Biological studies on molophilus ater meigen: (diptera : tipulidae)

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BIOLOGICAL STUDIES ON MOLOPHILUS ATER MEIGEN

(DIPTERA : TIPULIDAE)

by

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..... being a thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham, 1966.

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to Dr. J.C. Coulson for his direction and criticism throughout the study, and to Professor D. Barker for providing facilities in the Department of Zoology, Durham.

I would also like to thank :

Colleagues and friends of the Department of Zoology for much helpful discussion and advice,

The Staff of Moor House Research Station for their unfailing assistance and hospitality, and particularly Mr. D. Welch for providing information on the vegetation of the Moor House Reserve,

Mrs. Ruth L. Reed for typing the final draft,

and Cally, for many reasons.

The work was carried out whilst holding a Durham Colleges Research Studentship.

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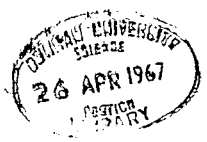
APPENDIX

I. INTRODUCTION

Most of the work described in this thesis was carried out on the Moor House National Nature Reserve, an area of moorland typical of the northern Pennines with a severe climate. Since 1952, investigations have been made on the Reserve on a number of groups representative of the fauna of moorland (see Cragg, 1961), investigations undertaken not merely to provide a faunal list, but to evaluate the influence of the biotic and physical environment on the numbers and distribution of these organisms. Several workers at Moor House have stated that predation and parasitism appear to have a negligible effect on the numbers of dominant moorland insects, and have demonstrated how single environmental factors dominate changes in density, and may be used to predict future densities.

The background to the present study was the work of Coulson (1959, 1962), who catalogued the crane-fly fauna of the Reserve and investigated the biology of certain Tipula species. The British Tipulidae are represented by nearly 300 species, but the family has received scant attention from ecologists. Early workers quite naturally concentrated their studies on the description and exploration



of the fauna, which is still only partially recorded even for the adult stage. In general, crane-flies are of only minor economic importance, and there has consequently been no impetus for studies on the biology of the group. Studies have mainly been restricted to the Tipulinae ("long-palped crane-flies"), and more particularly to Tipula oleracea Linnaeus and Tipula paludosa Meigen, two species which do cause damage to certain crops in Europe. Several authors have drawn attention to the susceptibility of egg and first instar stages of Tipula spp. to desiccation (e.g. Rennie, 1917; Maercks, 1939; Laughlin, 1958), and large changes in yearly densities and distribution have been correlated with the rainfall during these early stages (Maercks, 1943; Coulson, 1962; Milne, Laughlin & Coggins, 1965). The seasonal occurrence of adult crane-flies has been studied using light traps (Pinchin & Anderson, 1936; Robertson, 1939) and Hemmingsen (1952, 1956) has described the oviposition of crane-flies from different habitats.

The present study attempts to evaluate the biology of the brevi-palp crane-fly Molophilus ater Meigen. The brevi-palp group, composed mainly of the smaller species, is numerically larger than the Tipulinae, but apart from the studies of Cuthbertson (1926) on swarming, those of

Crisp & Lloyd (1954) on the species of woodland mud and occasional habitat records, most species of the group are known only to the taxonomist. Molophilus ater was noted by Coulson (1959) as a common member of the crane-fly fauna at Moor House, and has been previously recorded as being an important constituent of the food of young grouse (Committee of Inquiry on Grouse Disease, 1911). A characteristic of the species is that the adults of both sexes are sub-apterous. One major difficulty in the study of most adult crane-flies, as with other highly motile insects, is the accurate determination of densities; the fact that adults of Molophilus ater are incapable of flight enabled techniques to be used which could record the densities of adults. This thesis describes certain aspects of the biology of the species, including observations made under field conditions of the life cycle, the biology and occurrence of adults, and changes in density and distribution both within a generation and in succeeding years.

II. THE STUDY AREA AND SAMPLING SITES

1. LOCATION AND PHYSIOGRAPHY

The Moor House National Nature Reserve (N.R. 80 : Nat. Grid. Ref. NY/758329) occupies 10,000 acres (4,000hectares) of moorland typical of the northern Pennines. The Reserve is situated in Westmorland, 12 miles to the east of Penrith and 11 miles to the south of Alston. The greater part of the Reserve slopes in an easterly direction from the Pennine escarpment, which rises from the Vale of Eden to the summit ridge. The Reserve includes parts of both the western scarp and the eastern dip slopes of three principal fells, Knock Fell (2,604 ft.; 794 m.), Little Dun Fell (2,761 ft.; 842 m.) and Great Dun Fell (2,780 ft.; 845 m.). The summit ridge is continuous with Cross Fell (2,930 ft.; 893 m.), the highest peak of the Pennines which lies just to the north of the Reserve.

The entire area is dissected by numerous streams which flow into the River Tees on the east and the River Eden on the west. The bed rock consists of the Carboniferous Yoredale Series, which, except where exposed by streams and other erosive forces, is covered by an extensive cover of glacial drift overlaid by peat. Typically, the Reserve is covered by Blanket Bog, except on the higher slopes and adjacent to streams where shallower peat or mineral soils support rush and grass dominated areas.

General descriptions of the Reserve have been given by Conway (1955) and Cragg (1961), and the geology has been comprehensively studied by Johnson & Dunham (1963).

2. SAMPLING SITES

A preliminary survey indicated that Molophilus ater is limited in its distribution at Moor House to Blanket Bog and areas where the peat is better drained and shallower, where the dominant plant is often Juncus squarrosus; the species is not found on bare peat, on redistributed peat where Nardus stricta is dominant, or on mineral soils with Festuca and Agrostis as co-dominants.

In previous ecological studies at Moor House, all areas with Juncus squarrosus as a dominant plant species have been considered as one habitat type. Recent studies by Welch (1964) have shown that Juncus squarrosus cover is seldom greater than 50% in any habitat, and that it grows in association with a wide variety of other plants. There is often greater similarity between two communities, one with and one without Juncus squarrosus, than between two Juncus squarrosus communities. The use of Juncus squarrosus as one habitat type is undesirable. Though there is continuous variation between Juncus squarrosus communities, it is convenient to have fixed points, or noda, on these gradients for reference

in describing and comparing plant communities. Welch (1964) classified the Juncus squarrosus communities at Moor House into five different types, or noda, established by the method of successive approximation of Poore (1962). The noda are named after the typical soil type on which they occur.

In addition to Blanket Bog, two characteristic Juncus squarrosus noda were chosen as study areas, together with another site which is similar to a third nodum described by Welch, but where Carex spp. replace Juncus squarrosus as the dominant plant species. The sample sites selected are described below, and their location at Moor House shown in Fig. 1. A Domin scale analysis of the vegetation on each of the four sites is given in Appendix I.

a) PEATY GLEY SITE (1,800 ft.; 549 m.) PLATE 1.

This is the site which has been used in many ecological studies at Moor House as a typical Juncus squarrosus area. The site is, however, singularly atypical in its origin; the site comprises slightly flushed Blanket Bog which was used as a track in mining days, and has only in the last century been colonized by Juncus squarrosus. The Peaty Gley nodum is the most widespread at Moor House, and corresponds with the Juncetum squarrosi sub-alpinum shown by Eddy (unpublished) on his vegetation map of Moor House.

FIG. 1. MAP OF PART OF THE MOOR HOUSE NATURE RESERVE.

The letters refer to the sample sites.

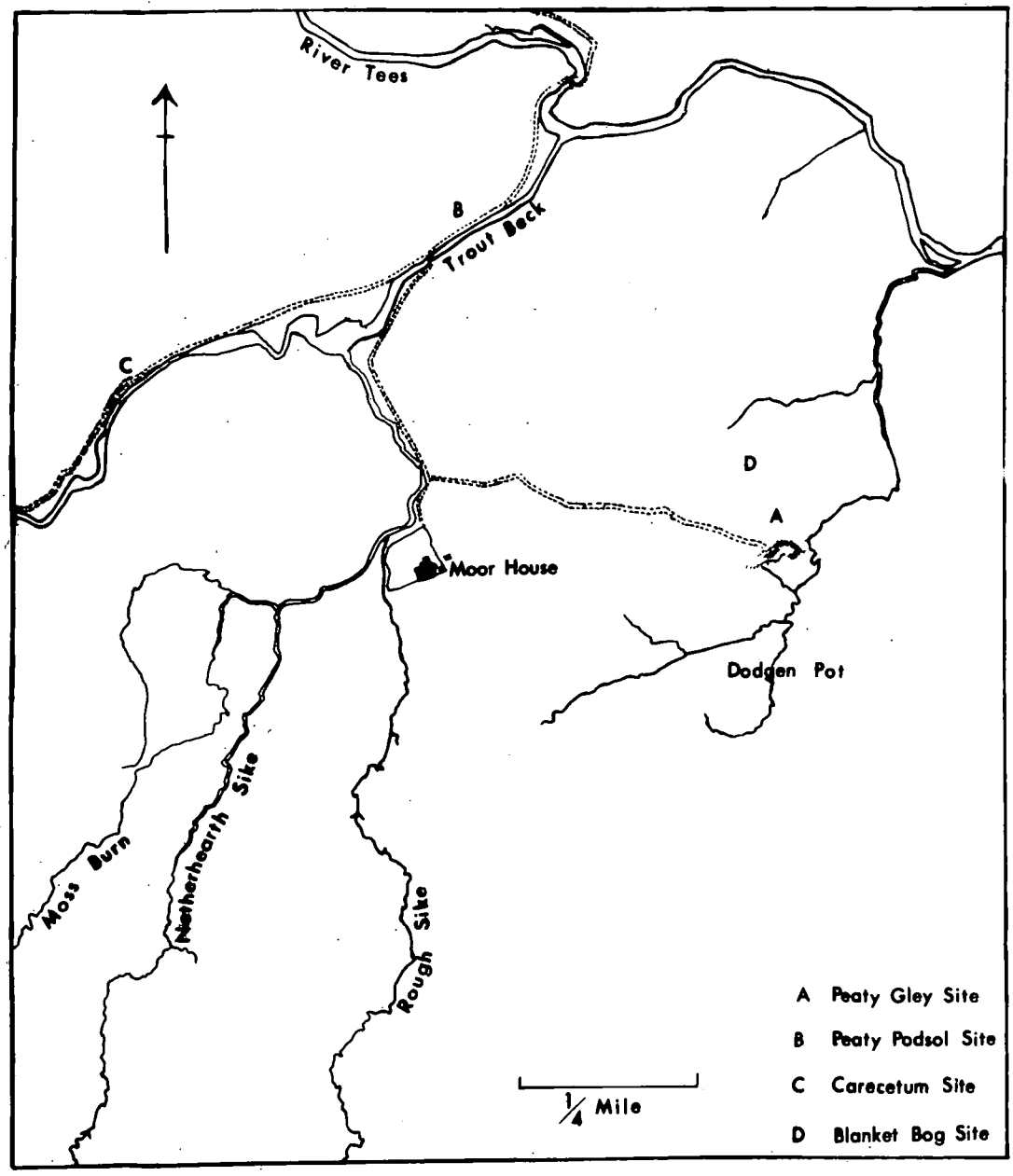

River Tees
B
Trout Beck
C
D
A
Moor House
Dodgen Pot
Moss Burn
Netherhearth Sike
Rough Sike
1/4 Mile
A Peaty Gley Site
B Peaty Podsol Site
C Carecetum Site
D Blanket Bog Site

PLATE 1. THE PEATY GLEY SITE.

A. General view. The sample area is bounded on the upper left and upper right by *Calluna* dominated Blanket Bog. In the foreground there is an area of *Juncus effusus*.

