Some aspects of the biology of molophilus ater meigen

R. J. Smith, Guy

SOME ASPECTS OF THE BIOLOGY OF *MOLOPHILUS ATER* MEIGEN.

BY

Guy R.J. Smith, B.Sc.

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C O N T E N T S

INTRODUCTION

The work presented in this thesis continues studies of the biology and the factors affecting population regulation in the brevi-palped crane-fly Molophilus ater Meigen.

It has been carried out on the Moor House National Nature Reserve in Westmorland where it has been suggested that extreme climatic conditions may prevent the population size increasing to a point where density dependent controls operate (Cragg 1961).

Cragg (1961) has summarised the many investigations into moorland fauna at Moor House and Coulson (1956, 1959, 1962) has catalogued the crane fly fauna of the reserve and studied the biology of some species there.

Most of the investigations on the family Tipulidae have been centred on the sub-family Tipulinae or long-palped crane flies and particularly those species which are of economic interest due to the damage their larvae can cause to certain crops. Barnes (1925, 1937) has investigated the distribution and bionomics of Tipula paludosa Meig., whilst Milne et al (1958, 1965) and Laughlin (1958, 1960, 1967) have made an extensive study of the biology of this species and also Tipula oleracea L.. Freeman (1964, 1967, 1968) has studied the ecology of a wider range of the Tipulinae species. Horobin (1971) has studied the emergence biology of Tipula subnodicornis Zett., T.paludosa and T. pagana Meig., at Moor House.

The other two sub-families of the Tipulidae, the Cylindrotominae and Linoniinae which comprise the short-palped crane flies have come in for less attention.

Cuthbertson (1926) studied swarming in various species, whilst Freeman's (1968) paper describes the distribution, emergence and ecology of some Limonids in a New Forest Reserve.

Crisp and Lloyd (1954) in a study of a patch of woodland mud recorded a wide range of short palped species, including seven species of the genus Molophilus, some features of development and general behaviour are recorded.

Hadley (1966), 1969, 1971) studied the biology of M.ater at Moor House between 1963 and 1966 and has elucidated the life cycle, emergence biology, growth rates and that the major generation mortality occurs in the egg and first instar stages, he estimated this as between 88% and 92%.

Horobin (1971) continued the population studies on M.ater from 1966 to 1970 and extended this with a series of sites on Great Dun Fell on the western side of the reserve. These varied in altitude from 1400 ft. to 2700 ft. (424M. to 818M.) and enabled him to describe the effects of altitude on the biology of M.ater and he related much of this to variations in temperature recorded at the sites. These temperature records also enabled him to postulate a temperature threshold for pupation as the factor controlling the date and synchrony of the adult emergence.

Using key factor analysis he has shown egg and first instar mortality to account for most of the variation in generation mortality from year to year and this is thought to be due to desiccation. Another component within this egg and first instar mortality, was thought to be due to predation, and this, together with a reduction in fecundity, acted in a density dependent manner in contributing to the regulation of population numbers.

The present study has continued the survey of populations on Hadley's Moor House sites, now making data available for 8 consecutive years. Sampling has continued on Horobin's Dun Fell sites making population data available on these areas for 5 consecutive years.

In addition, respiration and calorimetric measurements have enabled estimates of turnover and production efficiency to be made. Various aspects of the biology have been studied or checked and the variability in distribution of M.ater over the Blanket Bog and relative to the microhabitats within it have been investigated.

2. THE STUDY AREA AND SAMPLING SITES

2.1 Location and general physiography

The Moor House National Nature Reserve, Westmorland (N.R. 80 : Nat. Grid. Ref. N.Y. 758329) consists of 10,000 acres (4,000 hectares) of typical northern Pennine moorland and is situated twelve miles to the east of Penrith and eleven miles to the south of Alston. The greatest part of the reserve comprises the eastern dip slope descending from the summit ridge of three principal fells, Knock Fell (2604 ft., 794m), Great Dun Fell (2780 ft., 845m) and Little Dun Fell (2761 ft., 842m). Cross Fell (2930 ft., 893m), the highest peak in the Pennines, lies just outside the northern boundary of the reserve.

The scarp slope descends to the west into the Vale of Eden near Appleby. The reserve boundary on this side is provided by the upper limit of enclosed pasture which is at about 1,400 ft. (427m).

The dip slope has an extensive cover of peat, up to a depth of 12 ft. in places, this overlies a covering of glacial drift on a bedrock of the Carboniferous Yoredale series. This peat supports the Blanket Bog typical of the reserve but has been dissected by numerous streams flowing into the River Tees which provides the eastern and northern boundary of the reserve. Where the bedrock has been exposed peaty or mineral soils have been formed supporting a vegetation dominated by rushes and grasses. Above about 2,500 ft. (762m) on the dip slope and on the western scarp slope most of the peat has been eroded to produce thin fell top podsol soils. These are dominated by Festuca spp. on the summits, and a variety of peaty and mineral soils on the western slopes are dominated by Festuca spp., Nardus stricta or Juncus squarrosus. (Note: The species nomenclature for plants mentioned in this thesis is from Clapham et al (1962)).

General descriptions of the reserve have been given by Conway (1955) and Cragg (1961). The geology has been described by Johnson and Dunham (1963) and the vegetation by Eddy, Welch and Rawes (1969).

2.2 The study sites

The Moor House and Dun Fell sites used in this study have been adequately described by Hadley (1966) and Horobin (1971) in their theses. Their descriptions are summarised in Appendix I, complete with any necessary additions or notable changes.

The only new sites used in the present study are a series of Blanket Bog sites used to assess variations in *M.ater* populations on Blanket Bog. They were all situated within a mile of the Moor House field station, on the dip slope part of the reserve. They are described individually below:-

The Blanket Bog sites

1. The Bog End site

This is the same site that has been used by Horobin and Hadley and is fully described in the Appendix I.

2. The Troutbeck site

This level site is situated adjacent to the Moor House track in close proximity to the Troutbeck bridge. It is notably drier than the Bog End site and has been artifically drained. *Eriophorum vaginatum*, *E. angustifolium*, *Calluna vulgaris* and *Sphagnum* spp. all grow extensively here but it is noticable that it is difficult to divide the vegetation into the *E. vaginatum*, *Calluna*, and *Sphagnum* microhabitats that are conspicuous on most of the Blanket Bog. The *Calluna* growth is young and the *E.vaginatum* tussocks poorly developed.

3. The Neatherhearth site

This site is situated above the Neatherhearth area which lies alongside the Moor House track close to the actual field station. It is on the edge of the Blanket Bog and has a slight slope to the west.

The area is dominated by E.vaginatum with extensive E.angustifolium and C.vulgaris cover. Sphagum spp. and Trichophorum cespitosum are also present. The area is very hummocky and areas of wet bare peat are common.

4. The House Hill site

A level site situated on a peat hag between two eroding gullies on the hill directly behind the Moor House field station. There is an extensive Calluna canopy mainly of middle aged stems, Eriophorum vaginatum tussocks are common and well developed. The site is drier than the Bog End site and Sphagnum spp. though present are not so extensive. Polytrichium commune and Empetrum nigrum are also common.

5. The Valley Bog site

Valley Bog is situated alongside the track from Moor House to Bog End and is an area where the peat is very thick and over 20m deep in places. A site was set up at the eastern end of the bog. The area is very wet and the Calluna canopy extensive with many very old plants. E.vaginatum tussocks are large and isolated. A Sphagnum carpet covers most of the ground surface, in some cases it occurs as hummocks, whilst under the Calluna canopy the growth is very loose.

6. The Bog End Plantation

This is a well established plantation of Lodgepole pine (Pinus contorta), the trees are approximately 15 years old. Prior to planting the area was drained, and the channels are still distinct and effective. The area has also been fertilised. At ground level Calluna vulgaris and E. vaginatum are co-dominant. Sphagnum spp. are not common indicating the drier nature of the site. An exceptional growth of Rubus chamaemorus indicates the artifically produced high fertility.

3. CLIMATE

Meteorological records have been kept at Moor House since 1932 (Manley 1936, 1942, 1943); the climate is typical of the Montane regions of Britain (see Pearsall 1950). There is a high number of rain days each year and a mean annual rainfall in excess of 74 inches (1,900 mm). The average daily sunshine is less than 4 hours per day and strong winds are common throughout the year. On over 30% of days throughout the year, ground and air frosts are recorded. The climate at Moor House is severe and has been described by Manley (1936) as sub-arctic, having many features comparable to those at sea level in southern Iceland. The mean monthly temperatures and mean monthly rainfalls over the study period are given in Tables 1 and 2 along with the mean monthly temperatures and rainfalls for the period 1953 to 1965 for the purpose of comparison.

In the 1970-71 season, May and June were particularly warm and dry, May in fact showed a monthly mean water deficit, an unusual feature at Moor House. The autumn was windy, wet and relatively mild and the winter exceptionally mild with no monthly mean temperature below $0^{o}C$.

The 1971-72 season also experienced a dry May but it was not as warm as in 1970, the June rainfall was near normal but temperatures relatively low. July was exceptionally warm and dry. The autumn was mild and dry and was followed by another very mild winter.

Notable at the start of the 1972-73 season was the extremely wet and cold May and June.

The importance of a knowledge of soil temperatures, rather than air temperatures, to studies on the ecology of soil animals has been stressed by Macfadyen (1956) and it is fortunate for this study that Horobin (1971) has made an extensive study of soil temperature on all the main sites used. He recorded maximum and minimum soil temperatures at a depth of one centimetre with a mercury in steel thermograph and showed a reduction in mean soil temperature of

approximately 0.1°C for every 100 ft. increase in altitude, though exceptions were found in relation to different aspects and soil types. Using a method of chemical temperature inversion of sucrose solution, which had a precision of ± 0.1°C mean temperature estimates were obtained on all sites between October 1967 and May 1970. On a basis of average annual soil temperature the Peaty Podsol site was the warmest at 6.6°C and the other sites followed in the order Peaty Gley (6.4°C), 1,400 ft. (6.2°C), 1,700 ft. and Blanket Bog (5.8°C), 1,900 ft. and 2,050 ft. (5.5°C), 2,700 ft. (5.0°C.).

It was noted however that temperature differences were not consistent, in winter and spring there was a tendency for these differences to be smaller and during summer and autumn divergence occurred. Also deviations from the order of sites relative to annual average temperatures were noted in spring as some sites showed a tendency to warm up more quickly than others.

Table 1

Mean monthly temps. ^{o}C $\frac{1}{2}$(max. and min.) recorded at the Moor House Field Station over the study period. (Altitude 1832 ft. (558m))

\+ the mean monthly temps. over the period 1953-65 for comparison.

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
1970	-0.5	-2.5	-0.9	1.3	8.3	11.3	10.5	11.7	10.1	6.3	2.9	0.9	4.9
1971	1.2	1.2	1.0	3.6	7.0	7.5	12.2	11.1	10.2	7.3	2.2	3.3	5.6
1972	-0.1	-0.2	2.8	3.8	6.3	7.3	10.5						
1953-65	-0.7	-0.9	1.3	3.9	6.9	9.6	11.0	10.7	9.3	6.6	3.1	0.9	5.1

Table 2

Monthly rainfall in inches recorded at the Moor House Field Station over the study period.

\+ the mean monthly rainfall over the period 1953-65.

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	total for year
1970	6.18	11.03	6.06	7.99	2.41	3.77	6.71	7.29	6.69	10.50	9.47	6.80	84.3(
1971	5.47	6.07	5.01	2.11	3.01	5.09	2.51	7.35	1.62	5.52	6.80	2.43	52.9
1972	7.82	3.62	5.92	6.22	8.78	6.26	4.08						
1953-65	7.39	5.09	4.25	4.88	4.72	4.27	6.21	7.29	6.56	6.86	7.35	8.72	73.5(

4. CULTURE STUDIES

4.1 The biology of M.ater has been extensively studied by Hadley (1969, 1971) and Horobin (1971) both in the field and by laboratory experimentation. In the present study it was considered necessary to check and extend some of the studies of the previous authors.

M.ater larvae of all instars may be cultured in the laboratory in moist peat. The adults normally available in the field in late May and early June can be induced to emerge in the laboratory as early as January when given the correct conditions. These early adults will mate and provide fertile eggs which can be cultured to provide stocks of 1st and 2nd instar larvae by February and March. Although it was not attempted in this study it seems possible that M.ater could complete 2 generations in a year under controlled laboratory conditions. Using temperature control of the cultures it is possible to obtain most of the developmental stages throughout the year.

4.2 Studies on pupation

4.2.1 Pupation in M.ater was extensively studied in the laboratory by Hadley (1971) over a range of temperatures from 10°C to 23°C. He noted that the mean daily air temperature at Moor House in May, when pupation takes place, over the 14 year period 1952-65 was 6.9°C. Extrapolating back linearly from his laboratory results he suggested a pupal period in the field of the order of 14-17 days.

Horobin (1971) studied soil temperature on the various sampling sites over the period 1967-70 using both a sucrose inversion method and Cambridge thermographs. In each case soil temperature was measured at a depth of 1 cm.. Weekly means in May were in the range 4 - 9°C.

Little seems to be known of the actual position of the pupae in the field, but they must be near to the soil surface for ease of adult emergence, and larvae in April are certainly concentrated in the top 3 cms.

The mean temperature experience of the pupae therefore seems likely to be in the range of 6 - 7°C, though it is realised that daily excursion around the mean may be considerable.

In view of the lack of actual data on the duration of pupation at temperatures comparable to those experienced in the field, it was decided to study pupation at 5°C and 7°C as well as the 10°C and 20°C which would allow a check with Hadley's results.

4.2.2. Practical Details

In April 1972 larval cultures were set up on moist filter paper in glass petri dishes. A small amount of peat was included in each culture to provide food, but not so much as to make it difficult to find pupae. The larvae were obtained from an area of Juncus squarrosus moor adjacent to the 1,900 ft. site. Sods approximately 30 cms square and 4 cms thick were extracted using large Berlese type funnels with a 100 watt light bulb as the heat source. This technique though not fully quantitative, proved exceptionally useful in several of the studies in this thesis as it allowed the bulk collection of larvae for culture in a year when larval densities were very low.

The larval cultures were kept at 10°C and in an 18 hour photoperiod. They were checked twice daily and any pupae removed. The pupae were kept seperately on moist filter paper in small glass petri dishes in one of the 4 constant temperatures selected for the study. The individual pupal cultures were checked every afternoon for emergence as adults.

4.2.3 Results and Discussion

The results in Table 3 were obtained by the methods described, also included for the purpose of comparison are Hadley's results which have been marked with a triangle.

The results at 10°C and 20°C correspond very well with those obtained by Hadley, but when they are plotted in Figure 1 with the results at 5°C and 7°C the direct relationship previously postulated between temperature and pupal duration is not indicated.

