	4	16	10	25	26	17	43	12	173
Totals	31	18	36	23	21	62	51	32	64	20	358
x^2	0.06	0.78	9.65	2.02	0	0.78	0.06	0.14	4.42	0.51	18.42

$\sum x^2 = 18.42$ $P < 0.05 > 0.02$

Unlike L. ephippiatus and O. palpinalis, the catches of O. tridens from the two regions differed in every respect. Over twice as many were collected from region 2, and the difference between the diel distribution of the total catch in each region was highly significant (Table 49 $P < 0.001$).

Table 49. The distribution of the Oligolophus tridens ground layer totals over 'day' and 'night' in regions 1 and 2.

	Region 1	Region 2	Totals
'Day'	27	124	151
'Night'	321	597	918
Totals	348	721	1069

$x^2 = 16.47$ $P < 0.001$

The $\frac{\text{total 'night' captures}}{\text{total 'day' captures}}$ ratios of 11.9 and 4.8 for regions 1 and 2 respectively show that diel activity was less symmetrical in region 1. The individual regional totals did not bear the same relationship to each other throughout the season (Table 50, $P < 0.001$).

Relatively few N. lugubre were found in the pitfall traps and the seasonal totals from the two regions were too small to be examined by the χ^2 test (Table 51). However, the diel distribution was apparently similar in each region, the species being almost completely nocturnal.

Table 51 The distribution of the Nemastoma lugubre ground layer totals over 'day' and 'night' in regions 1 and 2.

	Region 1	Region 2	Totals
'Day'	1	2	3
'Night'	18	22	40
Totals	19	24	43

(ii) Numbers.

(p 113)

Figure 33 illustrates the captures from the fifty pitfall traps for all species except N. lugubre. The separate 'day' and 'night' totals are represented, respectively, by the broken and solid lines, and a small vertical arrow indicates the first sample consisting entirely of adults. Brief reference is occasionally made to the pitfall results of M. morio and O. agrestis although these have been

Table 50. The 24 hour totals of <u>Oligolophus tridens</u> from the ground layer in region 1 and 2.

	25.6 to 13.7	24.7	31.7	7.8	16.8	27.8	5.9	16.9	25.9	9.10	20.10	3.11	Totals
Region 1	1	17	29	38	33	58	53	45	12	27	31	4	348
Region 2	15	29	49	34	65	202	59	54	57	53	74	30	721
Totals	16	46	78	72	98	260	112	99	69	80	105	34	1069
x^2	3.39	0.29	0.51	9.11	0.04	8.36	7.46	5.09	4.90	5.58	0.29	4.54	130.15

$\sum x^2$ 130.15 $P < 0.001$

described earlier.

The patternof events was very similar in *M. morio* and *L. ephippiatus*, the two species which hatched in early spring. Both were virtually absent from the pitfall traps during April and May, then the numbers increased rapidly throughout June, reaching a maximum by early July. This was followed by a steady decline over the next two months, and both species had died out by the end of September.

The other species, *Oligolophus agrestis*, *O. tridens* and *Odiellus palpinalis* all hatched during the second half of May and first appeared in the pitfall traps, as fourth and fifth instars, towards the end of June.

The numbers of *O. palpinalis* and *O. agrestis* remained very similar to each other upto the end of August. After this time, those of the former increased considerably while those of the latter species remained very low, presumably as a result of the migration away from the ground described earlier. Some *O. agrestis* survived through to January and early February of the following year, but *O. palpinalis* was not found after early December.

O. tridens was numerically (at least from the point of view of pitfall captures) the most important of the ground dwelling harvest-spiders. The captures of this species increased rapidly after the middle of July, reaching the maximum of 260 on 27 August. Following a decrease during September, the numbers rose to a second but smaller peak at the end of October. The species was beginning to die off by early November and had disappeared completely by the end of the month.

(iii) Instars.

In all species, individuals of the second and third instars were absent from the pitfall trap collections. A few fourth instar juveniles were found, then the numbers increased progressively with the appearance of the fifth and sixth instars. In the purely ground dwelling species, the maximum was reached immediately after the disappearance of the sixth instars when the whole population had just reached maturity, but in the two migratory species the maxima occured a little earlier, before the sixth and final instars began to move away from the ground in large numbers.

(iv) Sex ratios.

The numbers of each sex, together with the results of χ^2 tests to determine the significance of any departure from an assumed sex ratio of 1, are given in Table 52. When adults first appeared in the traps, the number of females was greater than that of males in all three species, a situation also seen in M. morio. In L. ephippiatus, females disappeared rapidly during July resulting in an early and complete reversal of the sex ratios, but in

Table 52. The proportions of each sex in the ground layer collections of *Lacinius ephippiatus*, *Odiellus palpinalis* and *Oligolophus tridens*.

	Date	Adult males	Adult Females	χ^2	P
L. ephippiatus	7.7	16	79	41.78	<0.001
	13.7	30	46	3.37	ns
	24.7	32	13	8.02	<0.01
	31.7	19	12	1.58	ns
	7.8	11	10	0.05	ns
	16.8	5	5	–	–
	27.8	10	2	5.33	<0.05
	5.9	3	0	–	–
O. Palpinalis	27.8	0	6	–	–
	5.9	1	17	14.22	<0.001
	16.9	17	45	12.64	<0.001
	25.9	9	42	21.35	<0.001
	9.10	7	25	10.12	<0.01
	20.10	23	41	5.06	<0.05
	3.11	12	5	2.88	ns
O. tridens	7.8	2	6	–	–
	16.8	8	79	57.94	<0.001
	27.8	56	204	84.25	<0.001
	5.9	32	80	20.57	<0.001
	16.9	33	66	11.00	<0.001
	25.9	22	47	9.06	<0.01
	9.10	27	53	8.45	<0.01
	20.10	67	38	8.01	<0.01
	3.11	29	5	16.94	<0.001

O. palpinalis and *O. tridens* females remained the predominant sex in the traps for several weeks, until they began to disappear a little earlier th^an males after mid-October.

5. Discussion of field results.

To avoid unnecessary complications the results for Mitopus morio and Oligolophus agrestis are considered separately, followed by those of the remaining species together.

A Mitopus morio

Because of the variety of sampling methods necessarily involved in this study, direct comparisons between the data of collections from the different field levels cannot be made. However, by examining for each date in turn the results of collections from all levels, it is still possible to build up a qualitative picture of the vertical movement of Mitopus morio within the study area, and at the same time to suggest a correlation between the age of the population and its general type of behaviour. Comparisons are facilitated by reference to Figs. 32 (p111) and 34 (p117) and by examination of Table 53 p116. This table shows the percentage of adults in the population, together with a ratio illustrating the distribution of the catch over the 'day' and 'night' periods. The figures in parentheses show the proportion of adults expressed as a percentage of the total catch of adults and juveniles on each occasion. (The latter were all in the sixth instar except in the first two ground layer samples). The other figures show the ratios obtained by dividing the 'night' mean by the 'day' mean in the case of the surface, field and shrub layer collections (see Tables 23, 26 and 29), and in the case of the ground layer collections by dividing the total 'night' captures by the total 'day' captures. (see Table 17). No ratios are given for the tree trunk samples, all individuals having been found during the hours of darkness.

Table 53. The relationship between 'night' and 'day' captures of <u>Mitopus morio</u> and the percentage of adults in each collection (in parentheses). See text for explanation.

Date	Ground layer	Surface layer	Field layer	Shrub layer	Tree Trunks
11.6	1.9 (0)	-	-	-	0
16.6	1.7 (3)	32.0 (32)	37.5 (44)	-	75
25.6	6.9 (34)	3.9 (87)	3.7 (85)	2.5 (32)	96
7.7	5.8 (83)	1.3 (99)	0.8 (100)	0.7 (100)	100
13.7	4.0 (89)	1.1 (99)	1.3 (100)	0.8 (100)	100
24.7	1.3 (100)	0.7 (100)	0.5 (100)	1.1 (100)	100
31.7	1.8 (100)	1.4 (100)	2.5 (100)	0.8 (100)	100

(c) Survey of events by time.

Juveniles upto and including the fifth instar were almost completely restricted to the ground layer, although, for reasons given below, they were seldom caught in the pitfall traps.

During the first half of June, the majority of the population was undergoing the moult into the sixth instar (see Fig. 13) but on 11 June, in general, this instar was apparently not yet able to leave the ground. (It is thought that the few individuals found on the trees were slightly older than the majority, with the result that their behaviour pattern was slightly in advance of that of the general population).

A few adults appeared on 16 June, the proportion of the total catch in each layer ranging from 3% in the ground layer, upto 75% on the tree trunks, but as yet there were relatively fewer M. morio on the trees, and most of the population was still in the sixth instar. By this time, although migration into the surface and field layers was taking place, it can be seen by examination of Fig. 34 and from the high values of the $\frac{\text{'night' mean}}{\text{'day' mean}}$ ratios of Table 53 (32.0 and 37.5) that this was almost exclusively nocturnal, individuals returning to the ground again before full daylight. (Again the few M. morio on the trunks were probably slightly older than the majority of the population).

By 25 June, a large part of the population above ground had reached maturity. The extent of the nocturnal vertical migration was increasing, many adults moving into the trees, and both juveniles and adults moving, for the first time, into the scrub bushes. Some individuals now remained in the surface, field and shrub layers during the hours of daylight, with the result that the $\frac{\text{'night' mean}}{\text{'day' mean}}$

ratios fell to between 2 and 4.

During the first two weeks of July a few juveniles were still in the ground layer and on the surface, but elsewhere had completely disappeared. The numbers from the ground, field and shrub layers reached their maxima on 7 July although the ground layer maximum could reflect a peak of activity rather than one of density. The numbers from the tree trunks reached their maximum a week later (13 July), coinciding in time with a considerable fall in numbers at all other levels except the surface layer. This suggests that the net result of the movement in both directions over the tree trunks was the transfer of much of the population of the lower levels of the field to the tree canopy. (The slight increase in numbers in the surface layer at the same time cannot be explained). Although the diel population fluctuations in the field and shrub layers were still considerable during the first half of July, there was no apparent association with either the light-dark periods such as that seen in June, or with the recorded changes of temperature and humidity (Table 9). The graphs of Fig. 34 themselves now have very little in common, and as the $\frac{\text{'night' mean}}{\text{'day' mean}}$ ratios are all fairly close to unity, the fluctuations were probably chance events.

? [illegible]

The pattern of distribution underwent no further change after the middle of July. Juveniles had by now completely disappeared and the numbers of adults fell steadily. By mid- August they were virtually absent from the tree trunks, but upto this time were still fairly common elsewhere. However, at the end of August a sudden drop in numbers in the surface, field and shrub layer collections coincided with a slight increase in the ground layer, suggesting a return to the ground from the rest of the field. Relatively few adults were found during September, and the species had completely disappeared by the end of the month.

(b) Pitfall trap data.

The totals collected from the surface, field, shrub and tree layers would have been proportional to the density of *M. morio* within the region sampled, but collections from the pitfall traps would, in addition, have been influenced by changes in the efficiency of trapping for the different instars and by changes in the intensity of locomotor activity. Although it is not possible to isolate the contribution of each of these two factors, some measure of the possible influence of each can be detected by a closer examination of the results.

(i) Efficiency of trapping for different life stages.

The progressive increase, during the life history, in the numbers caught in thetraps may have arisen through a corresponding increase in the efficiency of trapping. During March, April and May pitfall traps were left out almost continuously, yet upto the third week in May only one or two specimens of *M. morio* were caught per week. However, during the last week of May, large numbers of juveniles suddenly appeared, of which the majority was in the sixth instar. Throughout this period, the species was restricted to the vegetation of the ground layer. The sudden increase in captures, occuring at a time when the population density would presumably have undergone relatively little change, is thought to have been associated with behaviour differences between the fifth and sixth instars. If it is assumed that the timing of the major stages of the life history of *M. morio* in the study area was similar to that previously described for this species in Great High Wood, then it can be seen from Fig. 13 that the sixth instar first appeared during the same period as the initial increase in captures. This suggests that the chance of an individual falling into a trap increased following the change from the fifth to the sixth instar.

A further similar increase occured following the change from the sixth to the final instar. From mid - June to early July, *M. morio* appeared in progressivly larger numbers in the field, shrub and tree layers as a result of the migration away from the ground, yet over this same period, the numbers caught in the pitfall traps continued to increase. In mid June adults comprised only 3% of the ground layer total, while by the first week in July the proportion had risen to over 80%, and again there was probably an association between the continued rise in captures and the change from one instar to the next.

As a result of laboratory experiments described later, it is known that adults were slightly more active than juveniles. However it is believed that the virtual absence from the traps of second, third and fourth instar juveniles followed by the progressive increase in captures from the fifth to the final instar simply reflected an increase in the efficiency of the trapping method with age. This probably resulted from the increase in size and weight following each moult. In support of this explanation, it was frequently noticed in the field that a small harvest-spider which moved onto the rim of the pitfall trap would pull itself back over the edge and escape, whereas a larger specimen in a similar situation would tend to slip and drop into the bottom of the trap.

(ii) Changes of activity with age.

The direct effect of the intensity of movement on the numbers caught in the pitfall traps is illustrated by differences, within any one 24 hour period, in the numbers caught by 'day' and by 'night'. It can be seen from Table 53 that there was an apparent increase in the level of nocturnal activity on all occasions, but only on 11 June, when the population was still virtually restricted to the ground layer through-out the diel, can the $\frac{\text{'night' mean}}{\text{'day' mean}}$ ratio of 1.9 be a true measure of the difference between the intensity of nocturnal and diurnal movement. Throughout the rest of June and July, this ratio would also have been influenced by changes in the density of the ground layer population associated with the nocturnal migration into the rest of the field. On 16 and 25 June movement was predominantly away from the ground, while during July, although nocturnal catches were still greater than those of the day, the volume of nocturnal migration into the canopy reached a very high level. Therefore, the size of the ground layer population on any one night would have been smaller than that on the preceding day, and the ratios, as indicators of the relative levels of nocturnal and diurnal activity will be rather low. Nevertheless, the changes in the ratios are of such magnitude that they almost certainly indicate definite changes in the distribution of diel activity with age.

In early June, when mainly juveniles were present, nocturnal activity was approximately twice as intense as that of the day, but by 25 June, when adults comprised 54% of the ground layer population, the proportion had risen to nearly seven. This was followed by a gradual decrease, and by the time the whole population was adult, the proportion was less than two. It would therefore seem that the level of nocturnal activity, (at least in the ground layer population and probably also among all individuals) increased to a maximum around the time of the final moult, then subsequently decreased to a level similar to that of the sixth instar.

(c) Vertical migration and the distribution of the species at different levels during the diel.

The movement of sixth and final instar M. morio on the tree trunks was actually observed: this was always exclusively nocturnal, most of the movement, both upwards and downwards, occuring soon after complete darkness had set in. However, the nature of any movement between the ground layer, and the field and shrub layers, can only be inferred by indirect means, the totals collected on any one occasion reflecting the net result of vertical migration in both directions. The results for June clearly show the direction of movement to have been predominantly away from the ground during the night and early morning, and back to the ground after dawn. The results for July are less easy to interpret, but it should not be inferred from the absence of an association with the 'day' and 'Night' periods (Fig. 34) that there was relatively little movement between the ground, and the field and shrub layers. Despite the lack of evidence on this point, there is every possibility that the migratory behaviour of M. morio in the lower levels of the field was similar to that recorded on the tree trunks, in which case, a considerable volume of traffic probably passed in both directions between the ground, and the field and shrub layers, especially during the first part of the night.

Nocturnal vertical migration is presumably associated with, but not necessarily caused by, the increase in the intensity of nocturnal locomotor activity described earlier. This is discussed after presentation of the results of laboratory studies on activity levels.

(d) Sex ratios.

Examination of the sex ratios throws further light on the behaviour of the adults. Figure 39 illustrates the ratios for the samples in which the totals were of sufficient size for application of the χ^2 test (expected > 5). The parts of the rectangle to the left and right of the centre line are proportional to the percentage of males and females respectively. Where the χ^2 test indicated

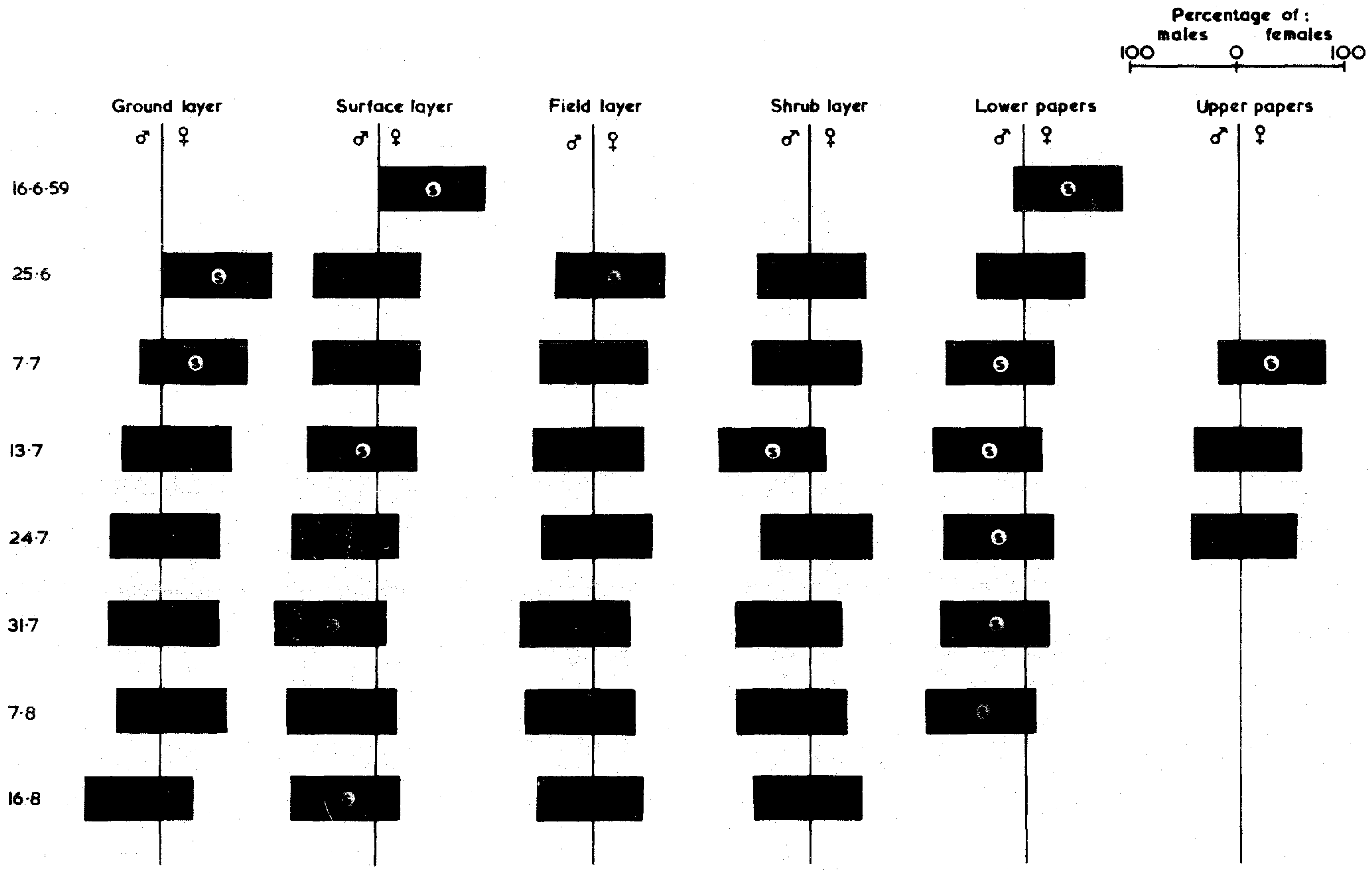


Fig. 39. The proportions of the sexes in each collection of adult <u>Mitopus morio</u>. (See text for explanation).

a significant deviation of the ratio from 1 ($P < 0.05$) a letter S is shown inside the rectangle. It is possible that the pitfall captures were biased as a result of a difference between the activity levels of the sexes. However, the general impression is that the ratios indicated by the figure are quite representative of the proportions of the sexes actually seen during the collections by hand from the ground layer.

The almost complete absence of males on 16 June indicates that females reached maturity slightly earlier than males. All but one of the adults found were on the surface vegetation and on the tree trunks, suggesting that, at least on this occasion, the penultimate instar moved just above the ground layer, moulted, then moved directly onto the trunks rather than into the ground or shrub layer.

On 25 June males were appearing and the sexes were equally distributed throughout the field and shrub layers, but only females were found in the ground layer. Two weeks later males had moved into this layer, but the excess of females was still significant.

During July most of the adult population was living above the ground. It can be seen from Fig. 39 that there was no consistent deviation of the sex ratios from 1 in samples from the field and shrub layers. The apparently significant excess of males on the surface is believed to have been due to males preferring the upper, females the lower surface of the bramble leaves. However, on the tree trunks, there were always significantly fewer females than males. As the sex ratio of the rest of the M. morio population did not apparently differ from 1, this suggests that some females may never have migrated as high as the tree canopy, remaining on or near the ground throughout the course of their life.

It is probable that those females which did move into the canopy would ultimately have had to return to the ground in order to deposit their eggs, whereas males would not necessarily have had to make the return journey. Such a situation is, to some extent, indicated by Table 54 in which, for each sex, the number of adults descending the trunks is expressed as a percentage of the number ascending on the same occasion.

Table 54. The number of adult Mitopus morio descending the tree trunks, expressed as a percentage of the number ascending.

Date	Males	Females
25.6	4.2%	6.4%
7.7	3.4%	36.4%
13.7	28.9%	182.6%
24.7	29.0%	91.7%
31 .7	27.8%	-

Except on 31 July, when no females descended, the proportion returning to the ground via the trunks on any one occasion was considerably higher in females than in males. However, this need not necessarily reflect a difference of behaviour between the sexes, but could have resulted from a relatively greater loss of males from the canopy as a result of predation - certainly to the human eye, the males of *M. morio* are more conspicuous than the females.

(e) Site of the final moult.

It can be seen from Table 53 that in general, on any one ocassion, the proportion of adults at each level of the field increased progressively with height above the ground. This was most pronounced on 16 June when adults first began to appear, and it suggests that the penultimate instar probably moved onto or above the surface for the final moult. This is in close agreement with the observation made in the field, that throughout the second half of June, *M. morio* undergoing the final moult were frequently seen during the night in the field layer but never elsewhere. Close inspection of the vegetation during the day revealed large numbers of cast skins attached just below the tips of grass blades and to both upper and lower surfaces of bramble leaves, but cast skins were never seen on the scrub bushes or on the tree trunks. The absence from the trunks would be expected, as an individual settling down to moult on the main migration route from the ground to the canopy would be easy prey for a potential predator of its own species. The apparent absence from the shrub layer might have simply reflected the efficiency of the cryptic colouration of *M. morio* although this is considered unlikely. If the absence was real, it would provide further support for the suggestion that the final moult occured mainly in the field layer. It would also help to explain the complete absence of *M. morio* from the shrub layer on 16 June, at a time when the species was quite common in the field layer.

B. Oligolophus agrestis.

The procedure adopted for analysing the data was the same as that used for M. morio.

(a) Survey of events by time.

There is likely to have been little difference between the course of the life history of O. agrestis in the study area and that previously described for this species based on material collected at Great High Wood. The graph of 'mean instar' against time (Fig. 19) presumably applies equally to the study area material. Figure 19 can thus be used to estimate the time at which the majority of the population was at any particular stage, but as the hatching period extended over two or three weeks, two or three instars would normally be present at the same time. Fig. 19 shows that hatching was almost complete by the first week in June, but upto 7 July, only two juveniles were found in the pitfall traps and none at any other level of the field. However, juveniles were easily found by hand searching of the ground layer vegetation, and it was clear that second and third and fourth instar juveniles never left the ground.

By 13 July, the majority of the population was in the fourth instar, but perhaps as the result of a progressive increase in the chance of capture with age, fifth instar juveniles formed the bulk of the pitfall collections. The species was still absent from the field and shrub layers, although two sixth instars were found on the tree trunks.

The population was probably changing to the fifth instar by 24 July, and over half the total from the pitfall traps was at this stage. Two individuals were found in shrub layer but in general, the fifth instar was still restricted to the ground. Sixth instar juveniles also appeared in larger numbers, and while a few were found on the ground, the majority had probably moved into the tree canopy rather than into the field and shrub layers.

This movement of sixth instars into the trees reached its highest intensity on 31 July, while, at the same time, a few also moved into the shrub layer. After this time, it is believed that the greater part of the population was living in the tree canopy, although as in M. morio, some individuals probably remained nearer the ground throughout their life.