B. Detail of the vegetation. The darker coloured *Juncus squarrosus* and the associated *Festuca ovina* (lighter colour) can be distinguished.

Juncus squarrosus is the clear dominant, and Polytrichum commune has a high cover value. Between the Juncus rosettes there are clumps containing Carex nigra, Deschampsia flexuosa and Festuca ovina. Herbs and lichens are rare, but there is a rich variety of bryophytes. There are only five constants; namely, Deschampsia flexuosa, Festuca ovina, Juncus squarrosus, Lophocolea bidentata and Polytrichum commune. There are four near constants, Aulacomnium palustre, Calypogeia trichomanis, Eriophorum angustifolium and Ptilidium ciliare.

b) PEATY PODSOL SITE (1,820 ft.; 555m.)

On this site mineral soil is covered by only a thin layer of peat, varying between 8 and 20 cm. deep, contrasting with the Peaty Gley site where the peat may be up to 100 cm. in depth. The site shares several constants with the Peaty Gley nodum (e.g. Festuca ovina, Juncus squarrosus, Lophocolea bidentata and Polytrichum commune), but is characterized by the absence of Eriophorum spp. and the presence of Nardus stricta, the latter being indicative of the drier, more mineral substrate of the Peaty Podsol site. Agrostis tenuis, Anthoxanthum odoratum, Galium saxatile and Hynum cupressiforme are characteristic species absent on the Peaty Gley nodum.

c) CARECETUM FLUSHED PEAT SITE (1,800 ft.; 549 m.)

This is similar to the Juncus squarrosus flushed peat nodum described by Welch (1964), except that Carex spp. are the clear dominants, and not Juncus squarrosus. The area is a typical marginal community separating calcareous flushes from the surrounding Blanket Bog. There are many more species than on the other two sites described previously, with a considerable group of base-demanding species. Characteristic species include Mnium punctatum, Pontentilla erecta and Trifolium repens. This site will be referred to as the Carecetum site in succeeding sections.

d) BLANKET BOG SITE (1,840 ft.; 561 m.)

This comprises the major vegetation type at Moor House, and is included under the general term of mixed-moor by Pearsall (1950). Calluna vulgaris is the main dominant, and, on the site chosen for study (closely adjacent to the Peaty Gley site), Eriophorum angustifolium, Eriophorum vaginatum, Juncus squarrosus, and Sphagnum plumulosum were constants.

e) THE DORTHGILL TRANSECT

In 1965 and 1966, a transect on the eastern facing slopes to the north of the Reserve at Hill Farm was used to investigate the influence of altitude on the adult emergence of Molophilus

ater. The transect, which approximates to the "East Transect" of Jordan (1962), rises from the bridge across Dorthgill (1,500 ft.; 457 m.) to the summit ridge (2,000 ft.; 610 m.). Six stations were chosen at 100 ft. vertical intervals up this transect, but though Juncus squarrosus was present at each station, there were considerable differences in the soil type and accompanying plant species.

At 1,500 and 1,600 ft., the soil was not peaty, but comprised a species rich gley. The vegetation was species rich, with Juncus squarrosus and Nardus stricta as co-dominants. Accompanying species included Anthoxanthum odoratum, Bellis perennis, Ranunculus repens, Rumex acetosella, Taraxacum officinale and Viola palustris. These species are all typical members of species rich gley soils. At both stations there was no Sphagnum spp., and Polytrichum commune had a very low cover value.

At 1,700 and 1,800 ft., the soil type was a species poor peaty gley, peat extending to a depth of about 40 cm. Nardus stricta was absent, and Juncus squarrosus had a large cover value. There were large amounts of Sphagnum spp. and Polytrichum commune, and adjacent to each site were Sphagnum flushes containing Juncus effusus. Characteristic plants included Aulacomnium palustre,

Eriophorum vaginatum, Ptilidium ciliare and Rhytidiadelphus squarrosus, all indicative of acid, wet, peaty gley soils.

Near the summit ridge, at 1,900 and 2,000 ft., the soil type had changed to a dry podsol and the vegetation to a Species Poor Festucetum. Though Juncus squarrosus was present, the species had a very low cover value and only occurred as isolated tufts between Festuca spp. Accompanying species, characteristic of thin podsol soils found near the dry summits of fells, included Dicranum scoparium, Hypnum cupressiforme, Pleurozium schreberi and Vaccinium myrtillus.

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). In Table 1, meteorological data for 1964 and 1965 have been summarised, and are compared with the average figures, taken from The Nature Conservancy's records, over the 1953-65 period. There is a high number of rain days each year, with an annual rainfall of over 74 inches. The average daily sunshine is less than four hours per day, and strong winds are common throughout the year. On average, snow is still lying

TABLE 1. SUMMARY OF MOORHOUSE METEOROLOGICAL DATA FOR 1964 AND 1965, COMPARED WITH THE THIRTEEN YEAR AVERAGE, 1953-65.

	1964	1965	Average 1953-65
Mean maximum temperature °C	8.2	7.6	8.4
Mean Minimum temperature °C	1.8	1.4	1.4
½(max.+min.) temperature °C	5.0	4.5	4.9
Average daily sunshine,hours	2.9	2.9	3.7
Rainfall, inches	73.0	83.0	74.5
Number of rain days	242	259	248
Mean monthly wind speed,knots	14.8	13.5	13.4
Days with snow lying	53	104	63
Days with air frost	127	134	131
Days with ground frost	173	198	169

on the ground at 09.00 hours G.M.T. on 63 days, and on over 30% of days throughout the year, ground and air frost is recorded.

The average monthly figures for certain climatic factors for the period 1953-65 are given in Table 2. Both summer and winter temperatures are low. The average mean temperature in January is 30.9°F (-0.6°C) and in July 51.6°F (10.9°C). Another feature of the temperature

TABLE 2. AVERAGE MONTHLY FIGURES FOR CERTAIN COMPONENTS OF THE CLIMATE OVER THE PERIOD 1953-65

Month	Mean daily maximum temperature °C	Mean daily minimum temp. °C	Average temperature °C	Rain-fall inches	Daily sunshine hours
J	1.9	-3.1	-0.6	7.6	1.2
F	1.8	-3.6	-0.9	5.2	1.7
M	4.3	-1.7	1.3	4.3	2.7
A	7.6	0.2	3.9	4.9	4.1
M	11.2	2.7	6.9	4.7	5.4
J	13.8	5.5	9.6	4.3	5.8
J	14.6	7.2	10.9	6.2	4.4
A	14.3	7.1	10.7	7.2	4.1
S	12.7	5.8	9.4	6.6	3.5
O	9.6	3.7	6.7	7.6	2.8
N	5.5	0.5	3.0	7.3	1.4
D	3.5	-2.0	0.8	8.7	1.0

records is the marked range that may occur within a twenty four hour period, diurnal fluctuations of up to 40°F (22°C) having been recorded. The climate at Moor House may be fairly described as severe, a climate which has been described by Manley (1936) as sub-arctic, having many features comparable to those at sea-level in southern Iceland.

III. THE ADULT STAGE

A. QUANTITATIVE SAMPLING OF ADULTS

1. INTRODUCTION

The great diversity in the life cycles, behaviour and habitats of different insect species, and in the particular objectives of specific field investigations, has led to an equally great diversity in techniques for population sampling. Sampling has no intrinsic merit; it is only a tool which provides the means of obtaining certain information, to be used only when there is no easier way of obtaining the information. Morris (1960) has stressed the importance of clearly defining the objective for which sampling is required. An important distinction is that between sampling of population density and sampling designed to study particular aspects of an animal's ecology such as development stages and degrees of parasitism and disease.

Most adult members of the Tipulidae are highly motile and, as with many ecological studies of non-sessile animals, there is great difficulty in obtaining an absolute measure of population density. The majority of sampling techniques used in studies on the ecology of adult Tipulidae may be included in the second of the categories mentioned above. Sweep nets and traps employing light, suction and adhesive substances have been used in investigations of such topics

as the seasonal incidence of adults, in describing relative numbers on different vegetation types and in work on daily rhythms of activity (e.g. Williams, 1935; Pinchin & Anderson, 1936; Lewis & Taylor, 1965).

From these techniques it is possible to derive a population index, (called also a relative estimate), that is any sort of measurement or count which is related to population density. A population index is, however, of limited value by itself; almost invariably it is related to other factors in addition to density. Many authors have commented that the numbers of insects caught depends not only on the population available for trapping, but also on activity, which in turn depends on various components of the weather (e.g. Williams, 1940; Hughes, 1955; Taylor, 1963). Though it is possible to standardize population indices to provide information on relative populations available for trapping in different periods or different areas, they cannot provide an absolute measure of numbers present as was required in the present study. In many studies, no improvement either in field methods, or in consideration of results can overcome the basic difficulty that the number of animals recorded depends not only on the density of the population, but also on the activity of individuals within it.

2. SUCTION SAMPLING OF ADULTS

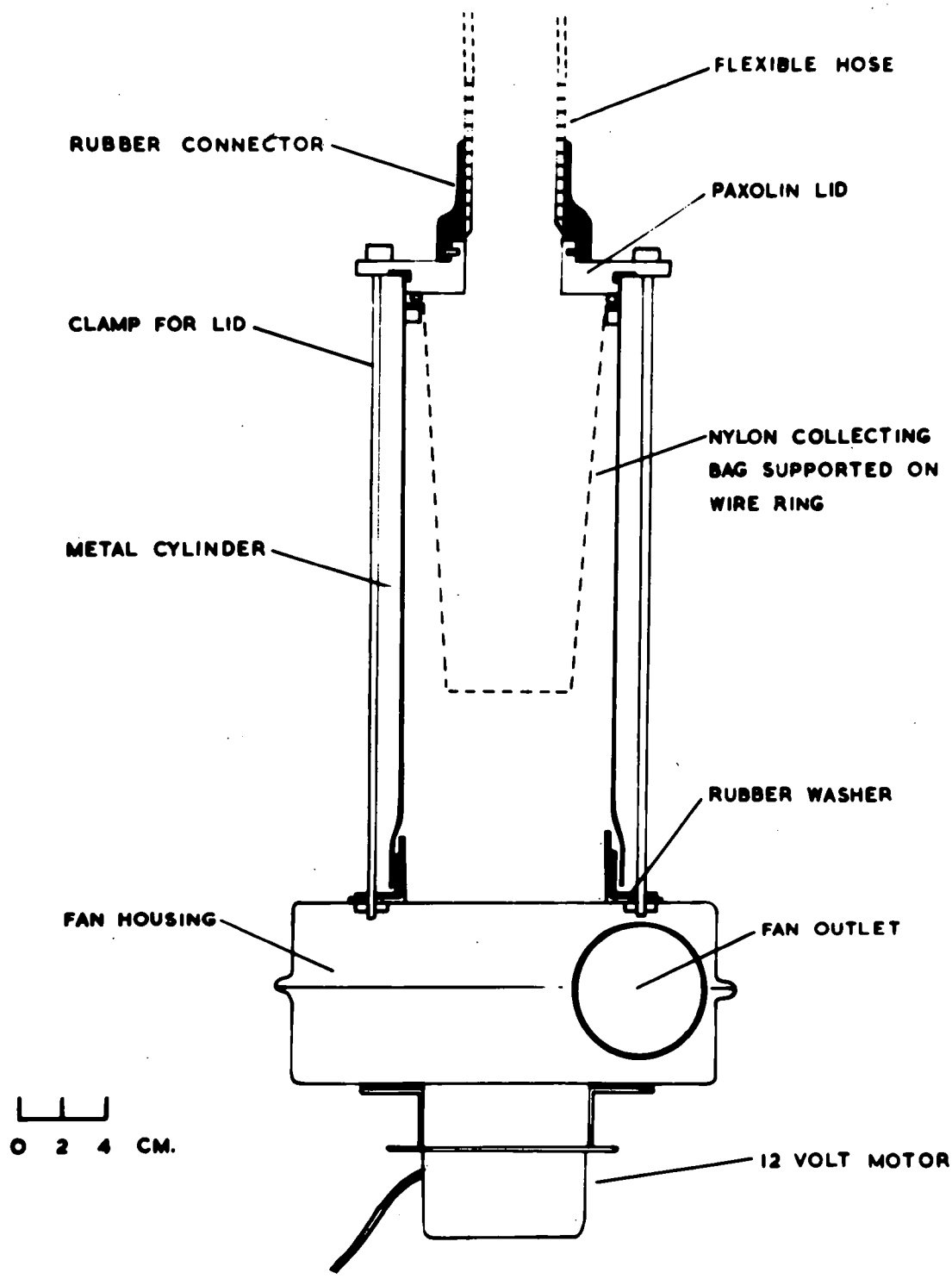
a) THE APPARATUS

The adults of both sexes of Molophilus ater possess abbreviated wings and are flightless; consequently it is possible to determine accurately numbers per unit area of habitat. A variety of electric or hand driven suction pumps which can achieve a precise measure of population density have been developed, and have been reviewed by Southwood & Pleasance (1962).