Figure 1

The relationship between temperature ^{o}C and pupal duration for M.ater in the laboratory.
(Hadley's findings (1971) are shown with a triangular mark for comparison)

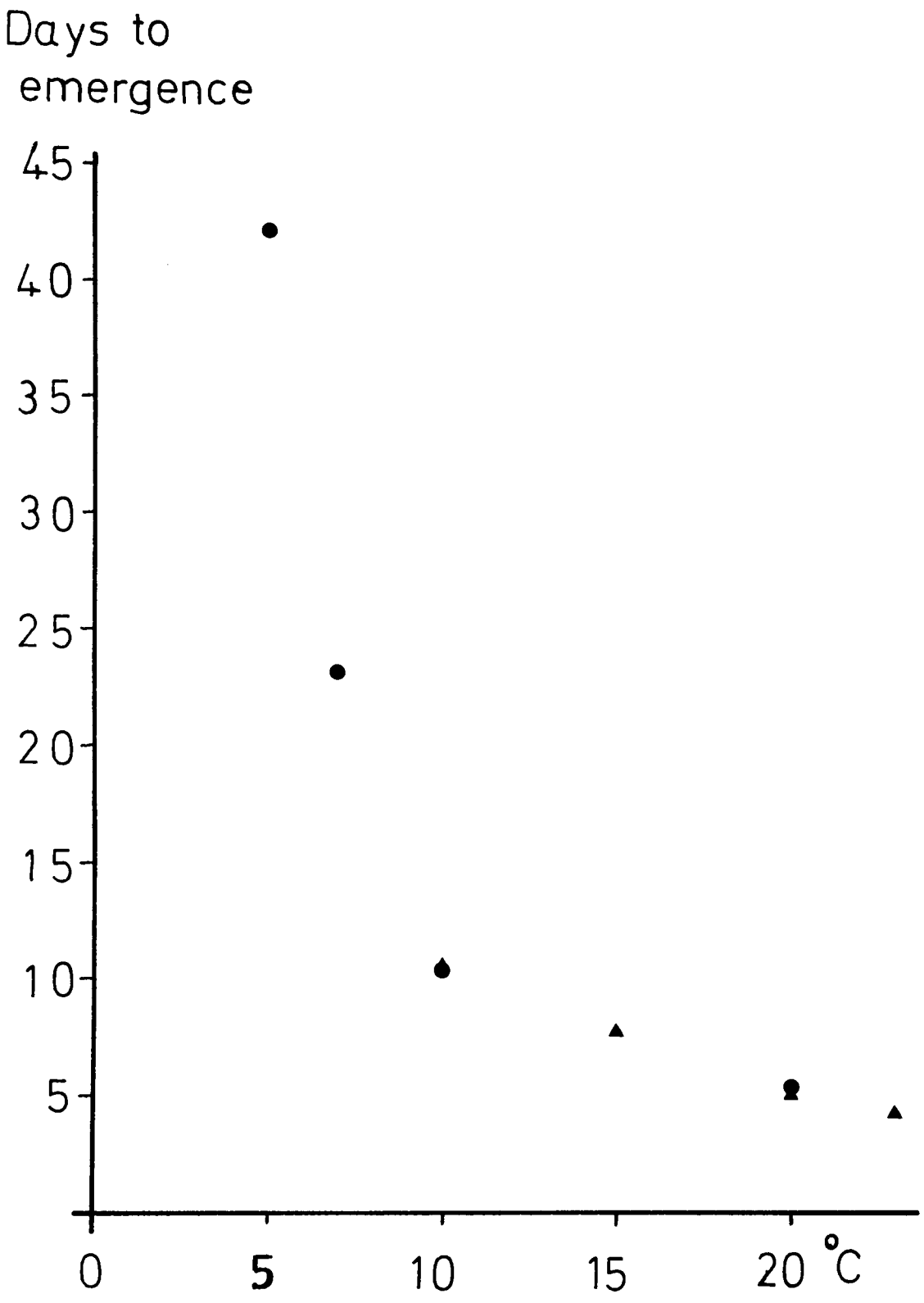

Days to
emergence
45
40
35
30
25
20
15
10
5
0
5
10
15
20 °C

Table 3

The effect of temperature on the duration of the pupal stage in the laboratory.

Temperature °C	Mean duration of pupal stage in days (± S.E.) Males	Females	Number of pupae
5	41.38 ± .48	43.00 ± .35	15
7	22.94 ± .27	23.67 ± .23	31
10	10.17 ± .35	10.56 ± .27	36
10 ▲	10.56 ± .34	10.74 ± .27	32
15 ▲	7.57 ± .19	7.72 ± .12	70
20	5.10 ± .17	5.22 ± .21	19
20 ▲	5.11 ± .20	5.21 ± .18	42
23 ▲	4.43 ± .17	4.38 ± .12	29

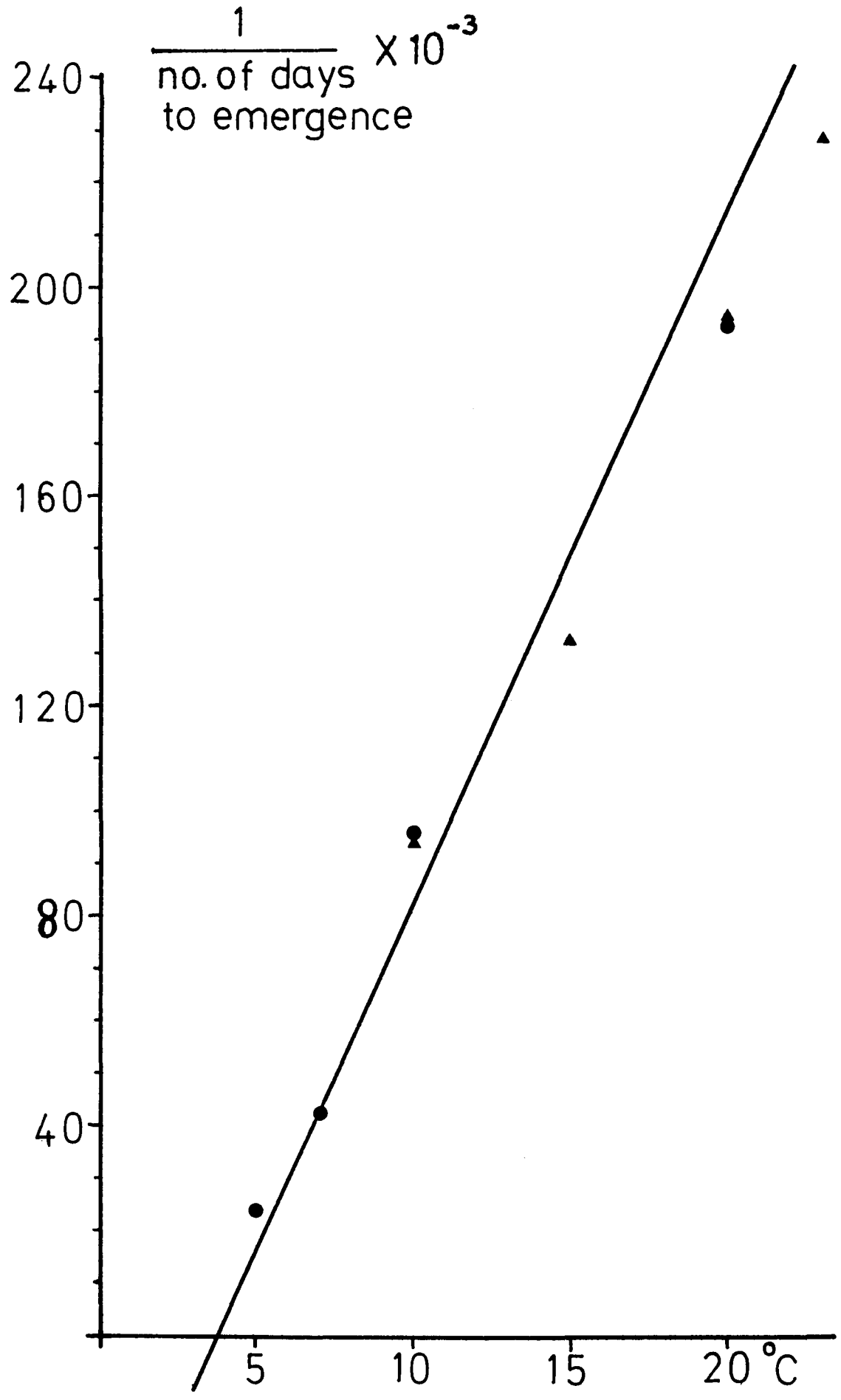
▲ = data obtained by Hadley

At temperatures below 10°C pupal duration is shown to be prolonged increasingly by decrease in temperature.

In Figure 2 where pupal duration is plotted as a reciprocal of the number of days taken to emergence, giving a measure of the rate of pupal development, a direct relationship is indicated which Hadley's high temperature results will also fit. This line crosses the temperature axis at 3.75°C indicating this as likely to be the threshold for pupal development. This low threshold for pupal development is particularly interesting as it was noted by Horobin and in the present study that the threshold for pupation from the 4th instar larva lies between 5 and 6°C. The results in Table 3 show that once pupation has occured development will continue and emergence can take place even at 5°C.

Figure 2

The relationship between rate of pupal development and temperature ^{o}C. The equation of the line is $y = 12.5x - 46.9$ and the correlation coefficient $r = + 0.99$. The slope of the line is significantly different from zero $t = 52.174$ $df = 6$ $P < 0.001$.
(Hadley's findings (1971) are shown with a triangular mark and for comparison only.)


1
no. of days
to emergence
X 10^-3
240
200
160
120
80
40
5
10
15
20 °C

The main significance of the extended pupal duration at low temperatures to the previous work on M.ater at Moor House is in Horobin's considerations of the factors affecting delay of adult emergence with altitude. He concluded that the delays observed between the emergence at 2,050 ft. and 2,700 ft., which varied between 6 and 12 days in the 1967-70 period, were due primarily to the delay in the arrival of the threshold temperature for pupation at the higher site. He discounts any differences taken in pupal duration as, extrapolating linearly from Hadley's results, he gives a relationship of one day delay for every 2.5°C fall in temperature, and his soil temperature studies only indicate a difference in the order of 1-2°C between the sites in May. As the mean soil temperatures he recorded in May fall in the range 6-9°C the present study indicates a delay in the order of 6 days for every 1°C. It seems likely therefore that the increase in pupal duration shown at field temperatures can contribute substantially to the observed different emergence dates between sites.

Over the temperature range 10°C to 23°C Hadley found no significant differences in pupal duration between males and females, though at 20°, 15°, and 10°C the females took longer. A study on the onset of pupation showed that males pupated about 1 day earlier than females and this was thought to explain the later recruitment of females into the adult population. This phenomenon has been observed by many workers on the Tipulidae (e.g. Maercks, 1939; Hemmingsen, 1952; Hemmingsen & Jensen, 1957; Freeman, 1964). In the present study however pupal duration was significantly different ($p < 0.01$) between males and females at the two temperatures nearest those occuring in the field, 5°C and 7°C. The percentage differences between male and female pupal duration for all the temperatures in the present study and for Hadley's data are given in Table 4.

Table 4

The differences in pupal duration between male and female M.ater under laboratory study at various temperatures. Hadley's results are included and marked with a ▲

Temperature °C	% Difference in male pupal duration $\left(\frac{♂}{♀} \times 100\right)$
5	- 4.21
7	- 3.08
10	- 3.73
10 ▲	- 1.60
15 ▲	- 1.94
20	- 2.30
20 ▲	- 1.98
23 ▲	+ 1.22

Only at 23°C was male pupal duration longer than female (but not significantly so) and the other figures indicate that female pupal duration is generally 2-3% longer than that recorded for males, but tends to be less at the higher temperature.

It, therefore, seems likely that this combined with the earlier pupation of males shown by Hadley effects the latter recruitment of females observed in M.ater populations.

4.3 PHOTOPERIOD EFFECTS

4.3.1 Introduction

Photoperiodic reaction is one of the most general ecological adaptions of a wide range of animals. Photoperiodic effects in insects have been extensively studied by Danilevskii (1965) and his lists of species known to show a photoperiodic effect include many Diptera, but do not include any members of the family Tipulidae. In most of the studies photoperiod is effective in the opening or breaking of diapause, though Houston (1970) related gonad development in several species of Carabid beetles to the length of photoperiod they were receiving.

Horobin (1971) states that he has not observed any photoperiodic effect on pupation in M.ater and that pupae were obtained equally well from larval cultures kept in continuous light, continuous dark, and a varying photoperiod. In the present study large numbers of instar IV larvae were available and it was considered worthwhile to check these results because recently such effects have been found in Tipula subnodicornis (J. Butterfield, pers. comm. 1972).

4.3.2 Methods and Results

Larvae were collected from a site adjacent to the 1900 ft. Dun Fell Site over the period November 1971 to April 1972. Sods were taken and bulk extracted in large Berlese funnels as was described in the section on pupation.

The larvae were cultured in peat, known to contain no other larvae, in glass petri dishes lined with filter paper. The cultures were watered and kept moist throughout the culture period. They were kept in constant temperature cabinets each lit by an 8 watt fluorescent tube controlled by a time switch. The cultures were placed so that the intensity of light reaching them was similar, though Lees (1955) found that in general photoperiodic reaction in arthropods is independent of light intensity above a low critical level.

Two photoperiods were used, one with 6 hours light, 18 hours dark and one with 18 hours light and 6 hours dark. These were intended to represent short and long day conditions. There were no twilight periods, the lighting being switched directly on or off.

The photoperiods were kept to a 24 hour rhythm, being illuminated for the same period each day. Where possible the cultures were examined daily and during the photophase, any M.ater that had emerged were noted and removed.

Interpolating back from the emergence dates the mean date for pupation can be estimated, taking a pupal duration of 10 days at 10°C (see page 11).

The results of the cultures are given in full in Table 5 and summarised in Table 6.

Table 5.

The emergence of M.ater adults from larval cultures kept at different temperatures and photoperiods.

Culture No.	Date Culture set up	Temp. °C	Photoperiod hours	Date of Transfer if transferred to another regime	Mean date of emergence ± S.E. in days	No. of emergences	Minimum days to pupation
1.	10/11/71	10°C	18	-	9/2/72± 2.2	7	81
2.	10/11/71	10°C	6	-	-	0	223
3.	20/12/71	10°C	18	-	12/2/72± 0.9	30	44
4.	20/12/71	10°C	6	-	-	0	226
5.	20/12/71	10°C	6)				
		10°C	18)	10/3/72	27/4/72± 1.7	6	128
6.	15/1/72	5°C	18	-	-	0	200
7.	15/1/72	5°C	18)				
		10°C	6)	10/2/72	13/4/72 ±1.8	6	88
8.	20/1/72	10°C	18	-	11/3/72± 0.9	23	40
9.	20/1/72	10°C	6	-	13/4/72± 1.5	9	73
10.	9/3/72	10°C	18	-	14/4/72± 0.5	10	26
11.	9/3/72	10°C	6	-	29/4/72± 1.5	9	41
12.	9/3/72	5°C	18	-	-	0	14
13.	24/4/72	10°C	18	-	22/5/72± 0.4	22	18
14.	24/4/72	10°C	6	-	22/5/72± 0.4	21	18

Table 6

The effects of temperature and photoperiod in inducing pupation of M.ater larvae in the laboratory

Date brought into culture	DAYS TO PUPATION		
	5°C	10°C	
	18 hr. photo-period	6 hr. photo-period	18 hr. photo-period
10/11/71	-	F	81
20/12/71	-	F	44
15/1/72	F	-	-
20/1/72	-	73	40
9/3/72	F	41	26
24/4/72	-	18	18

Note: F = failure to pupate

4.3.3 Discussion

Between November 1971 and April 1972 samples of larvae were taken from the field situation and cultured in the laboratory under different light and temperature regimes. The object of these studies was to investigate the effects of these two factors and their interaction in inducing pupation in the fourth instar larvae of M.ater.

Horobin (1971) studying the importance of temperature relative to pupation concluded that a threshold between 5^{o} - $6^{o}C$ existed and he related certain aspects of field behaviour to this. The existance of this threshold has been substantiated in the present study, with no culture kept continuously at $5^{o}C$ producing pupae. The larvae in these cultures survived and grew for up to 7 months, and eventually death appeared to be due to the larvae stopping feeding, the gut appeared empty. Removal of the larvae into fresh peat did not induce renewed feeding.

The results given in Tables 5 and 6 do however indicate that photoperiod also plays an important part in larval development prior to pupation and the following model for the development of larvae in spring is suggested.

Larvae in the field in November and December appear to be making progress towards pupation despite the low temperatures. Cultures 1 and 3 taken on the 10 November, 1971 and the 20 December, 1971 respectively, were both cultured at $10^{o}C$ (field temp. c.$2^{o}C$) and with an 18 hour photoperiod did not show a significant difference in their mean date of emergence, although culture 1 had been at $10^{o}C$ for 40 days more.

Clearly at this stage, 6 hours light a day inhibits pupation whilst 18 hours light induces eventual pupation. To complicate the situation exposure in the field to a low temperature ($2^{o}C$) and about 9 hours a day light require less high temperature and long day treatment to induce pupation. It may be that a state of diapause exists but

this has not been demonstrated in the larvae of any other tipulid species, and the mean larval weights calculated from the monthly site samplings taken for the population study show that between November and December, and between December and January, larval growth continues, mean weights increasing by approximately 15% per month.