Adults made their first appearance in the ground layer on 16 August and by 27 August juveniles had disappeared from all the samples, although a few were still found by hand searching of the ground layer vegetation. With the appearance of the adults, the numbers from all levels increased slightly, and for the first time a few individuals moved into the field layer. However, throughout the rest of the season, the density in the field and ground layers remained fairly low, most of the population by now dwelling in the shrub layer and the tree canopy. The density in the shrub layer increased steadily, and despite the absence of complete samples during the second half of September, it is believed that a peak in the numbers occured at this time.

Although the main migration into the tree canopy was carried out by the penultimate instar, adults continued to move into it for over two months after the time of the final moult, and a peak was reached in early October, just before the species disappeared completely from the trees. As a similar, but smaller, peak in the numbers returning to the ground was recorded at about the same time, it is possible that a general increase in activity, perhaps associated with senescense, occured in all animals at this time.

The disappearance of adults from the shrub layer and the trees in late October was perhaps due to a return to the ground layer, as a slight increase in pitfall captures occured at this time. However, the main cause is thought to have been the death of most of the population. The disappearance coincided with the period of leaf fall, and the loss of leaves, by removing the primary component of the food chain of the whole canopy fauna would, both directly and indirectly, have resulted in the loss of O. agrestis. Death would have been accelerated by the increasing shortage of food, which, at the same time, would also have been felt by other components of the canopy fauna, especially insectivorous birds. The resulting increase in the pressure of predation on O. agrestis might have been reinforced by the progressive loss of cover caused by leaf fall. In addition to these essentially biological factors, the microclimatic conditions of the shrub layer and the canopy might have been such that survival inthese layers was no longer possible. The fact that the species survived into December and early January in the ground layer, suggests that food might still have been readily available, or that the conditions of temperature and humidity in the ground were less unfavourable than those of the atmosphere above it.

(b) Vertical migration and the distribution of the species at different levels during the diel.

In general, both juveniles and adults were more abundant in samples taken by night than by day. The nocturnal collections from the pitfall traps were always slightly larger than those of the day, but the totals were generally so small, that it would be unwise to conclude from this that the level of nocturnal activity was definitely greater than that of the day. Too few juveniles ascended into the shrub layer to show the existence of any particular pattern of movement, but in the two complete collections of adults from this layer, there was a quite distinct increase in numbers after dusk, followed by a corresponding decrease around dawn. The situation on the tree trunks was quite clear, movement of both juveniles and adults in both directions, occuring exclusively by night.

(c) Sex ratios.

It is not possible to suggest the proportions of the sexes in the population as a whole, as the juveniles which ascended the trees in July were not sexed. However, examination of adults collected from a variety of sites suggests that it would not have differed noticeably from 1. There was never any significant difference between the numbers of each sex from the ground layer, but such differences did occur among adults from the shrub layer, and the tree trunks. Of the latter, the majority on all occasions were female, while of the former, the first two September samples consisted largely of males. This could imply the existence of a tendency for females to move into the canopy and for males to remain nearer the ground, but as the main ascent of trees was carried out by juveniles of undetermined sex, no estimate of the sex ratio of the canopy fauna is possible.

In all the samples of the second half of August, in which adults appeared for the first time, the sex ratios, while not differing significantly from 1, all showed a slight excess of females. This tendency, being common to collections from all parts of the field, suggests, as in *M. morio* that females reached maturity a little earlier than males.

It is known that the eggs of *O. agrestis* are deposited in the litter of the ground layer (Phillipson 1959) and it is therefore surprising that so few adults were found in this layer. This scarcity was confirmed by hand searching of the vegetation, and was therefore real, and not simply due to a low level of sampling efficiency, associated with the use of pitfall traps. A possible explanation is that females only moved from the rest of the field into the ground layer for oviposition, leaving immediately afterwards, while obviously males would have no need to return to the ground. Males might therefore be expected to be less common than females in this layer, but although this was usually the case, the differences were too small to be of statistical significance.

C. Species other than M. morio and O. agrestis.

In the following survey of the results for the three common ground dwelling species, *Lacinius ephippiatus*, *Odiellus palpinalis* and *Oligolophus tridens*, occasional reference is also made to the pitfall trap data of *Mitopus morio* and *Oligolophus agrestis*, the two migratory species already described.

(a) Survey of events by time.

The numbers of the three ground dwelling species caught in the pitfall traps rose progressively with age (instar) reaching a maximum around the time of the final moult. These increases could have resulted from corresponding increases in both activity level and trapping efficiency with age, and as suggested for *M. morio*, the latter was probably the most important factor. However, once the whole population had reached maturity, trapping efficiency would presumably remain constant, and variations in the rate of capture of adults would then largely reflect changes in density and activity levels.

Examination of Fig. 33 shows that the relative importance of these factors probably varied between species. For example; of the ground dwelling species, the activity level of *O. tridens* probably varied the most, that of

L. ephippiatus the least. *O. tridens* reached maturity by mid August, and from then on the density would certainly not have increased. Nevertheless considerable fluctuations in captures were apparent, and the peak at the end of August suggests a very high level of activity among young adults.

In *L. ephippiatus* on the other hand, the steady fall in the numbers of adults suggests that the graph reflects a steady fall in population density, the activity level either remaining fairly constant, or declining at a steady rate throughout.

Figure 33 also shows that, in all species, a second smaller peak in pitfall captures was recorded towards the end of the life history, over a month after the whole population had reached maturity. In the two migratory species this probably represented a return of specimens to the ground: this was shown to have been likely in *Mitopus morio* (Fig. 32) but the evidence for *Oligolophus agrestis* was not so clear. In the ground dwelling species, the second peak presumably represented a final burst of activity just before the species died out. This was probably associated with senescence, although the fact that the peaks occured on the same dates in the two spring species (27 August) and the three summer species (20 October) could mean that microclimatic conditions were responsible.

It is perhaps significant that Williams (1962), in a field study of the ground layer harvest-spider population, noted a similar bimodality in the temporal distribution of *Oligolophus agrestis* and *Oligolophus tridens* (the numbers of most of the other species were too low for consideration). Although his samples were only taken once a month, the timing of the two peaks in his and in the present study correspond reasonably well: for *O. agrestis*, they occured in August and November (compare August and October in the Durham study), for *O. tridens* in July and October (compare August and October). He attributed this bimodality to changes in the exclusiveness of the ground dwelling habit, the fall in numbers between peaks being due to vertical movement of part of the population away from the ground, the subsequent rise in numbers representing a return to the ground as the field layer vegetation died back. However, if, as in the present study, *O. tridens* actually remained in the ground layer throughout its life history, the peak in this species, at least, would have been one of activity rather than of population density.

(b) The distribution of each species over 'day' and 'night' periods.

In all the species studied the nocturnal pitfall catches were larger than those of the day. The distribution of the 24 hourly catch over the day and night on seperate occasions was not examined (other than in *M. morio*, Table 53), but considering only the annual totals, the degree of nocturnalism varied considerably both within and between species. This can be seen from Table 55 which shows the percentage of the total diel catch which was taken during the night.

Table 55. The degree of nocturnalism in harvest-spiders from the ground layer. The totals caught by night are expressed as a percentage of the 24 hour totals.

Species	Mean of regions 1 and 2	Region 1	Region 2
Mitopus morio	74.5 %	78 %	71 %
Oligolophus agrestis	76.0 %	84 %	68 %
Lacinius ephippiatus	81.5 %	90 %	73 %
Odiellus palpinalis	86.5 %	89 %	84 %
Oligolophus tridens	87.5 %	92 %	83 %
Nemastoma lugubre	93.5 %	95 %	92 %

In terms of the percentages based on the totals from both regions 1 and 2, *Mitopus morio* was the least nocturnal species, *Nemastoma lugubre* the most nocturnal. The degree of nocturnalism in the two regions differed slightly, all species being apparently more strongly nocturnal in region 1. These differences were probably associated with the slight floristic differences between the two parts of the study area: region 1 had a light covering of grass, contained large areas of bare litter and was fairly open, while region 2 had a deeper, fairly uniform cover of grass and was less open. Thus the floor surface of region 1 would have been relatively less well insulated from climatic changes than that of region 2, and the 24 hourly fluctuations of temperature, relative humidity and light intensity would have been less extreme in the former. This probably forced a higher proportion of the region 1 ground layer population to seek protection below the litter surface during the day, during which time they would not have been susceptible to capture by pitfall traps.

On the other hand, the vegetational differences may have produced distinct differences in the diel distribution of locomotor activity in the two regions. Williams (1959 a) showed that diel activity of the total arthropod ground layer fauna was more evenly balanced in woodland than in open scrub, and while region 1 of the present study does not represent such a vegetational extreme as open scrub, there are certain similarities. Assuming therefore region 1 to be approaching the scrub condition, and region 2 to be woodland, the present results are in accord with those of Williams.

Unfortunately, in a later paper (Williams 1962), it was shown that the harvest-spider component of the fauna behaved contrary to the general trend, activity being more evenly spread in the open scrub. To explain this apparent anomaly, it was suggested that while most feeding would take place at night, food was relatively more difficult to obtain in the scrub so that food searching activity in this area persisted into the day in order to satisfy hunger. In the present study at Nanny's Plantation, observations made during the night left little doubt that suitable food (Phillipson 1960 a.) was always apparently abundant, which could account for these harvest-spiders conforming to the trend for ground dwelling arthropods in general.

(c) Sex ratios.

In all the species of which reasonable numbers were obtained from the pitfall traps (L. ephippiatus, M. morio, O. tridens, and O. palpinalis), adult females were more abundent than adult males, at least initially. This could have resulted either from a numerical superiority of females in the ground layer or from a higher rate of capture of females from a population with a real sex ratio of 1. In the case of M. morio, as previously explained, the excess was probably numerical, but this was not necessarily the case in the ground dwelling species. In these, although females might have matured slightly earlier than males, Table 52 shows that the highest individual total of males was never more than half that of females, and clearly this explanation alone cannot account for the observed differences. Either females were more readily caught in the traps, because of their greater body weight and perhaps higher activity level, or the population actually contained a higher proportion of females. The latter explanation is unlikely to be correct, as the sex ratios were always approximately 1 in collections made by hand from other parts of Nanny's Plantation as well as from Great High Wood (Appendix A). At the same time however, laboratory experiments (described later) did not indicate a higher level of activity among females, although relatively minor differences may not have been revealed by experiments based on relatively low numbers of specimens. Clearly, more information is required before a sound explanation of the differences can be put forward.

IVb BEHAVIOUR STUDIES: LABORATORY INVESTIGATIONS

IVb BEHAVIOUR STUDIES: LABORATORY INVESTIGATIONS.

1. Temperature and relative humidity preferenda.

For the adults of several species of harvest-spider Todd (1949) showed a correlation between their laboratory determined humidity preferendum and the range of humidity within their normal habitat. The existence of a similar correlation between temperature preferenda and field temperatures was also suggested.

Todd's experiments were carried out mainly on adults. In the present work, it was hoped that results obtained by extending it to juveniles would help to explain why only certain species of harvest-spider move away from the ground layer during their life history.

Temperature and humidity gradient chambers were constructed as described by Todd (1949) and over a period of several weeks adults of Lacinius ephippiatus, Mitopus morio, Oligolophus agrestis and Oligolophus tridens were subjected to experiment. The results were inconclusive: apart from a slight 'end preference' individuals settled down apparently at random within the chambers. Despite considerable modification of both apparatus and methods of testing the same type of result was always obtained. It is unlikely that these species are indifferent to gradients of temperature and humidity, and in view of

Todds findings (1949, Tables 9 and 10) it is assumed that for reasons unknown, the experiments failed to demonstrate preferences which must surely exist.

In the absence of 'preference' data for adults, no experiments were carried out on juveniles.

2. Survival at different humidities and temperatures.

Todd (1949) also investigated survival at different humidities. Among the three species on which both humidity preference and survival experiments were carried out, the order of survival time was inversely related to the preferred relative humidity. Some of the data from Todd (1949) are reproduced in Table 56.

Table 56. Data from Table 8 and Appendix 2c in Todd (1949).

	Mean humidity preference (% R.H.)	Mean survival time (h) at 94% R.H.
Odiellus spinosus	55.5	350.0
Leiobunum rotundum	64.8	86.6
Oligolophus tridens	67.8	61.4

Clearly *O. tridens* had the shortest survival time and the highest humidity preference while, conversely, *Odiellus spinosus* had the longest survival time and the lowest humidity preference.

On the assumption that a similar relationship existed among other species of harvest-spider, survival experiments were carried out. It was hoped that the results would give an indication of the relative order of preferenda which could not be determined by more direct means.

(a) Methods.

Specimens were exposed, in samples of six, to one of a combination of three temperatures (5°, 16° and 25°C) and four relative humidities (30%, 60%, 90% and 100% R.H.) For *Mitopus morio*, *Oligolophus agrestis* and *Oligolophus tridens* samples of each instar from the fourth to the seventh were examined. *Lacinius ephippiatus* was very scarce in 1959 and only adults were found in sufficient numbers for testing.

Each specimen was put in a 5 x 1.5 cm glass specimen tube with a small strip of filter paper in the bottom to provide a foothold. Tubes were held together in groups of six and the open ends were covered by a circle of fine transparent nylon net secured by an elastic band. Each group was placed inside a small glass jar, and was supported 1 cm above the base by a plastic stand. The different humidities were produced by the use of water-sulphuric acid mixtures (Solomon 1951), sufficient liquid being used to just cover the base of the jar. Each jar was sealed by an 8 cm square glass plate pressed onto the vaseline smeared rim, and was then placed in the appropriate constant temperature enclosure (a cold room at 5°C, a water bath at $16^\circ \pm 0.5^\circ$C or a small incubator at $25^\circ \pm 0.5^\circ$C). The numbers of dead specimens were noted at intervals of four hours (except 0400h G.M.T.) for the experiments at 16° and 25°C, and once a day for those at 5°C.

(b) Preliminary experiments.

Two preliminary experiments were carried out. In the first, a group of twenty fourth instar Mitopus morio was exposed to each of three different humidities (30%, 60% and 90% R.H.) at 16°C. Ten of each group were given no food, the other ten were given a freshly killed Drosophila adult once a day. The results are illustrated in Fig. 40. There was no significant difference between the survival times at any one relative humidity and it was decided that food would not be provided in subsequent experiments.

In the second case, three identical sets of survival experiments were carried out at 25°C using ten fifth instar Mitopus morio for each condition. The results are illustrated in Fig. 41. Despite the wide 95% confidence limits there was a greater similarity between mean survival times at any one relative humidity than between those at different humidities. Although confidence limits of this size were typical of subsequent experiments, these results suggest that the means themselves were probably fairly reliable. However, to avoid confusion confidence limits are not shown in subsequent graphs, and descriptions are based on general trends rather than on individual mean values.

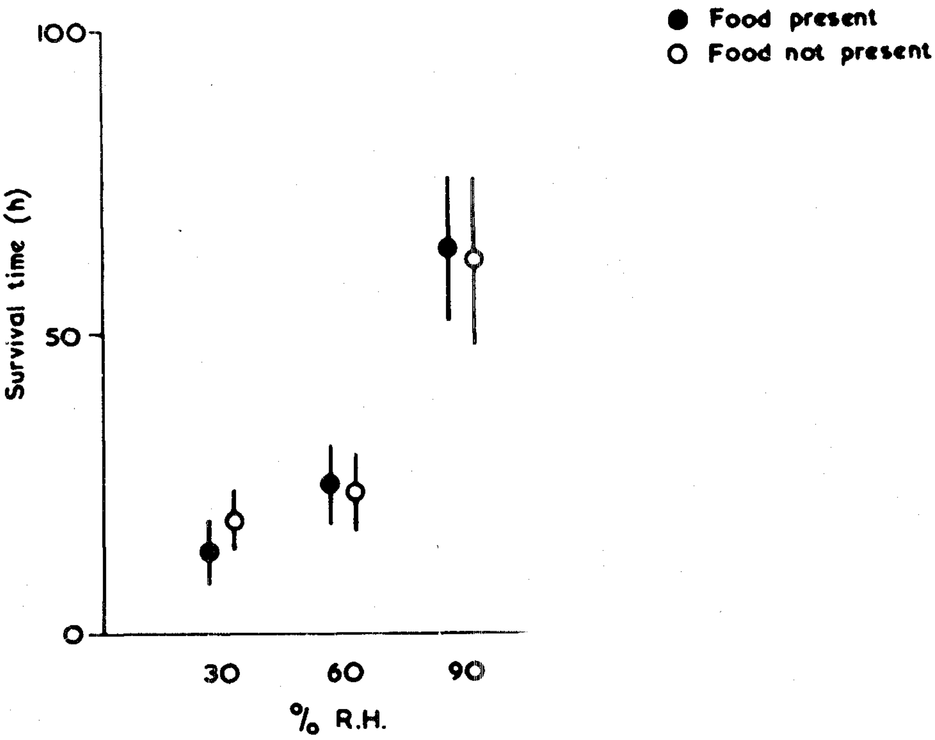


Fig. 40. Mean survival times (with 95% confidence limits) of fourth instar Mitopus morio in the presence and absence of food.

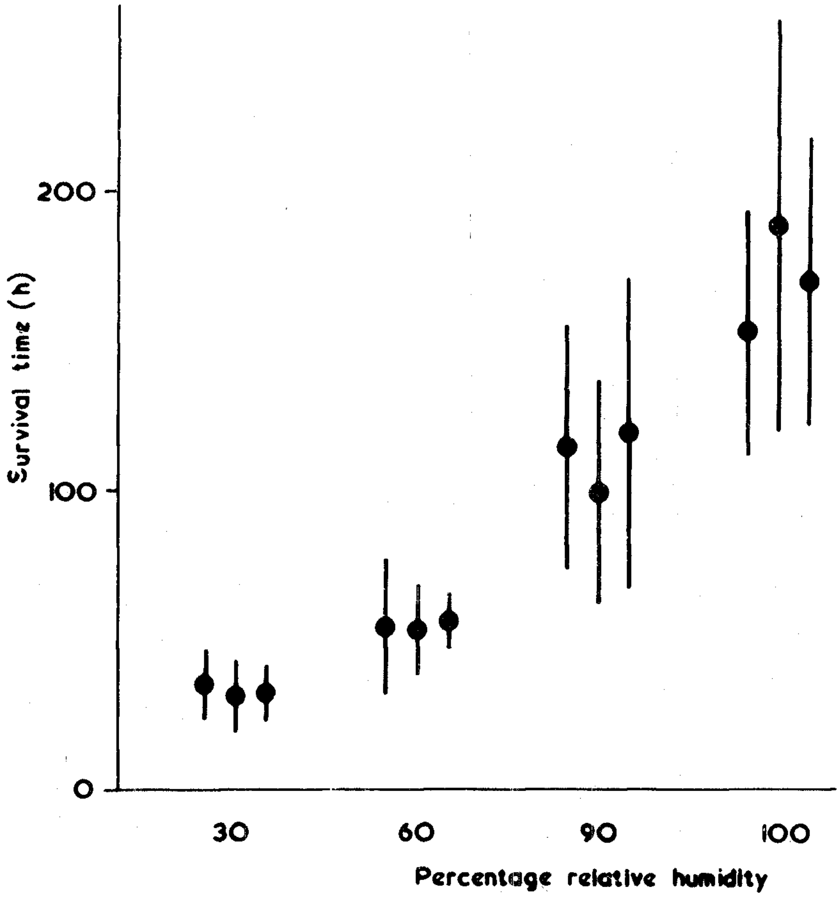


Fig. 41. Mean survival times (with 95% confidence limits) of fifth instar Mitopus morio when exposed to the same conditions.

(c) Results.

The results for all specimens are given in Tables 57 to 60. The absence of records for the fourth instar of *Oligolophus tridens* at 5°C is due to a fault in the constant temperature room which caused the temperature to rise to 14°C overnight.

(i) Relationship between survival time and age at constant temperature and humidity.

The changes in mean survival times from the fourth to the seventh instars at the same temperature and humidity are illustrated in Figs. 42 to 44.

In *Mitopus morio* survival times under the same conditions generally increased with age, the maximum being reached in the final instar. However, exceptions occured at 16°C - 100% R.H. when relatively little change was apparent, and at 25°C - 90% and 100% R.H. when adults did not survive as long as the penultimate instar. The atypical trend at 5°C - 100% R.H. was probably of little importance, the standard errors of the first two means being large: for example that of the fourth imstar was 715.2 ± 122.1 h while that of 343.9 ± 18.1 h for the sixth instar was more typical.

The trends in the two species of *Oligolophus* were similar to each other. At 5°C both differed from *M. morio*

Table 57. Mean survival times (in hours) of *Mitopus morio*.

Instar	% R.H.	5°C	16°C	25°C
IV	30	57.6 ± 10.7	24.8 ± 2.5	14.2 ± 1.6
	60	84.0 ± 17.7	36.0 ± 4.6	17.2 ± 0.8
	90	130.6 ± 19.2	72.0 ± 11.8	40.8 ± 6.5
	100	715.2 ± 122.1	163.4 ± 31.4	71.6 ± 11.2
V	30	67.2 ± 7.9	34.4 ± 2.6	15.2 ± 1.3
	60	108.0 ± 9.8	50.2 ± 2.7	17.2 ± 1.5
	90	158.4 ± 15.2	104.8 ± 10.5	43.2 ± 5.6
	100	794.4 ± 106.6	160.0 ± 29.1	78.0 ± 12.8
VI	30	72.0 ± 8.8	34.7 ± 3.8	26.7 ± 3.5
	60	103.9 ± 13.1	50.0 ± 5.1	34.0 ± 1.4
	90	192.0 ± 23.9	94.7 ± 13.6	90.7 ± 11.7
	100	343.9 ± 18.1	166.0 ± 39.6	175.0 ± 39.4
VII male	30	84.0 ± 16.4	43.3 ± 4.9	24.7 ± 5.2
	60	127.9 ± 14.5	51.3 ± 4.1	31.3 ± 5.6
	90	331.9 ± 46.9	124.0 ± 13.0	76.8 ± 4.3
	100	528.0 ± 30.3	156.0 ± 15.4	59.0 ± 8.3
VII female	30	151.2 ± 34.2	77.6 ± 3.5	40.7 ± 4.9
	60	259.2 ± 22.1	115.3 ± 14.9	46.2 ± 6.2
	90	559.2 ± 20.1	176.3 ± 13.0	77.0 ± 13.4
	100	559.2 ± 9.8	182.7 ± 22.6	85.3 ± 9.4

Table 58. Mean survival times (in hours) of *Lacinius ephippiatus*.

Instar	% R.H.	5°C	16°C	25°C
VII male	30	31.9 ± 4.9	25.3 ± 3.4	8.0 ± 0
	60	64.1 ± 4.9	40.0 ± 5.0	12.0 ± 0
	90	96.0 ± 8.8	72.0 ± 2.5	38.7 ± 3.8
	100	192.0 ± 52.6	198.7 ± 4.2	96.0 ± 6.7
VII female	30	48.0 ± 8.8	37.3 ± 3.4	24.0 ± 2.5
	60	96.0 ± 3.1	53.3 ± 1.7	29.3 ± 1.7
	90	192.0 ± 8.8	176.0 ± 10.1	57.5 ± 1.9
	100	504.0 ± 30.9	280.0 ± 13.4	154.7 ± 13.2

Table 59. Mean survival times (in hours) of <u>Oligolophus agrestis</u>.

Instar	% R.H.	5°C	16°C	25°C
IV	30	283.9 ± 72.7	51.3 ± 2.2	21.3 ± 1.3
	60	463.9 ± 147.6	87.3 ± 8.5	42.7 ± 4.6
	90	823.9 ± 362.0	161.3 ± 27.9	66.5 ± 9.3
	100	930.0 ± 154.6	289.7 ± 37.7	114.7 ± 8.3
V	30	271.9 ± 29.4	56.0 ± 9.1	35.3 ± 6.5
	60	307.9 ± 28.7	92.3 ± 20.0	62.0 ± 9.9
	90	618.0 ± 42.1	202.0 ± 34.4	112.3 ± 9.6
	100	904.1 ± 72.7	338.3 ± 25.2	180.7 ± 24.1
VI	30	136.1 ± 18.1	106.7 ± 18.5	53.3 ± 0.4
	60	196.1 ± 53.1	131.3 ± 16.6	61.6 ± 11.1
	90	295.9 ± 77.3	215.3 ± 33.9	126.5 ± 18.2
	100	648.0 ± 42.9	364.0 ± 46.9	230.4 ± 26.9
VII male	30	120.0 ± 12.0	49.1 ± 5.8	30.7 ± 3.7
	60	182.0 ± 29.4	106.1 ± 13.9	43.1 ± 2.8
	90	472.1 ± 73.3	176.4 ± 6.1	74.7 ± 14.1
	100	796.1 ± 44.9	222.0 ± 17.7	122.4 ± 18.4
VII female	30	151.9 ± 20.1	94.3 ± 4.9	48.2 ± 2.9
	60	317.0 ± 81.1	110.5 ± 20.9	64.4 ± 5.7
	90	628.1 ± 95.5	261.7 ± 29.5	135.1 ± 19.2
	100	1015.9 ± 111.3	256.3 ± 20.6	205.3 ± 36.4

Table 60. Mean survival times (in hours) of *Oligolophus tridens*.