The apparatus used in the present study (Fig. 2, Plate 2) was a modified form of the machine described by Johnson, Southwood & Entwistle (1957) for quantitative sampling of organisms inhabiting herb and ground stata, and the surface layers of certain kinds of litter.

The suction unit consists of a Smith's F350 centrifugal blower, capable of passing 165 cubic ft./min. of free air, powered by a 12 volt battery. A rubber collar seals the intake opening of the unit to a 14 cm. metal cylinder. A nylon collecting bag, suspended on a metal ring, rests inside the mouth of the cylinder, and is held in position by a "Tufnell" lid with detachable wing nuts. The unit is air sealed except for intake through a flexible hose (Wolf No. 470), attached to the lid by a rubber connector and terminating in a rubber nozzle

FIG. 2. SECTIONAL DRAWING OF THE VACUUM EXTRACTOR.



SECTIONAL DRAWING OF VACUUM EXTRACTOR

PLATE 2. THE SUCTION SAMPLER.

On the right is the flexible hose attached to the vacuum extractor, on the right the 12 volt battery mounted on a pack frame.

of diameter 3.5 centimetres. Organisms and debris are carried down the flexible hose into the metal cylinder. The larger diameter of this cylinder, compared with that of the nozzle, results in a radical fall in the air speed, and organisms are collected in the nylon bag without damage.

Estimates of density of two separate components of the population were measured daily during the emergence period; namely, the total number of adults and the number of newly emerged adults.

b) THE OPERATION OF THE APPARATUS

i. Total adults

Sampling procedure consisted of drawing the nozzle through vegetation enclosed by an open aluminium cylinder of known area (0.1 sq.m. or 0.05 sq.m.) placed randomly and pushed down immediately into the vegetation and soil to a depth of about 5 centimetres. The organisms and debris contained in the nylon collecting bag were transferred to screw top jars of the same diameter as the top of the nylon bag. Ten samples were taken daily from each sampling site.

Initially, the samples were returned to the laboratory, the contents of each jar transferred to trays, and the number of Molophilus counted. With greater experience, numbers were counted in the field, using an aspirator to

remove all individuals out of each sample jar; the species may be readily identified and the sexes distinguished by the naked eye and, being active, the individuals were easily seen. After counting, the animals were returned to the area from which they were extracted.

ii. Newly emerged adults

Prior to the start of the emergence period, open aluminium cylinders of the type already described were distributed randomly over the sampling area and pushed down into the vegetation and soil. Each trap remained in its determined position, enclosing the same known area of vegetation, throughout the adult period. Each trap was emptied of Molophilus daily using the vacuum extractor, enabling daily estimates to be made of the density of newly emerged adults.

The cylinders were sufficiently high (35 cm.) to prevent adults entering or leaving the cylinders via overhanging vegetation. The possibility of them doing so by crawling up the sides of the cylinders was precluded by smearing a layer of adhesive, about 3 cm. wide, on the inner and outer surfaces of the upper rim of the cylinders. Only those adults caught on the inner surface were counted as emergences from the delimited area under surveyance;

those caught on the outer surface were ignored.

The effect of diurnal rhythms of emergence must obviously be considered in any sampling programme designed to study quantitatively a population's emergence pattern. A preliminary survey suggested that almost the total daily emergence was completed between dawn and 12.00 G.M.T.; consequently samples, both of newly emerged and total adults, were taken between 12.00 and 16.00 hours. After extraction and counting, newly emerged adults were either used in laboratory experiments or returned to vegetation outside of the sampling site being investigated.

Southwood & Siddorn (1965) have commented that the validity of measurements by emergence traps on the numbers of insects emerging from soil or growing vegetation will depend on the degree to which the presence of the trap has altered the climate of the micro-habitat of the insect. It is feasible that emergence traps could significantly advance or retard an insect's development. Measurements taken 3 cm. above soil level suggested that though the temperatures inside the emergence traps used were slightly lower by day and higher by night than those of unshielded vegetation, the net discrepancy between the two was very small. Unlike the traps compared by Southwood & Siddorn (1965), the traps used in the present study had no tops and were open to the atmosphere; the influence of any

culmative temperature difference on the onset of emergence was discounted for Molophilus, where the entire population emerges within a period of about 16 days. As a further precaution, the traps were not placed into position until the latest possible moment prior to emergence starting.

c) EFFICIENCY OF APPARATUS

The efficiency of any method of population estimation is the percentage of the animals present that are actually recorded. It was found impossible to mark individual Molophilus using spots of paint, owing to the size of the adult flies. A satisfactory marking procedure was that used by Dalmat (1950, 1952) where an aniline dye dust was blown on to a known number of adults, contained in a glass screw-top jar, using a rubber bulb syringe. The dye is detected by passing individuals through a solvent, a mixture of absolute alcohol, glycerine and chloroform. The marked flies impart the characteristic colour of the dye to the solvent.

Several sampling regimes were compared for each site under investigation. For the Peaty Gley and Peaty Podsol sites, and for sample unit areas of 0.05 sq.m., a regime of 1½ minutes extraction, after which the collecting bag was emptied of Molophilus, followed by another one minute's extraction, gave the best compromise between efficiency and

use of time. On the Carecetum site, the regime adopted comprised two separate one minute periods of extraction, between which the nylon collecting bag was emptied. The efficiency was estimated by suction sampling known numbers of marked adults which had been allowed to re-distribute themselves within the herbage. The mean efficiency of suction sampling was found to be 91 per cent (Table 3).

TABLE 3 THE EFFICIENCY OF THE VACUUM EXTRACTOR

Site	Peaty Podsol	Carecetum
No. of adults marked	150	150
No. recovered	134	139
Per cent recovered	89	93

3. OTHER METHODS

Vacuum sampling was found impossible on Calluna dominated Blanket Bog, due to the varying height and toughness of the vegetation. In order to study the emergence period on Blanket Bog, and other selected sites also, trapping techniques relying on the locomotor activity of Molophilus were used. From the two methods employed, sticky traps and detergent traps, population indices could be derived.

a) STICKY TRAPS

Results obtained from any trapping method relying on locomotive activity may be effected by many factors other than population size. Catches by sticky traps have been shown to be influenced by the exposure of the trap (Heathcote, 1957a), the colour of the trap (Lewis, 1959; Entwistle, 1963), the trap size (Heathcote, 1957b; Staples & Allington, 1959) and wind speed (Taylor, 1962). A variety of resins and greases have been used as adhesive mechanisms for sticky traps (Ibbotson, 1958; Maxwell, 1965), and traps of several basic designs have been developed (Golding, 1946; Moreland, 1954).

The use of "Sellotape" as the adhesive medium was discarded after preliminary tests showed that the traps were of little use when wet. In addition, some individual adults were able to walk short distances over the adhesive, making any results on the height of capture on the trap invalid. Traps using "Stictite", a fruit-tree banding resin, proved more satisfactory for catching Molophilus, and this was used as the adhesive medium.

The traps were similar to those used by Broadbent et al. (1948), Lewis (1959) and Cornwell (1960). They consisted of aluminium cylinders, 18 cm. high and 5.5 cm. in diameter. Each trap was supported vertically by a wooden stake, with the base of the trap flush with the soil surface.

b) DETERGENT TRAPS

These consisted of glass jars (7.5 cm. high with a diameter at the mouth of 9 cm.), sunk in the ground with their rims level with the soil surface. The jars were filled with water, and a small quantity of detergent, which serves to lower the surface tension of the water, added. Omission of the detergent has been shown to drastically reduce the number of insects caught (Harper & Storey, 1962).

Detergent traps have certain advantages over sticky traps; they have been shown to make catches when sticky traps of a manageable size would not (Heathcote, 1957a), and the insects caught are in good condition, and are easily removed by a pair of forceps. One major criticism of detergent traps, that they overflow in heavy rain or dry out in warm weather, was not considered important in the present study, where individuals were removed daily.

4. PRELIMINARY COMPARISON OF DIFFERENT TRAPPING METHODS

The only precise method of measuring quantitatively the adult emergence of Molophilus is to use the emergence traps already described. It was not possible to use emergence traps either on Blanket Bog, or on privately owned "East Transect" where the effect of altitude on emergence was studied. On these sites use had to be made of measurements of components of the population other than the density of newly emerged adults;

namely, estimates of density of total adults present, and the number of individuals caught by sticky traps and detergent traps. The validity of using these methods to study the emergence pattern of the species will depend on how accurately they reflect the emergence of adults. In Table 4, the numbers of newly emerged adults extracted daily are compared with the numbers recorded by the other methods for the Peaty Podsol site in 1965.

TABLE 4 COMPARISON OF NUMBERS RECORDED BY DIFFERENT SAMPLING METHODS ON THE PEATY PODSOL SITE IN 1965

Date	No.of newly emerged adults extracted from ten,0·05 sq.m. emergence traps	No.of total adults extracted from ten,0·05 sq.m.random samples	No.of adults caught in 8 detergent traps	No.of adults caught by 8 sticky traps
30 May	1	4	3	3
31 May	16	17	9	7
1 June	22	20	8	4
2 June	34	36	15	9
3 June	78	74	51	7
4 June	86	104	42	16
5 June	142	165	69	30
6 June	144	165	42	33
7 June	177	188	73	23
8 June	113	139	42	33
9 June	70	79	46	12
10 June	33	47	17	6
11 June	11	17	12	7
12 June	2	3	4	2
13 June	4	3	4	0
14 June	0	0	2	1
Total caught	933	1,061	439	193

TABLE 5 ANALYSIS OF RESULTS OBTAINED BY DIFFERENT TRAPPING METHODS ON THE PEATY PODSOL SITE IN 1965

	Density of newly emerged adults	Density of total adults	No. caught by detergent traps	No. caught by sticky traps
Date of first capture	30 May	30 May	30 May	30 May
Date of last capture	13 June	13 June	14 June	14 June
Range of captures	15 days	15 days	16 days	16 days
Date when 50% of total taken	6 June	6 June	6 June	6 June
Middle 67% of total catch recorded (days)	5	5	6	5
Middle 95% of total catch recorded (days)	10	11	11	12

Analysis of the pattern of results obtained from each trapping method shows a close measure of agreement (Table 5). The short life span of adults makes all methods similar, and though estimates of density of daily and total emergences can only be derived using emergency traps, it is considered valid to use the other methods described to investigate the range and pattern of the emergence period of the species.