During January the larvae from the field continue to be photosensitive, probably in response to increasing daylength, the maximum field exposure at this time would be between 8 and 9 hours light. Larval cultures taken into the laboratory before 20 January, 1972 and kept continuously at a 6 hour photoperiod, 10°C, failed to pupate and eventually after 7 months died indicating that it is essential to M.ater to receive a daylength somewhat in excess of 6 hours if development in spring is to be completed. Culture 5, however, taken from the field on 20 January 1972, and cultured at 10°C first at 6 hours light, until 10 March, 1972 when it was transferred to 18 hours light, took 38 days from the date of transfer to the date for pupation. When compared with 44 days taken by culture 3 put straight into an 18 hour regime on the 20 January, 1972, it is notable that an advance of 6 days towards pupation has occured in 80 days at 10°C, 6 hours light. Though the advance is very small for the time taken, it indicates that avery small but significant amount of development can occur at a 6 hour light regime. Culture 10 was taken from the field on 9 March, 1972, this compares with the date of transfer of Culture 5 to 18 hours light (10 March, 1972). The cultures took 38 (from date of transfer) and 26 days to pupation respectively, indicating the greater influence of the light regime in the field on speeding up the rate of development than the raised temperature in the laboratory.

All larvae taken after the 20 January, 1972, and kept at 10°C produced pupae whether in 6 or 18 hour photoperiods, it is thought that these must all have received the required day length to stimulate development whilst in the field station. The larvae kept at the 18 hour day length did however pupate sooner than those taken at the same time and kept in 6 hour daylight showing that

photoperiod is still influencing the rate of development in this stage. From January on the larvae in the field are thought to be accumulating their light requirement as it is available to them, this varying with climatic conditions and photoperiod. This continues through February and March when samplings still showed larvae to reach pupation sooner in the 18 hour photoperiod than the 6 hour though development was not directly related to the photoperiod length. By the 24 April, 1972, however, larvae taken from the field and kept in 6 and 18 hour photoperiods showed no difference in the time taken to pupation.

In table 7 development up to this period is shown in relation to the time that the larvae were brought from the field into the laboratory, in days prior to 24 April 1972; also in relation to the temperature sum in degree-days (the temperature sum is calculated by halving the sum of maximum and minimum daily temperatures recorded in the screen at Moor House between sampling dates it assumes the developmental threshold postulated by Horobin of $0^{o}C$), and in relation to the photoperiod conditions given to the larvae in the laboratory.

From the figures in table 7, development towards pupation in the field cannot be significantly correlated with temperature sum, but after 20 December 1971 the number of days taken in the laboratory to pupate is positively and significantly correlated, for both the 6 and 18 hour photoperiods, with the number of days before 24 April 1972 that the larvae were removed from the field, see Figure 3. Progress towards pupation during this period would therefore seem to be correlated with the number of days of photoperiod, during this stage. The slower rate of development in the laboratory on the shorter photoperiod would support the idea of development being related to photoperiod sum.

Table 7

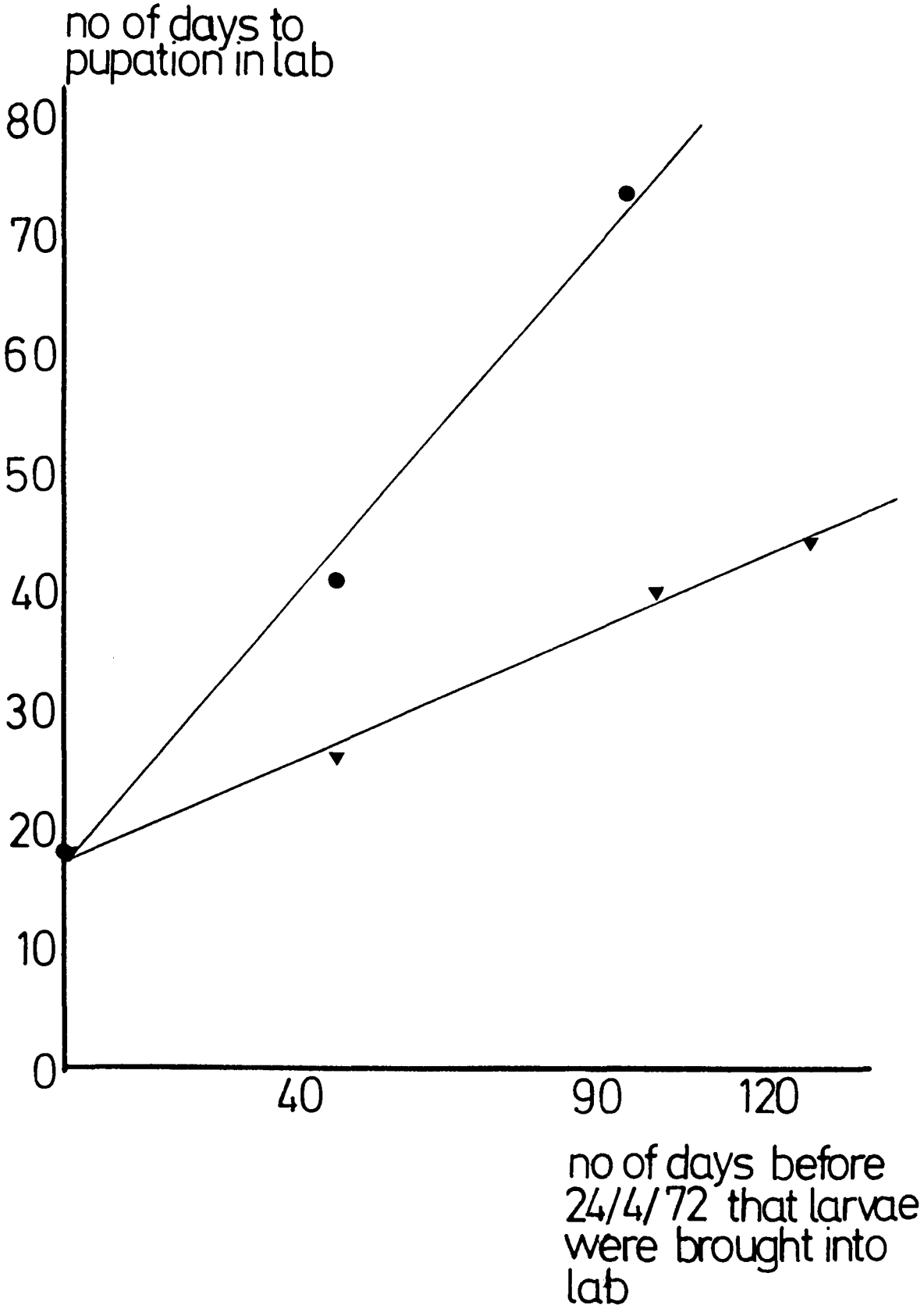
Rate of development in M.ater larvae relative to temperature and photoperiod experience.

Date brought into lab.	No. of days from 24/4/72	Temp. sum in field between consecutive dates (°days)	No. of days to pupation 10°C and 18 hours light	No. of days to pupation 10°C and 6 hours light
10/11/71	166		81	do not pupate
20/12/71	126	112	44	do not pupate
20/1/71	95	53	40	73
9/3/72	46	31	26	41
24/4/72	0	155	18	18

Figure 3.

The relationship between the date of removal of larvae from the field and the time taken to pupation in the laboratory in two photoperiods at 10°C (I) 18 hours light 6 hours dark
(II) 6 hours light 18 hours dark

The equation of line (I) is $y = 0.22x + 17.5$
$r = +0.992$, $p =< 0.001$
The equation of line (II) is $y = 0.58x + 16.8$
$r = +0.997$, $p =< 0.01$


no of days to pupation in lab
80
70
60
50
40
30
20
10
0
40
90
120
no of days before 24/4/72 that larvae were brought into lab

It appears that larvae in April (though the timing of this may vary from year to year) have completed the part of their development that is light dependant and at this stage development to pupation is dependant on temperature only. Horobin when describing his experiments in which he could observe no photoperiodic effect does not give the date for the field sampling from which he obtained his larvae, it may have been that they were in this stage.

This photosensitive stage of development prior to pupation may be ecologically significant as a safe guard mechanism preventing pupation in the case of warm periods in early spring. These might still be followed by severe weather conditions which the larvae can probably escape, but might be fatal to pupae. Also along with the temperature threshold for pupation it may contribute to the synchrony of the adult emergence, which is of prime importance to an insect with a short adult life as has M.ater.

Another question raised by the photoperiod reaction in M.ater fourth instar larvae is that of how they actually receive the light stimulus and what systems are involved in producing the effects. Here there is a need for investigation on the physiological level.

There is a need for further experimentation in the involvement of day length with larval development in M.ater if the exact timing and requirements of the developmental stages are to be discovered. Large numbers of larvae would need to be collected in November and cultured through to pupation in a wide range of photoperiods and with several temperatures regimes. Such an experiment was not possible within the time available for the present study.

4.4 STUDIES ON LARVAL GROWTH

4.4.1 Hadley (1966) produced a growth curve for M.ater larvae at Moor House by sampling larval populations monthly and calculating mean larval weights. Growth rate was rapid from hatching in June up to the onset of winter, when increases in weight were small though the larvae did still appear to be growing. In spring growth rate accelerated again until pupation occured in May.

Coulson (1962) working on T.subnodicornis, another very common crane fly at Moor House, produced a growth curve which was similar to that subsequently produced by Hadley for M.ater with the exception that T.subnodicornis does not step up its growth rate again with the arrival of spring.

It was decided to investigate this spring growth in M.ater as in Hadley's results it was noticable that at the same time as growth was taking place the variance in the individual larval weights was increasing. It was thought that perhaps one section of the population was responsible for the increase in mean weight whilst some of the population were already fully developed.

4.4.2 Practical details and results

The technique used to investigate this spring growth involved the setting up of a large number of individual larval cultures. The larvae were taken from the field situation on 24 January, 1972 and were kept in culture at $5^{o}C$ until the 22 March, 1972, when they were transferred to $10^{o}C$ to induce pupation. On pupation the sex of adult to be produced was determined. Weighings were made on a sensitive electro-microbalance (accurate to .001 mg) after excess water on the larval cuticle had been removed by rolling them on filter paper.

The larvae came from a Juncus squarrosus site adjacent to the 1900 ft. Dun Fell site, and the culture media consisted merely of peat taken from the same site and dried to ensure there were no larvae surviving in it. The exact food of M.ater has not been determined, in this or the previous studies, but the larvae ingest the organic debris of the peat and it may be that they feed directly on the organic material or on the microflora present on it. Which ever is the case the larvae survived and grew well in the cultures, each of which consisted of 5 x 1 cm glass tube lined with filter paper and three-quarters filled with the dried peat, the whole culture was thoroughly moistened and kept moist throughout the culture period. The tubes were stoppered with a pierced nylon bung.

The results are given in Table 8 and the growth rates of male and female larvae compared.

Table 8

Growth of ♂ and ♀ *M.ater* instar IV larvae whilst in laboratory culture at 5°C.

Sex	Number that survived to pupation	Mean live wt. 24 Jan. 1972 mgs ± S.E.	Mean live wt. 22 March 1972 mgs ± S.E.	Mean wt. gain between 24 Jan. and 22 March mgs ± S.E.	% wt. gain over period 24 Jan. to 22 March ± S.E.
♂	45	1.15 ± .03	1.41 ± .03	0.26 ± .02	23.8% ± 2.0
♀	22	1.56 ± .05	1.95 ± .05	0.39 ± .04	26.8% ± 2.9

4.4.3 Discussion

Out of 100 larvae originally placed in culture 67 reached pupation and could be sexed, 7 failed to pupate and the remainder either died or could not be found in the culture. It is thought that a large number of the deaths may have been due to damage inflicted during handling, but generally the culture method can be considered successful. From the weight gains recorded the larvae were obviously feeding well and the weights at the March weighing are comparable with field weights at that time.

The mean larval weights of males and females are significantly different at both the January and March weighings, this tendancy for the larger larvae to be female was first noted by Horobin (1971) who also related larval weight to female fecundity.

Both the males and the females show significant weight gains over the culture period and these gains were not only due to growth of the smaller larvae of each type, but it appears that all the larvae are still feeding and developing over the spring period. Only one of the 67 larvae that pupated was recorded as showing a weight loss.

The mean weight gains of the males and females are however significantly different with the females gaining on average 0.39± .04 mg compared with a male gain of only 0.26± .02 mg. When converted into a percentage weight gain the difference is not significant. These larger total weight increases of the females would seem to be responsible for the increase in the variance of larval weights which has been recorded during the spring period by Hadley.

As increased larval weight was shown by Horobin to be related to increased fecundity, this continued spring growth of the already large larvae may be of importance in channeling the growth available to the population into egg production. Growth of the smaller larvae, i.e. the males, is unlikely to be so useful to the population where males probably carry an excess of gametes anyway, though increased reserves in the males might prolong their life span.

4.5 LONGEVITY OF ADULTS

4.5.1 In the laboratory

Casual observation of the adults emerging from the pupal cultures indicated that they were surviving for considerable periods. This did not seem to be in accord with the results obtained by Hadley (1969). He had kept newly emerged adults in culture at temperatures between 9 and 12°C and humidities in the range 55-77% and recorded daily elimination rates between 66 and 78%. It was, therefore, decided to set up a series of experiments to determine how long M.ater adults can in fact live under favourable conditions.

Practical Details and Results

The adult material used was not from any single source, but adults emerging from the photoperiod, pupation and individual weight gain experiments were all kept and cultured in the following manner. The adult was removed from the pupal culture [redacted] on the day it emerged, and placed in a small plastic petri dish which contained two circles of saturated filter paper in the base. It was kept either on its own or with one individual of the opposite sex, depending on whether it was to be mated or not. Mated pairs were kept together until one of the individuals died. All the cultures were kept at 10°C and in an 18 hour photoperiod in a constant temperature cabinet, they were checked daily to see which individuals were still surviving and to wet the filter paper if necessary.

It is appreciated that the histories in terms of temperature and photoperiod, of the larvae from which the adults were derived were often different, but the adults from each source were as equally as possible divided amongst the 4 groups for culture i.e. males, mated males, females and mated females and the results (Table 9) achieved are so different from those of Hadley as to make them worthy of consideration.

Table 9

Longevity in days of *M.ater* adults in the laboratory (10° C)

	Males ♂	Mated Males ♂	Females ♀	Mated Females ♀
Longevity in days ± S.E.	7.71 (±0.40)	8.00 (±0.83)	8.56 (±0.63)	8.53 (±0.59)
No. of individuals cultured	17	15	16	15

Discussion

The results indicate that M.ater adults have a potential longevity much in excess of that indicated by Hadley's results, and individuals were recorded that lived for up to 15 days. The reason for the discrepency in the results is thought to be that in Hadley's experiments though the adults were kept at relatively high humidities they did not have access to free water. In the present study M.ater adults were regularly noticed to be drinking from the filter paper layer in the bottom of the petri dish, and any adult kept without water for a short period would avidly drink as soon as placed on damp filter paper. Adults refused access to water died, usually within 2 days. In view of the nature of the climate at Moor House it seems unlikely that this necessity to obtain water is of any importance in effecting the short life expectancy of M.ater adults in the field, but it is clear from these studies that some environmental factor is responsible for the short field life and that it is not due to the inability of the species to survive more than 1 or 2 days.

Mating did not reduce the life expectancy of either males or females, and in fact there are no differences of significance between any of the 4 groups.

4.5.2 In the Field

Introduction

In addition to the laboratory experiments already described it was decided to run an experiment during the adult field season to acertain how long the adults were surviving under field conditions. This aspect of the biology of M.ater had been previously investigated by Hadley (1969) on 3 of the Moor House sites during the 1965 adult season. He recorded an average daily elimination rate of 80% for ♂'s and 89% for ♀'s when the data from the 3 sites are combined. The lowest average daily elimination rate of the 3 sites for males was 74% and for females 85%.

Practical Details and Results

The experiment was carried out on the 1700 ft. Dun Fell site and samples of both the numbers of adults emerging and of the standing crop were taken daily over the period 2-15 June, 1972.