Instar	% R.H.	5°C	16°C	25°C
IV	30	—	35.2 ± 4.4	18.7 ± 1.3
	60	—	49.3 ± 7.7	28.0 ± 2.5
	90	—	88.8 ± 29.8	65.3 ± 10.0
	100	—	159.3 ± 26.1	105.2 ± 20.4
V	30	195.0 ± 10.2	42.0 ± 7.7	16.2 ± 2.2
	60	319.9 ± 15.2	48.9 ± 6.4	26.0 ± 3.7
	90	457.1 ± 84.7	129.7 ± 12.9	60.0 ± 14.5
	100	858.0 ± 92.4	240.0 ± 28.4	99.2 ± 14.7
VI	30	127.9 ± 9.8	48.0 ± 3.1	37.0 ± 4.0
	60	151.9 ± 18.1	103.7 ± 12.4	56.0 ± 2.5
	90	264.0 ± 27.2	185.3 ± 28.0	67.3 ± 5.5
	100	475.0 ± 44.3	408.7 ± 31.6	132.8 ± 39.1
VII male	30	66.1 ± 8.4	37.3 ± 4.2	17.3 ± 2.2
	60	112.1 ± 20.1	58.7 ± 5.1	44.0 ± 1.5
	90	199.9 ± 9.8	128.0 ± 10.1	64.7 ± 4.6
	100	441.6 ± 97.2	240.0 ± 15.2	156.0 ± 15.2
VII female	30	125.9 ± 9.6	64.0 ± 2.5	25.3 ± 3.7
	60	192.0 ± 30.3	122.7 ± 8.4	51.3 ± 2.9
	90	400.1 ± 35.6	160.0 ± 5.0	94.7 ± 18.2
	100	456.0 ± 83.6	296.0 ± 5.0	214.7 ± 14.9

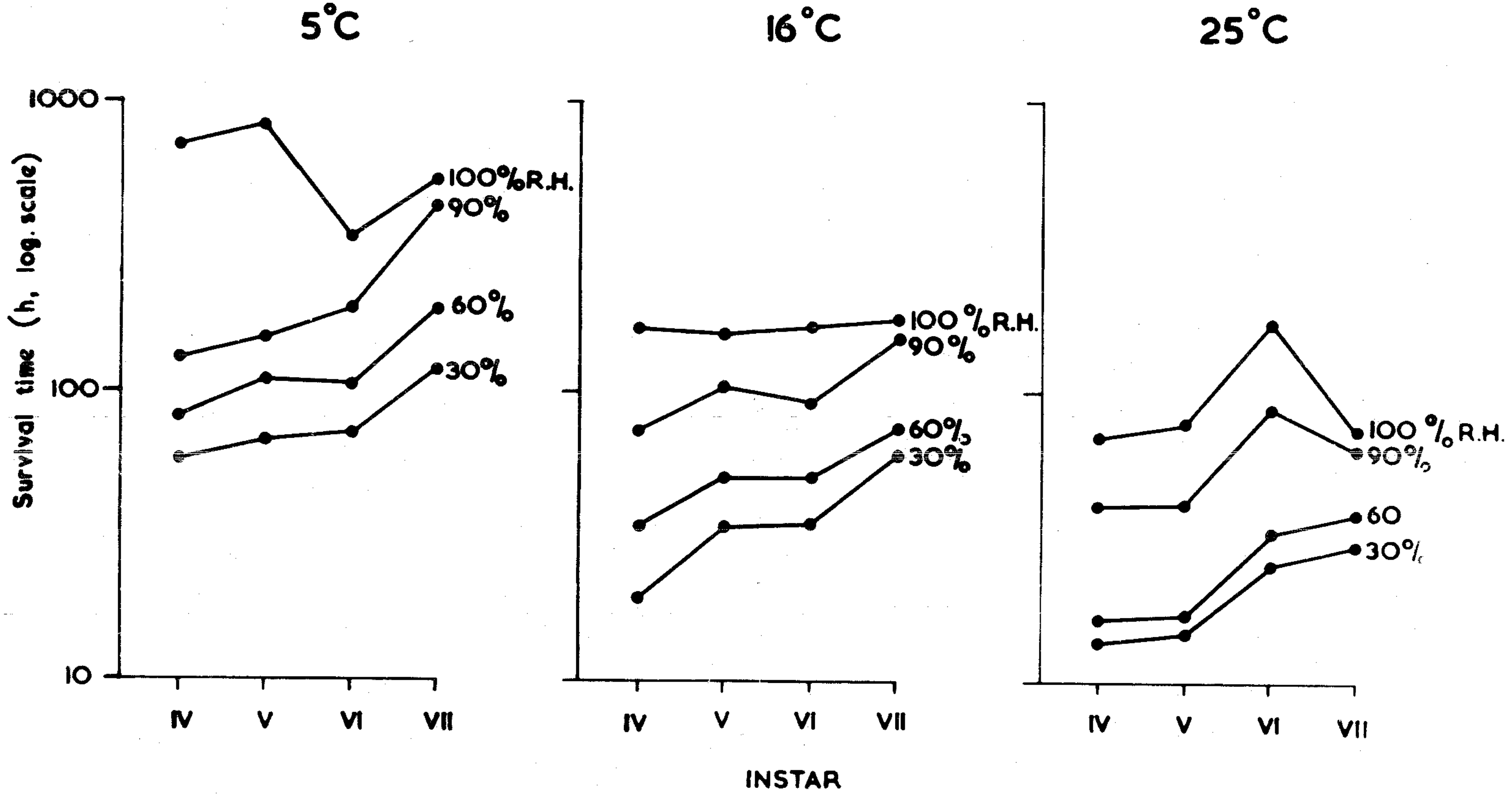


Fig. 42. Changes in mean survival time with age in Mitopus morio.

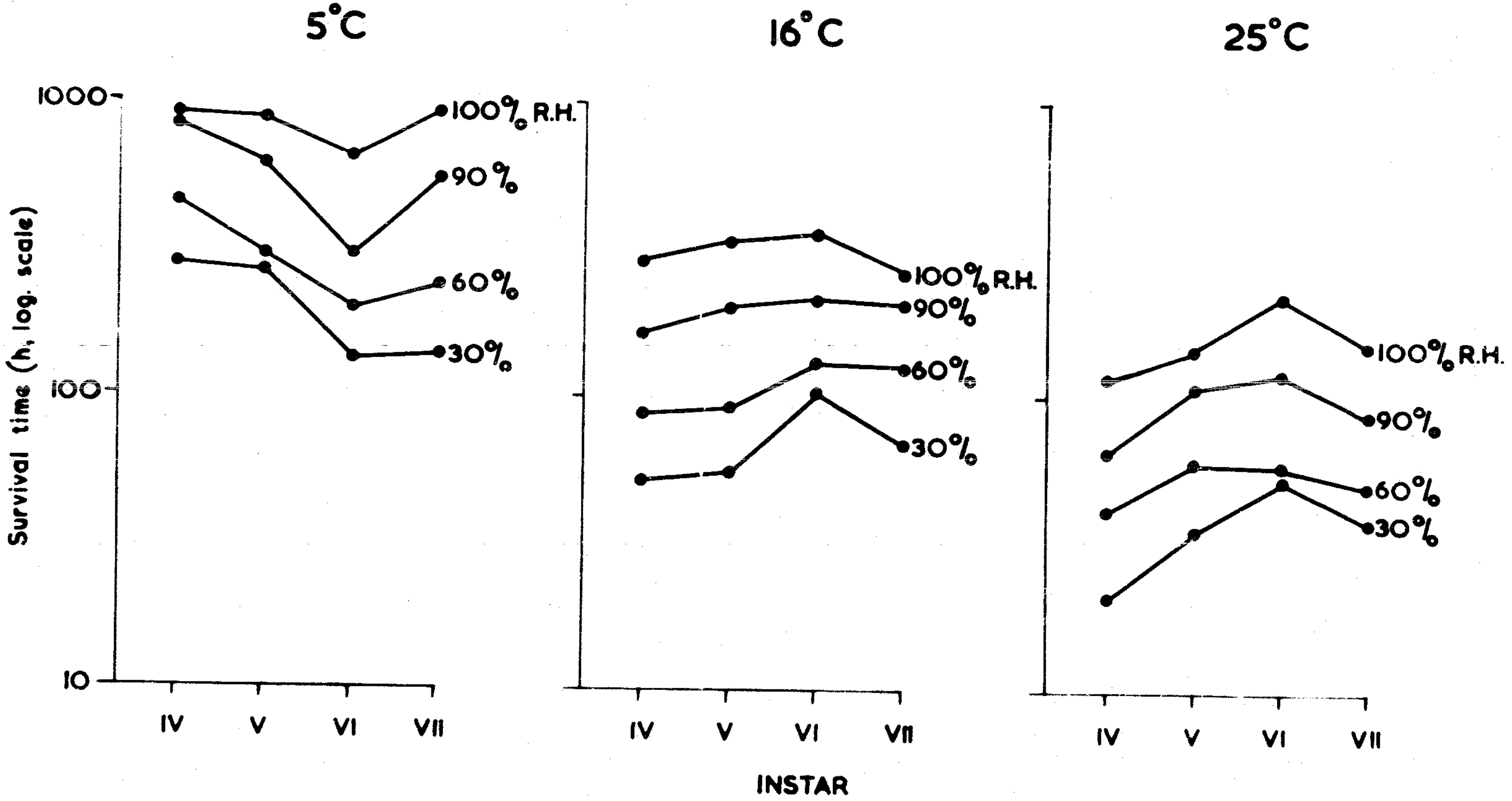


Fig. 43. Changes in mean survival time with age in Oligolophus agrestis.

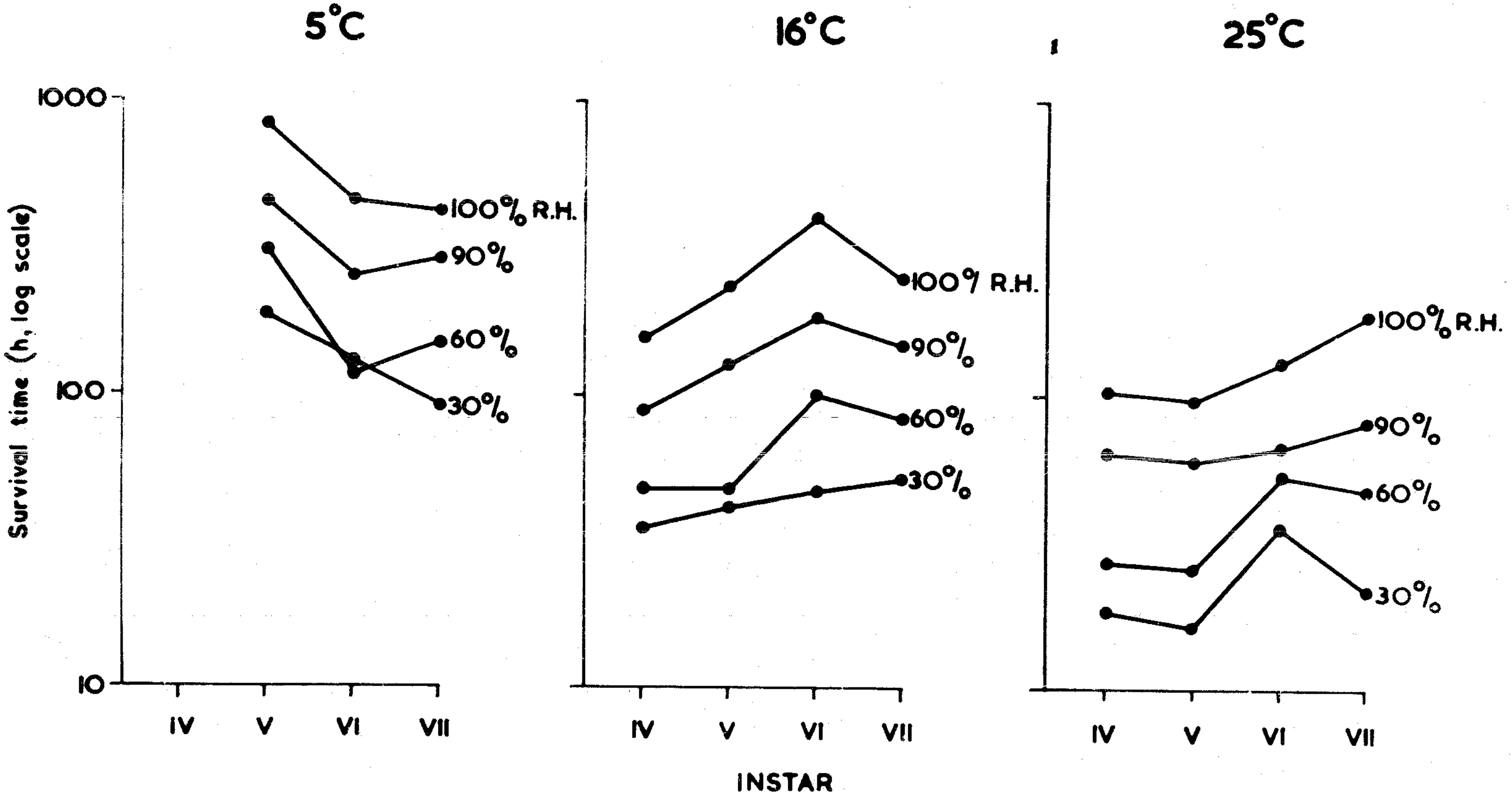


Fig. 44. Changes in mean survival time with age in *Oligolophus tridens*.

in that survival times decreased upto the sixth instar before rising slightly in the adults. At 16° and 25°C the trends in the juvenile stages were similar to those of M. morio, the means increasing upto a maximum in the sixth instar. However, in adults a slight decrease was generally apparent.

(ii) Relationship between survival time and temperature at constant humidity.

For each instar at any one relative humidity, the relationship between mean survival time and temperature is shown as a ratio obtained by dividing the mean survival time at the higher temperature by that at the next lowest temperature. For example, in adult female M. morio at 30% R.H. the means at 25°, 16° and 5°C respectively were 40.7 hours 77.6 hours and 151.1 hours, and the corresponding ratios are $\frac{40.7}{77.6} = 0.52$ and $\frac{77.6}{151.1} = 0.51$.

The ratios for all species are given in Table 61. Clearly these were generally in the region of 0.5, and because of the considerable variability between individual survival times, the occasional atypical ratio was probably of little significance. Such minor differences were smoothed by calculating the mean of all the ratios for each species. (Table 62). These proved to be very similar, ranging from 0.49 to 0.61 and clearly survival

Table 61. Ratios obtained by dividing the mean survival time at one temperature by that at the next lowest temperature.

Instar	% R.H.	*Mitopus morio*		*Lacinius ephippiatus*	
		$\frac{16^{\circ}C \text{ mean}}{5^{\circ}C \text{ mean}}$	$\frac{25^{\circ}C \text{ mean}}{16^{\circ}C \text{ mean}}$	$\frac{16^{\circ}C \text{ mean}}{5^{\circ}C \text{ mean}}$	$\frac{25^{\circ}C \text{ mean}}{16^{\circ}C \text{ mean}}$
IV	30	0.43	0.57	–	–
	60	0.43	0.48	–	–
	90	0.55	0.57	–	–
	100	0.23	0.44	–	–
V	30	0.51	0.44	–	–
	60	0.46	0.34	–	–
	90	0.66	0.41	–	–
	100	0.20	0.49	–	–
VI	30	0.48	0.77	–	–
	60	0.48	0.68	–	–
	90	0.49	0.96	–	–
	100	0.48	0.05	–	–
VII male	30	0.51	0.57	0.79	0.32
	60	0.40	0.61	0.62	0.30
	90	0.37	0.62	0.75	0.54
	100	0.29	0.38	1.03	0.48
VII female	30	0.51	0.52	0.78	0.64
	60	0.44	0.40	0.55	0.55
	90	0.31	0.44	0.92	0.33
	100	0.33	0.47	0.55	0.55

Table 61 Continued.

Instar	% R.H.	*Oligolophus agrestis*		*Oligolophus tridens*	
		16°C mean / 5°C mean	25°C mean / 16°C mean	16°C mean / 5°C mean	25°C mean / 16°C mean
IV	30	0.18	0.41	-	0.53
	60	0.19	0.49	-	0.57
	90	0.19	0.41	-	0.73
	100	0.31	0.39	-	0.66
V	30	0.20	0.63	0.21	0.38
	60	0.29	0.67	0.15	0.53
	90	0.33	0.55	0.28	0.46
	100	0.37	0.53	0.28	0.41
VI	30	0.78	0.49	0.37	0.77
	60	0.67	0.47	0.68	0.54
	90	0.73	0.59	0.70	0.36
	100	0.56	0.63	0.86	0.32
VII male	30	0.41	0.62	0.56	0.46
	60	0.58	0.41	0.52	0.75
	90	0.37	0.42	0.64	0.50
	100	0.28	0.55	0.54	0.65
VII female	30	0.62	0.51	0.51	0.39
	60	0.35	0.58	0.64	0.42
	90	0.42	0.52	0.39	0.59
	100	0.25	0.80	0.65	0.72

Table 62. Means of all the ratios given in Table 61.

Species	Mean ratio
Mitopus morio	0.49
Lacinius ephippiatus	0.61
Oligolophus agrestis	0.48
Oligolophus tridens	0.52

times, on average, were virtually halved for each temperature increase of approximately 10°C.

(iii) Relationship between survival time and humidity at constant temperature.

For each instar at any one temperature, the relationship between mean survival time and humidity can be seen by examination of the data shown in Tables 57 to 60. In all instars of all species, survival times increased progressively with increase of humidity, the rate of increase being illustrated in Fig. 45.

In all adults under all conditions examined, females outlived males, although the differences between the two were not always of statistical significance.

(iv) Comparison of survival times of different species under the same condtions of temperature and humidity.

Differences between species were illustrated by comparing

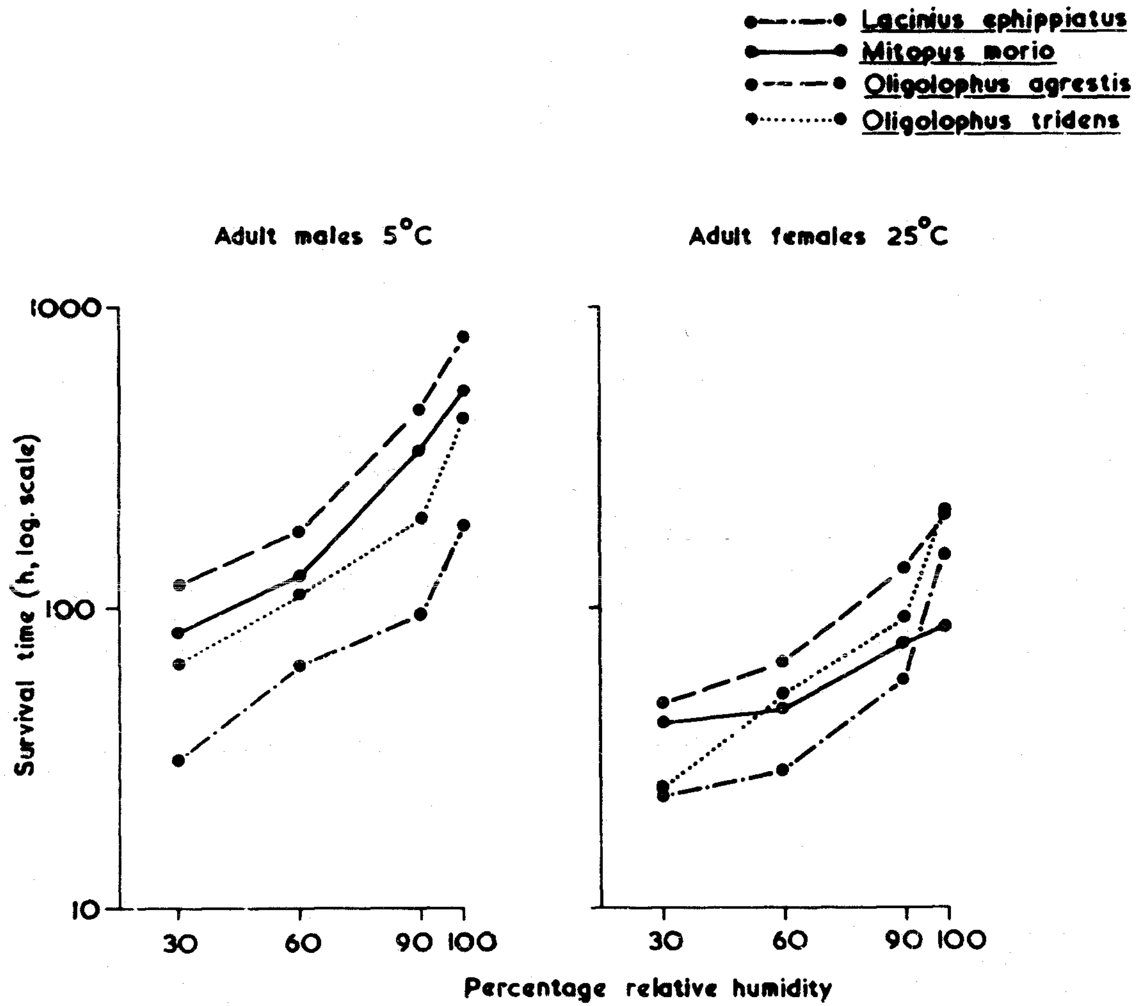


Fig. 45. Survival times of equivalent instars of the various species.

the mean survival times of equivalent instars when exposed to the same conditions. A separate graph was drawn for each instar at each different temperature, mean survival times being plotted (on a logarithmic scale) against the percentage relative humidity. The graphs were so similar that of the fifteen drawn, only two representative examples are given (Fig. 45). In general, the survival time of any one instar of *Oligolophus agrestis* was the highest, that of *Lacinius ephippiatus* the lowest, with those of *Mitopus morio* and *Oligolophus tridens* intermediate between the two extremes.

(d) Discussion.

Although survival times as determined in the laboratory would not necessarily apply in the field, it is believed that exposure of any one instar to the microclimatic conditions of its normal habitat would be unlikely to bring about death. Nevertheless, individuals would presumably move away from unfavourable conditions long before death could result, and the relationship between laboratory determined survival times of the various species might reflect the relative order of field preferenda.

For example, species with shortest survival times would occur in regions of highest humidity, those with the longest survival times in regions of lowest humidity.

Thus, considering equivalent instars of the species studied, *Lacinius ephippiatus* had the shortest survival times and was exclusively restricted to the ground layer, where the relative humidity ranged between 72 and 100% R.H. (see Table 9). At the other extreme *Oligolophus agrestis* had the longest survival times and, in the later instars, moved into the shrub and tree layers where midday humidities as low as 55% R.H. were recorded. *Mitopus morio* and *Oligolophus tridens* were intemediate between the two extremes, both in choice of habitat and survival time. *M. morio* did move into the shrub and tree layers in the later instars, but unlike *O. agrestis* still occured commonly in the ground and field layers. *O. tridens* occasionally moved from the ground to the field layer, although this was not observed in the study area itself. (Todd described this species as an inhabitant of the ground and field layers.)

It was shown that for any one instar the mean survival time was virtually halved for each temperature increase from 5° to 16°C and 16° to 25°C. At 100% R.H. any evaporation of water from the body was eliminated and death presumably occured when all the food reserves had been utilised. As harvest-spiders are poikilothermal, the rate of utilisation would depend largely on the outside temperature. Assuming a Q_{10} of approximately 2, each temperature increase was close enough to 10°C to predict that the rate would be approximately doubled at each step. Thus food reserves would be utilised twice as rapidly, and at 100% R.H. only, this could account for the observed halving of survival times.

At the lower relative humidities survival times were never as great as at saturation point. The food reserves were probably never exhausted and death would have resulted largely from dessication rather than starvation. An attempt was made to explain the relationship between survival times at these humidities on the basis that the rate of dessication was directly related either to the relative humidity or to the saturation deficit (= evaporating power) of the atmosphere. There proved to be no consistent relationship with either.

Within any one species at constant relative humidity and temperature (except 5°C in the two species of *Oligolophus*), the mean survival time tended to increase progressively from the fourth to the sixth instar, followed by a greater variability on reaching maturity. No satisfactory explanation can be offered for the reduction in *Oligolophus* at 5°C, while the variability in adults was probably associated with the approach of senescence in some individuals.

At humidities below saturation point some of the initial increase could have resulted from a progressive reduction, with age, in the rate of water loss per unit body weight. However, as a similar increase also frequently occured at saturation point, this cannot be the complete answer.

Clearly, the nature of the survival data precludes any precise analysis of the influence of age, temperature and relative humidity on survival times. Similarly, in the absence of data on actual water loss rates under different conditions, speculation on the probable influence of various biological factors (cuticle permeability, rates of respiration and of defaecation) can be of little value. Above all else, the survival experiments have shown the extent of the problems involved, the answers to which can only be found by more carefully planned laboratory investigations.