B. THE EMERGENCE PERIOD

1. EMERGENCE AT MOOR HOUSE

In 1964, the emergence period of adults of Molophilus ater at Moor House was investigated in detail on only one site, the Peaty Gley nodum at Bog End. The following year, the emergence period was studied quantitatively on three sites, namely, the Peaty Gley, the Peaty Podsol and the Carecetum noda. Newly emerged adults were removed daily from emergence traps using the vacuum extractor, and the numbers taken recorded (Figs. 3 and 4). This enabled daily estimates to be made of the density of newly emerged adults throughout the emergence period (Table 6). In 1964, the emergence traps comprised 5 aluminium cylinders, each enclosing 0.1 sq.m. of vegetation; in 1965, 10 cylinders, each covering 0.05 sq.m., were used on each site. On the Blanket Bog in 1966, 10 detergent traps were emptied of adults each day, since suction sampling was found to be technically impossible on this site. Though detergent trapping cannot quantitatively describe the densities of either daily or total adult emergences, they do accurately record the pattern and duration of the emergence period. The numbers of adults caught daily are included on Fig. 4.

Any emergence pattern may be readily described using a small number of parameters. Each of the five emergence periods studied has been analysed separately. (Table 7).

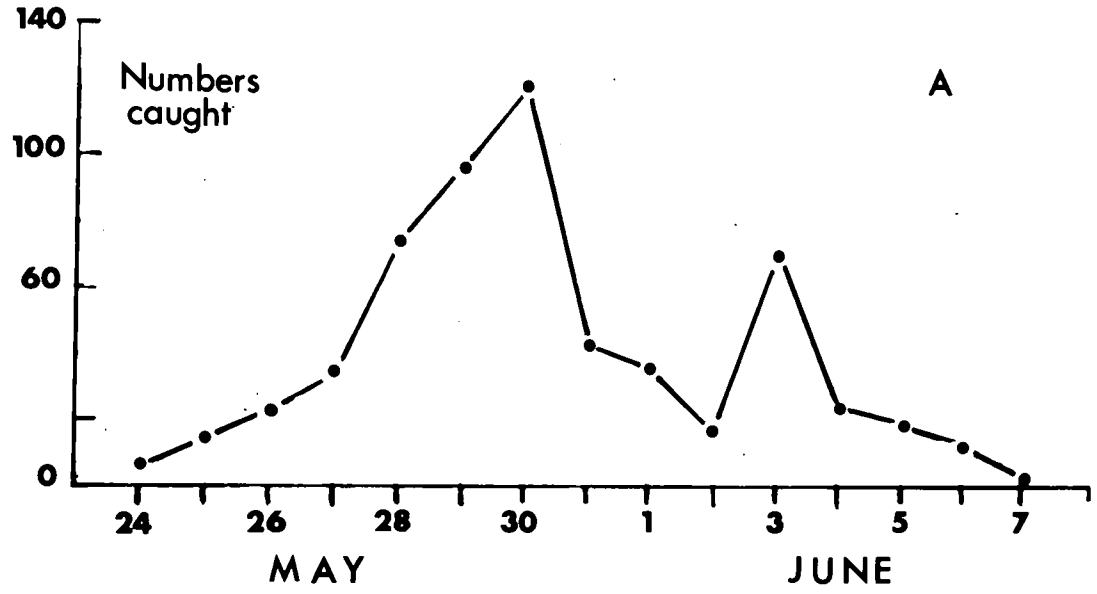
FIG. 3. THE EMERGENCE PERIOD OF ADULTS AT MOOR HOUSE.

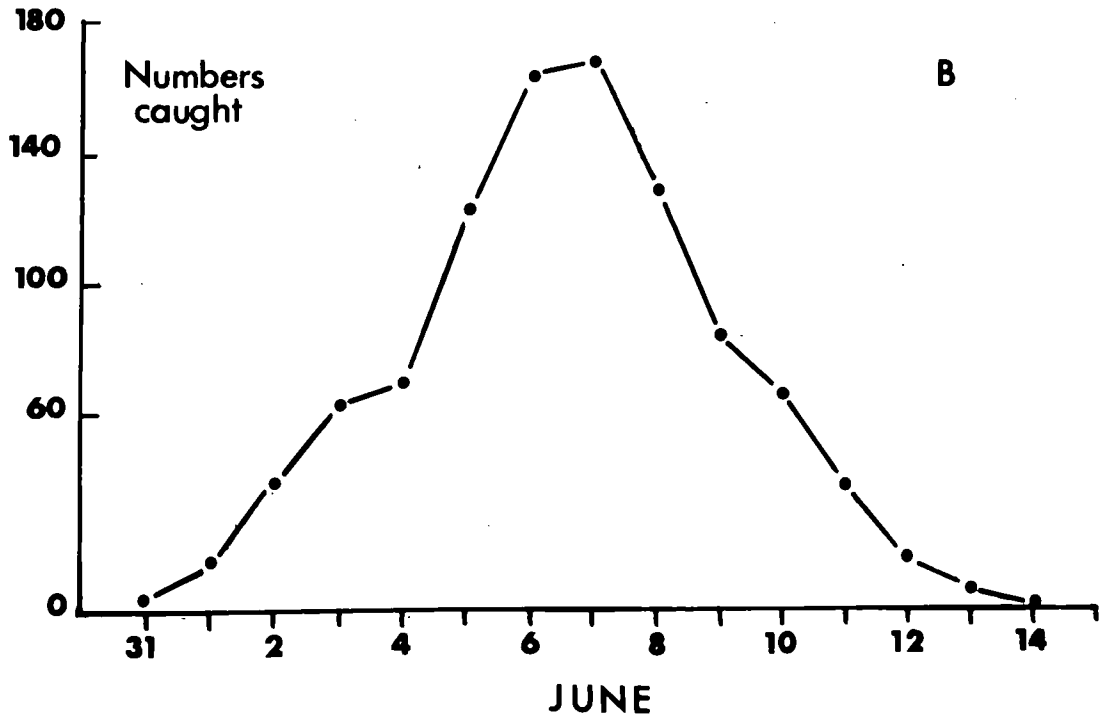
A. PEATY GLEY SITE, 1964.

The numbers of newly emerged adults extracted daily from five, 0.1 sq.m. emergence traps are shown.

B. PEATY GLEY SITE, 1965.

The numbers of newly emerged adults extracted daily from ten, 0.05 sq.m. emergence traps are shown.


140
100
60
0
Numbers caught
A
24
26
28
30
1
3
5
7
MAY
JUNE


180
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100
60
0
Numbers caught
B
31
2
4
6
8
10
12
14
JUNE

FIG. 4. THE EMERGENCE PERIOD OF ADULTS AT MOOR HOUSE.

A. PEATY PODSOL SITE, 1965.

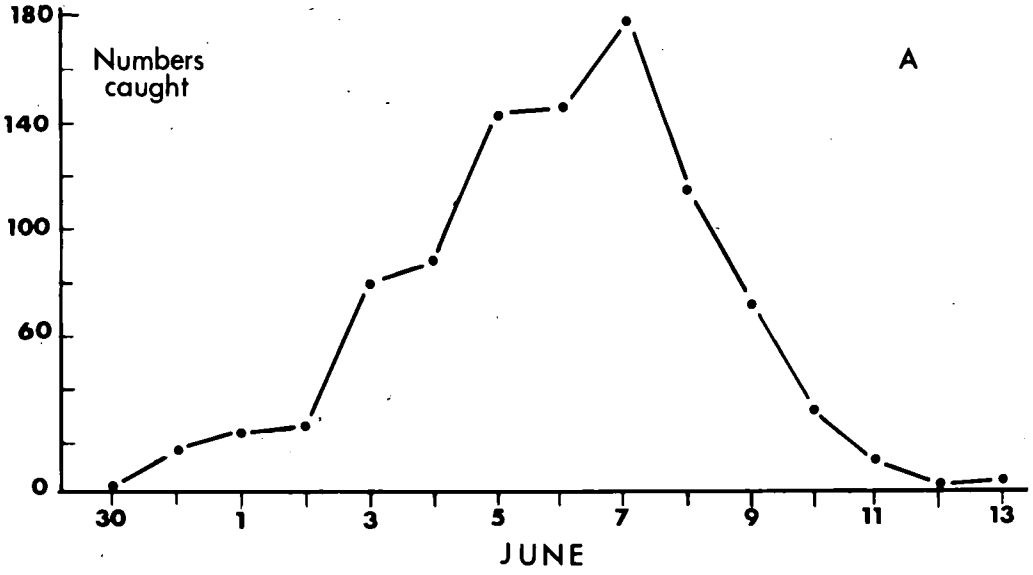
The numbers of newly emerged adults extracted daily from ten, 0.05 sq.m. emergence traps are shown.

B. CARECETUM SITE, 1965.

The numbers of newly emerged adults extracted daily from ten, 0.05 sq.m. emergence traps are shown.

C. BLANKET BOG SITE, 1965.

The numbers of adults caught daily by 10 detergent traps are shown.


180
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Numbers caught
A
30
1
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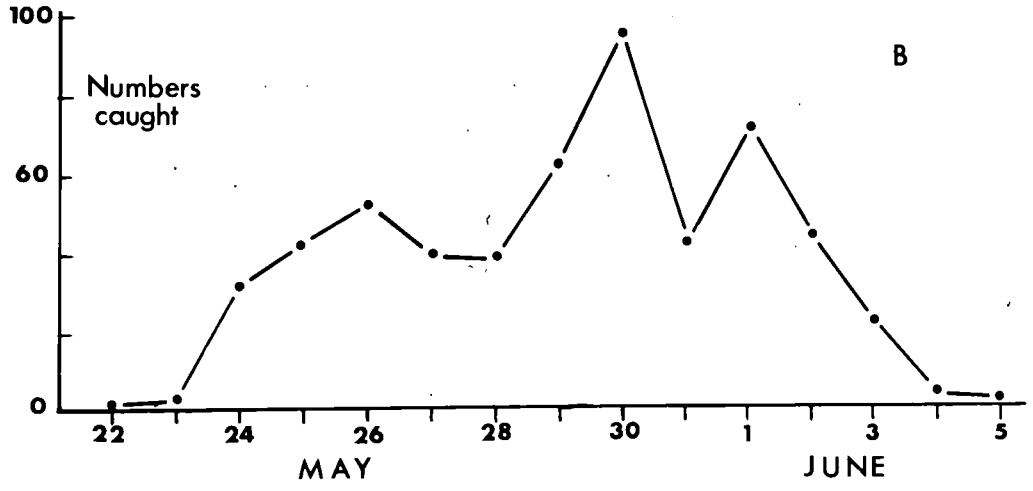
11
13
JUNE


100
60
0
Numbers caught
B
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30
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MAY
JUNE