The results from 4 x 1/4 sq. metre emergence traps, present on the site for the estimation of annual population, are used to give the numbers emerging daily. Standing crop was estimated by taking 10 x 1/20 sq. metre random samples of the adult population daily. Extraction of adults was in both cases by the vacuum technique described fully in section 5.2.4 In the standing crop samples only adults that were alive were counted.

The results from the traps were converted to numbers of adults per square metre and are given in Table 10 :-

The numbers of adults per sq. metre taken from emergence traps and standing crop,samples on the 1700' Dun Fell site over the period June 2-15 1972.

	Emergence traps		Standing Crop samples	
No. of M.ater adults per m^2 over period 2-15 June, 1972	405		698	
	♂	♀	♂	♀
	266	139	517	181
Mean numbers per day ± S.E.	29 ± 5.2		50 ± 4.8	
	♂	♀	♂	♀
	19±4.3	10±1.5	37±4.1	13±1.7
Average daily elimination rates	♂ 0.51	♀ 0.77	Total = 0.58	

Discussion

The field mean daily elimination rate recorded for M.ater adults in this study is 58% showing M.ater to have a very short lived adult stage, the function of which appears to be mainly to effect mating and to a limited extent dispersion. The results are however rather different from those recorded by Hadley in 1965 when the mean daily elimination rate was about 80%. The reason for the difference is not clear, but it is thought that climatic factors at the time of the emergence may be partially responsible. The emergence period in 1965 was both warmer and drier than in 1972, which was exceptionally cold and wet. It is thought that the 1972 conditions may have reduced activity and mating and the adults limited energy reserves may have been conserved resulting in a prolonged adult stage. Another factor may have been the relatively low larval density in 1972 which may have resulted in the production of larger adults with more energy reserves than the 1965 adults.

Also of interest is that the increased longevity of the population was almost entirely due to male survival. The mean daily number of males emerging per m^2 was only 19, compared with a standing crop population per day of 37, the difference is significant ($P < 0.01$). Whereas the female numbers were 10 a day emerging and 13 per m^2 in the standing crop samples, the difference is not significant. This prolonged male survival may be very useful in ensuring that all females available get fertilised, and it has been noticed by casual observation that males are inclined to mate on more than one occasion if the opportunity is presented. It seems likely that the rigours of oviposition combined with the harsh climate are the reasons for the short life expectancy of females under the field situation.

5. POPULATION STUDIES

5.1 The life cycle of M.ater in the field has been described by Hadley (1971). The eggs are laid in late May and early June and these hatch into first instar larvae in approximately 4 weeks, the second and third instar larvae also take about 4 weeks each to develop and fourth instar larvae appear in October. The fourth instar larva is the over wintering stage and continues until early May when there is a 3 week pupal phase prior to adult emergence in late May and early June.

Throughout the present study the densities of the different developmental stages of M.ater have been recorded on 8 sites. Three of these sites (the Moor House sites) were previously studied by both Hadley (1969) and Horobin (1971) and data on population levels are now available for 8 consecutive years. The other 5 sites (the Dun Fell sites) were started by Horobin and data are now available for 5 consecutive years. This section is a review of the previous authors considerations on the population biology of M.ater in the light of two more years data.

5.2. Practical Details

Technique for density estimation.

5.2.1 The Egg stage

The eggs of M.ater are soft and whitish, with a mean length ± S.E. off 221±9μ and mean maximum breadth of 134± 2μ (Hadley 1966). Horobin (1971) made several attempts to estimate egg numbers in the soil after adult emergence using both sieving and flotation techniques but met with little success. He attributed this to the soft nature of the egg and thought they were breaking up under the extraction technique. He therefore estimated egg density indirectly, using a knowledge of the density of adult females and their fecundity. The same technique has been used in this study. Fecundity is estimated by dissecting individual newly emerged females under a binocular microscope and counting the number of eggs they contain. The results are based on at least 15 females for each site. Adult female density is obtained from the emergence trap data obtained as in 5.2.3.

5.2.2
The larval stages

The larvae of M.ater are yellowish brown in colour and about 8 mm long and 0. 5 mm in diameter at their maximum in the 4th instar. The body is noticably constricted before the spiracular disc, the pigmentation of which is characteristic of the genus Molophilus (see Horobin 1971).

The pigmentation of the disc does not change through the instars and as Hadley (1966), Horobin (1971) and the present author have found no other representative of the genus Molophilus on the Moor House reserve identification of larvae to a species level was not considered necessary. Coulson (1956) found one adult female specimen of the genus which was probably M.griseus (Meigen).

The determination of instars was done on the basis of the maximum diameter of the spiracular disc as described by Hadley (1971). The larvae were killed by a quick immersion in hot water and then held for examination and measurement by placing them upright in a dish of very small glass beads.

Several other genera of small tipulid larvae were found on both the Moor House and Dun Fell sites. The commonest and most likely to be confused with Molophilus have been drawn and described by Horobin (1971). The key of Brindle (1967) is also useful for the separation of the genera of the British Limoniinae.

It was attempted to sample larval populations at monthly intervals throughout the study period, but unfortunately some gaps have occurred due to periods of inclement weather and difficulties in financing the work. Nevertheless, the records are complete from June 1970 which represents the last recorded work (Horobin 1971).

Soil cores were taken randomly from each site. The surface area of the core used was 1/1000sq. metre (shown by Horobin (1971) to be the most efficient in the subsequent extraction process). Cores were taken to a depth of 6 cm., M.ater seldom occurring below this depth. Initially 26 cores from each site

gave reasonable estimates of larval density but with the decrease in larval numbers in the 1971-72 season it was necessary to increase this to 50 cores.

The cores were returned to the laboratory in plastic trays and stored at a temperature close to that prevailing in the field. The previous experience of Hadley (1966) and Horobin (1971) has shown a dynamic extraction process using the wet funnel method developed by O'Connor (1955, 1962) to be the best suited to the extraction of M.ater larvae. The use of this technique was continued.

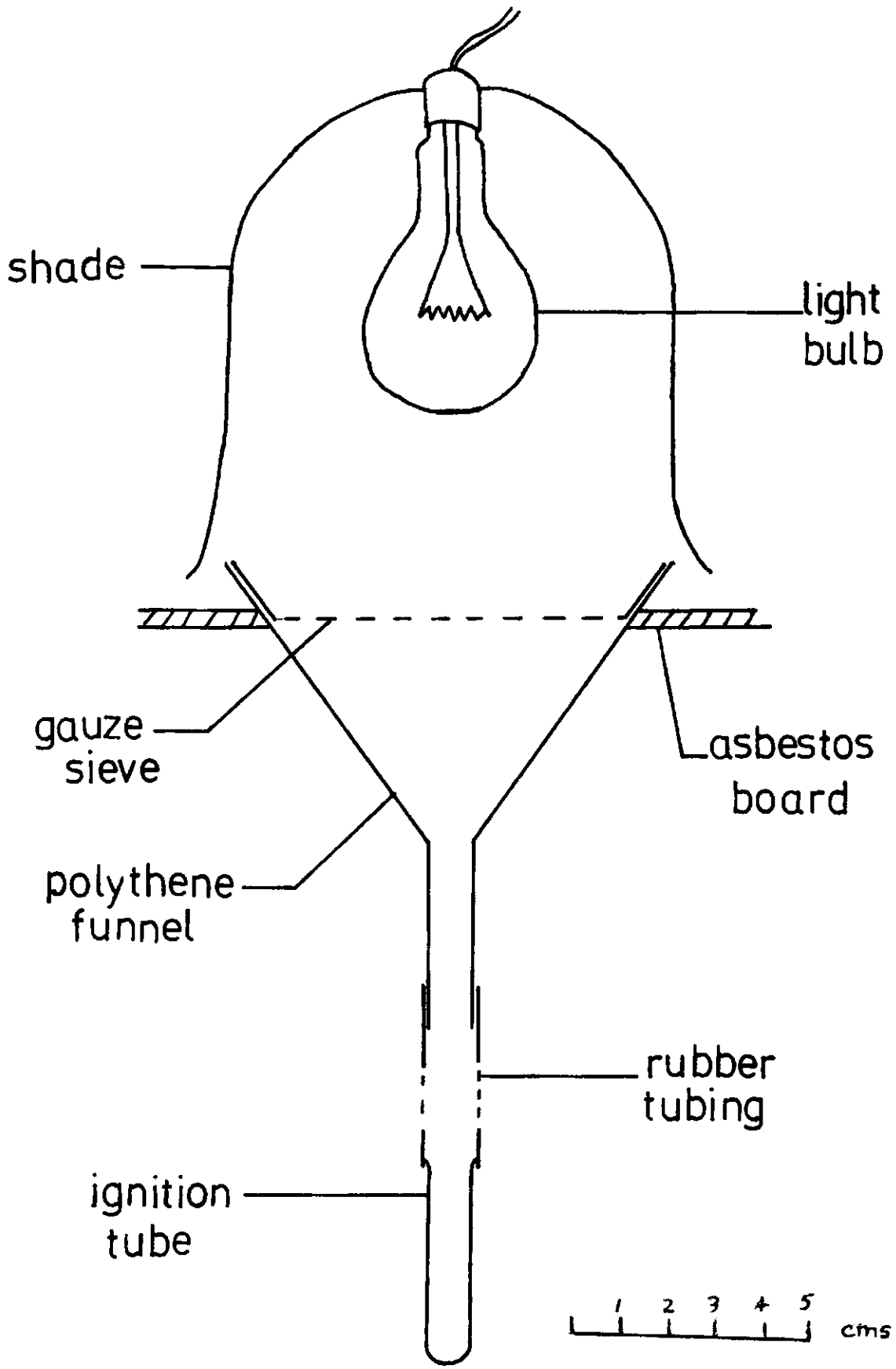
In this method heat is applied from a shaded light bulb to the soil, which is spread on a seive and submerged in a funnel filled with water, see Fig. 4. The larvae move away from the heat and pass down through the soil and seive and fall through the water to be collected in an ignition tube fitted to the funnel base by rubber tubing. Lateral temperature gradients are avoided by obtaining a close fit between the lamp shade and the funnel top, and by operating the apparatus in a draught free room of relatively constant temperature.

The heat regime is controlled by changing the voltage to the light bulbs, using a Variac transformer. Horobin (1971) experimented with several heat regimes but concluded that a 3 hour regime involving a gradual increase in voltage from 100 to 250 with 30 minutes at 250 volts was the most efficient. A steady voltage increase was effected by using a geared time clock to advance the variac. He estimated efficiency at 80% and all the larval densities given in this study have been estimated by this technique and corrected to give 100% values.

Several authors have commented on the importance of using only a thin layer of substrate in each funnel (e.g. Dinaburg 1942; Peachey 1962) so the 6 cm. cores taken in the field were first divided into two 3 cm lengths and each half extracted in seperate funnels. The 3 cm pieces were further broken down

Fig. 4

Sectional Drawing of a Single Unit of the wet Funnel Extraction Apparatus.


shade
light bulb
gauze sieve
asbestos board
polythene funnel
rubber tubing
ignition tube
1 2 3 4 5
cms

by gently separating them into 3 approximately 1 cm thick pieces before placing them in the sieves.

Twenty-six wet funnels were available mounted as a battery in asbestos board and wired in parallel, this allowed 13 cores to be extracted at a time.

On occasions when a severe drop in larval numbers was recorded from one month to the next the result was checked using a petrol flotation method originally devised by Salt & Hollick (1944), and adapted by Horobin (1971), for use with M.ater. This method has an estimated 92% efficiency but is too unpleasant in use and time consuming to be used as the main method for larval population estimates.

5.2.3 The pupal stage

No direct measurements of pupal numbers in the field was possible in this study, but mortality in this stage can be estimated by comparing the numbers of fourth instar larvae recorded in April with the number of adults taken in the emergence traps in June. The majority of mortality between these two times is likely to be due to pupal and emergence mortality and is usually small.

5.2.4. The adult stage

Hadley (1966) has shown M.ater to be univoltine at Moor House, with pupation taking place in May and the adults emerging in late May or early June in a highly synchronised manner, the middle 67% of the emergence occurring in 5 to 7 days. In both sexes the wings are abbreviated, and neither is capable of flight, consequently it is possible to determine accurately the number of adults per unit area of habitat. This was done using a vacuum cleaner unit as a suction apparatus to collect adults from emergence traps.

Two types of emergence trap were used. Hadley and Horobin both used open cylinders of galvanized steel, enclosing 0.05 m^2 of habitat. These traps were used in the present study on all the sites for the 1971 emergence period and on the Moor House sites in the 1972 season. The traps were fitted flush to the ground surface and secured with stakes, they are 35 cm high, thus preventing entry of adults from the surrounding vegetation and a band of "Stictite" fruit tree grease smeared around the top of the cylinder prevented any adults from walking in or out. Hadley concluded that the alteration in microclimate that these traps produced was negligible as they were placed in position only a short time before the expected beginning of emergence.

In 1972 on the Dun Fell sites in view of the low larval densities it was thought necessary to use a larger trap size. This ensured that there were enough specimens for an accurate determination of the sex ratio and for dissection to count egg numbers. A trap was designed using 4 pieces of galvanized steel 50 cm x 20 cm, these were inserted into the ground to form a box enclosing 0.25 m^2 of habitat. The pieces were inserted into the ground so that about 7 cm was below the surface and 13 cm above. The box was tied round the outside with strong cord and staked on opposite sides to give it rigidity and

to prevent the possibility of removal by sheep. The inside corners were sealed with 5 cm wide masking tape and a band of 'Stictite' put round the top edge of the trap. In view of the height of this trap it was necessary to trim vegetation inside and out to prevent access and escape of the adults. The numbers of traps used on each site was varied according to the population and the demands of the study. All traps were positioned randomly.

The suction apparatus used consisted of a 'Hoover Dustette' vacuum cleaner operated at 240 volts A.C. by a Honda E IV 300 portable generator. The insects were trapped in a piece of muslin spread over the nozzle of the vacuum and secured there with an elastic band. Obviously considerable amounts of plant debris are also picked up, but the material in the muslin was roughly sorted on the site, and if Molophilus were present the debris was stored in labelled bags to be sorted on returning to the laboratory. Each trap was vacuumed on each occasion until no more Molophilus were found in the plant debris.

Hadley (1966) showed that nearly the whole daily emergence occurred between dawn and 12.00 G.M.T., sampling was therefore, done in the early afternoon and except in conditions of extremely bad weather was done daily.

In addition to the suction sampling of the study sites, a series of 10 pitfall traps were maintained at each site. This gave an additional measure of the emergence of M.ater and also gives an indication of adult activity. Each trap consisted of a jam jar sunk into the ground so that its rim is flush with the ground surface. A weak detergent solution was placed in each jar to wet the insects and prevent them escaping.

5.3. Results and Discussion

The details of the site populations over the study period have been laid out in the form of life tables in Appendices II and III. The usual criteria of density in numbers living per square metre and the percentage mortality are given. The values for mortality have been calculated by subtracting successive density estimates. Sex ratios have also been considered as a mortality factor and reduction in fecundity has been expressed in the life table by calculating the number of females of maximum mean fecundity (e.g. for the Peaty Podsol site between 1965 and 1972 it was 93), that would be required to produce the same number of eggs into the next generation. This practice was also adopted by Klomp (1966).

Thus: Density of ♀ (93) = $\frac{\text{No. of eggs laid}}{93}$

It is recognised that in the life tables any one developmental stage does not have a monopoly of any given month, but the stage indicated represents the majority present at that time. The egg stage has been taken as the basis of each generation. The most notable feature of the 1970-71 and the 1971-72 populations is that over these two seasons there has been a marked decline in the numbers of M.ater on all sites, with the exception of the Blanket Bog. In Table 11 the adult populations of each site in 1971 and 1972 are compared with the mean adult population of the previous years in which the site has been studied. These changes in populations from one year to the next reveal a situation in the population biology of the species which is different from that envisaged by Hadley and further supported by Horobin's results where M.ater populations appeared relatively constant from year to year, though it was noted that no exceptionally harsh climatic conditions had prevailed during their study periods.