3. Activity over the 24 hour period.

General observations during field and laboratory investigations suggested the existence of both seasonal and 24 hourly variations in the intensity of movement in some species. To investigate this, a series of experiments was carried out in which the activity of both juvenile and adult harvest-spiders was recorded by means of an aktograph. The primary aim was to aid interpretation of the field results: thus the experiments were carried out under conditions as near as possible to those encountered in the field. A full investigation of the factors influencing activity was beyond the scope of the present study, although a few experiments were made with adult *Mitopus morio*.

(a) The aktograph.

The aktograph used had to be equally sensitive for the relatively small juveniles as well as the adult harvest-spiders. Several types of aktograph were tested before a suitable one was found.

The normal system, in which the movement of an animal enclosed in a tilting arena is recorded by mechanical or electrical means, was considered to be insufficiently sensitive for the smallest harvest-spiders. An attempt was therefore made to build a sensitive mechanical aktograph using part of a wrist watch movement. The balance wheel, supported between its jewelled bearings, was mounted with the spindle in the horizontal plane. A 30 cm length of strong but thin wire was fixed across the diameter of the wheel with 8 cm on one side of the pivot, 22 cm on the other. A small celluloid animal chamber was suspended from the end of the short arm. A single small bristle was attached to the end of the long arm, and was made to move against smoked paper on a barograph drum. When the animal was in the chamber the arm was brought to rest in a horizontal position by movement of a small counterbalance weight. This system did not prove to be satisfactory. With a large harvest-spider (pre-adult *Platybunus triangularis*), movement could only be recorded over short periods as the bristle tended to drift away from the drum, while the only movement recorded with a small animal was that caused by outside vibrations.

Two 'electronic' aktographs were then built. The first was that described by Backlund and Ekerood (1950) in which the movement of an animal near metal wires acting as one plate of a condenser, brought about slight changes in its capacitance. This change was converted ultimately to one of current which was used to operate a recording device. All attempts to obtain results with this system failed. It was later discovered that the value of a resistor in the oscillator section of the published circuit was such that the degree of damping would have been too heavy, and the apparatus could not therefore have been expected to work.

The second 'electronic' aktograph used a principle similar to that described by Backlund and Ekerood, but was based on a circuit described by French (1957). This system seemed to be extremely sensitive, but long term frequency drift resulted in a progresive loss of sensitivity over a period of several hours. This would presumably have been reduced or eliminated by enclosing the chassis of the amplifier in a draught free, constant temperature enclosure but lack of time prevented this being carried out.

In the aktograph finally used, each passage of an animal through a beam of light was recorded. The method described by Williams (1959) was first tried. In this, a beam of infra-red light was projected across a circular runway and focussed onto a phototransistor (Mullard OCP 71). Current changes in the transistor, caused by the passage of an animal across the beam, were amplified by a power transistor, (Pye V15/20P) which operated a relay in its collector circuit. This in turn actuated a second relay with a short extension arm 'writing' on the smoked paper of a barograph drum. Although this system worked extremely well with large harvest-spiders, it was difficult to adjust the sensitivity control so that every passage of a very small specimen (e.g. third instar Mitopus morio) was recorded.

A greater sensitivity was achieved by placing a micro-relay (shunted by a 5 k Ω potentiometer) directly in the collector circuit of the phototransistor rather than in that of the power transistor. The latter was then disconnected. However, even this system was not completely satisfactory with small specimens.

Finally, current changes in the collector circuit were recorded directly by using a sensitive moving coil meter movement with an extended 'writing' arm in place of the micro-relay. This system worked perfectly with animals of all sizes and was therefore adopted for the main study.

(b) Constructional details of the aktograph.

Three identical aktogrphs were built, and the activity records from all three were made simultaneously on the same smoked barograph paper. The wiring diagram and the various parts of the apparatus are illustrated in Figs. 46 and 47.

(i) The recording device.

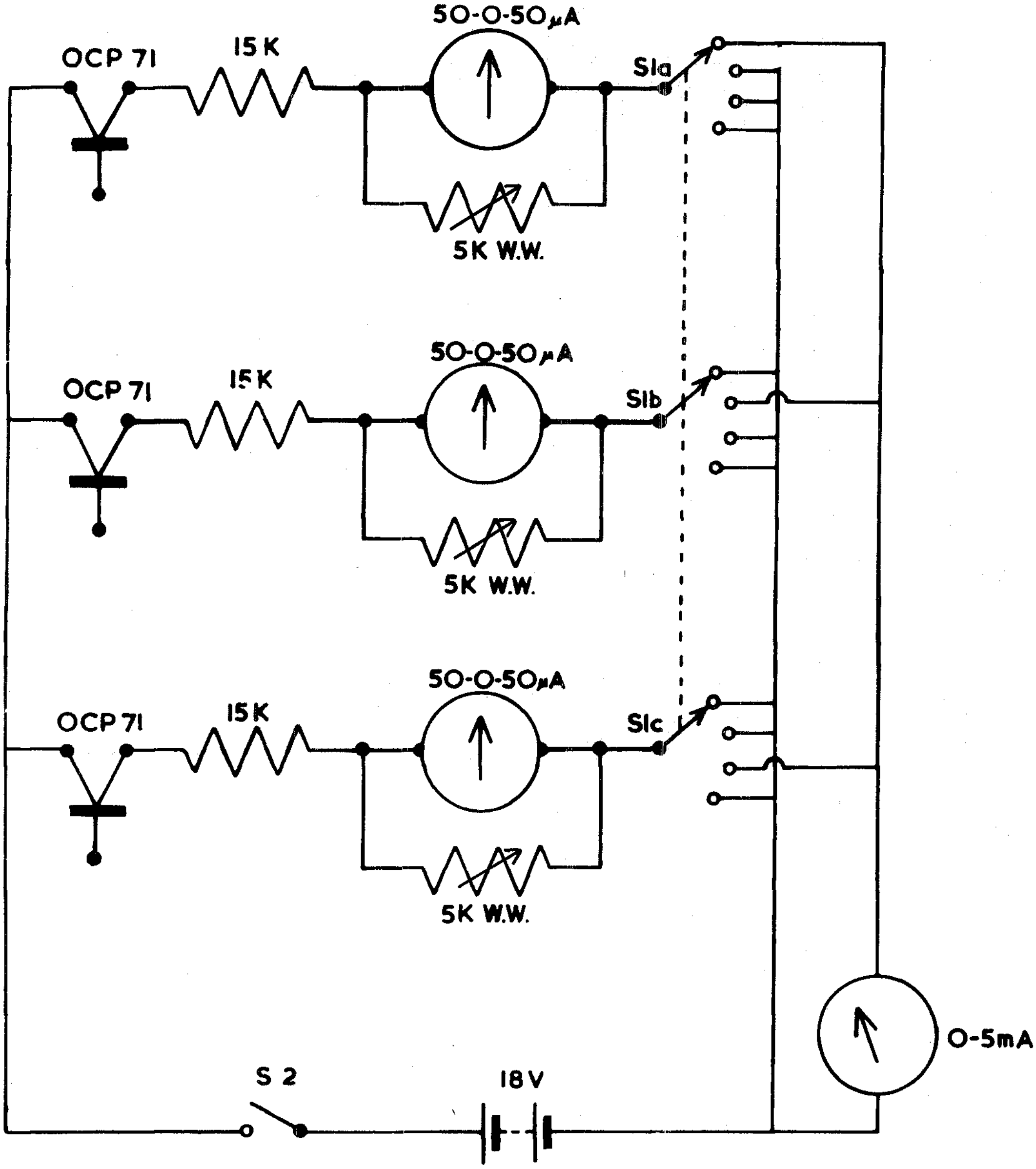


Fig. 46. The circuit diagram of the aktographs.

Key to Fig. 47.

a. Phototransistor mount.

b. Phototransistor.

c. Lens.

d. Wooden block.

e. Water filled Petri dish.

f. Glass cover of animal chamber.

g. Circle of black paper.

h. Light filter.

i. Lens.

j. Bulb.

k. Lamp housing.

l. Strip of filter paper.

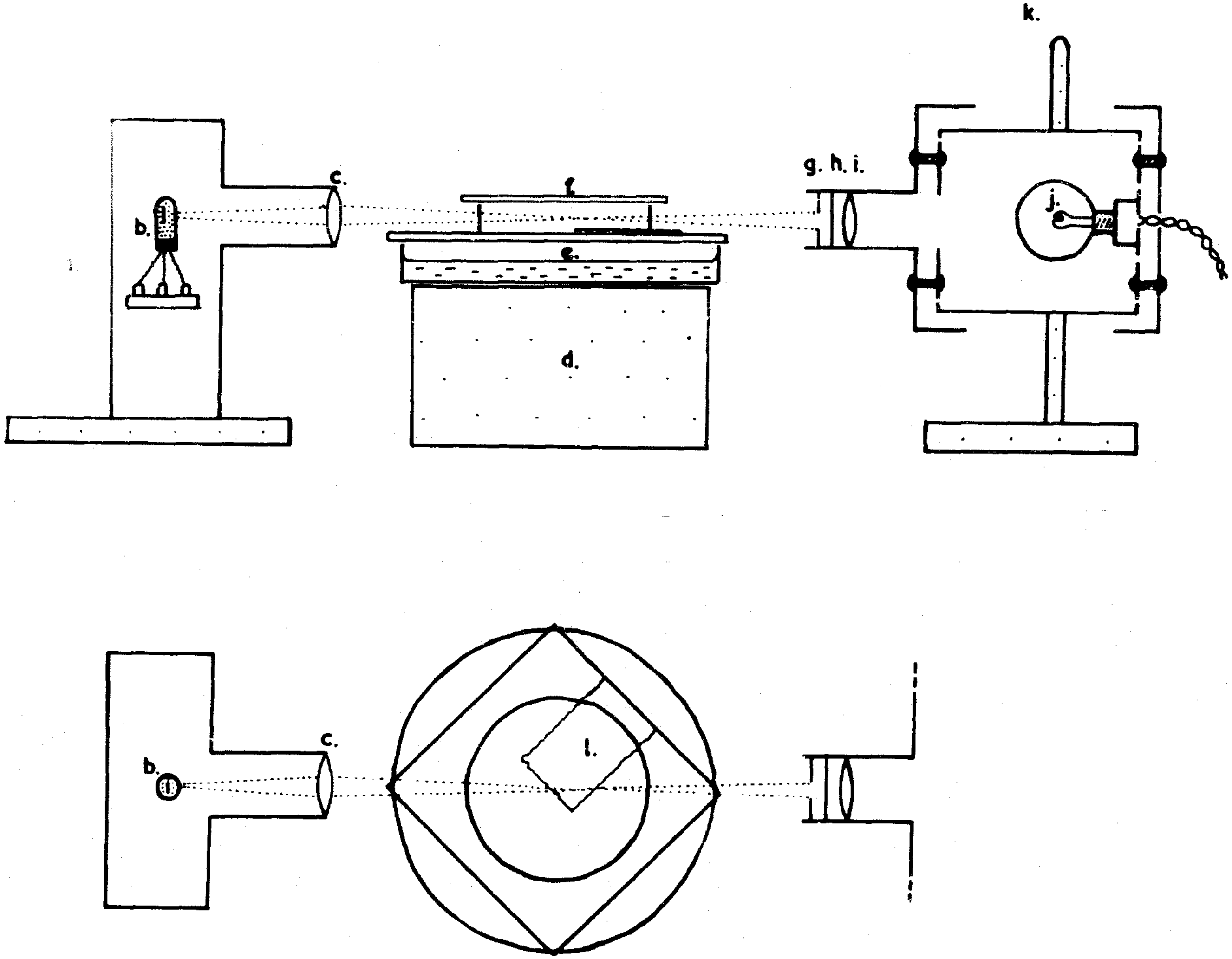


Fig. 47. Diagram of aktograph. (Not to scale.)

The movement of a centre-zero 50 micro-amp meter was removed from its case, and the metal needle cut off 5 mm from the pivot. A 12 cm length of drawn out glass tubing was glued onto the cut end of the needle and a single bristle from a camel hair paint brush was cemented to its free end. The movement was then mounted at the side of the barograph drum and the counterbalance weight of the meter was increased until the arm rested in the horizontal position. When the bristle was working against the smoked paper, it was found that the springs of the movement were too weak to return the arm to its resting position after each deflection. To rectify this, one end of a 2.5 cm length of 16 S.W.G. copper wire was soldered to the meter frame with its free end 1 cm above the cut end of the needle. A partly stretched wristwatch hairspring was soldered between this free end and the needle. By bending the wire, the tension of the spring was adjusted until the arm would return to the horizontal position without the initial deflection having been appreciably retarded.

The wiring diagram of the three meter movements and phototransistors is given in Fig. 46. The transistor feeders were left floating. The movements were shunted by 5 kΩ wire - wound potentiometers to permit adjustment of the intensity of the 'kick'. All three movements were connected via a 3 pole 4 way rotary switch (S1) to a

0-5 milliamp meter which was used when setting up the apparatus. Most of the components were mounted on one chassis from which wires were taken out to the phototransistors and the meter movements.

(ii) The barograph.

The three meter movements were clamped to the same vertical rod fixed to an extension arm of a barograph. Thus, once the pressure of each bristle on the smoke^d paper had been individually adjusted, the three could then be moved away from the drum as a unit when replacing the smoked paper. An attachment allowed a 1.25 m length of recording paper to be used which, moving at a speed of 5 cm per hour, gave a continuous 24 hour record. However, at this speed, the traces made by the bristle were extremely close together, and after 'fixing' the carbon , they had to be counted by examination under a low power binocular microscope.

(iii) The time marker.

To enable time marks to be made at half hour intervals on the paper, two contacts were fitted to the face of a Smiths alarm clock so that a circuit was completed each time the minute hand passed the 6 and 12 hour positions. The resulting current flow actuated a 6 volt relay, to the armature of which was attached a short arm which made a mark on the smoked paper.

(iv) The phototransistor mount.

The phototransistor mount was made by bending stiff cardboard into the shape of a box, 10 cm high 5 cm wide and 5 cm deep. A small hole was made just below the top on one side and a 3 cm diameter cardboard tube, 5 cm long, was glued over it. Both the inside and outside were painted black and the box was mounted on a heavy metal retort stand base. The phototransistor itself was soldered to a 3 way tag strip fixed inside the box directly behind the opening, and light was focussed onto it by a lens fitted in the end of the tube.

(v) The lamp.

The lamp housing was made from a treacle tin with ventilation holes in each end, over which two large tin lids with a 3 cm flange were fixed to act as light traps. A 10 cm long metal tube containing the lens was fitted to one end. The lamp holder, wired with asbestos covered wire, was fitted to the other end. The whole unit was painted inside and out with heat resistant black crackle paint and was mounted on a stand. The light source was a compact filament 6 volt 36 watt bulb. This was fed from a 6 volt D.C. supply through a 1.5 Ω 10 amp rheostat. A narrow beam of red and infrared light was obtained by mounting, in front of the lens, a small circle of black paper with a central 3 mm diameter hole, and a light filter. This was cut from a sheet of Ilford spectrum deep red gelatin filter which only passes light with a wavelength greater than 6,500 A.U.

The rating of the phototransistor allowed a maximum current flow of 1.8 m A when illuminated. However, by slowly reducing the intensity of illumination, it was found that the 'light current' could be reduced to 0.8 mA before the sensitivity of the system was in any way affected. At this setting the bulb filament merely glowed dull red, and the beam of light across the arena, having passed through the red filter, was quite invisible to the human eye. There was no evidence to suggest that the experimental animals were aware of this beam.

(vi) The animal arena.

Each animal under test was housed in a small arena, made by bending a strip of celluloid into a circle and welding the ends together with ethyl acetate. 7.5 cm square glass plates were used for the floor and roof. The lower square rested by its corners on a small water filled Petri dish, supported on a wooden block, and a strip of filter paper covering part of the floor trailed over the edge into this water. The relative humidity in the chamber was occasionally determined with cobalt thiocyanate paper, and was found to range between 98% and 100% R.H.

(vii) The time switch.

While carrying out preliminary experiments, in which the light was switched on and off by an ordinary time switch, it was noticed that occasionally the sudden change in light intensity produced an intense burst of activity. To reduce the risk of such a reaction, a system was devised whereby the light intensity was slowly reduced or increased over a period of one hour. The light bulb was fed via a variable transformer (Variac), to the spindle of which was attached a 12.5 cm diameter pulley wheel. One end of a length of string was attached to and wound several times round its rim, while the other end was fixed to the spindle of a barograph standing beside the Variac. The speed of the barograph was adjusted so that it took one hour to turn the Variac through its complete range of movement. An ordinary time switch was modified to bring the system into operation for two predetermined one hour periods during each 24 hours, so that artificial dusk and dawn was produced quite automatically.

(viii) Preliminary experiments.

The whole apparatus was set up on a bench in a small constant temperature room maintained at about 18°C. Trial experiments were carried out on three specimens chosen at random from the field (two *Mitopus morio* and one *Platybunus triangularis*). They were collected in the late morning, kept in a large covered glass dish with plenty of freshly killed food available until 1800 h GMT, when each was transferred directly to an arena in the aktograph. Activity records were obtained over the next 48 hours, the recording paper being renewed half way through. To avoid the effect of hunger on activity, a small freshly killed fly was put in each arena at the start of the experiment and the remains replaced by another fly 24 hours later.

The activity record for each individual is shown in Fig. 48. The histograms clearly illustrate a diel rhythm in each case. Although for any one specimen the general form of this rhythm was similar over both first and second 24 hour periods, that of the latter was more sharply defined, perhaps due to the animals having settled down and hence having become acclimatised to laboratory conditions.

In the light of the preliminary experiments it was decided that for the main investigation, animals would be

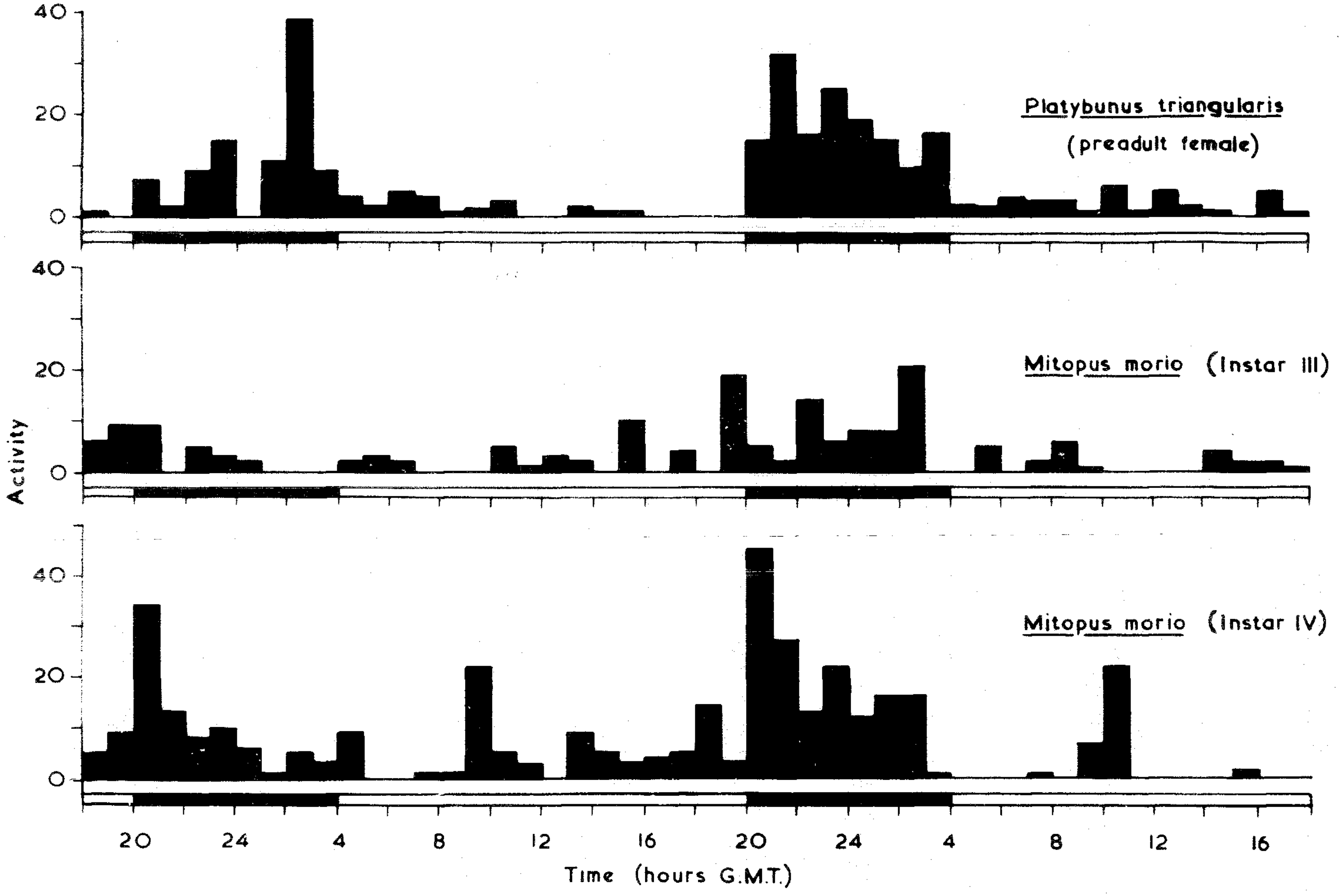


Fig. 48. Locomotor activity of three harvest-spiders. The solid black lines represent the periods of darkness.

allowed 24 hours in which to settle down before activity was recorded over the subsequent 24 hour period.

(c) Methods.

All animals were collected from the field between 0800 h and 0900 h GMT and placed directly, with freshly killed flies, in a large covered glass dish in the constant temperature room. They were left there for approximately 8 hours and then each one was transferred to a separate animal arena. The arena was later placed in the light beam of the aktograph and recording was started at 0800 h the following morning.

As in the trial experiments, a freshly killed fly was always placed in the arena with the experimental animal.

Constant conditions of temperature (18°C) and relative humidity (98% to 100% R.H.) were maintained throughout all experiments, but the lighting conditions were varied.

For the main investigation, animals were subjected to periods of light and dark similar to those experienced in the field. However, as these periods were to remain the same throughout, the timing of the laboratory day and night could not always coincide precisely with the day and night conditions of the field. A suitable average was therefore chosen, and the light was reduced from 2000 h to 2100 h GMT and increased again from 0300 h to 0400 h GMT.

For the purpose of this study, the period from 2000 h to 0400 h GMT, which includes both crepuscular periods, is referred to a 'normal night', the period from 0400 h to 2000 h GMT as 'normal day'.

Animals tested under these 'normal' conditions were transferred to the arenas at 1700 h GMT on the day of capture. They were subjected to a 'normal night' before the arenas were moved into the aktographs at 0800 h the following morning.

Experiments were also carried out in the absence of light, in continuous light and with the light and dark periods reversed.

Animals tested in continuous dark were transferred to the arenas and placed directly in the aktographs at 1700 h GMT on the day of capture. They were subjected to the usual 'dusk' at 2000 h, but the light was not brought on again at 0300 h the following morning. To avoid entering the room on the second morning (when it was still in darkness) the running speed of the barograph was reduced, enabling a continuous 39 hour record to be obtained, although only the results startimg at 0800 h GMT were used.

Animals tested in continuous light were placed in the arenas at 1700 h and moved into the beam at 0800 h the next morning, the light having been kept on throughout the night.

Those examined under 'reversed day and night' lighting conditions were first subjected to a period of darkness from 1100 h to 1900 h GMT on the day of capture, before being placed in the arenas. The light was left on throughout the night and the arenas were placed in the beams at 0800 h the following morning. The subsequent dark period was given as on the first day.

For the investigation of activity under 'normal day and night' conditions, two migratory species (*Mitopus morio* and *Oligolophus agrestis*), and two ground dwelling species (*Lacinius ephippiatus* and *Oligolophus tridens*) were chosen. For each, ten individuals of the fourth, fifth and sixth instars, and five adults of each sex were examined. However, *L. ephippiatus* was so scarce in 1960 that fourth and fifth instars could not be found in adequate numbers for testing.

The investigation of activity under the abnormal lighting conditions could only be carried out on adult *Mitopus morio*. For each condition, five males and five females were tested.

The actual records of activity are not given, but are illustrated by a series of histograms, in which each vertical column represents the total number of moves per hour made by all ten individuals. The mean and standard error of the numbers of moves per 'day' hour and per 'night' hour were calculated to enable comparisons to be made by Student's t test.

(c) Results.

(i) Mitopus morio

The results for Mitopus morio under 'normal' conditions are illustrated in Fig. 49. From this it can be seen that movement in the adults was almost completely restricted to the hours of darkness, whereas in the three juvenile stages it was spread over the whole 24 hour period, tending to be more intense by night than by day.

Table 63. Comparisons of nocturnal and diurnal activity levels in Mitopus morio.