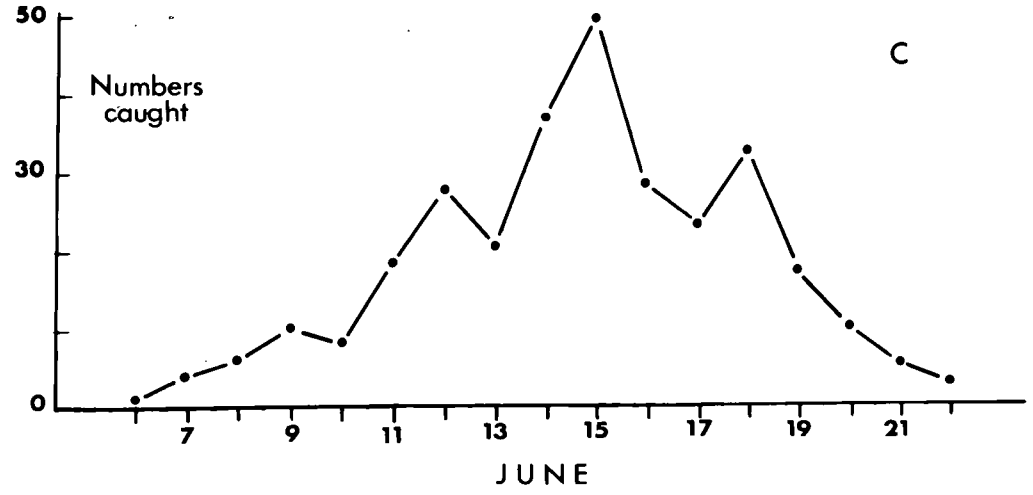

50
30
0
Numbers caught
C
7
9
11
13
15
17
19
21
JUNE

TABLE 6. DAILY DENSITY PER SQ.M. (± S.E.) OF NEWLY EMERGED ADULTS AT MOOR HOUSE

	Peaty Gley Site, 1964	Peaty Gley Site, 1965	Peaty Podsol Site, 1965	Carecetum Site, 1965
22 May				2 ± 1.9
23 May	0			32 ± 6.2
24 May	14 ± 3.6			66 ± 14.2
25 May	32 ± 5.2			86 ± 18.3
26 May	48 ± 8.2			106 ± 22.4
27 May	68 ± 10.4			78 ± 21.6
28 May	152 ± 12.5			76 ± 17.6
29 May	196 ± 30.0		0	126 ± 25.9
30 May	242 ± 12.1	0	2 ± 1.9	188 ± 54.9
31 May	88 ± 17.8	8 ± 5.1	32 ± 11.0	86 ± 28.0
1 June	74 ± 3.6	30 ± 6.5	44 ± 14.4	144 ± 35.6
2 June	36 ± 9.4	78 ± 30.8	68 ± 24.7	90 ± 20.8
3 June	142 ± 15.6	126 ± 31.6	154 ± 38.8	46 ± 14.1
4 June	50 ± 12.2	138 ± 12.1	172 ± 22.7	12 ± 3.9
5 June	40 ± 11.3	244 ± 22.8	284 ± 30.4	8 ± 3.9
6 June	26 ± 9.6	328 ± 33.1	288 ± 15.5	0
7 June	2 ± 1.9	336 ± 20.4	354 ± 28.1	0
8 June	0	258 ± 25.7	226 ± 22.1	
9 June	0	164 ± 17.9	140 ± 20.2	
10 June		130 ± 12.1	66 ± 12.6	
11 June		78 ± 18.2	22 ± 4.4	
12 June		28 ± 9.0	4 ± 2.5	
13 June		10 ± 5.1	8 ± 4.2	
14 June		2 ± 1.9	0	
15 June		0	0	

TABLE 7 ANALYSIS OF THE EMERGENCE PERIOD ON DIFFERENT SITES AT MOOR HOUSE

Site and Year	Date of first emergence	Date of last emergence	Range of Emergences (days)	Middle 67% of total emergence (days)	Middle 95% of total emergence (days)	Mean date of emergence	Median date of emergence
Peaty Gley 1964	24 May	7 June	15	6	12	30 May	31 May
Peaty Gley 1965	31 May	14 June	15	5	10	6 June	7 June
Peaty Podsol 1965	30 May	13 June	15	5	10	6 June	6 June
Carecetum 1965	22 May	5 June	15	7	11	29 May	30 May
Blanket Bog 1965	6 June	22 June	17	7	12	14 June	15 June

The findings indicate a remarkable constancy in the duration and pattern of the emergence period of Molophilus ater. The entire population on each site investigated completes its emergence within 15 to 17 days during late May and early June. The middle two-thirds emerge within a period of 5 to 7 days, the middle 95% within a period of 10 to 12 days. The distribution of adult emergences is symmetrical. There is close agreement between the median and mean values, and there is no evidence of a marked asymmetry or skew in the emergence of adults on any site studied.

Though for each emergence period studied the pattern and duration of emergences are similar, there are differences in the timing of emergence from year to year and from one site to another. In 1965, emergence on the Peaty Gley site was delayed about 8 days compared with the emergence period on the same sampling site in the previous year. In 1965, 50% of the total emergence had occurred by 6 June, compared with 30 May in 1964. Though a precise explanation of this phenomenon would require a detailed comparison of the degree of development throughout the larval stadium in the two years, it seems possible that the earlier emergence in 1964 is due to the slightly higher temperatures recorded in the spring of that year compared with 1965. The average mean daily temperature for April and May in 1964 was 42.9°F (6.1°C); in 1965 the corresponding temperature was 41.4°F (5.2°C).

It is perhaps interesting to note that in 1965 the emergence period on the Carecetum nodum is 8 days earlier than on the Peaty Gley and Peaty Podsol noda, that on the Blanket Bog some 9 days later. All these sites are approximately at the same altitude; the discrepancies of the timing of the emergence period seem likely to be due to differences in vegetation on individual sites. The vegetation on the Carecetum site, as well as being on a slight slope facing south, is lower and less dense than on the Peaty Gley and Peaty Podsol sites. On Blanket Bog, Calluna probably acts as an insulator of the soil during the spring, resulting in a retardation of the emergence period on this site. The matter requires investigation.

Though the sex ratio at emergence is discussed in detail in later pages, it is perhaps pertinent to consider here any differences in the pattern and duration of the male and female emergence periods. In Table 8, the numbers, and the accumulative percentages, of male and female daily emergences on the Peaty Podsol site in 1965 are recorded. Two differences between the sexes are apparent. Firstly, the range of emergence is one day shorter for females than for males. The first male emergence was recorded on 30 May, the first female emergence on 31 May. The last male and female emergences were recorded on the same day, 13 June. The second feature is the earlier emergence of the males. On 6th June, the median day of the whole emergence period, 59.7% of the total male emergence, but only 49.9 ~~41~~.0% of

TABLE 8 THE NUMBERS, AND ACCUMULATIVE PERCENTAGES, OF MALE AND FEMALE EMERGENCES RECORDED DAILY ON THE PEATY PODSOL SITE IN 1965

	MALES		FEMALES		TOTAL	
Date	No.	Accumulative %	No.	Accumulative %	No.	Accumulative %
30 May	1	0.2	0	0	1	0.1
31 May	15	2.7	1	0.3	16	1.8
1 June	17	5.6	5	1.7	22	4.2
2 June	25	9.8	9	4.4	34	7.8
3 June	47	17.8	31	13.4	78	16.2
4 June	58	27.6	28	21.6	86	25.4
5 June	92	43.2	50	36.2	142	40.6
6 June	97	59.7	47	49.9	144	56.1
7 June	120	80.0	57	66.5	177	75.0
8 June	64	90.8	49	80.8	113	87.1
9 June	37	97.1	33	90.4	70	94.6
10 June	11	99.0	22	96.8	33	98.2
11 June	4	99.7	7	98.8	11	99.4
12 June	0	99.7	2	99.4	2	99.6
13 June	2	100.0	2	100.0	4	100.0
Total	590		343		933	

the total female, had been recorded. The peak emergence for both males and females occurred on the same day, 7 June. For both sexes, the middle 67% of the total emergence took place within 5 days. For the male emergence, the middle 95% of the

total occurred within 10 days, whilst for females the same percentage was recorded within a period of 9 days, emphasizing the slightly shorter period of the female emergence.

Similar findings to these were reported on the other sites investigated in 1965. On the Peaty Gley site, the female emergence, though ending on the same day, started one day later than the male emergence, on 1 June. By the median day of the emergence period, 71.3% of the total male, but only 56.2% of the total female, emergence had taken place. Similarly, on the Carecetum site, only 36.0% of the total female, but 57.1% of the total male, emergence had been recorded by the median day of the entire emergence period.

The estimated numbers of total emergences are recorded for each site where quantitative measurements of the density of newly emerged adults are available (Table 9). Each sampling site supported very high numbers of Molophilus ater. The density of emergences per sq.m. ($\pm$ S.E.) range from 1130 $\pm$ 153 on the Carecetum site in 1965, to 1958 $\pm$ 75 on the Peaty Gley site in 1965. There are very few references in the literature to the numbers of crane-flies in their natural habitats. Coulson (1962) recorded for Tipula subnodicornis Zetterstedt at Moor House a density of 111 larvae per sq.m., four weeks before emergence, and Freeman (1964) reported mean adult densities for Tipula luna Westhoff of 0.27 per sq.m. and 0.45 per sq.m. on two different areas of the Matley and Denny Forest

TABLE 9 COMPARISON OF THE ESTIMATED DENSITY OF TOTAL EMERGENCES WITH THE MAXIMUM DAILY EMERGENCE

Site and Year	Density of total emergences per sq.m. (± S.E.)	Maximum daily emergence per sq.m. (± S.E.)	Percentage
PEATY GLEY, 1964			
Total	1212 ± 87	242 ± 31	20.0
Males	858 ± 51	152 ± 18	17.7
Females	354 ± 26	90 ± 12	25.4
PEATY GLEY, 1965			
Total	1958 ± 75	336 ± 20	17.2
Males	1240 ± 50	218 ± 24	17.6
Females	718 ± 39	124 ± 12	17.3
PEATY PODSOL, 1965			
Total	1866 ± 154	354 ± 28	19.0
Males	1180 ± 93	240 ± 23	20.3
Females	686 ± 66	114 ± 13	16.6
CARECETUM, 1965			
Total	1130 ± 153	188 ± 59	16.6
Males	708 ± 32	106 ± 38	15.0
Females	422 ± 71	82 ± 21	19.4

Nature Reserve. These contrast greatly with the densities recorded for Molophilus ater, though it must be remembered that there is a large difference in size between Molophilus ater and Tipula spp..

Included in Table 9 is a comparison of the peak daily emergence and the total emergence recorded for the entire adult period. For each emergence period studied, between 16% and 20% of the total number of emergences occurred on a single day. The average maximum daily emergence, for each of the four sites combined, accounts for 18.2% of the total number of adults which emerge. These figures emphasise the highly synchronised nature of the emergence of Molophilus ater; the entire population, comprising densities of between 1000 and 2000 individuals per sq.m., emerge within a period of about 15 days, with the middle two-thirds of the emergence taking place within 5 to 7 days.

2. THE EFFECT OF ALTITUDE ON EMERGENCE

Much of the literature on the influence of altitude on many aspects of insect life has been reviewed by Mani (1962). Several workers at Moor House have investigated the effect of altitude on the distribution and life cycles of certain moorland insects. Intensive studies on the tineoid moth Coleophora alticolella Zell. have emphasised the importance of climatic and environmental factors in determining the yearly altitudinal

limit of the species (Jordan, 1958, 1962; Reay, 1964; Welch, 1965). Egg hatching of the homopteran Neophilaenus lineatus (L.) is progressively delayed, and nymphal development progressively retarded, at higher altitudes (Whittaker, 1965). At a certain altitude, which is determined in any particular year by climatic factors, the species cannot complete its life cycle.