Horobin (1971) using his and Hadley's population figures was able to draw up complete age specific life tables for the

Table **11**

The adult populations on the Dun Fell and Moor House sites in 1971 and 1972

Site	Mean adult population of years previously studied. Nos. per sq.m.	Nos. of years previously studied.	Adult population 1971 Nos. per sq.m.	Adult population 1972 Nos. per sq.m.	Population change 1971 - 1972 No.	%
1400 ft.	679	2	1040	183	-857	-82
1700 ft.	1073	3	590	443	-147	-25
1900 ft.	2697	3	300	210	- 90	-30
2050 ft.	980	3	95	51	- 44	-46
2700 ft.	992	3	660	32	-628	-95
Peaty Podsol	2066	6	1210	375	-835	-69
Peaty Gley	1181	6	890	440	-450	-51
Blanket Bog	306	4	198	363	+165	+83

various sites. Using the key factor analysis method of Varley & Gradwell (1960) he compared the age interval mortality rates (k) with the generation mortality (K) for both the Peaty Podsol and Peaty Gley sites for which he had six years data available. The analyses concluded that at both sites egg and first instar mortality is the key factor, i.e. the one that accounts for the main fluctuations in population size. When combined with the second instar mortality this factor accounted for about 90% of the variation in generation mortality from year to year. His studies on the Dun Fell sites also indicated the importance of mortality in the egg and early larval stages and he postulated infertility and desiccation as the key factors whilst he thought predation another contributory factor which he suspected to be operating in a density dependent manner. The other age interval mortalities when related to generation mortality were shown to have little importance in the population dynamics of M.ater. However, consideration of individual sites and years did reveal one or two divergences from the general trend and Horobin noted that pupation and emergence mortality was particularly high in 1969 on the Podsol site and this one event brought it into consideration as a secondary key factor. Also in 1969 the Gley site suffered an unusually high overwinter mortality.

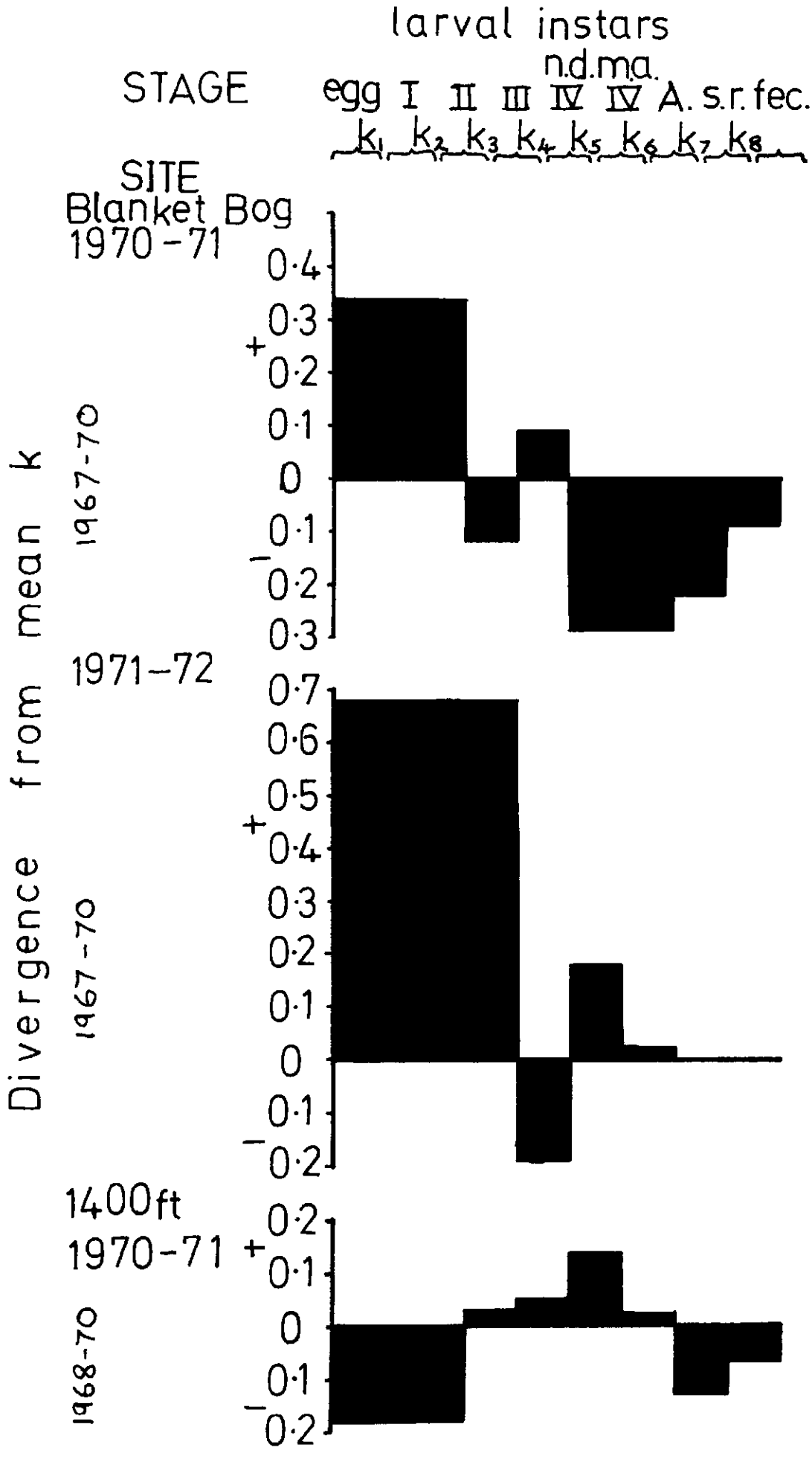
In the present study where all the sites have suffered a decrease in population, this has not been attributable to any single cause, and indeed the stage and time of the drop is not the same for each site. From the life tables in the appendix II it has been possible to calculate age interval mortality rates (k) for all the sites during the 1970-71 and 1971-72 seasons. In Figure 5 these mortality rates are compared with the mean mortality rate for the same stages in the years prior to 1970 when that site was under study. The results are expressed as divergence from the mean k of previous years. Departure from zero above the line indicates reduced mortality and below the line increased mortality. From the histograms it is possible to observe where the abnormal mortalities, responsible for population decline at any site, have occurred.

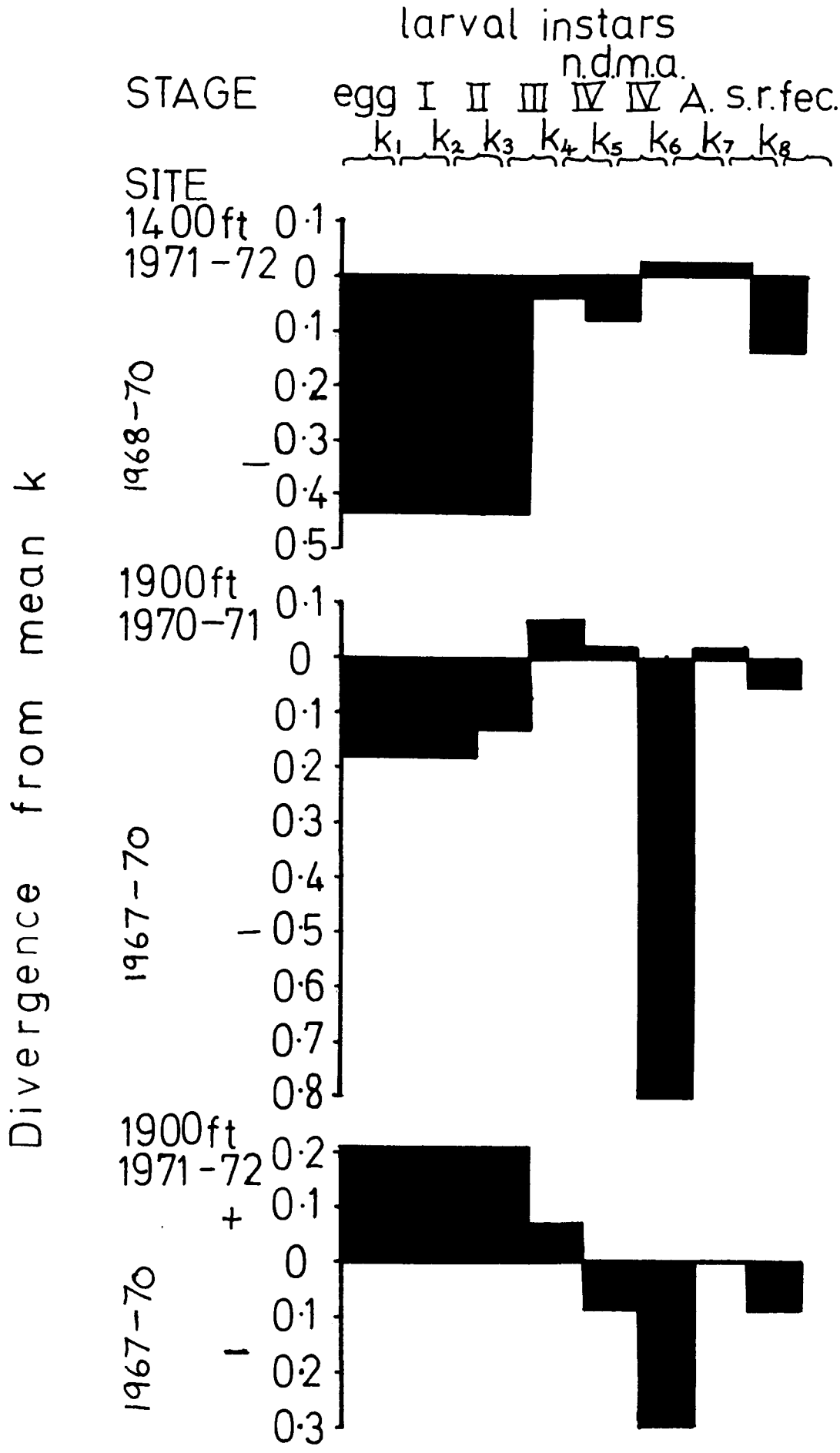
Fig. 5

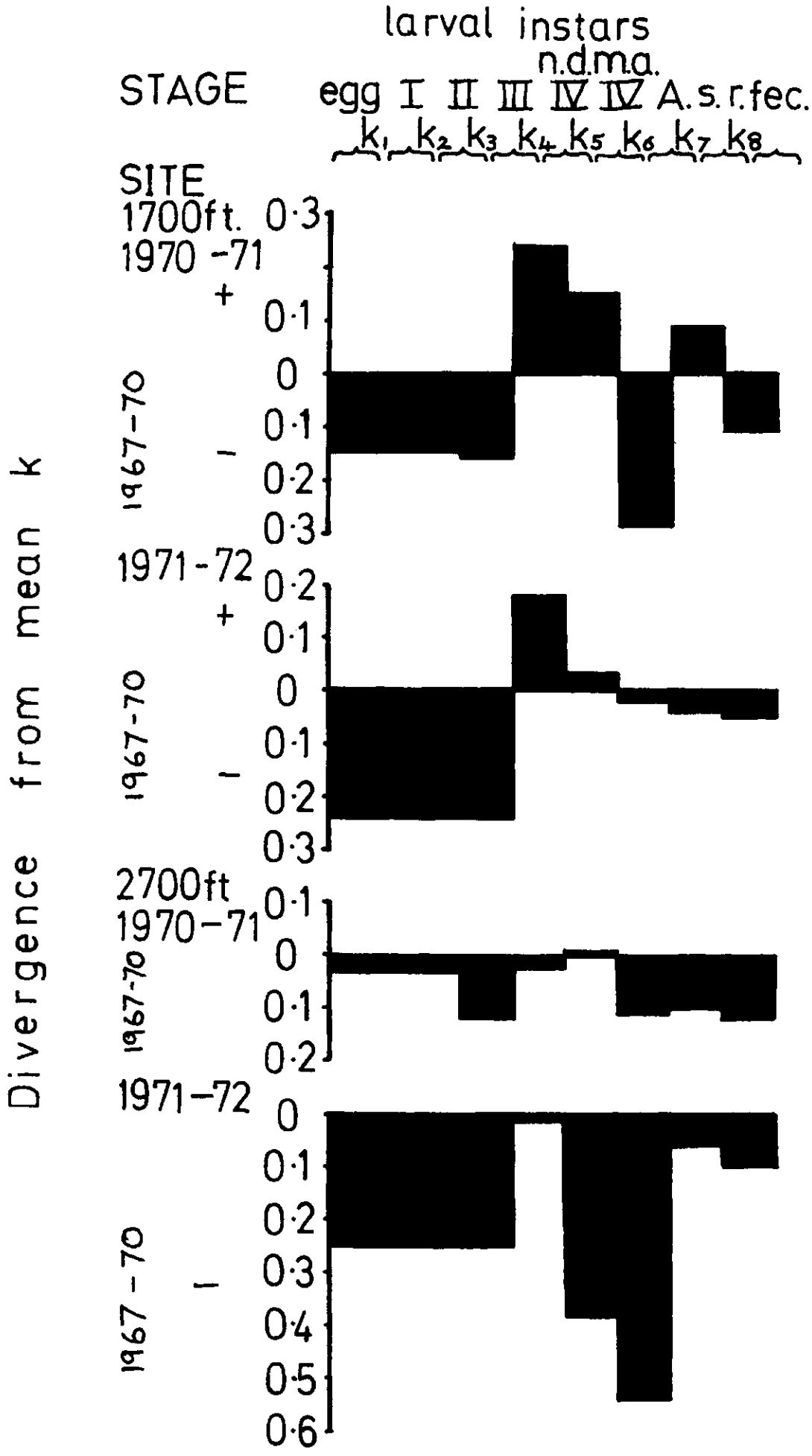
A comparison of age interval mortality rates for M.ater at the Moor House and Dun Fell sites in the 1970-71 and 1971-72 seasons, with the mean age interval mortality rates from previous studies.

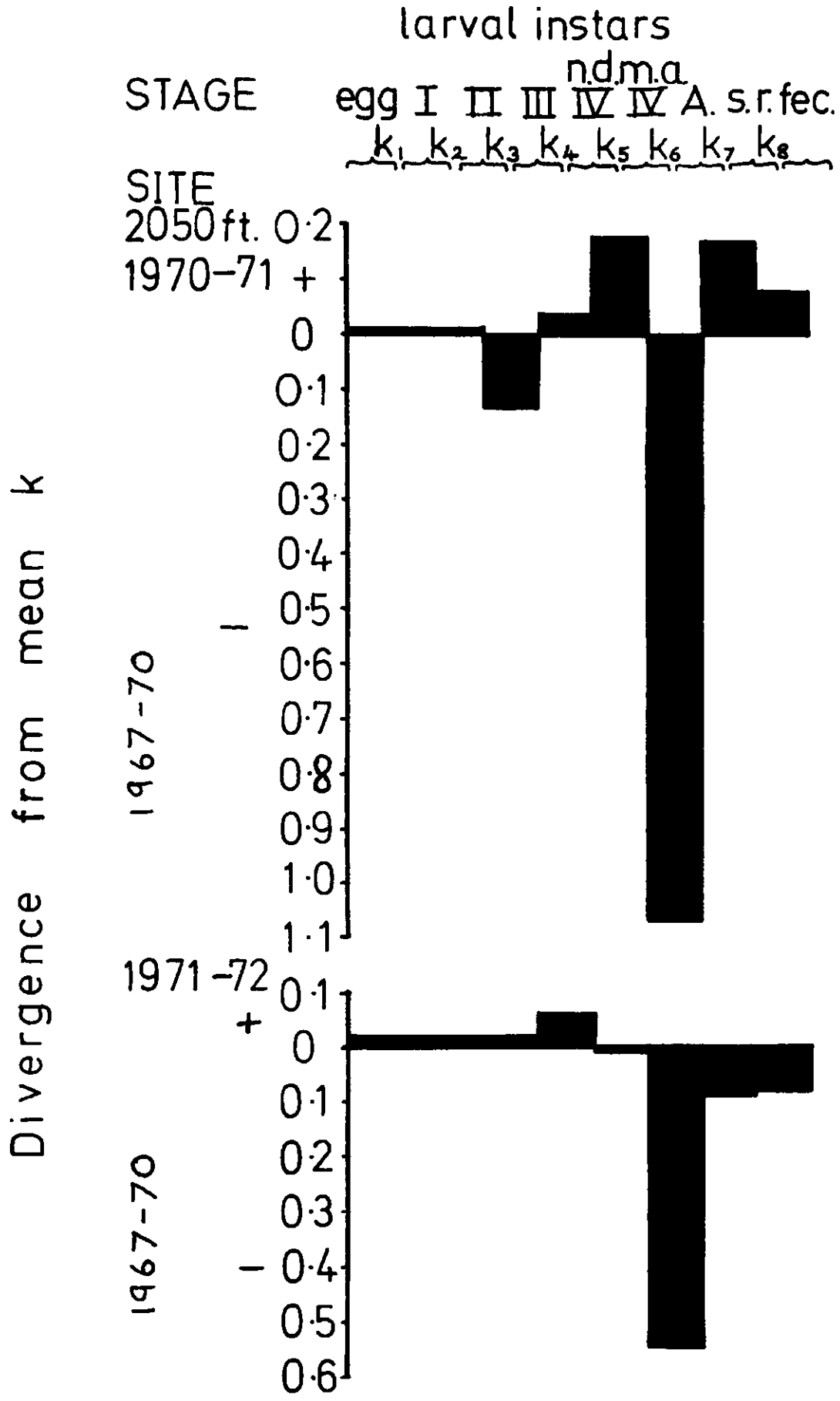
k = age interval mortality rate
n.d. = November/December
m.a. = March/April
A. = adult
s.r. = sex ratio
fec. = fecundity