Instar	Mean no. of moves per hour		t	P	'Night' mean / 'Day' mean
IV	'Day' mean 'Night' mean	4.24 ± 0.65 6.61 ± 1.12	1.939	ns	1.56
V	'Day' mean 'Night' mean	4.60 ± 0.67 12.22 ± 2.23	4.120	<0.001	2.66
VI	'Day' mean 'Night' mean	3.45 ± 0.54 6.14 ± 1.13	2.421	<0.05	1.78
VII	'Day' mean 'Night' mean	0.73 ± 0.11 23.29 ± 1.93	16.376	<0.001	31.90

Examination of Table 63 shows that the mean number of moves per 'night' hour (subsequently referred to as

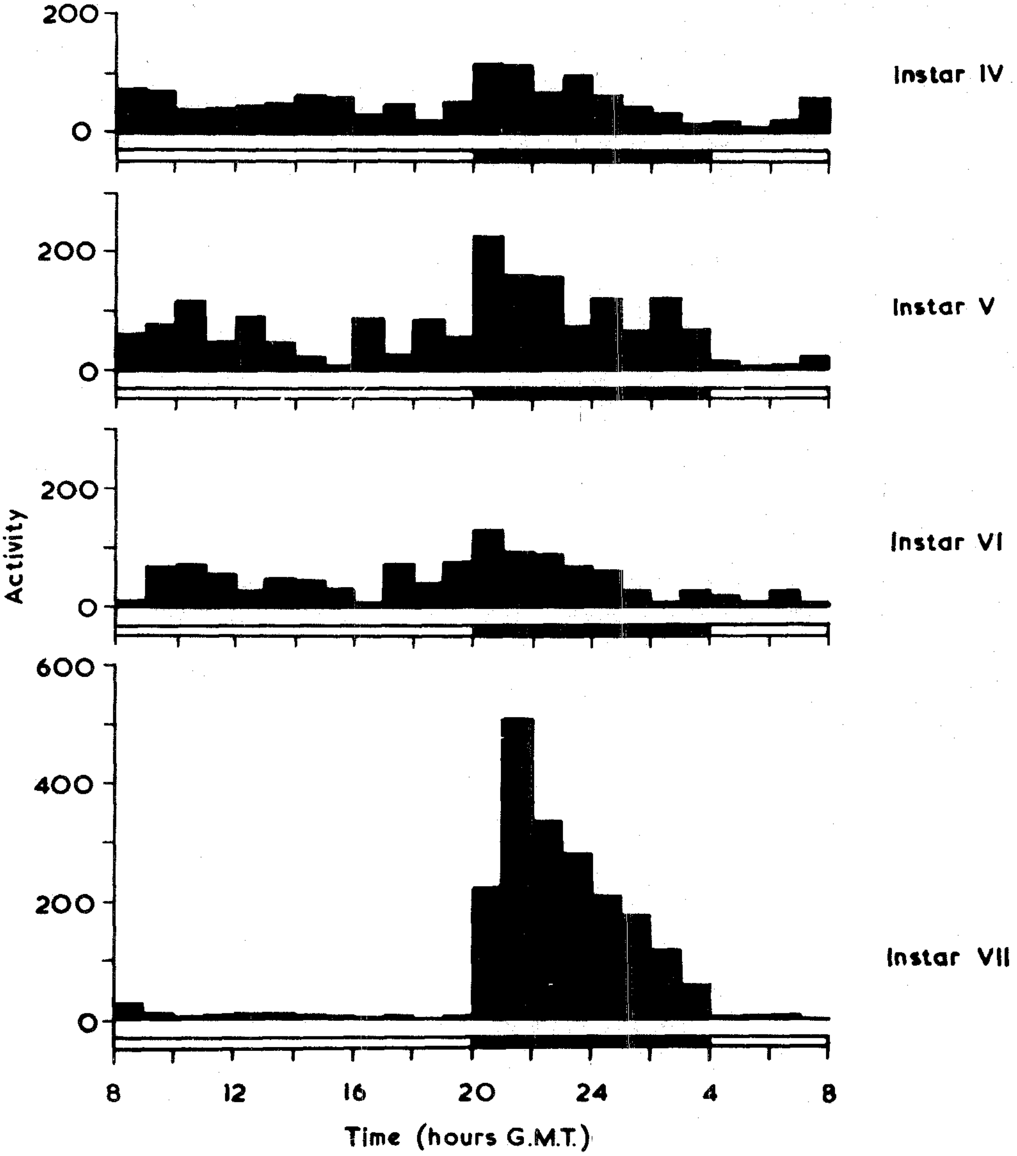


Fig. 49. Locomotor activity of Mitopus morio. The solid black lines represent the periods of darkness. Each vertical column represents the total numbers of moves per hour, made by ten individuals.

the mean intensity of nocturnal movement) was significantly greater than that of the day in all insters other than the fourth.

Comparison of the activity levels of adjacent juvenile insters (Table 64) shows that there was no change in the level of daytime activity ($P > 0.05$) and the apparent increase in nocturnal activity in the fifth inster was probably no more than a chance fluctuation (P between 0.05 and 0.02).

Table 64. Comparisons of activity levels of adjacent insters in *Mitopus morio*.

	Instar	Mean no. of moves per hour	t	P
'Day' means	IV	4.24 ± 0.65	0.269	ns
	V	4.60 ± 0.67	0.936	ns
	VI	3.45 ± 0.54	3.452	
	VII	0.73 ± 0.11		<0.002
'Night' means	IV	6.61 ± 1.12	2.233	<0.05, >0.02
	V	12.22 ± 2.23	2.416	<0.05, >0.02
	VI	6.14 ± 1.15	7.632	<0.001
	VII	23.29 ± 1.93		

However, a highly significant change occured in the adults, when the mean intensity of daytime movement dropped to a very low level ($P < 0.002$) while that of the night increased considerably ($P < 0.001$). This change is illustrated by comparing the ratios of the 'night' mean divided by the 'day' mean (Table 63).

These were very similar in the juveniles, being 1.56, 2.66 and 1.78 in the fourth, fifth and sixth instars respectively, but that of the adults rose to 31.90. It can be seen from Table 65 that the mean intensity of movement over the whole 24 hour period in the adults was only approximately twice that of the penultimate instar and the sudden increase in the ratio on becoming adult must largely reflect a change in behaviour on reaching maturity.

Table 65. Mean number of moves per hour based on activity over the whole 24 hour period.

Instar	*Mitopus morio*	*Lacinius ephippiatus*	*Oligolophus agrestis*	*Oligolophus tridens*
IV	5.03	–	6.07	7.91
V	7.14	–	19.55	9.77
VI	4.34	9.20	25.07	18.88
VII	8.25	4.60	13.69	29.13

(ii) *Lacinius ephippiatus*

In *Lacinius ephippiatus* it can be seen from Fig. 50 and Table 66 that both instars examined were more active by night than by day ($P < 0.001$) and activity reached a peak just before midnight. The difference between the $\frac{\text{'night' mean}}{\text{'day' mean}}$ ratios of 5.32 for the adults and 2.22 for the penultimate instar shows that the

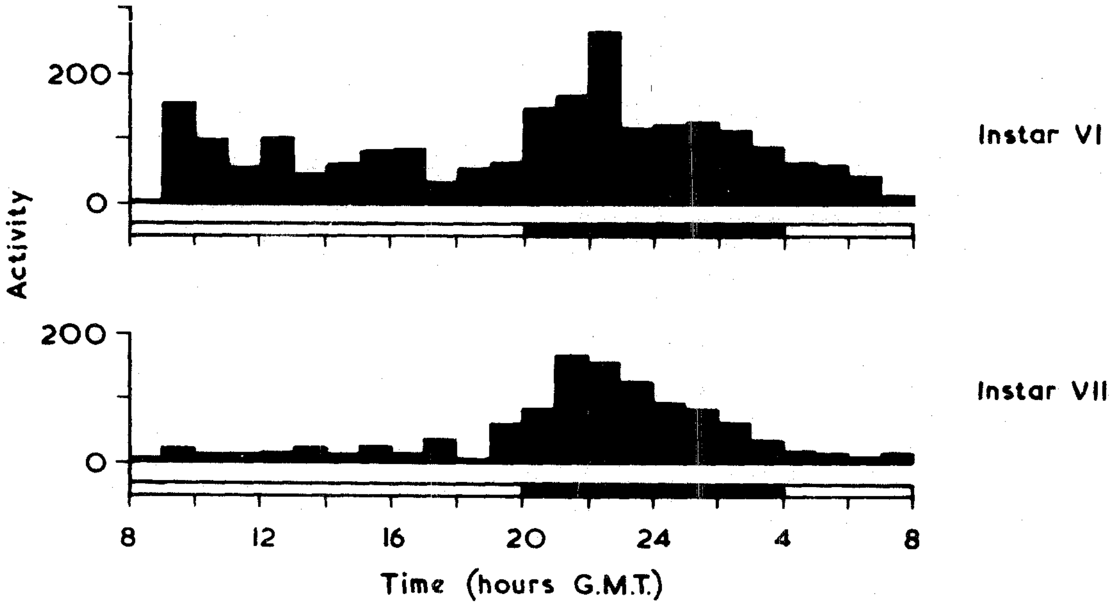


Fig. 50. Locomotor activity of *Lacinius ephippiatus*. The solid black lines represent the periods of darkness. Each vertical column represents the total number of moves per hour, made by ten individuals.

adults were slightly more nocturnal. Although, as in *M. morio*, this was due largely to a decrease in the intensity of diurnal activity on becoming adult, it can be seen from Table 67 that there was, at the same time, a significant fall in the intensity of nocturnal movement ($P < 0.001$).

Table 66. Comparisons of nocturnal and diurnal activity levels in *Lacinius ephippiatus*

Instar	Mean no. of moves per hour	t	P	'Night' mean / 'Day' mean
VI	'Day' mean 6.52 ± 0.82 'Night' mean 14.50 ± 1.76	4.667	< 0.001	2.22
VII	'Day' mean 1.92 ± 1.27 'Night' mean 10.21 ± 1.55	7.134	< 0.001	5.32

In terms of activity over the whole 24 hours (Table 65) the situation is the reverse of that seen in *M. morio*, in that the adults were slightly less active than the penultimate instar.

Table 67. Comparisons of activity of adjacent instars in *Lacinius ephippiatus*

	Instar	Mean no. of moves per hour	t	P
'Day' means	VI VII	6.52 ± 0.82 1.92 ± 0.27	2.583	<0.02>0.01
'Night' means	VI VII	14.50 ± 1.76 10.21 ± 1.55	3.735	<0.001

(iii) *Oligolophus tridens.*

In *Oligolophus tridens* the intensity of nocturnal activity was always significantly greater than that of the day (Fig. 51 and Table 68) and in all instars except the sixth, maximum activity occured between dusk and midnight. The $\frac{\text{'night' mean}}{\text{'day' mean}}$ ratios (Table 68) range between approximately two and five and there is no sign of a change in the distribution of movement over the diel on becoming adult such as that seen in *M. morio.*

Table 68. Comparisons of nocturnal and diurnal activity levels in *Oligolophus tridens.*

Instar	Mean no. of moves per hour	t	P	$\frac{\text{'Night' mean}}{\text{'Day' mean}}$
IV	'Day' mean 6.11 ± 0.78 'Night' mean 11.50 ± 1.61	3.370	<0.01	1.88
V	'Day' mean 4.40 ± 0.77 'Night' mean 20.37 ± 4.48	4.749	<0.001	4.63
VI	'Day' mean 11.44 ± 1.96 'Night' mean 33.76 ± 5.69	14.392	<0.001	2.95
VII	'Day' mean 18.01 ± 2.21 'Night' mean 51.39 ± 5.24	6.865	<0.001	2.85

Table 69 shows that in general, there was a progressive increase in activity from the fourth to the final instar, and the differences between the activity levels of adjacent instars cannot be completely disregarded despite the lack of clear statistically significant differences. This

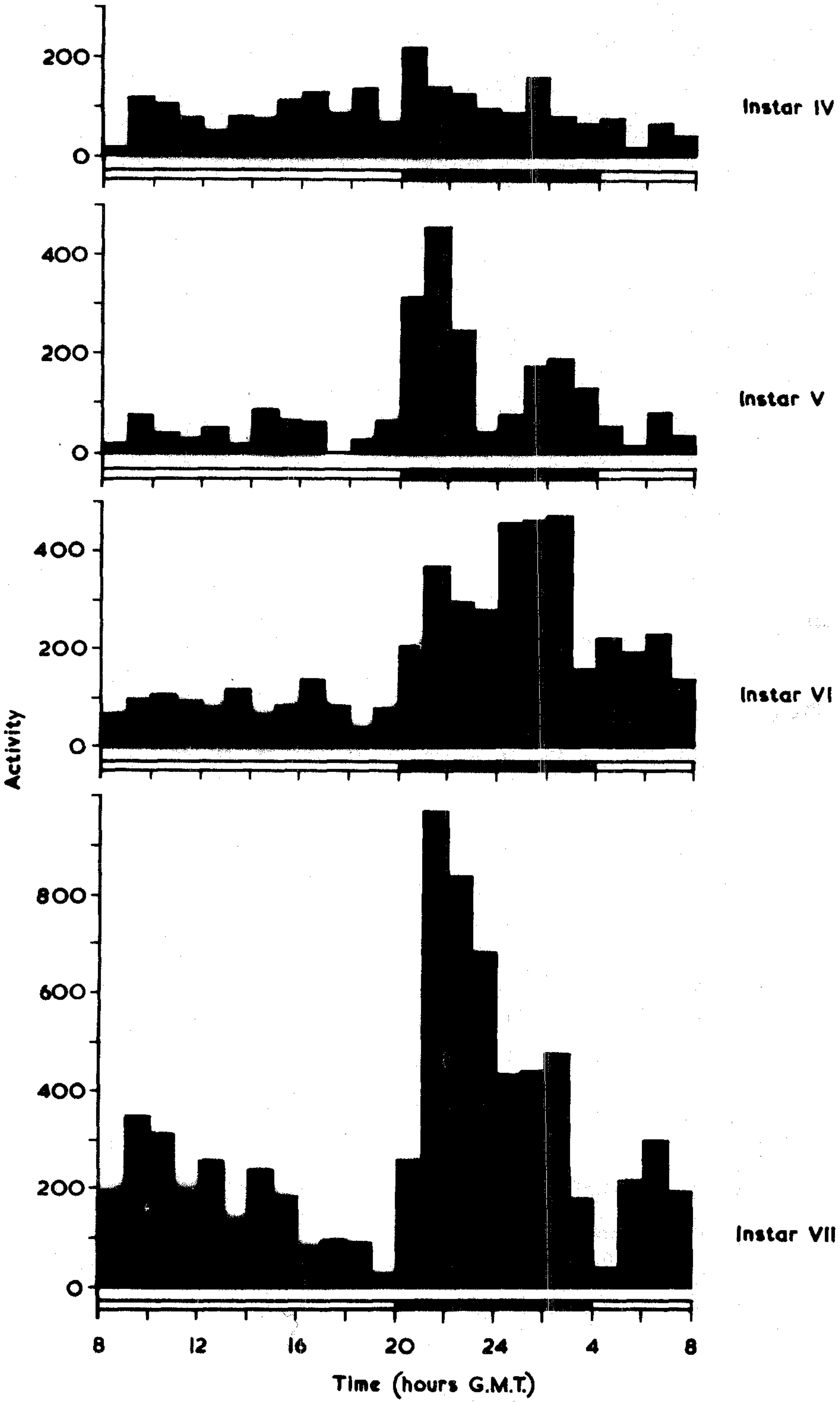


Fig. 51. Locomotor activity of Oligolophus tridens. The solid black lines represent the periods of darkness. Each vertical column represents the total number of moves per hour, made by ten individuals.

situation had been anticipated, as compared to all other species examined, the variation between the records of individual specimens is quite considerable, thereby producing correspondingly large variances.

Table 69. Comparisons of activity levels of adjacent instars in Oligolophus tridens.

	Instar	Mean no. of moves per hour	t	P
'Day' means	IV	6.11 ± 0.78	2.099	<0.05 >0.02
	V	4.11 ± 0.77	3.335	<0.01
	VI	11.44 ± 1.96	2.220	<0.05 >0.02
	VII	18.01 ± 2.21		
'Night' means	IV	11.50 ± 1.61	1.953	ns
	V	20.37 ± 4.48	1.838	ns
	VI	33.76 ± 5.69	2.365	<0.05 >0.02
	VII	51.34 ± 5.24		

However, it was not possible to test more than ten individuals of each instar and this would seem to be a situation in which too rigid an interpretation of the results of statistical tests would be misleading.

(iv) Oligolophus agrestis.

The pattern of activity in Oligolophus agrestis was quite different from that of the species described above. All instars were active throughout the 24 hours. Although it seems, on examination of Fig. 52, that irregular bursts of activity occured, quite unrelated to the periods oflight

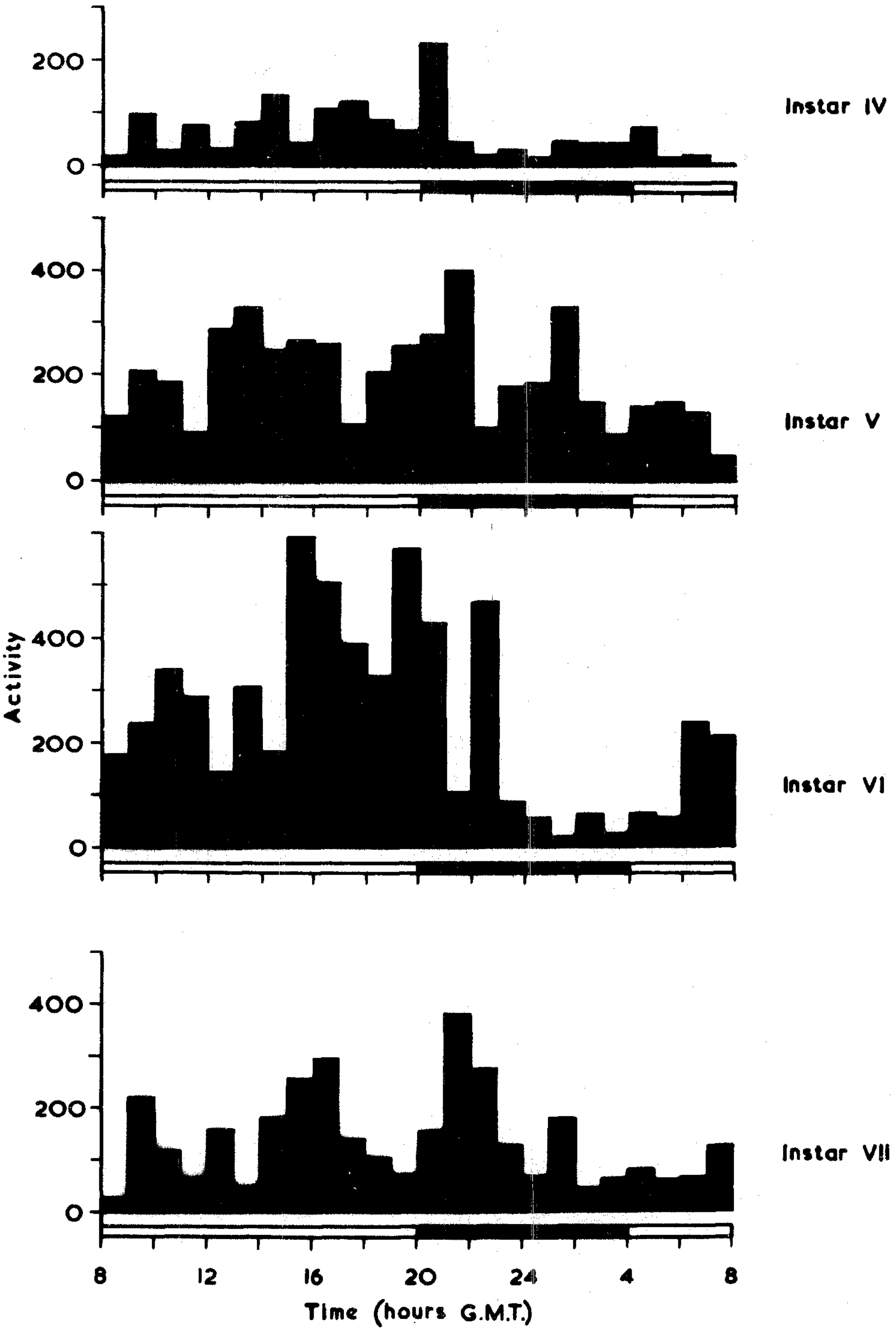


Fig. 52. Locomotor activity of Oligolophus agrestis. The solid black lines represent the periods of darkness. Each vertical column represents the total number of moves per hour, made by ten individuals.

and dark, in all but the sixth instar maximum activity occured soon after dusk. This suggests that the removal of light produced a slight increase in the intensity of movement. However, Table 70 shows that there was no evidence of a real difference between the mean intensity of nocturnal and diurnal movement in any one instar.

Table 70. Comparisons of nocturnal and diurnal activity levels in Oligolophus agrestis.

Instar	Mean no. of moves per hour		t	P	'Night' mean / 'Day' mean
IV	'Day' mean	6.22 ± 1.05	0.239	ns	0.93
	'Night' mean	5.79 ± 1.41			
V	'Day' mean	18.79 ± 1.90	0.631	ns	1.12
	'Night' mean	21.07 ± 3.37			
VI	'Day' mean	29.86 ± 4.58	1.975	ns	0.52
	'Night' mean	15.50 ± 4.57			
VII	'Day' mean	12.44 ± 2.10	1.002	ns	1.30
	'Night' mean	16.19 ± 3.18			

Considerable differences existed between the mean activity levels of adjacent instars (Table 71) and the maximum intensity of movement by night occured in the fifth instar, and by day in the sixth instar. This difference cannot be explained, but in terms of movement over the whole 24 hour period (Table 65) the sixth instar was the most active stage of the life history.

Table 71. Comparisons of activity levels of adjacent instars in Oligolophus agrestis.

	Instar	Mean no. of moves per hour	t	P
'Day' means	IV	6.22 ± 1.05	5.761	<0.001
	V	18.79 ± 1.90	2.224	<0.05
	VI	29.86 ± 4.58	5.444	<0.002
	VII	12.44 ± 2.10		
'Night' means	IV	5.79 ± 1.41	4.152	<0.001
	V	21.07 ± 3.37	3.082	<0.01
	VI	15.50 ± 4.57	0.389	ns
	VII	16.19 ± 3.18		

(v) The nature of the diel rhythm in adult M. morio.

The nature of the activity rhythm observed in adult Mitopus morio was investigated further. The possible existence of an endogenous 24 hour rhythm of activity was first investigated by testing animals in continuous light and continuous dark. The effect of giving the period of darkness during the day was then examined.

The results are illustrated in Fig. 53. The histogram given earlier, showing activity of adults under a 'normal' light-dark regime, is included for the purpose of comparison.

Comparisons were made, by the t test, of the mean intensity of movement over the two parts of the 24 hour period and the means were then compared with those of adults tested under the 'normal' light-dark regime, (Table 72).