It was not possible in the present work to investigate the yearly altitudinal distribution of Molophilus ater. The study was limited to a determination of whether altitude influenced in any way the adult emergence of the species. The area sampled approximated to the "East Transect" of Jordan (1962), and is described in Section II. Though the range of altitude was from 1500 ft. to 2000 ft., preliminary sampling showed that no individuals were present above 1840 ft. This is not due to an altitudinal effect, since the species has been found at 2400 ft. on the Moor House Reserve. Rather it is referable to a change of soil and vegetation at this altitude from a Species Poor Peaty Gley, dominated by Juncus squarrosus, Polytrichum commune and Sphagnum spp., to a thin podsol soil dominated by Festuca spp. At Moor House, similar vegetation to the latter, termed a Species Poor Festucetum, did not support Molophilus ater.

Four sampling stations, each separated from the next by a vertical interval of 100 ft. (30.4 m.), were determined

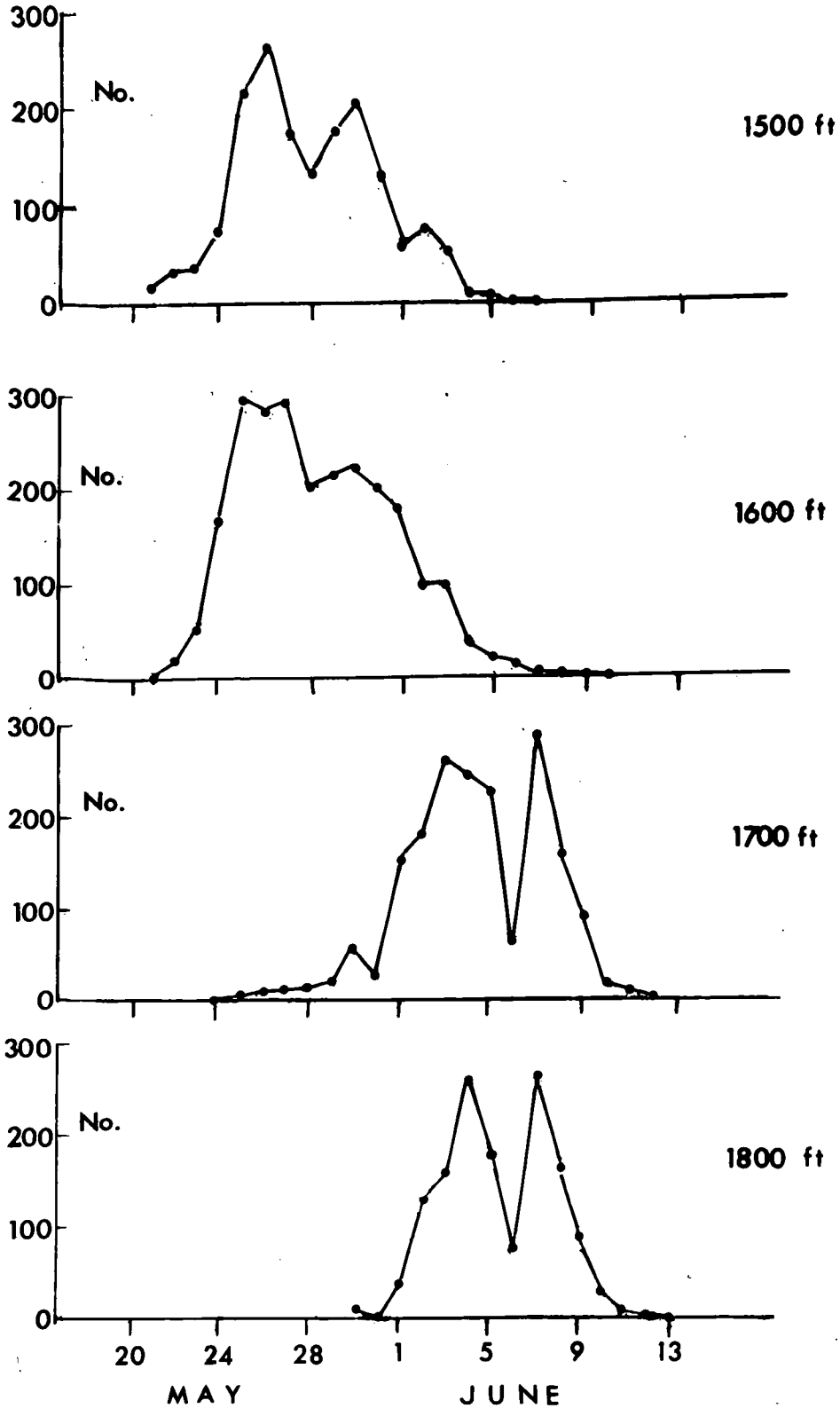
using an aneroid-barometer altimeter. The lowest station was at 1500 ft. (457 m.), the highest at 1800 ft. (549 m.). In 1965, the vacuum extractor was used to estimate the number of adults present. Ten random samples, each of 0.05 sq.m., were taken daily from each station throughout the adult period. The number of adults taken daily from each station was recorded (Fig. 5), and estimates of density determined (Table 10). In 1966, the time consuming measurement of absolute population density was discarded, and detergent traps were used to provide relative estimates of the population size. At each station 10 detergent traps were arranged in two rows of five, and were spaced at one metre intervals. The traps were emptied daily throughout the adult period, and the number of individuals caught was recorded (Fig. 6).

Though neither of the methods used in 1965 and 1966, namely the measurement of absolute densities and relative estimates of population size, are strictly measures of the density of newly emerged adults, they have been shown to reflect accurately the emergence pattern of the species. They cannot record daily and total estimates of adult emergences, but they do provide a satisfactory indication of the length and form of the emergence period.

The pattern and duration of the adult period at each altitudinal station in 1965 and 1966 have been analysed (Tables 11 and 12). The results in 1966 closely parallel those

FIG. 5. THE EMERGENCE PERIOD OF ADULTS ON THE "EAST TRANSECT", 1965.

At each station, the numbers of adults caught daily by suction sampling ten, 0.05 sq.m. random samples are shown.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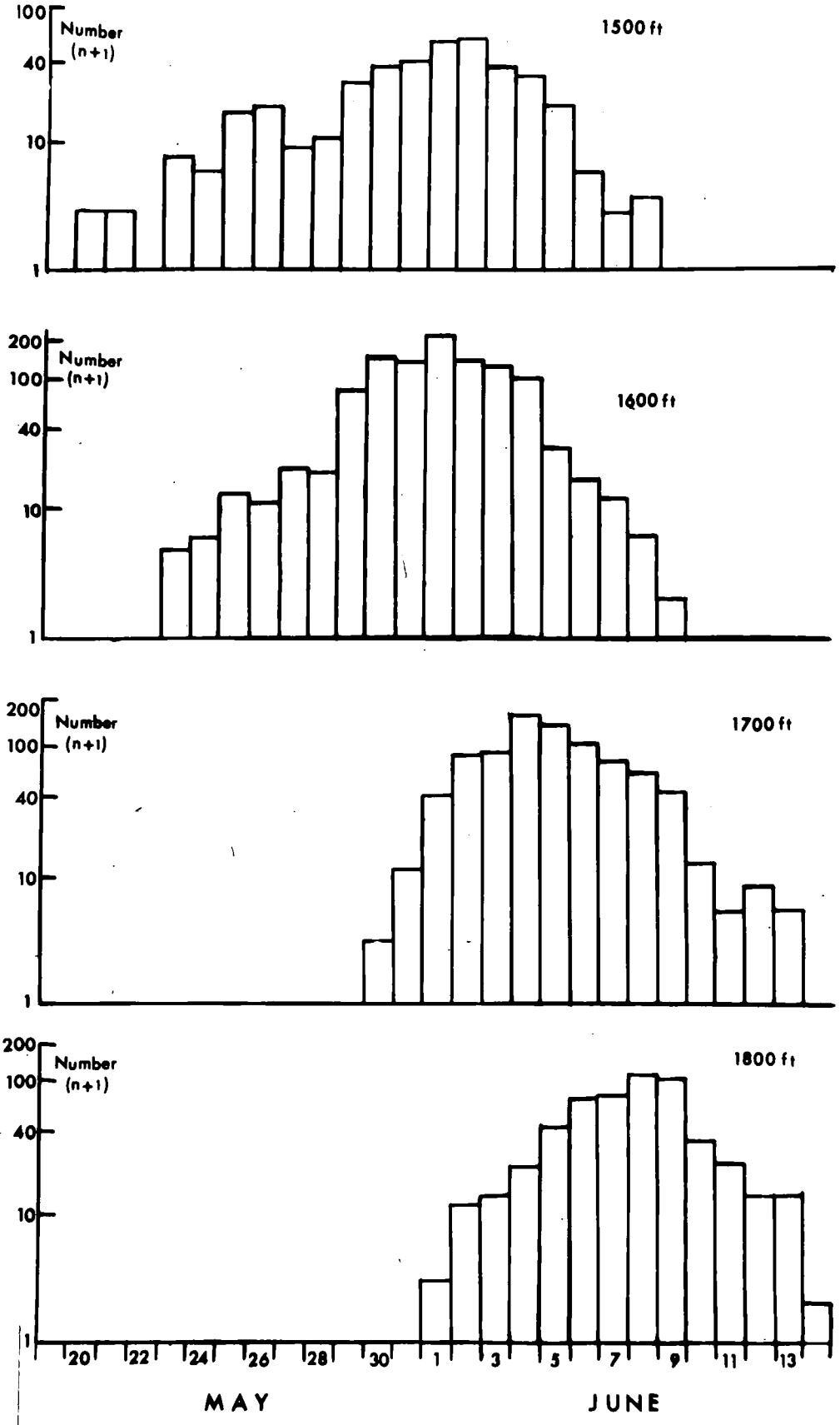
No.
1800 ft
20
24
28
1
5
9
13
MAY
JUNE

TABLE 10 DAILY DENSITY PER SQ. M. (± S.E.) OF ADULTS ON THE "EAST TRANSECT", 1965

Date	Altitude (ft.) 1500	1600	1700	1800
21 May	50 ± 15.3	14 ± 5.7	0	
22 May	82 ± 21.3	44 ± 13.2	0	
23 May	40 ± 24.4	118 ± 39.7	0	
24 May	178 ± 21.5	350 ± 51.2	4 ± 2.4	
25 May	452 ± 61.3	604 ± 91.7	8 ± 4.2	
26 May	556 ± 76.2	584 ± 35.4	24 ± 9.7	
27 May	370 ± 40.0	612 ± 40.6	22 ± 6.6	
28 May	258 ± 59.4	422 ± 55.1	28 ± 12.2	0
29 May	378 ± 45.6	438 ± 52.2	50 ± 18.6	0
30 May	438 ± 47.6	456 ± 55.1	130 ± 31.3	8 ± 4.2
31 May	270 ± 35.4	418 ± 44.1	66 ± 18.4	0
1 June	130 ± 26.4	370 ± 34.2	314 ± 31.4	108 ± 28.4
2 June	166 ± 34.2	206 ± 20.2	374 ± 32.7	270 ± 25.0
3 June	120 ± 21.9	212 ± 30.9	534 ± 53.8	322 ± 28.3
4 June	26 ± 9.4	86 ± 19.2	512 ± 51.6	548 ± 72.4
5 June	28 ± 8.6	54 ± 11.3	472 ± 39.4	368 ± 38.9
6 June	6 ± 2.9	40 ± 9.4	148 ± 14.7	172 ± 22.8
7 June	0	16 ± 6.8	588 ± 47.9	540 ± 38.1
8 June	0	12 ± 4.2	334 ± 35.1	356 ± 26.8
9 June		0	204 ± 26.4	186 ± 17.4
10 June		0	52 ± 11.7	70 ± 17.3
11 June			34 ± 8.3	28 ± 8.1
12 June			0	4 ± 2.4
13 June			0	2 ± 0.2
14 June			0	0

FIG. 6. THE EMERGENCE PERIOD OF ADULTS ON THE "EAST TRANSECT", 1966.