larval instars
n.d.m.a.
STAGE
egg I II III IV V A. s.r. fec.
k1 k2 k3 k4 k5 k6 k7 k8
SITE
Peaty Podsol
1970-71
1964-70
0·1
+
0
0·1
−
0·2
1971-72
1964-70
0·1
+
0
− 0·1
0·2
Peaty Gley
1970-71
1964-70
0·1
+
0
0·1
0·2
−
0·3
0·4
1971-72
1964-70
0·1
+
0
−
0·1
Divergence from mean k


larval instars
n.d.ma.
STAGE
egg I II III IV IV A. s.r. fec.
k1 k2 k3 k4 k5 k6 k7 k8
SITE
Blanket Bog
1970-71
1967-70
0·4
0·3
0·2
0·1
0
0·1
0·2
0·3
1971-72
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
0·1
0·2
1400ft
1970-71
1968-70
0·2
0·1
0
0·1
0·2
+
−
Divergence from mean k


larval instars
n.d.m.a.
STAGE egg I II III IV IV A. s.r.fec.
k1 k2 k3 k4 k5 k6 k7 k8
SITE
1400ft 1971-72
1968-70
1900ft 1970-71
1967-70
1900ft 1971-72
1967-70
Divergence from mean k
0·1
0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
+
−


larval instars
n.d.m.a.
STAGE
egg I II III IV IV A.s. r.fec.
k1 k2 k3 k4 k5 k6 k7 k8
SITE
1700ft.
1970 -71
1967-70
1971-72
1967-70
2700ft
1970-71
1967-70
1971-72
1967-70
Divergence from mean k
+
-
0·3
0·2
0·1
0
0·1
0·2
0·3
0·4
0·5
0·6


larval instars
n.d.m.a
STAGE egg I II III IV V A. s.r. fec.
k1 k2 k3 k4 k5 k6 k7 k8
SITE
2050 ft.
1970–71
1967–70
1971–72
1967–70
Divergence from mean k
0·2
+
0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0
1·1
0·1
+
0
0·1
0·2
0·3
0·4
0·5
0·6

Though no single factor or event was responsible for the decline in M.ater populations over the study period, some general conclusions can be drawn on the population dynamics of the species that have not been brought out in the previous studies, when populations remained relatively constant.

One of the most striking features is the very high mortalities that have occurred between the sampling of the fourth instar larvae in April and May, and the time of the adult emergence in June. This has been the major factor in the decline of several of the sites. No abundance of predators likely to cause such mortalities was noted in the field, and no evidence of parasitism or disease was seen in any of the large number of pupae examined in the laboratory. The most likely cuase of these mortalities is thought to be climatic, pupation takes place very close to the ground surface, and consequently the pupae are exposed to the weather conditions at that level. The pupa would seem particularly vunerable at two different stages of its development. Firstly, just at the point of pupation when the pupa is very delicate, it takes about 2 days for the cuticle to harden,at field temperatures, and it may be that there is a danger of dessication under very dry conditions. Secondly, at the point of emergence it is thought that very wet conditions may prevent successful emergence. This theory is backed up by laboratory observations, where pupae kept on saturated filter paper would develop normally up until the time when emergence was due, but failed to emerge though they would survive for a day or two past their emergence time. It is thought that the second of these possibilities may have been responsible for the very high pupal mortalities recorded in 1971 and 1972, as in both these years the emergence period was exceptionally wet.

Obviously the suggestions made can only be tentative and to form any definite conclusions there is a need for further experimentation. A study of pupal emergence and development in relation to controlled relative humidities

should reveal whether this is an important factor in pupal mortality. It is, however, clear that pupal mortality can play a very important part in generation mortality in some seasons.

Another factor that has undoubtedly contributed to population decline over the period 1970-72 is that of high mortality in the egg and early instar stages. Horobin (1971) in noting this as the key factor determining population numbers, showed that egg, 1st and 2nd instar mortality operated in a density dependent manner. It might, therefore, have been expected that with populations at their low level in 1970-72, that mortality in the early stages would have been reduced. This in fact has not occurred and mortality here has been as high or higher than in previous years, see Table A1 in appendix III.

Horobin when considering the causes of this mortality suggested three contributory factors, infertility, desiccation, and predation. He thought that probably only the predatory factor was density dependent. It is thought that under the conditions prevailing over the 1970-72 period, it is unlikely that any of these factors has been reduced and that this is what has caused the very high mortalities recorded.

In regard to predation, numerous species of small arthropods and nematodes are suspected of being involved. With the populations of M.ater having been fairly constant over several years it seems likely that predator populations may have been in balance, the sudden fall in M.ater population could mean rather heavier predation until populations of predators readjust. Also in both 1971 and 1972 the winters were extremely mild. M.ater is known to be under little pressure from the severe Moor House winter climate, but it may be that predatory species are, and that mild winters favoured their survival in numbers. The whole question of predation however is rather hypothetical, and there is a need for the positive identification of the species involved and of the factors affecting their population dynamics.

Mortality due to desiccation may well have been high in both 1970, when rainfall in May was exceptionally low, and low again in June and in 1971, when July rainfall was exceptionally low. That desiccation can be of importance as a mortality factor in an area of such high rainfall as the Moor House Reserve would at first seem unlikely. The ratio of potential evaporation to rainfall recorded at the Moor House field station rarely drops below unity when considered on a monthly basis. The use of the monthly mean however disregards day to day variations, which may produce ecologically important short periods of water deficit. Green & Millar writing in the Moor House fifteen year report overcame this problem by calculating water deficit on a pentade (5 day) basis, and showed that over the years 1957-66 during the months April to September only 8 months lacked a pentade with a water deficit, whereas on a monthly mean basis only 7 months during the same period showed a deficit. The same authors also noted the occasional occurrance of very low humidities of $<10\%$ at Moor House. It would, therefore, seem likely that the eggs and early instars of Molophilus living near the ground surface may well be exposed to the possibility of desiccation.

The possibility of an increase in egg infertility over the study period is also thought to be a real one. The details of the adult emergences in 1971 and 1972 have been given in Tables 12 & 13 respectively. Both mean and median dates are given along with the standard deviation and standard error of the mean, and the number of individuals on which results are based.

The start of the emergence in both years was early due to good weather in early May. The order of emergence of the sites in 1971 was the same as that recorded by Horobin, but in 1972 the 1700' emergence preceded that of the Peaty Podsol site. The most notable feature of both years' emergence periods however was the time taken between the first and last sites to emerge. Horobin (1971) records it as 13 days

Table 12

Mean and Median dates of emergence at the Moor House and Dun Fell sites in 1971.

Site	Median date	Mean date	S.D.	S.E.	No. of adults
1400 ft.	16 May	17 May	2.75	0.13	480
2050 ft.	22 May	23 May	3.43	0.79	19
Peaty Podsol	28 May	28 May	3.70	0.34	121
1700 ft.	1 June	1 June	2.76	0.25	118
1900 ft.	31 May	2 June	2.55	0.36	51
Peaty Gley	3 June	3 June	3.82	0.44	76
2700 ft.	9 June	9 June	3.70	0.32	132
Blanket Bog	11 June	12 June	4.56	0.57	63

Table 13

Mean and Median dates of emergence at the Moor House and Dun Fell sites in 1972.

Site	Median date	Mean date	S.D.	S.E.	No. of Adults
1400 ft.	20 May	20 May	2.32	0.12	367
2050 ft.	5 June	4 June	6.03	0.60	102
1700 ft.	7 June	7 June	5.28	0.25	443
Peaty Podsol	8 June	8 June	4.55	0.53	75
1900 ft.	8 June	8 June	2.93	0.20	210
Peaty Gley	10 June	10 June	2.70	0.26	109
2700 ft.	16 June	16 June	1.14	0.12	96
Blanket Bog	27 June	27 June	4.56	0.34	176

in 1969 and 17 days in 1970. In 1971 it was 23 days, and in 1972 27 days, with the Blanket Bog site emergence exceptionally late and continuing into July. Two standard deviations on the mean emergence date gives the duration of the middle 68% of the emergence, and this was recorded by both Hadley and Horobin as lasting between 5 and 7 days. In Table A2 in the Appendix the number of days taken for the middle 68% emergence at all the sites over the period 1967-72 are given. It is noticable that in 1971 and 1972 the time taken is in general longer than is usual, and at some sites the emergence has been extremley prolonged, e.g. the 2050' site in 1972 where the duration of the middle 68% of the adult emergence was in excess of 12 days. This partial breakdown of the synchrony of the adult emergence, in a year when populations were already low and catches in the pitfalls indicated that there was very little adult activity, must have reduced the chances of adults mating, which is dependant on chance meetings, considerably.

It is thought that both the prolongation of the emergence period and the lack of adult activity were due to the cold and wet conditions that prevailed during the 1971 and 72 emergence periods.

Overwinter mortality was considered by Horobin (1971) to be of little importance in population regulation in M.ater, though he did note its occasional occurrence at a high level. Generally overwinter mortality is low and M.ater appears not to be under great stress from the Moor House winter climate. No explanation can as yet be given for the occasional high mortalities over this period.

In Table A3 in the appendix the fecundity recorded at all sites for all the years studied are given. Horobin (1971) by plotting the relationship between the number of instar IV larvae in spring, and the mean fecundity of newly emerged females for each site, concluded that a density dependant reduction in fecundity was operating. With the present

population figures it might, therefore, have been expected that fecundity would be high. This has not in fact occurred and the fecundities recorded in 1971 and 1972 are generally very low, and it appears that the relationship does not hold where populations are below 500 per sq. m.. The reasons for these low fecundities recorded with low population levels is not clear, it is unlikely that food availability could be a limiting factor at these levels, as the sites have all previously supported much larger populations, and culture studies indicate that larvae will grow normally even in very small peat samples. However, it is known that the larger larvae produce female adults and Horobin (1971) demonstrated a relationship between increased weight and increased fecundity. It may be that one or more of the mortalities that have occurred has been selective against the larger larvae or pupae, a further project may be justifiable to test this.

From the histograms (Figure 5) sex ratio (k7) has shown itself to be rather variable from year to year, and at some sites has contributed to the population decline. A preponderance of males is general amongst the Tipulidae, (Barnes 1937, Hemmingsen 1956, Coulson 1962, Freeman 1964) and Hadley (1966), recorded a mean of 64% of males in his studies on M.ater. In the Appendix Table A4 gives the sex ratios recorded throughout the 8 years studies on the Moor House Reserve. The ratio has varied within the range 42% (2,050' 1970-71) to 85% (Peaty Gley 1970-71) males. The 42% is a single occurrence of a preponderance of females, but as this figure is based on a sample of only 51 adults not too much stress can be laid on it (S.E. = 6.9%).

As yet no reason or controlling factor responsible for the fluctuations of sex ratio from year to year and site to site has been found.

In August 1972 all the sites under study were resampled in order to judge whether any recovery of the population was likely to occur in the 1972-73 season. The larvae were mostly in instar II and the populations are given in the life tables. Almost all the sites showed a lower larval

density than recorded at a similar time in the previous year, though it is possible that if there is little mortality between sampling and emergence, some recovery will have been made. At the 2,700 ft. site no second instar larvae were found in 52 sample cores taken in August 1972, thus the population at this site appeared to have been virtually wiped out. However, these samples in August 1972 from the 2,700 ft. site did reveal a very considerable residue of instar IV larvae (173 $\pm$ 59 per sq. metre) across the 52 samples and as the instar IV larval population recorded in the samples taken from the site on 25 April 1972 was only 140 $\pm$ 85 per sq. metre it would appear that there has been an almost complete failure to pupate here and that this is another factor in the population decline. Considerable numbers of these larvae were kept in culture to see if they would survive through into 1973 to produce adults, but they followed the same fate as the normal residue (5% - 10%) of instar IV larvae and all had died off prior to January 1973.

The question of how recovery can now take place on these sites where the populations have reached such a low level that even in ideal conditions successful matings may be few is extremely interesting. Cragg (1961) summarising much of the previous work at Moor House made some general observations on the distribution and regulation of animal numbers at Moor House. He considered climate to be the major factor responsible for the local depletion or extinction of animal populations, but stressed the importance of the heterogeneity of the moorland environment in preserving pockets of a species which will recolonize the depleted areas on the return of favourable conditions.

Coulson (1961) studying the biology of Tipula subnodicornis described how in 1955 a drought extending over the egg and first instar stages were responsible for the virtual extinction of the species over considerable areas of the moor. On Sphagnum bog, however, populations were only reduced to about half and later sampling, 1962, of the depleted areas showed populations to have recovered to their pre-1956 level.

The populations of M.ater appeared not to fit in with this pattern for the Peaty Gley and Peaty Podsol sites studied by Horobin and Hadley for six years had shown remarkably constant populations, and Horobin (1971) had shown density dependent factors at work in population regulations. However, between 1970 and 1972 it seems that a series of climatic factors have prevailed that have produced a severe depletion of M.ater on the Juncus squarrosus moor at Moor House. In a similar way to Coulson's 1956 records for T.subnodicornis the Blanket Bog (the wettest site) has maintained its population at a normal level. It is difficult however to imagine how an insect with as limited a motility as M.ater can move out from these reservoir areas to recolonize the Juncus moor, much of which is not adjacent to a Blanket Bog area. It is to be hoped that population observations can be continued on some sites to see how long it takes and by what methods population numbers can increase again to reach their former levels.

5.4 POPULATION STUDIES ON BLANKET BOG

5.4.1 The studies on Molophilus ater at Moor House have been centred on the Juncus squarrosus vegetation areas. This however is not the dominant vegetation type on the reserve, which is extensively covered with a Blanket Bog vegetation in which Calluna vulgaris, Eriophorum vaginatum and Sphagum sp. are the dominant species. Both Hadley and Horobin maintained a single site on the Blanket Bog near Bog End and this was noted to support a low but fairly constant population of M.ater. In the present study several other sites were set up on the Bog with a view to comparing populations over the Bog itself, and a more intensive study was made of the Bog End site to determine if the larvae showed any distinct preference for any of the three microhabitats afforded by the three dominant vegetation species.

5.4.2 Sites, techniques and results

The sites used are described fully in Section 2-2. Six sites were involved, including the Bog End site of Hadley and Horobin. The larval populations only were sampled and the technique used was the same as in Section 5.2 with 1/1000 sq. metre cores taken randomly.

Three of the six sites were sampled on two occasions. 18th October, 1971 and 23rd April, 1972, and the other three sites were sampled only on the later date. The numbers of larvae obtained in numbers per square metre are given in Table 14 . The figures in brackets indicate the number of cores on which the density estimate is based.

Table 14

Density of larvae on various Blanket Bog sites (nos. per square metre ± S.E.). Sample sizes in parenthesis.