When kept in continuous darkness (Fig. 53 c) M. morio

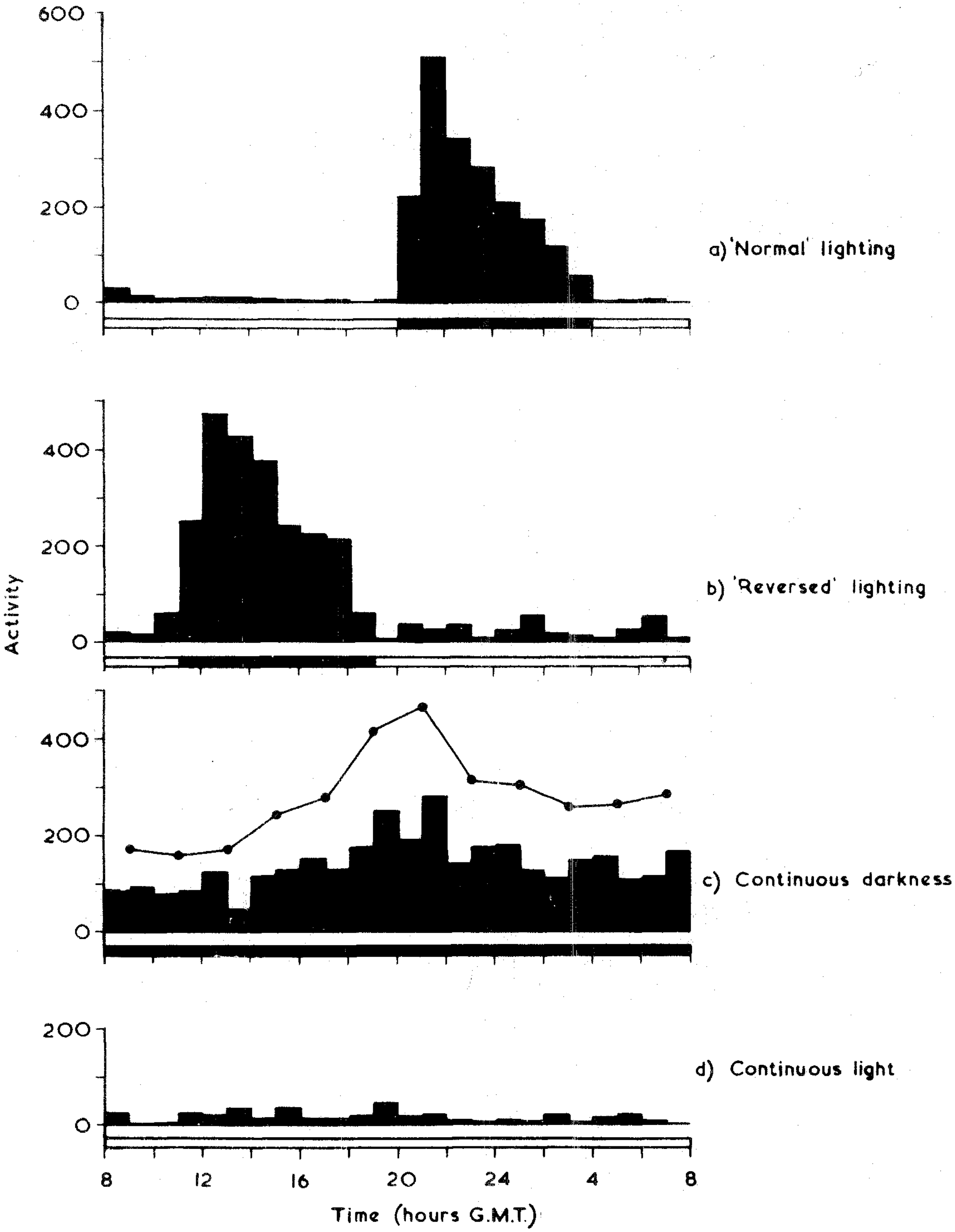


Fig. 53. The activity of adult Mitopus morio under various lighting conditions. Each vertical column represents the total number of moves per hour made by ten individuals. The solid black lines represent the periods of darkness.

maintained a fairly high level of activity throughout the whole 24 hour period. Although there was no difference between the mean number of moves during the two periods which would normally have been day and night (Table 72a $P > 0.05$), the highest level of activity during any one hour occured between 2100 h and 2200 h GMT. This is precisely the same period as that at which maximum activity under 'normal' conditions was recorded (Fig. 53a). Moreover, when the numbers of moves per two hour period were plotted above this histogram, on the same scale, a line drawn through the points clearly suggested the existence of a definite rhythm, activity rising to a peak just before midnight.

Exposure to continuous light (Fig. 53 d) caused a considerable reduction in activity over the whole 24 hours. There was no sign of any rhythm, and the mean intensity of movement over the two periods corresponding to the day and night was very similar (Table 72 b $P > 0.05$). However, the mean intensity during the day period was significantly greater than that of the day under 'normal' conditions (Table 72 g $P < 0.01$)

When tested under 'reversed' day and night conditions, the rhythm was transferred to the new time (Fig. 53 b). However, it was not a perfect replica of that seen under 'normal' conditions (Fig. 53 a). The progressive decrease in activity during the 'reverse night' was less pronounced than that occuring during 'normal night', although the mean intensity of movement over the two periods was about the same (Table 72 e). However, the intensity during the 'reverse day' was significantly greater than that of the 'normal day' (Table 72 d).

Table 72. Comparisons of activity of adult *Mitopus morio* under various conditions of light and dark.

		Times (GMT)	Mean no. of moves per hour	t	P
)	Continuous darkness	04-20	15.56 ± 1.15	1.900	ns
		20-04	16.81 ± 2.15		
)	Continuous light	04-20	1.82 ± 0.32	1.461	ns
		20-04	1.11 ± 0.22		
)	'Reversed' lighting	19-11	2.52 ± 0.43	14.206	< 0.001
		11-19	27.97 ± 2.37		
)	'Reverse day'	19-11	2.52 ± 0.43	3.986	< 0.001
	'Normal day'	04-20	0.73 ± 0.11		
)	'Reverse night'	11-19	27.97 ± 2.37	1.516	ns
	'Normal night'	20-04	23.29 ± 1.93		
)	'Dark night'	20-04	16.81 ± 2.15	2.49	< 0.02
	'Normal night'	20-04	23.29 ± 1.93		
)	'Light day'	04-20	1.82 ± 0.32	3.161	< 0.01
	'Normal day'	04-20	0.73 ± 0.11		

(e) Discussion.

The results are first briefly surveyed. In terms of the total volume of movement over the 24 hours, the two species of *Oligolophus* were considerably more active than *Lacinius erhippiatus* and *Mitopus morio*. The intensity of movement in *Oligolophus* increased steadily from the fourth instar onwards, reaching a maximum in the penultimate instar of *O. agrestis* and in the final instar of *O. tridens*. Only the last two instars of *Lacinius ephippiatus* were examined and pre-adults were slightly more active than adults. In *M. morio* adults were slightly more active than any of the juvenile stages.

There was no apparent 24 hour rhythm of activity in *O. agrestis*, movement occuring, in general, fairly evenly throughout the diel. All instars of *L. ephippiatus*, *M. morio* and *O. tridens* showed maximum activity between dusk and midnight. In all instars of these three species except the seventh of *M. morio*, the intensity of movement by night was between approximately two and five times greater than that of the day. In adult *M. morio*, this proportion increased to approximately 32.

The change, between the penultimate and final instars of *M. morio* by which activity in the latter became almost exclusively nocturnal, presumably represented a redistribution of diel activity on reaching maturity. As both juveniles and adults were subjected to the same conditions of temperature, relative humidity and light, this was clearly not a simple behaviour change caused by changing physical factors. The cause is suggested to have been a change, between juveniles and adults, in the response made to light ie. while light almost completely suppressed movement in the adults, it probably had much less effect on the juveniles which remained fairly active in its presence. Thes explanation was not tested by further experiments on juveniles.

The cause of the observed 'normal' diel activity rhythm in adult M. morio was investigated. When tested in continuous darkness a fairly distinct rhythm was still apparent, with a peak of activity about three hours before midnight (Fig. 53 c). Although this rhythm could represent the partial persistence of one previously induced by field conditions, it is thought likely to be essentially endogenous in origin.

This (endogenous?) rhythm was accentuated by exposure to the light of the normal day (Fig. 53 a). The mean intensity of daytime activity dropped to a very low level, while that of the 'normal night' was significantly greater than that during the equivalent period in continuous dark

(Table 72 f). Exposure to continuous light produced an almost complete suppression of movement (Fig. 53 a) and it is obvious that the normal rhythm in adult M. morio was produced mainly by the alternating periods of light and dark. If, however, this was a simple response to changes in light intensity, it should have been possible to transfer the rhythm, unchanged in character, to any part of the 24 hours by altering the timing of the light changes. Although a transfer was made, (Fig. 53 b) the new rhythm differed in several respects from the 'normal', and clearly other factors, perhaps the endogenous rhythm itself, had some influence.

A few experiments were carried out on single specimens of adult M. morio under conditions other than 18°C and 100 % R.H. As a result of these, it is believed that fluctuations of temperature and humidity similar to those experienced in the field would only cause modification of detail to thelaboratory determined activity pattern without affecting the major trends. Therefore, in adult M. morio, it is concluded that the general form of the normal diel activity rhythm resulted from an endogenous rhythm accentuated by the alternating periods of light and dark.

However, it cannot be assumed that a similar mechanism is responsible for the apparent association between the diel rhythm and the light-dark periods in juveniles of *M. morio*, and indeed in adults and juveniles of *L. ephippiatus* and *O. tridens*. Clearly, all instars must be tested under continuous light and continuous dark before any conclusion as to the nature of the diel rhythm can be drawn.

4. Weight differences among adults of *Mitopus morio* and *Oligolophus agrestis*.

To see if the vertical migration of adults was associated with their physiological condition, the mean wet weights of adults of both sexes of *M. morio* and *O. agrestis* were determined. Some adult females were also dissected and egg counts made. Comparisons were then made between adults separated in space and time.

(a) Methods.

Wet weight determinations were made by weighing specimens individually. Each animal was rinsed in 96% alcohol, any debris being removed with a camel hair paint brush, and it was then allowed to dry in air for two minutes. Specimens from the surface, field and shrub layers were treated as one sample: specimens from the ground layer, the lower papers and the upper papers on the tree trunks were treated as separate samples. Representatives were weighed from all samples from the time of the first appearance of adults until they began to die off.

Egg counts were made on approximately ten females per sample, according to Phillipson (1959). In *O. agrestis*, females from all samples used in the wet weight determinations were examined, but in *M. morio*, due to poor preservation of body contents, counts were only possible on females of 25 June and 24 July. Three main types of egg could be distinguished: large eggs apparently ready for oviposition, eggs of a similar size on the surface of the ovary and therefore presumably not ready for oviposition, and very small eggs forming the bulk of the ovary. Complete egg counts have already been made by Phillipson (1959) and as the contribution of the small eggs towards the total body weight was found to be insignificant compared to that of the two larger types, the small eggs were not counted.

(b) Results of wet weight determinations.

(i) Mitopus morio.

The mean wet weights of Mitopus morio adults are given in Table 73. For each occasion, the weights of specimens from the various field levels were compared by the t test (Appendix G), but the nature of the differences are illustrated graphically. (Fig. 54). In the females, weight differences between those ascending and those descending the tree trunks were never of statistical significance ($P > 0.05$): thus in Fig. 54 only single means based on all females from the trunks are illustrated. So few males descended the trees that these specimens were

Table 73. Mean wet weight of adult <u>Mitopus morio</u>. The upper part of the Table refers to females, the lower part to males. The numbers weighed per sample are shown in parentheses.

Date	Ground layer	Surface-field -shrub layers	Lower papers	Upper papers
25.6	29.98 ± 1.40 (38)	31.85 ± 1.39 (62)	39.98 ± 1.58 (45)	-
7.7	41.06 ± 1.04 (88)	37.06 ± 1.14 (61)	50.51 ± 1.59 (22)	44.99 ± 1.48 (8)
13.7	38.77 ± 1.18 (44)	35.80 ± 1.14 (52)	46.94 ± 1.41 (18)	45.13 ± 2.16 (18)
24.7	42.14 ± 1.65 (32)	35.87 ± 1.37 (35)	51.31 ± 1.35 (15)	35.73 ± 1.54 (3)
31.7	38.02 ± 1.69 (8)	31.12 ± 1.88 (12)	38.20 ± 2.01 (5)	-
7.8	43.43 ± 2.70 (3)	31.50 ± 5.19 (5)	42.17 ± 2.41 (3)	39.30 (1)
25.6	-	16.83 ± 0.47 (40)	20.93 ± 1.64 (28)	-
7.7	16.61 ± 0.66 (10)	16.38 ± 0.49 (47)	21.79 ± 0.39 (43)	18.65 ± (2)
13.7	17.17 ± 0.81 (15)	16.76 ± 0.39 (50)	19.94 ± 0.67 (41)	21.40 (3)
24.7	19.64 ± 0.66 (24)	16.07 ± 0.48 (27)	20.57 ± 0.66 (23)	20.35 (4)
31.7	18.45 ± 0.93 (9)	15.54 ± 0.42 (38)	18.91 ± 0.69 (17)	19.05 (3)
7.8	17.42 ± 2.63 (4)	17.39 ± 1.17 (16)	19.71 ± 0.69 (13)	20.60 (1)

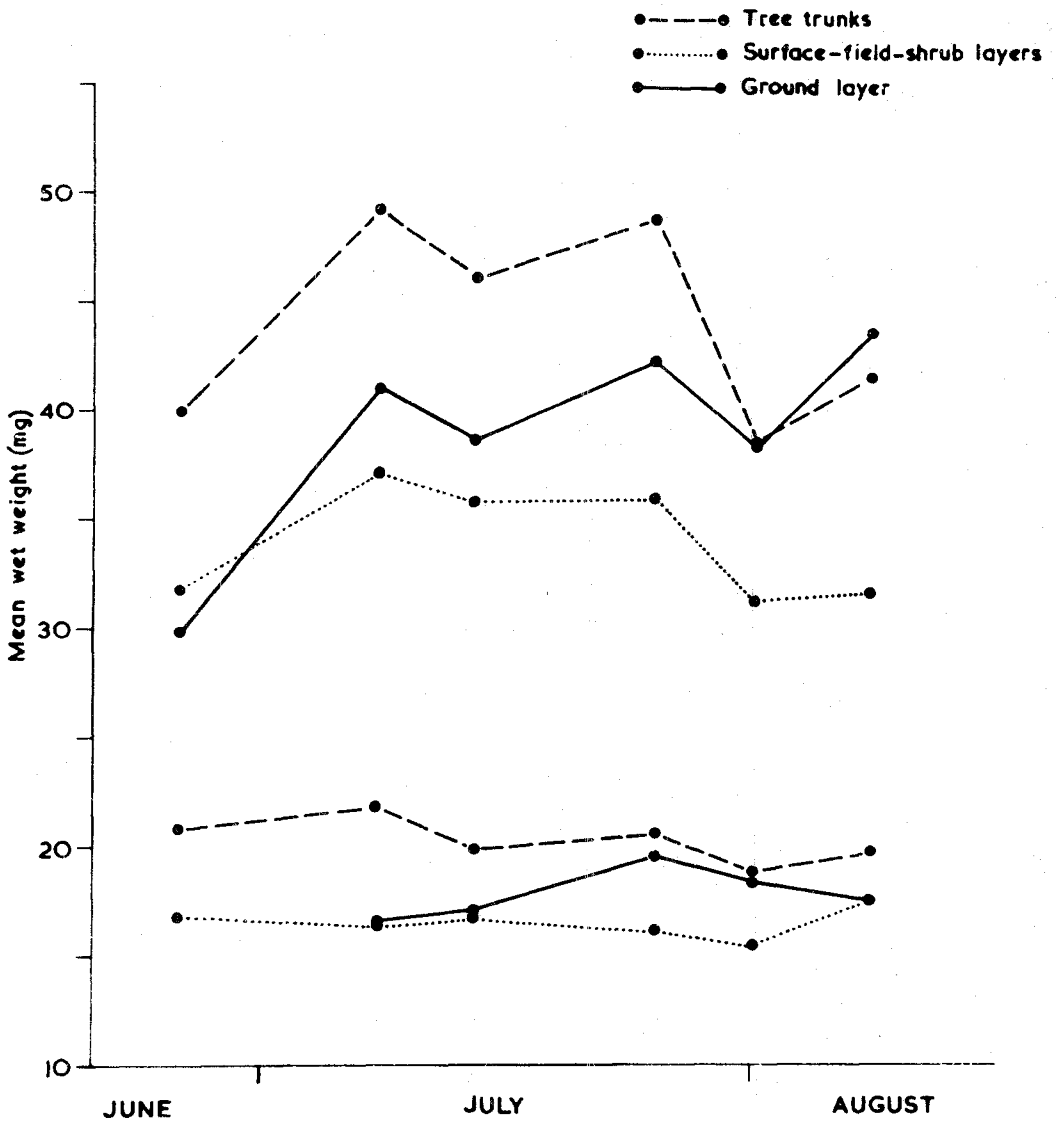


Fig. 54. Changes, with time, in the mean wet weight of adult Mitopus morio. The upper three lines represent females, the lower three, males.

not considered, either in Fig. 54 or in Appendix C.

The weight of males remained remarkably constant within each layer. On 25 June the mean weight of males from the trees was 20.93 mg which was significantly higher than the 16.83 mg of the surface - field - shrub layer specimens ($P < 0{\cdot}02$). There was little change on subsequent occasions, and the weight of ground layer males was always intermediate between those of males from the other two layers.

The weight of females ascending the trunks rose from 39.9 mg on 25 June to 50.51 mg on 7 July, then remained around this weight throughout most of the month before dropping to 38.2 mg on 31 July. On all occasions prior to 31 July, these specimens were always significantly heavier than those from the ground and the surface - field - shrub layers(P ranging from 0.02 to < 0.001).

The mean weight of females from the ground layer and from the surface - field - shrub layers on 25 June was approximately 30 mg. By 7 July the mean of the ground layer females had risen to 41.1 mg, that of the surface - field - shrub females to 37.0 mg. These weights remained of a similar order on 13 and 24 July, then dropped slightly at the end of the month.

On most occasions the relationship between the weight of females at the three levels remained very similar: those from the surface - field - shrub layers were the lightest, those from the trees were the heaviest, with those from the ground layer intermediate between the two extremes.

(ii) *Oligolophus agrestis.*

The mean wet weights of *Oligolophus agrestis* adults are given in Table 74. Where any sample of females from the trees was very small, individuals from the corresponding duplicate collection were also weighed. In the case of the males, the numbers from the trees were generally so small that only the complete set of samples of 9 October was examined.

For each occasion, the mean weights of specimens from the various field levels were compared by the t test, the results of which are given in Appendix D.

Table 74 shows that the mean weight of males was apparently very similar, ranging from 5.5 mg to 6.4 mg. However, it can be seem from Appendix D that those descending the trunks were significantly heavier than those ascending the trunks ($P < 0.01$) and those of the surface - field - shrub layers ($P < 0.001$).

The mean weight of adult females increased steadily from the time of their first appearance in August to reach a maximum in October. The maximum weight of females from both the ground layer and the surface - field - shrub layers was approximately 13 mg, that of females from the trees approximately 15 mg.

It can be seen from Appendix D that on most occasions females descending the trunks were significantly heavier than those from any of the other samples. At the same time, differences among these other samples were generally of no statistical significance.

Table 74. Mean wet weight of adult _Oligolophus agrestis_. The numbers weighed per sample are shown in parentheses. The bottom line refers to males - the rest of the Table to females.

Date	Ground layer	Surface-field -shrub layer	Lower papers	Upper papers
16.8	-	-	8.30 ± 0.28 (23)	-
27.8	10.14 ± 0.57 (9)	9.15 ± 0.26 (34)	9.62 ± 0.52 (10)	12.13 ± 0.26 (42)
5.9	11.40 ± 1.74 (3)	10.89 ± 0.44 (38)	10.64 ± 0.56 (16)	14.88 ±1.28 (5)
16.9	12.50 ± 0.79 (3)	13.05 ± 0.38 (13)	12.28 ± 0.34 (22)	12.47 ± 0.51 (7)
9.10	12.43 ± 0.58 (7)	12.73± 0.34 (39)	12.81 ± 0.32 (34)	15.32 ± 0.57 (16)
20.10	12.98 ± 0.42 (27)	10.80 ± 0.83 (5)	14.62 ± 0.39 (25)	-
9.10	-	5.36 ± 0.16 (11)	5.88 ± 0.12 (24)	6.45 ± 0.12 (10)

(b) Results of egg counts.

(i) *Mitopus morio*.

The results of egg counts made on female *Mitopus morio* are given in Table 75, each number being the total of the two larger types of egg.

The ovaries of all females on 25 June were packed with small eggs, but large eggs were completely absent from the surface - field - shrub layer females, and present in only one of the ten females from the ground layer. However they were present in every female from the trees, the mean number per animal being 24.0 ± 7.64.

By 24 July every specimen examined possessed the larger eggs. The mean numbers ranged from 12.40 ± 1.84 for the surface - field - shrub layer females upto 36.45 ± 4.11 for those ascending the tree trunks.

Although females of 7 and 13 July were not dissected, their body weights were so similar to those of 24 July (see Fig. 54) that they probably also contained similar numbers of eggs.

(ii) *Oligolophus agrestid*

The results of egg counts made on females of *Oligolophus agrestis* are given in Table 76. Although mature females first appeared 16 August, large eggs were not present until 27 August. The numbers increased steadily from this time onwards until, by 16 September, the mean number in females from all levels ranged between approximately 22 and 26. There was subsequently more variability between the samples, but the only further increase occurred in females descending the trunks in which the mean rose to 38.18 ± 5.52 on 9 October.

Table 75. The mean numbers of large eggs in adult females of *Mitopus morio*.

Date	Sample	Mean number of large eggs per specimen	Number dissected
25.6	Ground layer	2.10	10 (eggs in only one specimen)
	Surface-field - shrub layers	0	10
	Lower papers	24.0 ± 7.64	10
24.7	Ground layer	32.54 ± 4.89	13
	Surface-field - shrub layers	12.40 ± 1.84	10
	Lower papers	36.45 ± 4.11	11
	Upper papers	23.00 ± 1.99	3

Table 76. The mean numbers of large eggs in adult females of *Oligolophus agrestis*.

Date	Sample	Mean number of large eggs per specimen	Number dissected
27.8	Ground layer	0 –	9
	Surface-field -shrub layers	0 –	10
	Lower papers	0.90 ± 0.79	10
	Upper papers	4.55 ± 1.89	9
5.9	Ground layer	11.00 ± 6.35	3
	Surface-field -shrub layers	5.50 ± 2.19	10
	Lower papers	5.87 ± 2.89	8
	Upper papers	17.20 ± 5.95	5
16.9	Ground layer	23.33 ± 6.36	3
	Surface-field -shrub layers	22.10 ± 3.91	10
	Lower papers	25.40 ± 4.49	10
	Upper papers	25.71 ± 4.94	7
9.10	Ground layer	12.10 ± 1.18	10
	Surface-field -shrub layers	25.60 ± 2.26	10
	Lower papers	18.40 ± 1.49	10
	Upper papers	38.18 ± 5.52	10
30.10	Ground layer	18.20 ± 1.58	10
	Surface-field -shrub layers	16.90 ± 2.23	10
	Lower papers	23.20 ± 2.05	10
	Upper papers	–	

(d) Discussion.

(i) Males.

The weight differences among adult males could be due to differences in body size, gut contents and body food reserves. However, as growth presumably does not take place within the same instar, the last two factors are of most importance. No attempt was made to investigate this further.

If it is assumed that, as a result of feeding, the body weight increased progressively for some time following the final moult, the order of body weights might be directly related to the length of time since the final moult. Thus, in *M. morio* the heaviest males (those from the treetrunks) were probably the oldest, the lightest males (those from the surface - field - shrub layers) the youngest, with those of the ground layer intermediate in age between the two extremes. Applying the same reasoning to *O. agrestis* males, those descending the trunks were probably the oldest, those of the surface - field - shrub layers the youngest, with those ascending the trunks intermediate in age.

In *M. morio* the possibility of an association between the age of a male and its position in the field was supported by an observation for which, unfortunately, no quantitative information was obtained. It was noticed in the laboratory that the dorsal body surface of newly moulted males was a light yellow-brown colour and that this changed to dark brown or black after a few days. This same colour difference was noticed during laboratory examination of specimens taken in the field. Samples from the trees contained males which were, without exception, dark brown or black in colour, while those from the other levels contained males of both colour types. This suggests that male M. morio from the tree trunks were older than those from the rest of the field.

(ii) Females.

As suggested for males, the body weight of females would be influenced by the gut contents and food reserves. However, most of the observed differences in weight were believed due to differences in the number of large eggs in the body.

This is indicated for M. morio by comparing the data of Tables 73 and 75. On 25 June, there was clearly a similarity between both mean weight and egg counts of ground layer females (29.98 mg and 2.1 eggs) and females of the surface-field-shrub layers (31.85 mg and no eggs). At the same time, the greater the weight of females from the trees (39.98 mg) was presumably associated with the relatively large number of eggs present (24.0 eggs).

On 24 July, the explanation is not so simple. Despite the similarity between the egg counts of female M. morio ascending the trunks (36.45 eggs) and those of the ground layer (32.54 eggs) the former (mean weight 51.31 mg) were considerably heavier than the latter (mean weight 42.14 mg). Obviously other factors were involved, perhaps, as already suggested, differences in the amount of food in the body.

To show the relationship between body weight and egg counts in O. agrestis, the two sets of results were plotted together in Fig. 55, confidence limits being omitted for clarity. In general, weight changes tended to follow changes in the numbers of large eggs, although the relationship is not always simple. For example, in female O. agrestis descending the trunks, the mean body weight of those of 5 September (14.88 mg) was of the same order as those of 9 October (15.32 mg) yet the mean number of eggs in the former was 17.20, in the latter 38.18. Probably the amount of food in the body was greater in the September than in the October females.