At each station the number of adults caught daily by 10 detergent traps are shown.


100
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MAY
JUNE

recorded in 1965. In both years emergence is delayed at higher altitudes, the peak emergences occurring 7 to 9 days later at 1800 ft. than at 1500 ft. Similar findings, that the seasonal occurrence is earlier at lower than at higher altitudes, have been recorded for Tipula lesnei Pierre in the Canary Isles by Hemmingsen (1958).

The emergence period at 1800 ft. on the"East Transect" in 1965 followed very closely the emergence period at a similar vegetation site at the same altitude at Moor House. At 1800 ft. on the "East Transect", emergence began on 30 May and ended on 13 June, an emergence period of duration 15 days. Exactly similar results were recorded on the Peaty Podsol site at Moor House; on the Peaty Gley site, the emergence period was again of similar duration, but emergence began one day later, starting on 31 May and ending on 14 June.

Another feature of the influence of altitude on the emergence period of Molophilus is that though the middle two-thirds of the total adults are present at each altitude within a small period of 4 to 6 days, there is a progressive decrease with increasing altitude in the number of days within which the middle 95% emerge. There appears to be a narrowing of the total active phase of the life cycle at higher altitudes. A further effect of altitude is the bringing together of the male and female emergence. In 1965, at 1500 ft. 50% of the male emergence had taken place by 27 May and 50% of the female emergence by 29 May, a difference of 2 days. At 1800 ft. this difference between the mean male and

TABLE 11 ANALYSIS OF THE ADULT PERIOD AT DIFFERENT ALTITUDES ON THE "EAST TRANSECT", 1965

	1500 ft.	1600 ft.	1700 ft.	1800 ft.
Date of first capture	21 May	21 May	24 May	30 May
Date of last capture	7 June	9 June	11 June	13 June
Range of captures	18 days	20 days	19 days	15 days
Middle 67% of total adults recorded (days)	6	6	6	5
Middle 95% of total adults recorded (days)	15	13	12	8
Mean Date of adult period	27 May	28 May	4 June	5 June
Median date of adult period	30-31 May	31 May - 1 June	1 June	5 June

TABLE 12 ANALYSIS OF THE ADULT PERIOD AT DIFFERENT ALTITUDES ON THE "EAST TRANSECT", 1966

	1500 ft.	1600 ft.	1700 ft.	1800 ft.
Date of first capture	20 May	23 May	30 May	1 June
Date of last capture	8 June	9 June	13 June	14 June
Range of captures	20 days	18 days	15 days	14 days
Middle 67% of total adults recorded (days)	6	5	5	4
Middle 95% of total adults recorded (days)	14	11	9	9
Mean date of adult period	1 June	1 June	5 June	8 June
Median Date of adult period	30-31 May	31 May - 1 June	5 June	7-8 June

female emergence had narrowed to one day, 50% of males being recorded by 5 June and 50% of females by 6 June. The influence of a larger altitudinal range on this and other aspects of the emergence of adults would repay further investigation.

C. SEX RATIO

1. AVERAGE SEX RATIO

Coulson (1962) was able to determine the sex ratio of Tipula paludosa at the time of emergence by sexing pupal cases collected throughout the emergence period. The small size of the pupal case of Molophilus, and the difficulty of finding the same, precluded the use of this technique in the present study. The best estimate of the adult sex ratio for Molophilus was to use the results obtained by daily suction from emergence traps. The average sex ratios from various sites all give a preponderance of males. In each case the sex ratio is significantly different from unity (Table 13).

Similar findings of an excess of males have been reported for several other members of the Tipulidae (e.g. (Barnes, 1937; Hemmingsen, 1956; Freeman, 1964). The majority of these results are values estimated from studies on the total adult population, not on adults at the time of emergence, and any differential mortality between males and females could conceivably result in a distorted value for the true adult sex ratio. Any differential mortality for Molophilus was considered irrelevant in the present context since the average sex ratio was based on daily estimates of the sex ratio of newly emerged adults.

TABLE 13. THE NUMBERS OF MALES AND FEMALES EXTRACTED FROM EMERGENCE TRAPS

Site and Year	Number of males	Number of females	% males	χ^2	P
Peaty Gley, 1964	429	177	70.1	104.8	$\leq$0.001
Peaty Gley, 1965	620	359	63.3	67.0	<0.001
Peaty Podsol, 1965	590	343	63.2	65.4	<0.001
Carecetum, 1965	354	211	62.7	36.2	<0.001
Total	1993	1090	64.6	264.5	<0.001

The χ^2 value has been calculated using a null hypothesis that the sex ratio is equality.

A more valid criticism is that of Sellke (1936), who deprecates outdoor assessments of sex-ratios because the females are much less active than the males and often remain in other localities. Though it is true that the findings of detergent and sticky traps indicate that males of Molophilus are more active in a horizontal plane than females (see Section III, E), this could not affect the proportion of sexes extracted from permanently positioned emergence traps, or from pupal examination.

That the females remain in the lower levels of vegetation and escape detection is a more feasible possibility. However, prolonged suction sampling, after the initial sampling regime had been completed, failed to yield more than the very occasional adult. In addition, random samples, taken adjacent to the Peaty Podsol site, were subjected to vacuum extraction, immediately after which the sample turves were dug up and placed in polythene bags. These were then returned to the laboratory where the vegetation and soil was carefully searched for any individuals which may have escaped suction sampling. Suction sampling of five 0.05, sq.m. unit areas yielded 79 individuals, 48 males and 31 females. After investigation of these sample unit areas, in the laboratory, only a further 8 individuals were recovered, 3 males and 5 females. This is very much in accordance with the estimated efficiency of suction sampling on this site of 89%. Though not proven conclusively, it is considered doubtful that the excess of males recorded is the result of a large number of females escaping detection.

The pre-imago sex ratio of Tipula subnodicornis has been determined by dissection of final instar larvae (Coulson, 1962), that of Tipula luna by analysis of polymodal frequency distributions of the length of final instar head capsules (Freeman, 1964). Neither of these techniques proved successful for Molophilus ater.

The procedure adopted to determine the pre-imago sex ratio of Molophilus was to induce instar 4 larvae to pupate in the laboratory. These larvae were extracted from soil samples taken in late April - early May, immediately prior to the onset of pupation in the field. The sex of the pupae could be readily ascertained by examination of the prominent genitalia (Brindle, 1960).

Of 872 pupae examined in the laboratory, 480 were males and 392 were females, giving a sex ratio of 55.0% males. This is significantly different from unity at the 1% level ($\chi^2 = 8.9$, d.f. = 1, $P<0.01$). Though there is this preponderance of males in the pupal sex ratio in the laboratory, the difference between this and the sex ratio of total adult emergences, where of the total 3083 emergences recorded, 1993 were males and 1090 were females, is highly significant ($\chi^2 = 114.9$, d.f. = 1, $P<0.001$).

There is little evidence of a difference in mortality rate between the sexes during the pupal period. Of the 872 individuals which pupated in the laboratory, only 335, 38.4%, emerged as adults. Of the 392 female pupae, 148 emerged; of the 480 male pupae, 187 emerged. Though the recorded mortality is slightly lower for males than for females, 61.0% for males compared with 62.2% for females, this is not significant ($\chi^2 = 0.08$, d.f. = 1, $P>0.9$).

There is no evidence of a similarly large mortality during the pupal stage in the field. For each site where data are known, the estimated total density of newly emerged adults shows a close agreement with the estimated density of final instar larvae, (Table 14).

TABLE 14 COMPARISON OF DENSITIES OF FINAL INSTAR LARVAE AND OF ADULT EMERGENCES

Site and Year	Estimated Number per sq.m. (± S.E.) Instar 4 larvae	Adult emergences
Peaty Gley, 1964	1100 ± 143	1212 ± 87
Peaty Gley, 1965	1866 ± 329	1958 ± 75
Peaty Podsol, 1965	2040 ± 353	1866 ± 154
Carecetum, 1965	933 ± 172	1130 ± 153
Total	5939	6166

It is difficult to evaluate the validity of the finding of an excess of males for the species at the time of emergence. The preponderance of males recorded for the pupal stage in the laboratory is insufficient to wholly account for the sex ratio recorded in the field. Differential mortality of adults may be discounted, and neither of the other two hypotheses suggested, namely that a number of females may remain undetected or that there is a difference in mortality rates during the pupal period, has any conclusive evidence to support it. The results on the adult sex ratio may be recorded, but their explanation and and significance must remain uncertain.

2. CHANGE IN SEX RATIO

There is considerable evidence of a change in sex ratio during the emergence period of the species. There is a well defined trend towards a decrease in the proportion of males as the emergence period progresses.

In Fig. 7, the daily sex ratio recorded for newly emerged adults on the three sites investigated at Moor House in 1965 is expressed graphically, and regression lines drawn. The correlation coefficients for the relationship between the percentage of male emergences and the progression of the emergence period are given; on the Peaty Gley site the rate of change in the percentage of each sex at emergence was 3.3% per day, on the Peaty Podsol site 3.6% per day, and on the Carecetum site 5.0% per day. A similar decrease in the proportion of males with time was recorded at each of the four stations, at different altitudes, on the"East Transect" in 1965 (Fig. 8). The rate of change in sex ratio was remarkably constant at each station, ranging between 3.4 and 3.6% per day. Though these figures for the "East Transect" are based on measurements of the total adults present on each day, not of newly emerged adults, the mortality rates for both sexes are so high (see Section III D) that the increase in the proportion of females with time cannot be due to different survival rates for the two sexes. Rather must it be due to a slightly later recruitment of females into the adult population.

FIG. 7. THE CHANGE IN THE SEX RATIO OF NEWLY EMERGED ADULTS AT MOOR HOUSE.