Sampling date	Bog End	Valley Bog	Troutbeck	Neather-hearth Syke	House Hill	Plantation
18 Oct. 71	592±89 (77)	186±47 (71)	600±83 (78)	-	-	-
23 April 71	200±54 (48)	46±26 (52)	49±26 (49)	50±29 (48)	122±43 (49)	35±28 (35)

Between the dates 18 October 1971 and 23 April 1972 the Blanket Bog site at Bog End was sampled on 9 separate occasions. On each occasion prior to extraction each core was classified according to the dominant vegetation or litter which it contained. In this particular study at Bog End only the top 2 centimetres of the usual 6 cm core was considered, this part is believed to be where most M.ater activity takes place, and seemed likely to be where the influence of vegetation may be seen most clearly. Three distinct vegetation or litter types of sample were identifiable. There were those containing Sphagnum, which was usually still actively growing rather than litter; those containing mainly E.vaginatum litter and those consisting of C.vulgaris remains. A fourth, less distinct, core type was denoted as "mixed" where cores did not consist of virtually pure vegetation or litter.

The mean densities of M.ater larvae recorded over the period are given in Table 15.

Table 15.

The densities of M.ater larvae in 4 microhabitats in Blanket Bog at Bog End, 1971-72. Sample sizes are given in parenthesis.

	Nos. per sq. Metre ± S.E.			
	Sphagnum	Calluna	Mixed	Eriophorum
Oct./Nov.	250±65 (48)	285±85 (28)	807±151 (26)	740±164 (27)
Dec./Jan.	185±74 (27)	105±70 (19)	115±63 (26)	333±136 (12)
Mar./April	37±35 (27)	38±38 (26)	233±90 (30)	285±120 (14)
% Mortality Oct./April	85%	87%	71%	61%

5.4.3. Discussion

M.ater larvae were recorded on all six of the Blanket Bog sites sampled, indicating that the species is extensive in its coverage of this habitat, though Hadley (1966) did record that the species did not occur on eroding peat areas. Population levels however do vary from site to site as has been shown for the Juncus squarrosus dominated areas. The blanket bog site at Bog End appears to support a population higher than is general for such areas and on the 23rd April 1972 the House Hill site had a population that was not significantly lower. On the 18th October 1972 the Bog End and Troutbeck sites supported similar populations. Mortality between then and the April sampling was considerably higher at Troutbeck than at Bog End, no explanation can be offered, but it is interesting to note that different and very high mortalities can occur on the blanket bog.

The M.ater population recorded in the Larchpole Pine plantation near Bog End is the lowest in the Bog area, this site had been dressed with fertiliser prior to tree planting, but the raising of its nutrient status does not appear to have favoured M.ater. Similarly, another area, high in nutrient with limestone bed rock occurring close to the surface, at Knock Fell, and which is J.squarrosus dominated was found not to support a population of M.ater when pitfall traps were operated there in the 1971-72 adult season. It may be that the species is particularly well adapted to survival under low nutrient conditions and that other species are dominant where the mineral content is high.

The distribution of M.ater in the various microhabitats also confirm the view that Blanket Bog cannot be considered as a homogenous area in regard to M.ater populations. In Table 15 the October and November samplings show a significantly higher number of M.ater in the Eriophorum litter and mixed litter cores ($P < 0.01$), than in the Sphagnum and Calluna cores. The March, April and December, January sampling do not show any significant differences, but in both cases populations recorded are highest in the Eriophorum cores. The mixed litter cores show a high population in March and April, but the numbers that were recorded in December and January

were low, this it is thought may just be due to the inherent variability in a core classification such as 'mixed'. When the differences between the populations in the different core types are considered over the whole sampling period Eriophorum cores contain siginificantly more M.ater larvae than either the Sphagnum or Calluna cores ($P < 0.01$). The mortalities, or movements of larvae from one microhabitat to another, occurring over the whole sampling period are given in Table 15 and also indicate that Eriophorum litter as the most favoured microhabitat. (A similar preference for certain microhabitats within the Bog was shown by Hale (1966) for two species of Collembola.)

It may be that this selection against pure Calluna and Sphagnum litter areas are related to the unsuitability of the material as a food source or to variations in microclimate. That 3 distinct microclimates exist relative to Calluna, Eriophorum and Sphagnum has been shown by the recording made using a Grant recorder and temperature sensitive probes in the various microhabitats as part of the I.B.P. work on the Syke Hill site at Moor House (Smith 1973). The relationships between the microhabitats (based on mean weekly temperatures) are quite complex and alter at different phases of the seasonal temperature variation. Comparing the three probes, Calluna litter at a depth of 1.0 cm, Eriophorum litter at a depth of 1.0 cm and Sphagnum at a depth of 0.5 cm, the maximum variation occurs in the summer with the Eriophorum approx. $2^{\circ}C$ warmer than the Calluna and Sphagnum areas. The Sphagnum warms up quickest in spring, but is over-taken in about June by the Eriophorum. The Calluna remains coldest for approx. 9 months of the year but the Eriophorum and Sphagnum litters cool quickly in autumn, the Eriophorum running at about the same temperature as the Calluna during the winter months and the Sphagnum becoming the coldest of the 3 litters from October till January.

Standen (Moor House Annual Report No. 13 and pers. comm.) has shown that Enchytraeid worms, the other main detritus feeders in the Blanket Bog, grow better when feeding on

Eriophorum and Calluna litters than on Sphagnum litter and analysis done by the Chemical Section at the Merlewood Research Station (Nature Conservancy) on litter collected in April 1972, has shown the litters to have the following Carbon to Nitrogen ratios: Eriophorum 31.5, Calluna 35.1, Sphagnum 85.9. This very low nitrogen content indicates the Sphagnum as a poor food source, and it may be that it is the combination of the better quality of the Eriophorum litter and the warmer environment around the tussock that encourages the aggregation or survival of larvae around them.

6. RESPIRATION AND CALORIMETRIC STUDIES

6.1 As in the previous studies on M.ater no assessment has been made of annual production it was thought worthwhile, with several years data now available to calculate this at both a Blanket Bog site and a typical Juncus site. It was hoped that the figures obtained could then be compared with each other, with those available for other species at Moor House, and with the figures and conclusions of McNeil and Lawton (1970) in their paper on the annual production and respiration of animal populations.

The two sites selected for detailed examination were the Blanket Bog site at Bog End and the Peaty Gley site, a Juncus squarrosus dominated site nearby. Horobin (1971) gives full age specific life tables for these two sites over the periods 1966-1970 for the Bog and 1963-1970 for the Gley and also left details of mean larval weights at each stage, and figures indicating a mean wet weight to dry weight ratio of 4.9:1 for the larval stages. Tables 16 and 17 give the average populations , the mean weights, the numbers dying and the turnover at each stage for the two sites over the specified periods.

In order to convert the turnover details into figures for production it was necessary to determine values for the respiration of M.ater and also the calorific value of M.ater tissue.

6.2 Respiration Techniques and Results

To make a completely accurate calculation of the annual respiration of M.ater it would be necessary to determine the respiratory level for each life stage at field temperatures. This has not been possible within the limits of this study, both on the grounds of time available and equipment required. It was, therefore, decided to estimate the respiratory rate of the instar II larvae and the instar IV larvae at temperatures approximating to the mean field temperature experience of these stages, and to consider respiration of instar I

Table 16

The average populations and turnovers at the Blanket Bog site Bog End, 1966 - 1970.

Stage	Average Population per m^2	No. dying at each stage	Mean Wet Wt. per stage mg	Turnover mg/m^2 Wet Wt.
Eggs June/July	10,700	10,000	0.0016	16
Instars I and II July/August	700	250	0.2	50
Instars III and IV Sept./Oct.	450	50	0.6	30
Instar IV March/April	400	100	2.0	200
Adults June	300	300	0.67	201-16 = 185

Total turnover calculated ignoring adults = 16 + 50 + 30 + 800 = 896 mgs - 16 mgs eggs to next generation = 880 mg/m^2 wet weight = Total Annual Production

Table 17

The average populations and turnovers at the Peaty Gley site at Bog End, 1963 - 1970.

Stage	Average Population per m^2	No. dying at each stage	Mean Wet Wt. per stage mg	Turnover mg/m^2 Wet Wt.
Eggs June	20,000	17,000	0.0016	27.2
Instar I July	3,000	650	0.15	97.5
Instar II August	2,350	600	0.3	180.0
Instar III September	1,750	150	0.6	90.0
Instar III and IV October	1,600	50	1.0	50.0
Instar IV Nov./Dec.	1,550	200	1.3	260.0
Instar IV March/April	1,350	250	1.8	450.0
Adults May/June	1,100	1,100	0.72	792.0 - 27 = 765

Total turnover calculated ignoring adults = 27.2 + 97.5 + 180 + 90 + 50 + 260 + 2430 = 3134.7 - 38 mgs eggs to next generation = 3096.7 mg/m^2 wet weight = Total Annual Production.

larvae and eggs at the instar II rate and instar III larvae and pupae at the instar IV rate. Respiration of the adults has not been considered as it is thought that due to the short duration of this phase it would be negligible.

The figures given are as near accurate as could be obtained without a very large involvement in this part of the project and are thought to give a worthwhile basis for comparison with other species.

The respiration rates of the instar II and instar IV larvae were estimated by different techniques. The instar IV larvae were considered large enough to be handled in the Warburg manometer, whilst for the instar II larvae it was necessary to use the Cartesian Diver technique, Klekowski (1967), to obtain consistent results. The sensitivity of the Warburg was increased by the use of small flasks (10 ml), and the volume of these was further reduced to about 5 ml by part filling them with glass beads of known specific gravity. These beads served a dual purpose as they also encouraged the larvae to settle whilst in the respirometer, 20 larvae were placed in each flask on each occasion. The larvae were group weighed on an electro-microbalance and all had been acclimatized for 4 days previous at the temperature of the run. Two temperatures 10 and 5°C were used and these were kept constant to $\pm$ 0.1°C by immersion of the flasks in a thermostatically controlled water bath. Thirty-two flasks each containing 20 larvae were run at 10°C and 12 flasks at 5°C.

With the instar II larvae in the Cartesian Diver it was possible to measure the respiration of individual larvae. A single temperature of 10$\pm$ 1°C was used and the larvae were again weighed on the elctro-microbalance and had been acclimatised to the run temperature for 4 days. Diver capacity was between 4.5 and 7.0 μ litres and the respiration of 10 individual larvae was measured.

The results obtained by these two techniques are given in Table 18.

Table 18

Respiration of M.ater larvae in $\mu l O_2/g/hr.$ ± S.E.

	Temperature °C		
Instar	5	10	Technique
Instar II larvae	-	347 ±8	Cartesian Diver
Instar IV larvae	98±4	152 ±6	Warburg Manometer

6.3 CALORIMETRY

The calorific value of M.ater was determined using a micro-bomb calorimeter of the type described by Phillipson (1964).

Here again it was not possible to assess the calorific value of each life stage and the figure that has been obtained has been based solely on instar IV larvae. The collection of material for this study took considerable time as populations were low and it was necessary to extract sods $\frac{1}{2}$ metre sq., taken from a site adjacent to the 1900 ft. Dun Fell, in large Berlese funnels over several weeks in order to obtain sufficient material. For the smaller larval stages no bulk extraction technique is available and the time required to collect sufficient material was outside the scope of this study.

The extracted larvae were washed and then dried to constant weight at 80°C, and then stored over a dessicant. The total material was ground and thoroughly mixed, then made into pellets in the weight range 18 to 28 mgs. and weighed on an electro-microbalance.

Each weighed pellet was placed in the sample holder of the bomb and an approximately 3 cm length of platinum wire was used to join the two terminals and arranged so as to press against the pellet. The two halves of the bomb were screwed together and the bomb pressurized to 30 atmospheres with oxygen. Then the bomb was cooled in running water, dried with tissue, seated in the copper ring of the stand and the leads to the firing circuit connected. A stainless steel jacket was placed over the whole assembly.

The recording system was switched on and if the cooling of the bomb had been of the correct order a constant reading was soon obtained. When this equilibrium was reached the bomb was fired. The potentiometer recorded the heat rise in the bomb via the thermocouples and when cooling became apparent

the operation was stopped and the maximum reading was then compared with the potentiometer readings obtained by burning pellets of benzoic acid of known calorific value and the calorific value of the M.ater pellet calculated. Ten benzoic acid pellets were burnt to calibrate the potentiometer and 7 M.ater pellets burnt gave the calorific values given in Table 19.

Table 19

The calorific values of 7 M.ater pellets

Pellet No.	Wt. of pellet mgs.	Cals. in pellet	Cals. per gram.
1	24.40	135.6	5558
2	20.50	109.0	5319
3	21.65	122.7	5668
4	27.25	146.3	5369
5	29.35	160.5	5467
6	18.50	96.9	5237
7	27.20	148.5	5461

Mean Calorific Value Per Gram = 5440±51

6.4 Energy Budgets

The mean annual production figures as calculated in Tables 16 & 17 are given in Table 20 both as wet and dry weights for both sites. All these figures are based on calculations ignoring the adult stage, and assuming the instar IV larva to be the final life stage. As little if any growth takes place between the final larval measurement in April, and the adult emergence in late May and early June and there are considerable losses which would be difficult to measure, e.g. larval and pupal exuvaie, it is thought that this method gives the best estimate that can be easily obtained. The production figures given in kcals/m^2 have been calculated using the annual dry weight production figures and the calorific value for M.ater obtained by the bomb calorimeter method previously described.

To obtain figures for annual respiration it was necessary to calculate the biomass present at each life stage in grams. This was done using the figure given in Table 16 or 17 for the average population at each stage times the mean wet weight of that stage. The biomass was then multiplied by the duration of the stage in hours and by the figure previously obtained or assumed for respiration of that stage in $\mu l O_2/g/hr$. The total for all the life stages in one generation is the figure given as the annual respiration. This figure has been converted to kcals/m^2 by multiplication by the oxycalorific equivalent. The figure assumed in this study is 4.775 kcals/litre O_2, the figure given by Heilbrunn (1947) for general detritus feeders.

6.5 Discussion

From the figures in Table 20 annual production at the Peaty Gley Juncus site appears to run at about three times that on the Blanket Bog. Over the past six years however, the populations on the Bog have remained fairly constant, whilst on the Juncus sites, particularly in the 1970-71 and 1971-72 seasons (which have not been considered in the

Table 20

The annual production and respiration for M.ater, calorific equivalent 5,440 cal per gram dry weight, oxy-calorific equivalent 4.775 Kcals/litre oxygen, on two sites at Moor House.

SITE	PEATY GLEY	BLANKET BOG
Years	1963/70	1966-70
Mean annual production		
Wet weight	3.10 g/m^2	0.88 g/m^2
Dry weight	0.53 g/m^2	0.15 g/m^2
Kcals/m^2 (P)	2.883	0.816
Mean annual respiration		
lO_2/m^2	1.664	0.459
Kcals/m^2 (R)	7.946	2.192
Assimilation		
(P + R) = A Kcals/m^2 (R)	10.829	3.008
$\frac{P \times 100}{A}$	26.62	27.13

determination of mean annual production) considerable fluctuations have occurred. It seems likely that in some years production may be reduced by up to 50%, whereas on some Juncus sites, e.g. 1900 ft. Dun Fell and Peaty Podsol, which have been known to support very high populations, production in some seasons may run at double that of the mean annual estimate given for the Gley site.

Standen (1973) in a study of the production and respiration of the enchytraeid population on the Blanket Bog at Moor House has estimated the annual production as between 10-13 kcals/m^2. As enchytraeids are the other main detritus feeders in association with M.ater on both the Bog and Juncus sites, with a production in excess of 12 times that of Molophilus, they must be considered the major contributor to this part of the energy cycle on the Bog. The annual respiration of the enchytraeid population was estimated as around 60 kcals/m^2 and Standen noted that this gave the population an extremely low production efficiency (P/A x 100), 17.2 in the 1968-69 season, and 14.1 in the 1969-70 season. She considered this to be due to the life history of the enchytraeid where no egg stage is involved and multiplication is by segmentation and that this method of reproduction greatly reduced the energy cost to production.