Phillipson (1959) found that eggs of M. morio and O. agrestis were first laid in the field three to four

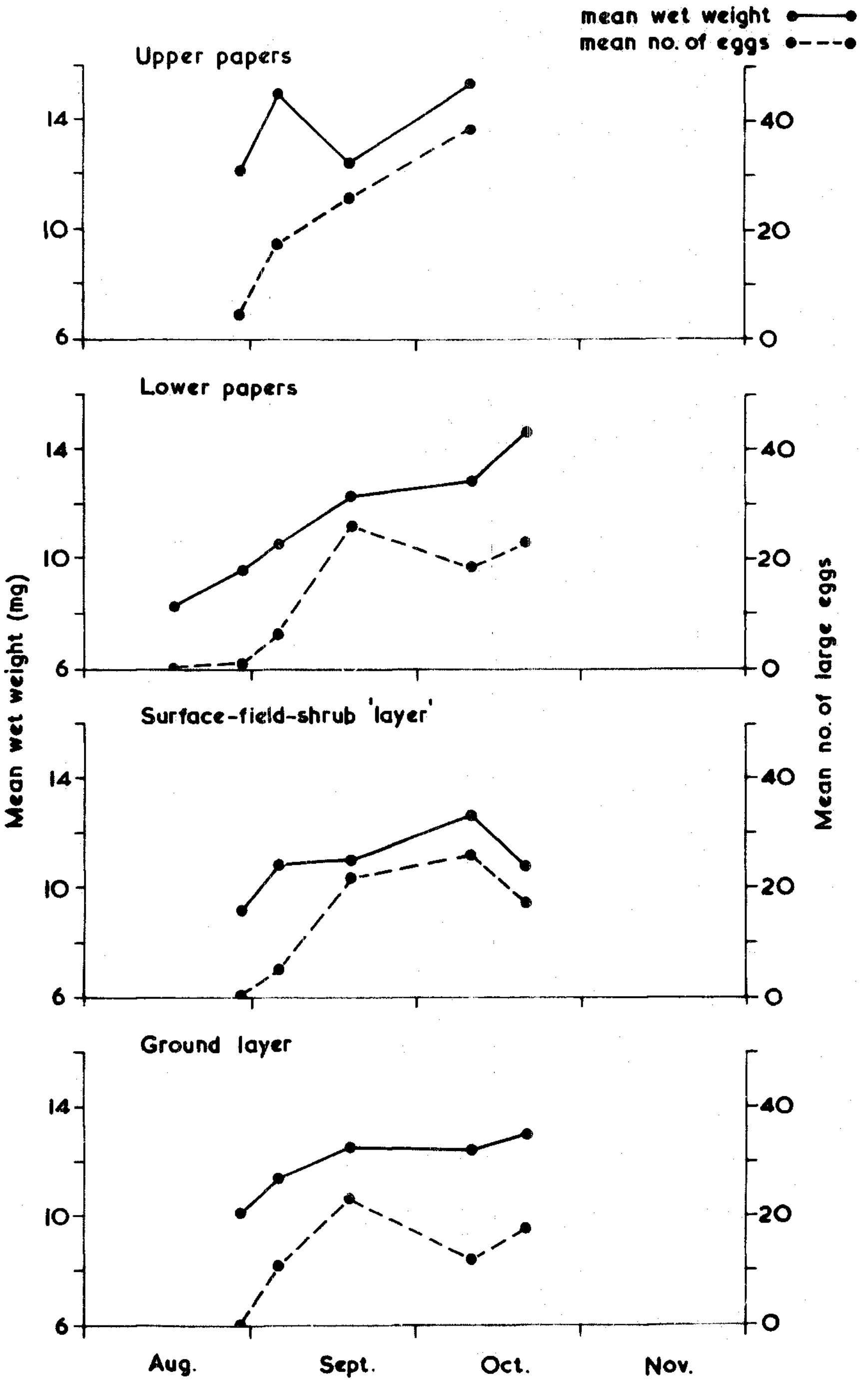


Fig. 55. The relationship between mean wet weight and egg numbers in adult females of *Oligolophus agrestis*.

weeks after the appearance of adults. He also estimated that the average number of eggs per batch was 37 in *M. morio* and 26 in *O. agrestis*. The results in the present study can be interpreted in the light of these findings. On any one occasion during the three or four weeks following the first appearance of adults, presumably only those females containing the equivalent of one batch of large (ripe) eggs were ready for oviposition. Thus in *O. agrestis*, although adults appeared on 16 August, it was not until a month later (16 September) that all females contained approximately 26 ripe eggs and were presumably ready for oviposition. Before 16 September the number of large eggs present on any one occasion might indicate the order of time since the final moult: for example, on 27 August female *O. agrestis* descending trunks (4.55 eggs) were probably slightly older than those ascending (o.55 eggs), while those of the ground and the surface-field-shrub layers (large eggs completely absent) were perhaps newly moulted. The egg count data are too limited in *M. morio*, to attempt a similar interpretation of the results. However, on 25 June, it is probable that only females from the tree trunks (24.0 eggs) were ready for oviposition, and were much older than females from the ground layer and the surface-field-shrub layers (large eggs absent from 19 of the 20 specimens dissected). On 24 July, and presumably also on the previous two occasions, all females except those of the surface-field-shrub layers (12.40 eggs) were presumably ready for oviposition.

V GENERAL DISCUSSION

V GENERAL DISCUSSION

The work of Todd (1949) is the only detailed published account of the general field biology of British harvest-spiders. Although excellent in general approach it was felt that the work had its limitations and that many of the questions raised required further investigation. For example, Todd (1949) outlined the seasonal development of many species and showed that some of them moved from the ground layer into the field and tree layers as development proceeded while others did not. However no attempt was made to explain this migration.

Todd (1949) also found that the temperature and humidity preferenda of the adults of the different species was correlated with the temperature and humidity regimes in the field. The question arises as to whether a similar correlation occurs among juveniles and indeed whether preferenda changes occur from instar to instar which might account for the seasonal change of microhabitat in certain species. It is equally important to know at what stage of the life history this seasonal migration begins.

A further complication arises in that a daily vertical migration also occurs in some species. It must be asked what governs this diel migration, whether it is related to corresponding diel changes in the levels of locomotor activity and how it affects the results obtained for seasonal migration.

Todd (1949) also gave estimates of the numbers and biomass of the ground layer population, but the instar composition of this fauna and the effect on it of the two types of migration still remained to be investigated.

Clearly before any of the questions posed above could be answered it was necessary to have a means of determining the different instars of the species to be examined.

The species of adult British harvest-spiders can be readily determined by any of several published keys. The earliest were those of Simon (1879), Pickard-Cambridge (1890) and Falconer (1910). Following the revision of the genus <u>Oligolophus</u> by Roewer (1923), keys incorporating this change were produced by Hull (1930) and Savory (1944). Todd disagreed with some of the changes made by Roewer and published a further key (1948). The latter, being the most recent, was used throughout the present study. While this worked satisfactorily with most juvenile stages, some difficulty was experienced in determining the very earliest stages of <u>Mitopus morio</u>, <u>Oligolophus agrestis</u> and <u>Oligolophus tridens</u>. By rearing animals in the laboratory from eggs produced by known species, the characteristic features of the juveniles of these three species were noted. and it was found that the juveniles could be satisfactorily separated by certain characteristic features of the ocularium, the genital plate and the dorsal surface of the prosoma.

No means of identifying the instars of any of the British species of harvest-spider has been published. Immel (1954) described in great detail the instars of <u>Nemastoma quadripunctatum,</u> a species not found in Britain, and for each life stage recorded the mean length of each leg and tarsus and the mean number of segments per tarsus. However, the range of values for each instar were not given and it is impossible to tell to what extent, if any, the values for adjacent instars overlap each other. The use of mean values alone are therefore clearly limited in their application to the determination of the instar of a particular individual of this species.

In an attempt to find a single feature by which the instars of the British species to be studied could be rapidly and reliably determined, the features used by Immel (1954) were examined further. Although it was felt that features frequently used for instar determination in some insects (particularly length and width of the body or part of the body) would be unreliable due to the softer nature of the body of harvest-spiders these were also examined. As a result of these investigations the femur length of the second walking leg alone was found to provide a satisfactory indication of the instar of an individual. Comparisons of the range of second femur length per instar were facilitated by presenting the data in a manner similar to that used by Ghent (1956) who determined the instars of two species of sawflies on the basis of the width of the head capsule.

Using the information presented in the above manner, the seasonal development of six species was studied in detail in order to provide a basis for the further investigation of vertical migration in certain species. In terms of the times at which eggs first hatched in the field, the onset of maturity and the disappearance of the various species from the field, the present results are in accord with those of both Todd (1949) and Phillipson (1959). However the present investigation went further in that the timing and the duration of the juvenile stages was defined. This was done by analysing the data on seasonal development by a method based on that used by Gabbutt (1959) for the wood cricket. *Nemobius sylvestris*.

All the species involved in the present study begin their life in the ground layer (Todd 1949). Todd paid special attention to seasonal changes in the population density of the ground layer fauna, but despite the fact that density changes in this stratum of the field would be influenced by the interstratal migration of certain species as well as by mortality and predation the relative importance of each of these factors was not investigated. Hence in this work the magnitude of the interstratal migration of the different life stages of the various species was investigated by following the relative population density changes, with season, in various field strata. Elton and Miller (1954) stressed that the fauna of a woodland habitat should be subdivided into the components of the various microhabitats within it. Of the several types of microhabitat classifications proposed, one of the most valuable was considered to be that in which the habitat was separated, vertically, into ground, field, shrub and tree layers. This classification was used, in a modified form, in the present study as it was ideally suited to a study of interstratal movement. The modification involved the addition of a surface layer and also a slight alteration to the limits of some of the other layers as defined by Elton and Miller (1954).

The sampling methods used for relative population density estimates in the case of the field layer and the tree branches were similar to those of Todd (1949). The method commonly used in agricultural practice for trapping small invertebrates moving on tree trunks (by the use of greasebands) was found to be unsatisfactory for harvest-spiders and a more efficient method was devised (page 100)

Todd's method of sampling the ground layer (by driving out animals from leaf litter in heated Tullgren funnels) was tried and found to be relatively less efficient than hand sorting for small harvest-spiders: by hand sorting, population densities approximately three times greater than those recorded by Todd from a similar habitat were found. In addition to hand sorting, pitfall trapping was also used for the ground layer.

Despite the fact that each level was sampled by a different method, so that the numbers from each were not strictly comparable, it was still possible to determine the pattern of vertical migration. This was done by comparing the relative changes, with time, in the numbers, species and instars of the harvest-spiders at the various levels. By using this approach, it was found that of the six common woodland species studied, only two (*Mitopus morio* and *Oligolophus agrestis*) moved above the ground, the movement occuring only in the penultimate (sixth) and final instars. Thus in the earlier instars of these two species and in all instars of the remaining species (*Lacinius ephippiatus*, *Nemastoma lugubre*, *Odiellus palpinalis* and *Oligolophus tridens*) the seasonal decline in ground layer population densities were presumably directly related to mortality.

The present work is believed to provide the first detailed account of seasonal changes in the ground layer population density of harvest-spiders. The only comparable work (Todd 1949) merely gives, for several species the "monthly mean count divided by the number of months in which the species was present" and the "maximummonthly mean count recorded".

For the adults of several species of harvest-spider Todd (1949) found some degree of correspondence between the humidity and temperature preferenda as measured in the laboratory and the rela^tive humidity and temperature measured in the corresponding habitats in the field. This suggests that habitat selection in ha^rvest-spiders may be governed more by the physical conditions of the environment than by the essentially biological needs, such as those of feeding and reproduction. Such relationships between the physical environment and laboratory determined preferenda ha^ve been found in several other invertebrate groups: For example, Backlund (1945) working on the wrack fauna of Swedan and Finland, concluded that "in the preferendum experiments the animals chose the temperature in which they prefer to live". Nørgaard (1951) working on the spiders of a Danish sphagnum bog found a close association between laboratory determined temperature preferenda of two species (<u>Lycosa pullata</u> and <u>Pirata piraticus</u>) and the temperatures of their habitats. Schaller (1950, as reported by Macfadyen 1963) found a similar association between microclimate and laboratory determined preferenda in several species of Collembola.

In the field, changes of light intensity are so closely associated with changes of temperature and relative humidity that it is difficult to assess the role of light alone as a factor influencing the selection of a habitat by a species. Hence there is little published work on this aspect although Cloudsley-Thompson (1961) found that in woodlice the humidity response (which plays an important part in habitat selection) in daylight differed from that in darkness.

In the present study Todd's microclimate and laboratory experiments were repeated and extended in order to define more precisely the relationships between the physical factors of the environment, habitat and behaviour.

Todd's field microclimate records were somewhat limited in scope. On only four separate occasions she recorded air and ground temperatures and relative humidities at intervals from late evening to early morning but gave no record of daytime conditions. Also, in view of the implied importance of light, it is surprising that the timing of the disappearance of light at dusk and its subsequent reappearance at dawn were not given. In the present study therefore, maximum scope for the correlation of physical conditions and behaviour was given by recording at three week intervals the light intensity, temperature and relative humidity on six occasions per 24 hour period. By expressing the results graphically, the 24 hourly temperature and relative humidity fluctuations were found to follow the characteristic pattern described by Geiger (1951).

The laboratory work carried out on certain species was intended to define the temperature and humidity preferenda and the pattern of diel locomotor activity of both juveniles and adults. Some adults from the field were weighed and egg counts were made to see if vertical migration could be associated with their physiological condition. In order that the present laboratory findings would be comparable with those already described in the literature, the preference experiments were carried out almost exactly as described by Todd (1949), the egg counts as described by Phillipson (1959). In the apparent absence of any published information on the determination of locomotor activity patterns in harvest-spiders, individuals were tested in several types of aktograph. These included the conventional mechanical type (Gunn and Kennedy 1936), the electronic type (Backlund and Eckerood 1950) and the infra red beam type (Williams 1959b). However no method was found which satisfactorily recorded the movements of very small individuals such as third instar <u>Mitopus morio</u> weighing approximately 2 mg, and a new system was devised (page 214). This was similar in principle to that used by Williams (1959b) in a study of the carabid Feronia madida but the method of recording permitted a much higher degree of sensitivity to be achieved.

During the three and a half year study, a considerable amount of information was compiled on both field and laboratory behaviour of certain species of harvest-spider and on field microclimate conditions. These findings must now be compared with each other in order to find reasons for the diel and seasonal vertical migration of only certain species.

Initially however, it is necessary to distinguish between these two types of migra^tion. In terms of seasonal migration juveniles of the only two migratory species studied (Mitopus morio and Oligolophus agrestis) upto and including the f^ifth instar were almost completely ground dwelling in habit, and the extension of vertical range really began in the sixth instar and continued in the seventh (adult) instar (Tables 21 and 36). In terms of diel migration most of the vertical movement occured during the hours of darkness, particularly between dusk and midnight (Figs. 34, 35 and 37).

The diel migration is considered first. Todd (1949) concluded that this was related to changes of locomotor activity. She sta^ted that the increase in activity "appears to be associated with the increase in the percentage relative humidity and the decrease in temperature........during the night " and that "activity begins with the approach of dusk and declines with the onset of dawn". However a more precise analysis was not attempted.

In the present study, it is clear that the onset of the diel vertical migration in preadult and young adult Mitopus morio (Figs. 34 and 35) coincided in time with a sudden increase in the intensity of locomotor activity as measured in the laboratory (Figs. 49 and 53). Under laboratory conditions this increase was brought about by the removal of light at'dusk', while similarly the reduction of activity at'dawn' was caused by the reappearance of light. A similar explanation seems to apply in the field, the relationship between field behaviour and microclimate being illustrated by comparing Figs 34 and 35 with Fig. 31. On 16 and 25 June a temperature decrease and relative humidity began at sunset (period 2) and continued steadily upto midnight (period 4) yet vertical migration did not begin until shortly after dusk (period 3). Thus, on both occasions, it seems likely that migration was triggered by the disappearance of light at dusk, although it is possible that it began only when a certain temperature or humidity had been reached. Such a situation was described by Gaul (1952) who found that certain Vesperine wasps only awoke in the morning when a certain temperature and humidity threshold was reached.

The movement of *M. morio* back to the ground layer at dawn (Fig. 34) is more easily understood. On 16 June the majority of individuals return from the surface and f^ield layers to the ground at dawn (between periods 4 and 5). However between these periods the relative humidity in the field layer remained at 93% RH, while the temperature rose by only 0.5°C. Clearly the return to the ground was synchronised with the reappearance of daylight rather than with a sudden change of temperature or relative humidity (Figs. 31 and 34).

The results of 24 June can be interpreted in a similar manner. Although a few *M. morio* now remained above ground during the day, a return of this species to the ground at dawn was clearly apparent. Due to the presence of early morning mist the humidity at all levels remained at 100% RH from midnight until after sunrise (periods 4 to 6), while between periods 4 and 5 the temperature rose by only 0.5°C. Again light was clearly the most important factor.

On all occasions after 24 June, after which time virtually the whole of the population above ground was adult, there was no longer any obvious association between movement between the ground and the lower levels of the field and changes of light intensity. However as movement of adults on the tree trunks was always nocturnal, part of the population presumably still responded to changes of light intensity. Probably the response made to light varies during the life history. Activity in the early sixth instar could be almost completely surpressed by light: this suppression could become progressively less intense in the la^te sixth and early seventh instars but then be renewed in older adults. Unfortunately the laboratory activity experiments were carried out on individuals of unknown age and the laboratory results cannot be used to support this explanation.

Oligolophus agrestis was relatively scarce in the study area in Nannys Plantation. However, on the few occasions when large numbers were obtained, the timing of vertical migration coincided with changes of the intensity of light rather than of temperature or relative humidity (Fig. 37 and Table 9). For example, at dawn the numbers in the shrub layer decrease at a time when temperatures and humidities changed only very slightly. Similarly movement over the tree trunks occured exclusively during the hours of darkness when changes of temperature and humidity were relatively small compared with those occuring around sunset and sunrise. However, unlike *M. morio*, the timing of vertical migration in *O. agrestis* did not coincide with any corresponding change of the intensity of locomotor activity, either in the f^ield (Fig. 33) or in the laboratory (Fig. 52).

Thus it is clear that the vertical movement in *M. morio* and *O. agrestis* was not necessarily caused by any change in t^he intensity of activity. Despite the association between migration and locomotor activity changes in the migratory stages of *M. morio*, a similar activity change occured in the non-migratory fifth instar and indeed in all instars tested of the exclusively ground dwelling species, *Lacinius ephippiatus* and *Oligolophus tridens*. At the same time, the vertical migration in *O. agrestis* was not accompanied by any activity change. Presumably innate differences in the behaviour patterns of the various species a^re therefore responsible for the observed differences.

Discussion of the nature of t^he diel rhythm of locomotor activity is beyond the scope of this work. However, such rhythms are of almost universal occurrence among living organisms, being particularly prominent in the Arthropods. The vast amount of literature on this subject has been recently reviewed by Harker (1958), Cloudsley-Thompson (1961) and Aschoff (1963). Briefly, it is clear that activity rhythms can be partly or completely endogenous in origin being governed by some internal physiological chronometer, or almost completely exogenous being controlled by periodic fluctuations of some physical factor of the environment. However, it is impossible to make any generalisation on the nature of the rhythm in any particular group and each species must be considered on its own account. For example, within the Millipedes, *Blaniulus guttulatus* and *Oxidus gracilis* exhibit a purely exogenous diurnal rhythm (as a response to alternating light and dark) while *Oxydesmus platycercus* and *Ophistreptus* sp. demonstrate an endogenous rhythm independent of any physical factors (Cloudsley-Thompson 1961). Any rhythm either partly or completely endogenous must be kept in phase with the daily environmental changes, and as a generalisation Aschoff (1963) concludes that there is "a form of coupling between the natural innate oscillator and the driving agent, the environmental fluctuation". He also concludes that the driving agent is normally light and that there is usually a remarkable independence of temperature. The results in the present study on harvest-spiders are in accord with these conclusions, the evidence indicating that except in *O. agrestis*, a diel rhythm of locomotor activity results largely from changes in the intensity of light (Figs. 49 to 53). Some degree of temperature independence may also occur: despite the lower nocturnal field temperatures (Table 9) with their resulting depression of metabolic activity rates, the nocturnal ground layer catches were still considerably greater than those of the day (Fig. 33).

Among the species of harvest-spider in the present study, it is impossible, from the evidence available to say whether the observed diel activity rhythm is exogenous or endogenous in origin. The persistent rhythm shown by adult *M. morio* when exposed to continuous darkness in the laboratory (Fig. 53) suggests that it could be endogenous. However, according to Aschoff (1963), the ease with which the phase of the rhythm was shifted would be evidence in favour of exogenous control. He concludes that a rhythm under endogenous control takes several days to be shifted through a 12 hour period, while in the few species reported to follow such a shift in only one or two days (the water skater Velia currens and the spider Arctosa perita) this may indicate the rhythm to be exogenously controlled. Clearly, further studies on the locomotor activity of harvest-spiders must be carried out before the nature of the rhythm can be elucidated.

The seasonal vertical migration is now considered. The change of microhabitat in the sixth and seventh instars of M. morio and O. agrestis could have resulted either from a change in the physical conditions of the environment affecting the non-migratory and the migratory phases of the life history, or from one in the physiological or ecological requirements of the different life stages.

In the case of M. morio, although microclimate readings were not made before 16 June, it is doubtful whether they would have differed sufficiently from those of this date to account for the sudden onset of migration in this species at this time. In O. agrestis, no association between microclimatic changes and the onset of migration was detected and it was concluded that the changes in behaviour with the approach of maturity were not the result of corresponding changes of the physical environment. In M. morio there was never any apparent shortage of suitable food in the ground layer and it is suggested that the needs of reproduction were primarily responsible for the extension of range of adults into the tree canopy. In harvest-spiders copulation only occurs as a result of random encounters between the sexes (Cloudsley-Thompson 1958), and any mechanism which would increase the chance of such encounters would be advantageous to the species. The movement of M. morio over the tree trunks, occurring only in adults and being restricted to a period of approximately three hours per diel admirably serves this purpose, animals being concentrated in both time and space. Certainly, in the field, copulation was frequently observed on the tree trunks at night, often the same male fertilizing more than one female. However, it is believed that not all members of the adult population moved onto the trunks (Page 172) and the evidence from weight determinations and egg counts indicated that only the oldest adults were involved (pages 258 and 262). Probably several days must elapse before newly moulted adults are in a condition suitable for copulation, and only then does the behaviour pattern change to allow migration into the canopy.

This explanation cannot apply to Oligolophus agrestis in which the main migration into the canopy occurred in the penultimate instar (Fig. 38). Perhaps this species moved away from the ground mainly to exploit the food resources of another microhabitat. Prior to the penultimate instar such a movement may have been prevented by, for example, an inability to control water loss from the body: on the other hand the sixth and final instars may have aquired the necessary waterproofing to move into regions of generally lower relative humidity - the shrub and tree layers.

It was expected that the changes of microhabitat noted during the life history of a single species would be reflected by corresponding changes in its preferred temperature and relative humidity. Such a change was discovered by Nørgaard (1951) in the spider *Pirata piraticus* but there is no record of any similar occurrence in harvest-spiders. Todd (1949) obtained preferred temperatures and relative humidities for adults of several species of harvest-spider, and it was hoped that by repeating and extending her work to the non-migratory juvenile stages of *M. morio* and *O. agrestis* a distinct change in preferred conditions would become apparent. However, the results of these experiments were inconclusive, animals being indifferent to gradients of both temperature and relative humidity. It is of interest that Nørgaard was unable to obtain any humidity preferences for the spiders *Lycosa pullata* and *Pirata piraticus* and he concluded that "the lack of a humidity preferendum is the more remarkable because humidity differences are so obvious in the environment of these spiders". This conclusion applies equally to the results in the present study. Cloudsley-Thompson (1957) suggested that the absence of a preferendum could be attributed to insufficient time having been allowed for the animals to respond. However, this was certainly not the cause in the present study on harvest-spiders, several experiments having been carried out over a 24 hour period in an attempt to obtain a 'preference'.

It is of interest to examine Todd's (1949) statement that laboratory determined humidity preferenda of the species are correlated with the relative humidity of their normal habitat. The ranges of rela^tive humidities given in Todd (1949) are q^uestionable: for example, that of the field la^yer is given as 70% to 80% RH yet the actual humidity records obtained during the night transects between 7 pm and 5 am were within the range 75% to 90% RH. It is suspected that the range 70% to 80% RH is that prevailing during the daytime only, when the animals were not out. Even assuming this criticism to be unjustified, there are still several other inconsistencies. For example *Leiobunum rotundum*, described as a tree trunk species, has a humidity preference of 60.7% to 68.9% RH, well within the range 60% to 75% RH given for the tree trunk humidities. However, in Todd's description of the night transects, she states that "proba^bly all *L. rotundum* leave the trees for the field layer at dusk and return there a^t dawn". As nocturnal field layer humidities were 75% to 90% RH, this species was therefore exposed to humidities well outside its preferred range for about half the diel. Similarly the upper limit of the humidity preference in Oligolophus tridens (72.1% RH), described as a field layer species, was well below that actually recorded in the field layer by night. It is therefore concluded that the existence of correlations between field conditions and laboratory determined preferenda are not as clear cut as Todd suggested.

In the absence of preference data it was believed that should any preferences actually exist, their relative order among the species would be revealed by comparing the survival times of corresponding instars when exposed to the same conditions. Thus it was expected that the survival experiments would reveal a distinct preference change between the fifth and sixth instars, exclusive to the two migratory species, sufficient to account for the onset of migration in the sixth instar. However, no such change was recorded (page 195). The only real point of interest to emerge from the survival experiments was the existence of a constant relationship between survival times of corresponding instars, O. agrestis surviving the longest time, L. ephippiatus at the other extreme, the shortest time. This suggests that the rates of water loss from the body may differ characteristically among the species and, to some extent, help to account for the difference in behaviour and distribution of the various species within the same woodland habitat. This type of relationship has been found by Tipton (1960, unpublished, reported in Williams 1962) in two species of Carabidae: *Nebria brevicollis* was nocturnal and was relatively less able to control its rate of water loss than the diurnal species *Feronia caerulescens*. Similarly, Cloudsley-Thompson (1957) found that, under the same conditions, the nocturnal spider *Ciniflo ferox* lost water more rapidly than the diurnal species *Ciniflo similis*. Clearly, corresponding studies could well be made on the two harvest-spiders *Oligolophus agrestis* and *Oligolophus tridens*.

Water is lost from the body by transpiration, respiration and defaecation. Among terrestrial arthropods the ability of many to control water loss has long been recognised as the prime factor influencing their distribution in the field. As a general rule, animals lacking a waterproofing layer in the cuticle are restricted to a moist environment and are usually nocturnal in habit, while those possessing such a la^yer are frequently diurnal (Cloudsley-Thompson 1954). However, as a result of competition with more efficient species, some of the latter may become secondarily adapted to the nocturnal habit. Cloudsley-Thompson (1954) divided nocturnal terristrial invertebrates into the primary nocturnal species which ha^ve not acquired a waterproof cuticle, and the secondary nocturnal species which may have acquired the necessary waterproofing for diurnalism but have nevertheless adopted the nocturnal habit. Williams (1962), noting the stress placed by other workers on the importance of high humidities to harvest-spiders, suggested that they were members of the primary nocturnal group. In the light of the results of the present study, it is believed that this cannot be true of harvest-spiders in general. For example, although adult M. morio only moved onto the tree trunks at night (Fig. 35) some remained in the canopy for at least 24 hours (Fig.36) where they would be exposed to strong winds, direct insolation, high temperatures and shade humidities at least as low as 55% RH (Table 9). It is difficult to see how individuals could survive for more than a few hours under these conditions unless some control over water loss could be exerted. The same conclusion applies to preadult and adult O. agrestis which also spent at least 24 hours in the tree canopy (Fig. 38).

However, it is expected that when studies of the physical and chemical properties of the cuticle of harvest-spiders are made, Nemastoma lugubre (a ground dwelling species not directly involved in this study) will prove to be a primary nocturnal species. This belief is based on the comparitive inability of N. lugubre to resist dessication when compared with the four species of the

Family Phalangiidae studies (Tables 57 to 60). *N. lugubre* was unable to withstand humidities much below 90% RH: for example, ten adult females exposed to 60% RH at 16°C were all dead within four hours, while a similar number at 30% RH 16°C were all dead within one hour. By contrast adult females of *Oligolophus tridens*, also a ground dwelling species, survived for approximately 123 hours at 60% RH 16°C and 64 hours at 30% RH 16°C (Table 60). Clearly an investigation of the structure and physical properties of the cuticle would be an invaluable aid towards the interpretation of the field behaviour recorded in this study.

In conclusion it must be admitted that, although positive results were obtained in the studies of seasonal development and population density changes, the studies intended to reveal the causes of, and the reasons for, the vertical migration of certain species gave inconclusive results. While migration occurring over the season is closely associated with that occurring over the diel, the present work has shown that each type must be considered separately.

The seasonal migration was caused by endogenous factors rather than by any change in the physical conditions affecting the various life stages. The diel vertical migration was 'triggered' by the removal of light at dusk but was not necessarily caused by the locomotor activity increase occurring at the same time - a similar activity increase at dusk was also apparent in the non-migratory harvest-spiders.

The reasons for the vertical migration are not known. It was suggested that the seasonal migration permitted the exploitation of the food resources of another microhabitat, while the diel migration, being restricted in both time and space, increased the chance of copulation and hence fertilisation of the eggs. However, neither explanation was fully tested and clearly much further work needs to be done before the behaviour patterns of the various species of harvest-spider can be satisfactorily explained.

VI SUMMARY

SUMMARY

1. Means of separating the different life stages (instars) are described for the following species: *Lacinius ephippiatus*, *Mitopus morio*, *Nemastoma lugubre*, *Odiellus palpinalis*, *Oligolophus agrestis* and *Oligolophus tridens*.

2. For each of the above species the course of seasonal development and seasonal changes in population density and dry weight were followed during 1958 and 1959.

   All species passed through their life history approximately two weeks earlier in 1959. The cause is suggested to have been an earlier hatch in 1959 resulting from the consistently higher field temperatures of that year.

   When compared with 1958, the population densities in 1959 were greater in *M. morio* and *O. agrestis*, similar in *O. tridens* and much smaller in *L. ephippiatus*, *N. lugubre* and *O. palpinalis*. It is suggested that juveniles of the last three species were the least able to resist dessication with the result that the unusually dry conditions of 1959 produced a very high level of juvenile mortality.

   The maximum population density for all species of harvest-spider combined was 167 per sq m (of beech litter). The corresponding maximum dry weight was 138.1 mg which is eqivalent to a live weight of approximately 690 mg per sq m.

3\. In the field the later instars of all the species studied except *O. agrestis* were more active by night than by day in the ground layer.

L. ephippiatus, *N. lugubre*, *O. palpinalis* and *O. tridens* were exclusively ground dwelling throughout their life. *M. morio* and *O. agrestis* were ground dwelling in the early juvenile stages but an extension of range into the field, shrub and tree layers occurred in the penultimate and final instars.

Movement of *M. morio* and *O. agrestis* between the ground and tree layers occurred only during the hours of darkness. Most individuals remained in the canopy for at least 24 hours: a large proportion never returned to the ground probably as a result of predation by birds. Light, rather than temperature or humidity, was suggested to be the stimulus controlling the vertical movement.

4\. In no species could any temperature or relative humidity preferendum be detected in the laboratory.

The survival times of both juveniles and adults of several species of harvest-spider were determined.
In any one instar the survival time at constant relative humidity was approximately halved for each temperature increase from 5° to 16°C and from 16° to 25°C.
In any one instar the survival time at constant temperature increased progressively from 30% to 100% RH.

Under the same conditions of temperature and relative humidity the survival times of corresponding instars of the species tested bore a constant relationship to each other, *O. agrestis* surviving the longest time, *L. ephippiatus* the shortest time with *M. morio* and *O. tridens* intermediate between the two extremes.

5. In the laboratory *Oligolophus agrestis* was equally active throughout the diel, while a diel rhythm of locomotor activity was demonstrated in both juveniles and adults of *L. ephippiatus*, *M. morio* and *O. tridens*. These results agree with the field observations on locomotor activity.

The activity increase was associated with the removal of light at 'dusk', the subsequent decrease with the reappearance of light at 'dawn'. It was shown that the rhythm in adult *M. morio* resulted largely from the suppression of activity by light.

6. Both adult males and females of *M. morio* and *O. agrestis* from the trees were generally heavier than those from the other strata of the field. In the case of *M. morio* it is suggested that only the oldest adults moved into the tree canopy.

In both species the mean weight of adult females increased for some time following the final moult. This increase was mainly due to an increase in the number of ripe eggs in the body.

Females of *O. agrestis* moving from the tree canopy to the ground contained more eggs than those moving in the reverse direction. This suggestssthat the reason for the return from the canopy was the need to deposit eggs on the ground.

The mean weight of adult male *M. morio* remained fairly constant following the final moult, while that of adult male *O. agrestis* was not studied in detail.

VII APPENDICES

Appendix A (i) The instars of Lacinius ephippiatus in each collection from Great High Wood, 1958 and 1959.

Date of sampling	Instar II	III	IV	V	VI	VII male	VII female
9.5.58	10	8					
15.5.58	3	25					
30.5.58	2	12	26				
8.6.58			30	5			
15.6.58			8	27			
3.7.58				4	27		
21.7.58					1	8	7
11.8.58						4	4
28.8.58						2	3
7.9.58						2	1
22.9.58							
9.10.58							
23.10.58							
5.11.58							
20.11.58							
5.12.58							
14.12.58							
19.2 .59							
13. 3.59							
3. 4.59	29						
24. 4.59	7	4					
11. 5.59		14	2				
28. 5.59			6				
13. 6.59				7			
30. 6.59					4		
15. 7.59						2	
4. 8.59						2	
20. 8.59							
2. 9.59							
16. 9.59							
22.9. 59							
11.10.59							
31.10.59							
11.11.59							
5.12.59							

Appendix A (ii) The instars of <u>Mitopus morio</u> in each collection from Great High Wood, 1958 and 1959.

Date of sampling	Instar II	III	IV	V	VI	VII male	VII female
9. 5.58	19	28					
15. 5.58	17	45	3				
30. 5.58		23	41	2			
8. 6.58		12	30	31			
15. 6.58		1	15	31	2		
3. 7.58			4	27	18		
21. 7.58				5	6	4	1
11. 8.58				1	2	10	6
28. 8.58						2	4
7. 9.58						4	6
22. 9.58						2	1
9.10.58						2	2
23.10.58						2	1
5.11.58							
20.11.58							
5.12.58							
14.12.58							
19. 2.59							
13. 3.59							
3. 4.59	30						
24. 4.59		84					
11. 5.59		23	30				
28. 5.59			25	19	1		
13. 6.59			5	16	17		
30. 6.59				2	23		
15. 7.59					4	7	4
4. 8.59						12	3
20. 8.59						7	2
2. 9.59						3	0
16. 9.59							1
22. 9.59							
11.10.59							
31.10.59							
11.11.59							
5.12.59							

Appendix A (iii) The instars of Nemastoma lugubre in each collection from Great High Wood, 1958 and 1959

Date of sampling	Instar II	III	IV	V preadults	V adult male	V adult female
9. 5.58	17				2	4
15. 5.58	12					2
30. 5.58	17	31	6			10
8. 6.58	5	12	26		7	10
15. 6.58	6	10	30	3	8	4
3. 7.58			13	31	2	3
21. 7.58			3	33	6	4
11. 8.58				8	26	20
28. 8.58					37	51
7. 9.58					49	38
22. 9.58					24	23
9.10.58					21	22
23.10.58					9	28
5.11.58					13	34
20.11.58					7	14
5.12.58					5	8
14.12.58					5	11
19. 2.59						4
13. 3.59						2
3. 4.59	1				5	3
24. 4.59					3	3
11. 5.59	8	9				2
28.5. 59	2	11	2		3	6
13. 6.59	1	4	10	1	2	1
30. 6.59			3	7		3
15. 7.59			2	4	3	3
4. 8.59				5	5	5
20. 8.59					6	6
2. 9.59					3	2
16. 9.59					3	4
22. 9.59					2	7
11.10.59						
31.10.59					2	3
11.11.59						1
5.12.59					1	1

Appendix A (iv). The instars of Odiellus palpinalis in each collection from Great High Wood, 1958 and 1959.

Date of sampling	Instar II	III	IV	V	VI	VII male	VII female
9. 5.58							
15. 5.58							
30. 5.58	10						
8. 6.58	28						
15. 6.58	37						
3. 7.58	2	42	4				
21. 7.58		3	17				
11. 8.58			1	21			
28. 8.58				1	38		
7. 9.58				2	16		7
22. 9.58					1	15	22
9.10.58						32	9
23.10.58						28	29
5.11.58						11	21
20.11.58						5	6
5.12.58							
14.12.58							
19. 2.59							
13. 3.59							
3. 4.59							
24. 4.59							
11. 5.59	1						
29. 5.59	20						
13. 6.59	2	23					
30. 6.59		13	10				
15. 7.59		2	10	1			
4. 8.59				9			
20. 8.59				3	4		
2. 9.59					2		
11. 9.59						1	
22. 9.59						5	4
11.10.59						5	
31.10.59						1	
11.11.59						3	1
5.12.59							

Appendix A (v) The instars of <u>Oligolophus agrestis</u> in each collection from Great High Wood, 1958 and 1959.

Date of sampling	Instar II	III	IV	V	VI	VII male	VII female
9. 5.58							
15. 5.58							
30. 5.58							
8. 6.58	18						
15. 6.58	16						
3. 7.58	5	37	2				
21. 7.58		14	14				
11. 8.58			12	13			
28. 8.58					24		
7. 9.58					20		2
22. 9.58						1	
9.10.58						16	8
23.10.58						10	11
5.11.58						8	15
20.11.58						2	6
5.12.58						2	2
14.12.58							1
19. 2.59							
13. 3.59							
3. 4.59							
24. 4.59							
11. 5.59	2						
28. 5.59	56						
13. 6.59	41	11	4				
30. 6.59		28	12				
15. 7.59		7	33	2			
4. 8.59		1		39	1		
20. 8.59				8	24		
2.9 .59					18		2
16. 9.59					1	13	5
22. 9.59						3	2
11.10.59						4	1
31.10.59						3	3
11.11.59						5	2
5.12.59							

Appendix A (vi) The instars of <u>Oligolophus tridens</u> in each collection from Great High Wood, 1958 and 1959.

Date of sampling	Instar II	III	IV	V	VI	VII male	VII female
9. 5.58							
15. 5.58							
30. 5.58							
8. 6.58	2						
15. 6.58	10						
3. 7.58	5	34					
21. 7.58		6	20				
11. 8.58			8	17			
28. 8.58					8		3
7. 9.58					6	4	12
22. 9.58						9	11
9.10.58						33	9
23.10.58						16	7
5.11.58						1	
20.11.58							1
5.12.58							
14.12.58							
19. 2.59							
13. 3.59							
3. 4.59							
24. 4.59							
11. 5.59							
28. 5.59	14						
13. 6.59	14	8					
30. 6.59		2	13				
15. 7.59		1	12	2			
4. 8.59				13			
20. 8.59					9	1	
2. 9.59					3	5	4
16. 9.59						11	3
22. 9.59						2	6
11.10.59						1	2
31.10.59							1
11.11.59							1
5.12.59							

Appendix B. The numbers of <u>Mitopus morio</u> seen on the tree trunks at each of the six periods of the diel.

	Greased Trees												Ungreased Trees.											
	Lower papers						Upper papers						Lower papers						Upper papers					
Period	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
16.6	0	0	1	19	7	0	0	0	0	0	0	0	0	0	7	2	0	0	0	0	0	0	0	0
25.6	0	0	26	35	5	1	0	0	0	0	0	0	0	0	3	7	0	0	0	0	0	0	0	0
7.7	0	0	46	55	0	0	0	0	12	4	0	0	0	0	23	6	0	0	0	0	12	1	0	0
13.7	0	0	82	51	0	0	0	0	7	21	0	0	0	0	32	3	0	0	0	0	14	1	0	0
24.7	0	0	48	69	0	0	0	0	2	1	0	0	0	0	10	2	0	0	0	0	1	1	0	0
31.7	0	0	33	26	0	0	0	0	2	1	0	0	0	0	5	3	0	0	0	0	3	1	0	0
7.8	0	0	41	11	0	0	0	0	2	4	0	0	0	0	2	1	0	0	0	0	0	0	0	0
16.8	0	0	14	12	0	0	0	0	4	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
27.8	0	0	2	12	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.9	0	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16.9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25.9	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix C Comparisons of mean wet weights of adult harvest-spiders.

(i) Male *Mitopus morio*.

Samples compared	Date	t	d f	P
Lower papers v Ground layer	7.7	5.7332	51	<0.001
	13.7	2.2401	54	<0.05
	24.7	0.9688	50	ns
	31.7	0.1886	24	ns
Lower papers v Surface-field -shrub layers	25.6	2.7195	66	<0.02
	7.7	8.2069	88	<0.001
	13.7	4.2068	89	<0.001
	24.7	5.3622	53	<0.001
	31.7	4.2213	53	<0.001
	7.8	1.5502	27	ns
Ground layer v Surface-field -shrub layers	7.7	0.2034	55	ns
	13.7	0.4790	63	ns
	24.7	3.5999	46	<0.002
	31.7	2.9074	45	<0.01

Appendix C Contd.

(ii) Female Mitopus morio

Samples compared	Date	t	d.f.	P
Lower paper v Upper paper	7.7	1.9044	28	ns
	13.7	0.6813	34	ns
	24.7	1.4944	16	ns
Lower papers v Surface-field -shrub layers	25.6	3.7894	105	<0.001
	7.7	5.3147	89	<0.001
	13.7	5.8168	86	<0.001
	24.7	5.4339	51	<0.001
	31.7	2.0822	15	ns
	7.8	1.4394	9	ns
Lower papers v Ground layer	25.6	4.4900	81	<0.001
	7.7	3.6168	116	<0.002
	13.7	12.9794	78	<0.001
	24.7	2.4913	48	<0.02
	31.7	0.6210	11	ns
	7.8	0.0180	7	ns
Surface-field -shrub layers v Ground layer	25.6	0.8824	98	ns
	7.7	2.5380	147	<0.02
	13.7	1.7796	94	ns
	24.7	2.8942	65	<0.01
	31.7	2.4343	18	<0.05
	7.8	1.0467	6	ns

Appendix D. Comparisons of mean wet weights of adult harvest-spiders.

(i) Male *Oligolophus agrestis*

Samples compared	Date	t	d.f.	P
Upper papers v Lower papers	9.10	2.7822	32	< 0.01
Upper papers v Surface-field -shrub layers	9.10	5.0249	19	< 0.001
Lower papers v Surface-field -shrub layers	9.10	2.4270	33	< 0.05

Appendix D Contd.

(ii) Female *Oligolophus agrestis*.

Samples compared	Date	t	d.f.	P
Upper papers v Lower papers	27.8	4.1387	50	< 0.01
	5.9	3.2644	19	< 0.01
	16.9	0.2728	27	ns
	9.10	4.0200	48	< 0.01
Upper papers v Surface-field -shrub layers	27.8	7.8538	74	< 0.001
	5.9	3.3153	31	< 0.01
	16.9	0.8648	18	ns
	9.10	4.9034	53	< 0.01
Upper papers v Ground layer	27.8	3.1199	49	< 0.01
	5.9	1.4101	6	ns
	16.9	0.0028	8	ns
	9.10	2.9345	21	< 0.02
Lower papers v Surface-field -shrub layers	27.8	0.8207	42	ns
	5.9	0.3047	42	ns
	16.9	1.4034	33	ns
	9.10	0.2002	71	ns
	20.10	3.8119	28	<0.001
Lower papers v Ground layer	27.8	0.6349	17	ns
	5.9	0.4786	17	ns
	16.9	0.2166	23	ns
	9.10	0.4876	39	ns
	20.10	2.7760	50	<0.01
Surface-field -shrub layers v Ground layer	27.8	1.6449	41	ns
	5.9	0.3401	29	ns
	16.9	0.5877	14	ns
	9.10	0.4969	44	ns
	20.10	2.0431	30	<0.05

VIII REFERENCES

REFERENCES

Allee, W.C. et al. (1949) Principles of Animal Ecology (New York).

Andrewartha, H.G. and Birch, L.C. (1954) The Distribution and Abundance of Animals (Chicago).

Backlund, H. O. and Ekerood, S. (1950) An aktograph for small terrestrial animals. Oikos, 2, 213-16.

Bailey, N. T. J. (1959) Statistical Methods in Biology (London, E.U.P.)

Baker, J.R. (1936) Normograms for saturation deficiency. J. Anim. Ecol. 5, 94.

Beament, J. (1958) Electronics for Biologists (Butterworth).

Bristowe, W. S. (1949) The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food. J. Anim. Ecol. 18, 100-14.

Broadhead, E. and Thornton, I.W.B. (1955) An ecological study of three closely related psocid species. Oikos 6, 1-50.

Broadhead, E. (1958) The psocid fauna of larch trees in Northern England, an ecological study of mixed species populations exploiting a common resource, J. Anim. Ecol., 27, 217-64.

Bullock, T.H. (1955) Compensation for temperature in the metabolism and activity of poikilotherms, Biol. Rev., 30, 311-42.

Cloudsley-Thompson, J. L. (1954) The ecological significance of diurnal rhythms in terrestrial arthropods. Sci. Progr. 42, 46-52.

Cloudsley-Thompson, J. L. (1958) Spiders, Scorpions, Centipedes and Mites, The ecology and natural history of woodlice, 'myriapods' and arachnids, Pergamon, London and New York.

Cloudsley-Thompson, J. L. (1961) Rhythmic Activity in Animal Physiology and Behaviour (Academic Press, New York and London.

Duffey, E. A. J. (1956) Aerial dispersal in a known spider population. J. Anim. Ecol., 25, 85-111.

Edney, E. B. (1957) The Water Relations of Terrestrial Arthropods.(C.U.P.).

Ellis, A. E. (1942) The natural history of Wheatfen Broad, Surlingham. Part IV. The woodlice and harvest-men. Trans. Norfolk Norw. Nat. Soc. 15, 291-300.

Elton, C. S. (1935) Animal Ecology, 2nd edn.(London).

Elton, C. S. and Miller, R. (1954) The ecological survey of animal communities: with a practical system of classifying habitats by structural characters, J. Ecol., 42, 460-96.

Falconer, W. (1910) Keys to the families and genera of British spiders, and to the families, genera and species of the British harvest-men and pseudoscorpions. Naturlist, Lond., 233-42, 323-32, 438-47.

Fisher, R. A. (1938) Statistical Methods for Research Workers, 7th edn. (Edinburgh).

French, G. A. (1957) A sensitive proximity detector. The Radio Constructor,Dec.302-5.

Gabbut, P. D. (1959) The bionomics of the wood cricket, *Nemobius sylvestris* (Orthoptera: Gryllidae). J. Anim. Ecol., 28, 15-42.

Geiger, R. (1951) The Climate near the Ground. (Harvard University Press).

Ghent, A. W. (1956) Linear Increment in Width of the Head Capsule of two Species of Sawflies. The Canadian Entomologist, 88, 17-23.

Harker, J. (1958) Diurnal rhythms in the animal kingdom. Biol. Rev. 33, 1-52.

Hull, J. E. (1930) A note on north country harvest-men. Vasculum, 16 (3), 100-3.

Immel, V. (1954) Zur Biologie and Physiologie von *Nemastoma quadripunctatum* (Opiliones, Dyspnoi). Zool. Jb. (Syst.), 83, 129-84.

Ladell, W. R. S. (1936) A new apparatus for separating insects and other Arthropods from the soil. Ann. Appl. Biol., 23, 862-79.

Lloyd, M. (1963) Numerical observations on movements of animals between beech litter and fallen branches. J. Anim. Ecol., 32, 157-63.

Macfadyen, A. (1963) Animal Ecology: Aims and Methods, 2nd edn. (Pitman, London).

Madge, D. S. (1961) "Preferred temperatures" of land Arthropods. Nature, Lond., 190, 106-7.

Meade, R. H. (1855) Monograph on the British species of Phalangiidae or harvest-men. Ann. Mag. Nat. Hist., 15, 393-416.

Mitchell, B. (1963) Ecology of two Carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). J. Anim. Ecol., 32, 377-92.

Nørgaard, E. (1951) On the ecology of two Lycosid spiders *Pirata piraticus* and *Lycosa pullata* from a Danish sphagnum bog, Oikos, 3, 1-21.

Parry, D. A.	(1951)	Factors determining the temperature of terrestrial Arthropods in sunlight. J. Exp. Biol., **28**, 445-62.
Phillipson, J.	(1959)	The seasonal occurance, life histories and fecundity of harvest-spiders (Phalangida). Ent. Mon. Mag., **95**, 134-8.
Phillipson, J.	(1960a)	A contribution to the feeding biology of *Mitopus morio* (F.) (Phalangida). J. Anim. Ecol. **29**, 35-43.
Phillipson J.	(1960b)	The food consumption of different instars of *Mitopus morio* (F.) (Phalangida) under natural conditions. J. Anim. Ecol. **29**, 299-307.
Phillipson, J.	(1962)	Respirometry and the Study of Energy Turnover in Natural Systems with Particular Reference to Harvest-spiders (Phalangiida). Oikos, **13**, 311-22.
Pickard-Cambridge, O.	(1890)	On the British species of Phalangidea or Harvest-man. Proc. Dorset nat. Hist. Fld. Cl., **11**, 163-216.
Sankey, J. H. P.	(1949)	British harvest spiders. Essex Nat., **28**, 181-91.
Savory, T. H.	(1938)	'Notes on the biology of harvest-men.' J. Quekett Micr. Cl., **1**, 89-94.
Savory, T. H.	(1944)	Synopses of the British fauna - No. 1. Opiliones, Proc. Linn. Soc. Lond., 1942-43 (2): 81-92.
Snedecor, G. W.	(1949)	Statistical Methods, 4th edn. (Iowa).
Solomon, M. E.	(1945)	The use of cobalt salts as indicators of humidity and moisture. Ann. Appl. Biol., **32**, 75-85.