The production efficiency at both the Juncus and the Bog sites are also very low when compared with the figures given by McNeil and Lawton (1970) for the relationship of annual production (P) to production efficiency (P/A x 100). They indicate that at the lower production levels the production efficiencies of comparatively short lived poikiotherms are markedly increased. This they suggest may be due to either to an attempt to compensate for restricted total annual production or may be caused by differences in life histories. In relation to the latter they point out that most comparatively short lived poiki lotherms with a $\log_{10} P$ below 0

overwinter as eggs and that those with $\log_{10}P$ above 0 overwinter as juveniles or adults. At Bog End, however, the situation is that two populations live adjacent to one another, one, the Bog with a $\log_{10}P$ of $\bar{1}$ .9117 and the other, the Gley with a $\log_{10}P$ 0.4599. At both these sites the life cycle is the same with M.ater overwintering as the instar IV larvae and it is thought that it is the continuance of respiration in this stage during the winter when production is near zero that is responsible for the low production efficiencies recorded. Production efficiencies at the two sites are similar, and the differences in production at these two sites would appear to be due merely to the inherent different natures of the sites and their ability to support populations of different sizes.

SUMMARY

1. Population studies on M.ater at the Moor House National Nature Reserve, Westmorland, have been continued. This study covers the period June 1970 to August 1973, and data are now available for eight consecutive years on two sites and five consecutive years on six other sites.

2. A sharp decline in populations on the Juncus squarrosus moor has been recorded with site populations running at between 3 and 50% of their pre-1970 levels. A single blanket bog site under study did not suffer a similar decline. Mortality on the Juncus sites has not been attributable to any single factor, but has operated at different stages at different sites. Egg, first and second instar mortality has been high and this may have been due to exceptionally low rainfall in May 1970 and July 1971, dessication is known to be a cause of mortality in these early stages. Mortality in the pupation-emergence stage has also acted at an exceptional level on some sites and on one site there is evidence of almost complete failure to pupate and larvae still surviving in the fourth instar well after the normal emergence date.

3. Previous studies had shown M.ater to maintain remarkably constant populations from year to year and Horobin had shown density dependant factors at work in population regulation. The present study however indicates that M.ater , like many other moorland animals, is subject to periodic declines, and it is thought that the variability of the moorland climate is the major factor responsible.

4. A study of M.ater populations over the blanket bog has shown that the species is extensive in its coverage of this habitat, but variations in spring fourth instar populations in the range 200-35 per sq. metre were recorded on 6 sites in 1971. An investigation of larval distribution relative to microhabitats within the bog has shown Eriophorum vaginatum litter areas to be prefered to Sphagnum or Calluna litter.

5. The relationship between pupal duration and temperature has been investigated at temperatures corresponding to those prevailing in the field. At temperatures below 10°C pupal duration is shown to be prolonged increasingly by decrease in temperature. As mean soil temperature in the field in May may vary between sites by as much as 2°C and a delay in pupation in the order of 6 days for every 1°C is indicated it seems likely that increase in pupal duration contributes substantially to the observed different emergence dates between sites.

6. Studies on the development of fourth instar larvae towards pupation relative to photoperiod and temperature have shown that a short daylength inhibits pupation but that a temperature threshold of between 5-6°C also exists. Larvae taken in November and December 1971 failed to pupate in a short day (6 hour) photoperiod even at 10°C whilst larvae taken at the same time but kept in 18 hours daylight did pupate. Larvae taken in late January, 1972 did however reach pupation in both 6 and 18 hour photoperiods at 10°C. It is thought that these larvae must all have received the required daylength to stimulate development whilst in the field situation The larvae in the 18 hour photoperiod did however pupate sooner than those in the 6 hour photoperiod, indicating that daylength is still influencing development at this stage. From this stage on larvae appeared to accumulate the light effect as light was available to them, up until 24 April 1972 when daylength ceased to have an effect on time taken to pupate and development to pupation appeared to be temperature dependant.

7. Data on the respiration and calorific value of M.ater have been collected and have been used along with details of populations to assess annual production, respiration and assimilation on both a blanket bog and a typical Juncus site The low production efficiencies given by these figures

was thought to be due to the high respiratory loss caused by overwintering as fourth instar larvae.

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APPENDIX

APPENDIX I The Sample Sites

The Moor House Sites

The three sites in this group had all been previously used and described by Hadley (1966) and Horobin (1971).

(1) The Peaty Gley Site (1800', 549m)

This is a level, slightly flushed site where the dominant plant is Juncus squarrosus. It is situated at the end of the old mining track to Bog End and has been used in many ecological studies at Moor House. Between the Juncus rosettes there are clumps containing Carex spp. Deschampsia flexuosa, Festuca ovina, and Polytrichium commune. Herbs and lichens are rare but the site supports a rich variety of bryophytes. M.ater has now been studied on this site for 8 consecutive years.

(2) The Peaty Podsol Site (1820', 555m)

On this site the mineral soil is covered by only a thin layer of peat, varying between 6 and 20 cms in thickness. The site slopes S.S.E. at an angle of approximately 7^{o}. Juncus squarrosus is again dominant and Festuca ovina and Polytrichium commune common.

The site is characterised by the presence of Nardus stricta, being indicative of the drier and more mineral substrate of this site. It has also been studied for 8 consecutive years.

(3) The Blanket Bog Site (1840' 561m)

Blanket Bog comprises the major vegetation type at Moor House. This site is level and situated adjacent to the Peaty Gley site at Bog End. Calluna vulgaris is dominant. Sphagnum spp. and Eriophorum vaginatum tussocks have a high cover value. Eriophorum angustifolium is also present. The M.ater population on this site have been studied for 6 years.

The Dun Fell Sites

These five sites were set up and have been previously described by Horobin (1971). They are referred to by their altitude.

(1) 1400' site (427m)

A site dominated by J.squarrosus with a slope of approximately 3° to the west, it also supports Festuca spp. and Vaccinium myrthillus and in one corner which is rather wet Juncus effusus and Sphagnum spp. M.ater has been studied for 4 years.

(2) 1700' site (518m)

A level site dominated by J.squarrosus. It is much the wettest of the Dun Fell sites and frequently suffers water logging due to impeded drainage. Other common plant species are E.angustifolium, V.myrtillus, Empetrum nigrum, Potentilla erecta, Polytrichium commune and Sphagnum spp.

The site has been studied for 5 years.

(3) 1900' site (579m)

A well drained level site with a very uniform cover of J.squarrosus, V.myrtillus and Festuca spp. are also present. This site supports a high density of Tipula subnodicornis. It has been studied for 5 consecutive years.

(4) 2050' site (625m)

This site is inclined at about 5° to the north west and has an alluvial soil underlaid by gravel in places. It is consequently well drained.

The vegetation here is distinctly different from the other 4 sites and it was chosen by Horobin (1971) as no suitable J.squarrosus site could be found around this altitude.

Deschampsia cespitosa and Holcus lanatus were dominant together with Gallium saxatile, Potentilla erecta, Ranunculus acris and Polytrichium commune. The site has been studied for 5 years.

(5) 2700' site (823m)

A level site dominated by J.squarrosus and the highest at which M.ater has been studied. E.vaginatum and E. angustifolium are common, and the latter has been increasing over the last few years now forming an almost pure belt across the site.

The site is sheltered to the north and east by the summit of Gt. Dun Fell and has been studied for 5 years.

APPENDIX II

Life Tables for M.ater 1970-72

The life tables comprise of the usual three colums:

l	numbers living per sq. metre
d	numbers dying per sq. metre.
100q	percentage mortality.

The Peaty Podsol Site

		1970-71			1971-72		
Stage	Time	l	d	100q	l	d	100q
Egg	June	52650			23220		
Instar I	July		49450	93.9		21916	94.4
Instar II	August	3200					
Instar III	Sept.	2385	815	25.5	1304		
Instar IV	Nov./Dec.	2131	254	10.6	822	482	37.0
Instar IV	Mar./April	1523	608	28.5	557	265	32.2
Adults	May/June	1210	313	20.6	375	182	32.7
Adult ♀♀	May/June	270	940	77.7	145	230	61.1
Adult ♀ (93)	May/June	250	20	7.5	111	34	23.4

		1972-73		
Egg	June	10300		
Instar I	July		9146	88.8
Instar II	August	1154		

THE PEATY GLEY SITE

		1970-71			1971-72		
Stage	Time	l	d	100q	l	d	100q
Egg	June	214120			11570		
Instar I	July		19520	91.1			
						10870	93.9
Instar II	Aug.	1900					
			440	23.2			
Instar III	Sept.	1460			700		
			229	15.7		44	6.3
Instar IV	Nov/Dec	1231			656		
			231	18.8		216	34.0
Instar IV	Mar/April	1000			440		
			110	11.0		0	0
Adults	May/June	890			440		
			760	85.4		325	73.9
Adult ♀♀	May/June	130			115		
			34	26.1		29	25.2
Adult ♀ (120)	May/June	96			86		

Egg	June	10350		
Instar I	July		9626	93.0
Instar II	August	624		

THE BLANKET BOG SITE

		1970-71			1971-72		
Stage	Time	l	d	100q	l	d	100q
Egg	June	8342			3320		
			7380	88.5			
Instar I	July					2628	79.2
			347	36.0			
Instar II	August	962					
			38	6.2	692	339	49.0
Instar III	Sept.	615					
			385	66.7	353		
Instar IV	Nov/Dec	577					
					200	0	0
Instar IV	Mar/April						
			152	79.1	363		
Adults	May/June	192					
			8	20.0			
Adult ♀♀	May/June	40					
Adulst ♀ (104)	May/June	32					

1400 ft. site

		1970-71			1971-72		
Stage	Time	l	d	100q	l	d	100q
Egg	June	32704			28992		
			30704	93.9			
Instar I	July					28542	98.4
		2000					
Instar II	Aug.		769	38.4			
		1231			450		
Instar III	Sept.		77	6.3		113	25.1
		1154			337		
Instar IV	Nov/Dec		114	9.9			
		1040			144	154	45.7
Instar IV	Mar/April		0	0			
		1040			183		
Adults	May/June		739	71.1		108	59.0
		301			75		
Adult ♀♀	May/June		42	10.6		22	29.2
Adult ♀ (112)	May/June	259			53		

		1972-73		
Egg	June	5925		
			5271	89.0
Instar I	July			
		654		
Instar II	Aug.			

1700 ft. site

		1970-71			1971-72		
Stage	Time	l	d	100q	l	d	100q
Egg	June	36848			18750		
Instar I	July		34384	93.3			
						17966	95.8
Instar II	Aug.	2464					
			1118	45.4			
Instar III	Sept.	1346			784		
			0	0		79	10.1
Instar IV	Nov/Dec	1346			705		
			154	11.4		230	32.6
Instar IV	Mar/April	1192			475		
			602	50.5		32	6.7
Adults	May/June	590			443		
			340	57.6		302	68.2
Adult ♀♀	May/June	250			141		
			64	25.6		20	14.2
Adult ♀ (1OI)	May/June	186			121		

	1972-73			
Egg	June	12267		
Instar I	July		11390	92.8
Instar II	Aug.	877		

1900 ft. site

Stage	Time	1970-71 l	1970-71 d	1970-71 100q	1971-72 l	1971-72 d	1971-72 100q
Egg	June	102912			8910		
Instar I	July		98512	95.7		8126	91.2
Instar II	Aug.	4400	1588	36.1	784		
Instar III	Sept.	2812	296	10.5	705	79	10.1
Instar IV	Nov/Dec	2516	401	15.9	475	230	32.6
Instar IV	Mar/April	2115	1815	85.8	210	265	55.8
Adults	May/June	300	190	63.3	74	136	64.7
Adult ♀♀	May/June	110	19	17.3	56	18	24.3
Adult ♀ (98)	May/June	91					

Stage	Time	1972-73 l	1972-73 d	1972-73 100q
Egg	June	5476		
Instar I	July		5376	98.1
Instar II	Aug.	100		

2050 ft. site

		1970-71			1971-72		
Stage	Time	l	d	100q	l	d	100q
Egg	June	35937		92.6	6050		
Instar I	July		33287			5678	93.8
Instar II	Aug	2650					
			1050	39.6			
Instar III	Sept.	1600			278		
			62	3.9		0	0
Instar IV	Nov/Dec	1538			372		
			307	20.0		178	47.8
Instar IV	Mar/April	1231			193		
			1136	92.3		142	73.6
Adults	May/June	95			51		
			40	42.1		35	68.6
Adult ♀♀	May/June	55			16		
			8	14.6		5	31.2
Adult ♀ (129)	May/June	47			11		

Egg	June	1376		
Instar I	July		1232	90.4
Instar II	Aug.	144		

2700 ft. site

		1970-71			1971-72		
Stage	Time	l	d	100q	l	d	100q
Egg	June	33335			14440		
Instar I	July		30823	92.5		13932	96.5
Instar II	Aug.	2512	1012	40.3			
Instar III	Sept.	1500	269	17.9	508	116	22.8
Instar IV	Nov/Dec	1231	311	25.3	392	272	69.3
Instar IV	Mar/April	920	260	28.2	120	88	73.3
Adults	May/June	660	470	71.2	32	22	68.7
Adult ♀♀	May/June	190	62	32.6	10	3	30.0
Adult ♀ (113)	May/June	128			7		

		1972-73		
Egg	June	760		
Instar I	July		741	97.5
Instar II	Aug.	Less than 19		

APPENDIX III
TABLES

Table A1

Mortality in the egg, Instar I and Instar II stages of M.ater at Moor House and Dun Fell 1964 to 1972.

The mortality is expressed as a percentage of the egg number laid in that generation.

	SITES							
Year	Peaty Podsol	Peaty Gley	Blanket Bog	1400 ft.	1700 ft.	1900 ft.	2050 ft.	2700 ft.
1964-65	95.7	91.1						
1965-66	95.0	94.7						
1966-67	95.6	97.3						
1967-68	94.2	96.2	95.8		94.2		93.2	89.0
1968-69	96.6	95.5	96.0		93.9	93.9	94.5	94.7
1969-70	92.4	93.8	95.2	96.1	89.3	95.1	94.6	95.7
1970-71	95.5	93.2	92.6	96.2	96.3	97.3	95.5	95.5
1971-72	94.5	93.9	79.2	99.0	95.8	91.2	95.4	96.5
Mean morlality	94.9	94.5	91.8		93.9	94.4	94.6	94.3

Table A2

The times, in days, taken for the middle 68% of the adult emergence at the Moor House and Dun Fell sites 1967-72.

	YEAR					
Site	1967	1968	1969	1970	1971	1972
1400 ft.	-	-	5.5	3.9	5.5	4.6
1700 ft.	4.6	4.6	5.7	3.4	5.6	10.6
1900 ft.	-	4.8	7.6	3.4	5.1	5.9
2050 ft.	9.0	5.2	6.4	5.2	6.9	12.1
2700 ft.	4.5	6.0	5.2	2.7	7.4	2.3
Peaty Podsol	4.8	6.4	6.6		7.4	9.1
Peaty Gley	4.4	6.0	5.4		7.6	5.4
Blanket Bog	6.6	6.5	-		9.1	9.1

Table A3

FECUNDITY: estimated by dissection, each figure based on at least 15 females

Year	SITE							
	Peaty Gley	Peaty Podsol	Blanket Bog	1400 ft.	1700 ft.	1900 ft.	2050 ft.	2700 ft.
1965	78	78						
1966	78	78						
1967	96	82	104					
1968	120	90	97		91	80	129	95
1969	107	93	97	104	101	98	99	89
1970	119	81	97	112	98	96	99	113
1971	89	86	83	96	75	81	110	76
1972	90	71	93	79	87	74	86	76
Mean	97	82	95	98	90	86	105	90

Table A4

SEX RATIOS

Adults % ♂ 1965 - 1972

	S I T E S							
Year	Peaty Podsol	Peaty Gley	Blanket Bog	1400 ft.	1700 ft.	1900 ft.	2050 ft.	2700 ft.
1965	63	63						
1966	63	65						
1967	74	71	68					
1968	75	71	62		71	72	60	60
1969	64	65	62	61	62	60	59	65
1970	74	73	66	60	62	60	64	60
1971	78	85	78	71	58	65	42	71
1972	61	70	-	59	68	65	70	68