A. PEATY GLEY SITE, 1965.

$y = 91.18 - 3.30x$

$r = -0.90$

B. PEATY PODSOL SITE, 1965.

$y = 91.31 - 3.63x$

$r = -0.76$

C. CARECETUM SITE, 1965.

$y = 102.94 - 4.97x$

$r = -0.97$

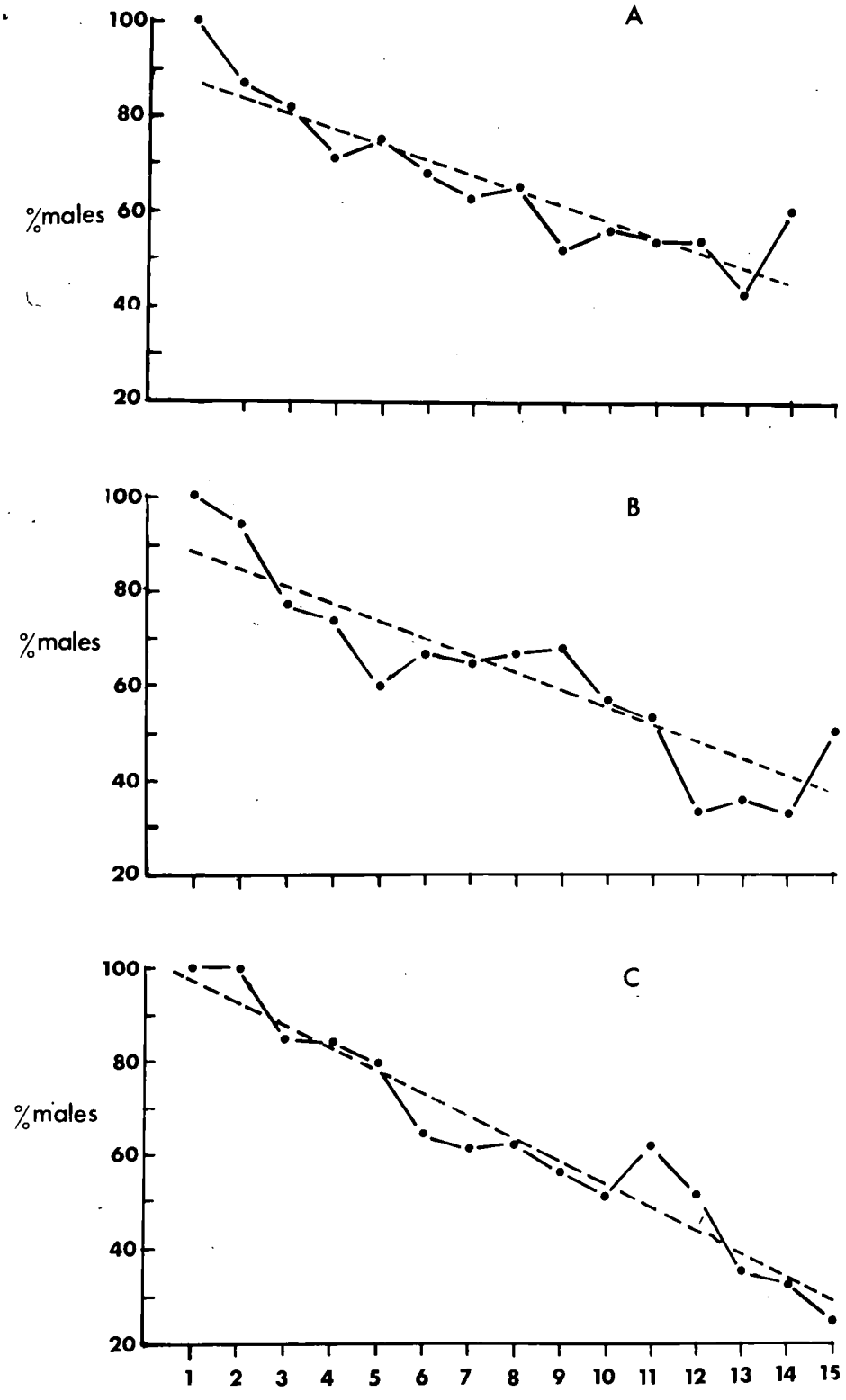

A
B
C
%males
100
80
60
40
20
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
DAY OF EMERGENCE PERIOD

FIG. 8. THE CHANGE IN SEX RATIO OF ADULTS ON THE "EAST TRANSECT" IN 1965.

At 1500 ft.

$y = 92.97 - 3.63x$

$r = -0.98$

At 1600 ft.

$y = 93.04 - 3.53x$

$r = -0.99$

At 1700 ft.

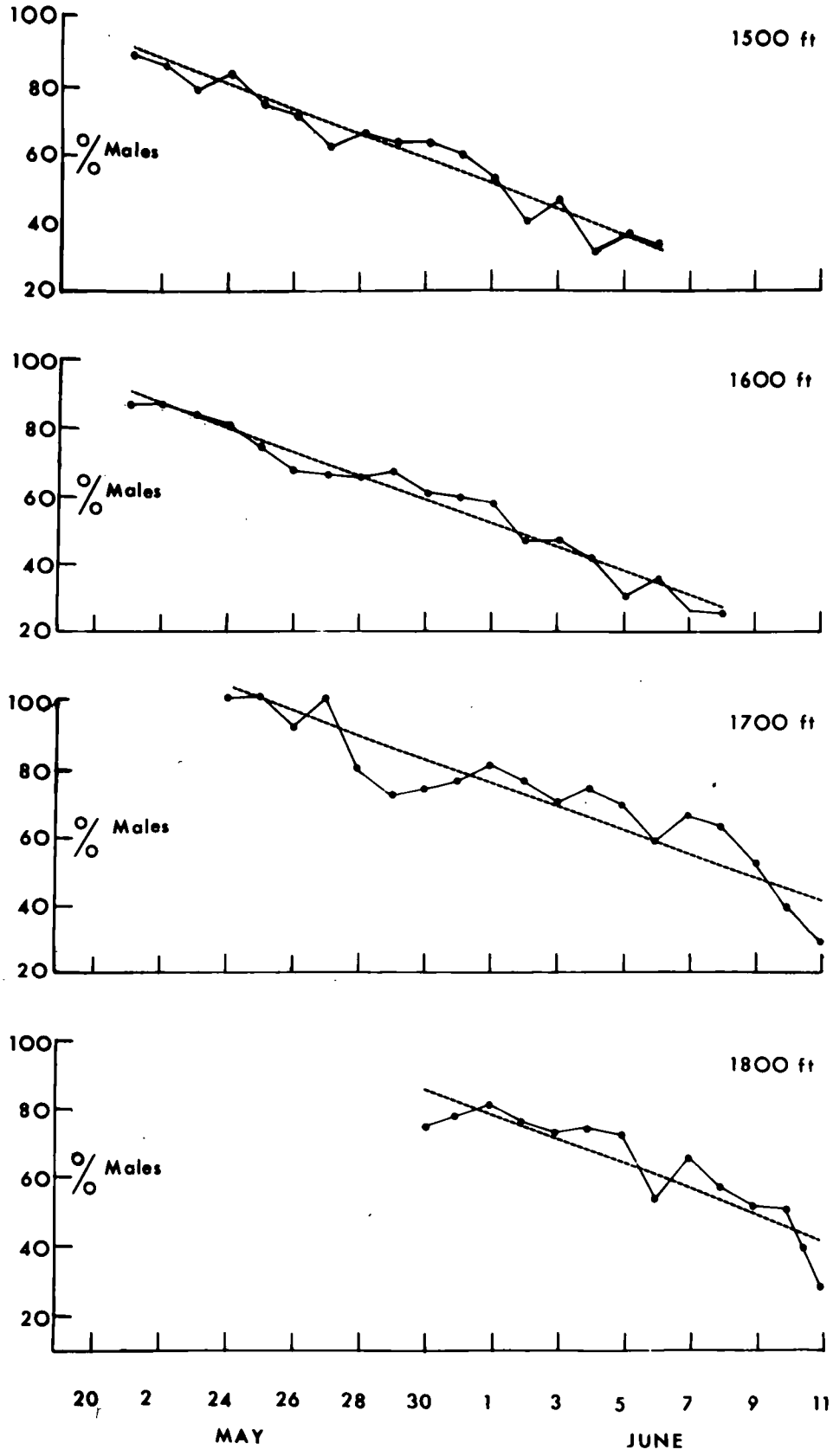
$y = 105.70 - 3.37x$

$r = -0.92$

At 1800 ft.

$y = 88.48 - 3.42x$

$r = -0.89$


100
80
60
40
20
% Males
1500 ft
1600 ft
1700 ft
1800 ft
20
2
24
26
28
30
1
3
5
7
9
11
MAY
JUNE

Similar observations, of a rise in the proportion of females in the population with time, have been reported for several members of the Tipulidae (e.g. Maercks, 1939; Hemmingsen, 1952; Hemmingsen & Jensen, 1957; Freeman, 1964). Though there is little discussion in these studies of male and female survival rates, it does seem probable that the males emerge slightly before the females. There has been no investigation in the Tipulidae of how this later recruitment of females is effected.

D. POPULATION DENSITY AND MORTALITY

Throughout the adult period in 1965, ten random samples, each of 0.05 sq.m. area, were taken daily using the vacuum extractor. This provided daily estimates of the density of adults on each of the sites under investigation (Table 15). The maximum density of adults on the Peaty Gley site was recorded on day 8 of the total adult period of 16 days; on the Peaty Podsol and Carecetum sites, the maximum number of adults occurred on day 9 of the 15 and 16 day adult periods respectively. These findings agree with the measurements on newly emerged adults, that the adult period is symmetrical with no marked skew in its distribution.

The maximum daily density of adults on the Peaty Gley site of 404 $\pm$ 18 per sq.m. ($\pm$ S.E.) on 7 June represented 20.6% of the total estimated emergence of 1958 $\pm$ 75 per sq.m. On the Peaty Podsol and Carecetum sites, the equivalent percentages were 20.1 and 18.2 respectively. Thus, between 18 and 20% of the total adult population is present on one particular day. These figures are similar to those reported by Coulson (1962) for Tipula subnodicornis, another common moorland crane-fly with a very short adult period. In this species, 13% of the possible adult population was present on a single day.

TABLE 15 DENSITY OF ADULTS IN 1965, EXPRESSED AS THE NUMBER PER SQ.M. (± S.E.)

	Peaty Gley Site	Peaty Podsol Site	Carecetum Site
22 May			6 ± 4.0
23 May			18 ± 7.7
24 May			92 ± 17.8
25 May			94 ± 20.4
26 May			112 ± 21.0
27 May			90 ± 15.8
28 May	0	0	90 ± 16.3
29 May	0	0	154 ± 31.2
30 May	0	8 ± 4.2	206 ± 38.3
31 May	10 ± 5.1	34 ± 9.4	148 ± 45.8
1 June	42 ± 11.5	40 ± 9.4	144 ± 33.9
2 June	120 ± 26.5	72 ± 18.2	98 ± 22.7
3 June	192 ± 27.0	144 ± 19.0	70 ± 17.7
4 June	194 ± 19.6	208 ± 18.6	14 ± 6.4
5 June	274 ± 18.8	330 ± 33.5	8 ± 6.4
6 June	370 ± 30.4	330 ± 19.8	2 ± 1.9
7 June	404 ± 17.6	376 ± 26.9	0
8 June	280 ± 18.3	278 ± 33.6	0
9 June	236 ± 29.2	158 ± 16.8	0
10 June	176 ± 13.8	94 ± 12.6	
11 June	94 ± 15.2	34 ± 9.8	
12 June	56 ± 8.4	6 ± 4.0	
13 June	22 ± 7.7	6 ± 2.9	
14 June	4 ± 2.5	0	
15 June	2 ± 1.9	0	
16 June	0	0	

Comparison of the daily densities of total adults with the daily densities of newly emerged adults enables estimates of mortality to be made. For both newly emerged and total adults, a similar area of vegetation was sampled daily, namely ten samples each of 0.05 sq.m. area. Direct comparison of the daily densities of these two components of the population was thus possible (Fig. 9). The close similarity between the numbers of newly emerged and total adults, both as regards the number of individuals caught and the number of days on which they were present, indicates the low daily survival of the species. The average daily mortality of adults has been computed by comparing the total emergence with the total adults taken by random sampling. The daily elimination rate for both sexes is high (Table 16). Combining the data for each of the three sites studied during 1965, the average daily mortality rate for adults was 83%. The average rate for males was 80%, and for females 89%.

Though no detailed investigation has been made on the viability of adults under different experimental conditions in the laboratory, it seems likely that the daily elimination rates recorded in the field reflect with some accuracy the normal duration of life of adults. Numbers of newly emerged adults were enclosed in chambers kept at relative humidities similar to those recorded in the field.

FIG. 9. COMPARISON OF THE NUMBERS OF NEWLY EMERGED AND TOTAL ADULTS.

Newly emerged adults were extracted daily from ten, 0.05 sq.m. emergence traps.

Total adults were extracted daily from ten, 0.05 sq.m. random samples.

A. Peaty Gley Site, 1965.

B. Peaty Podsol Site, 1965.

C. Carecetum Site, 1965.

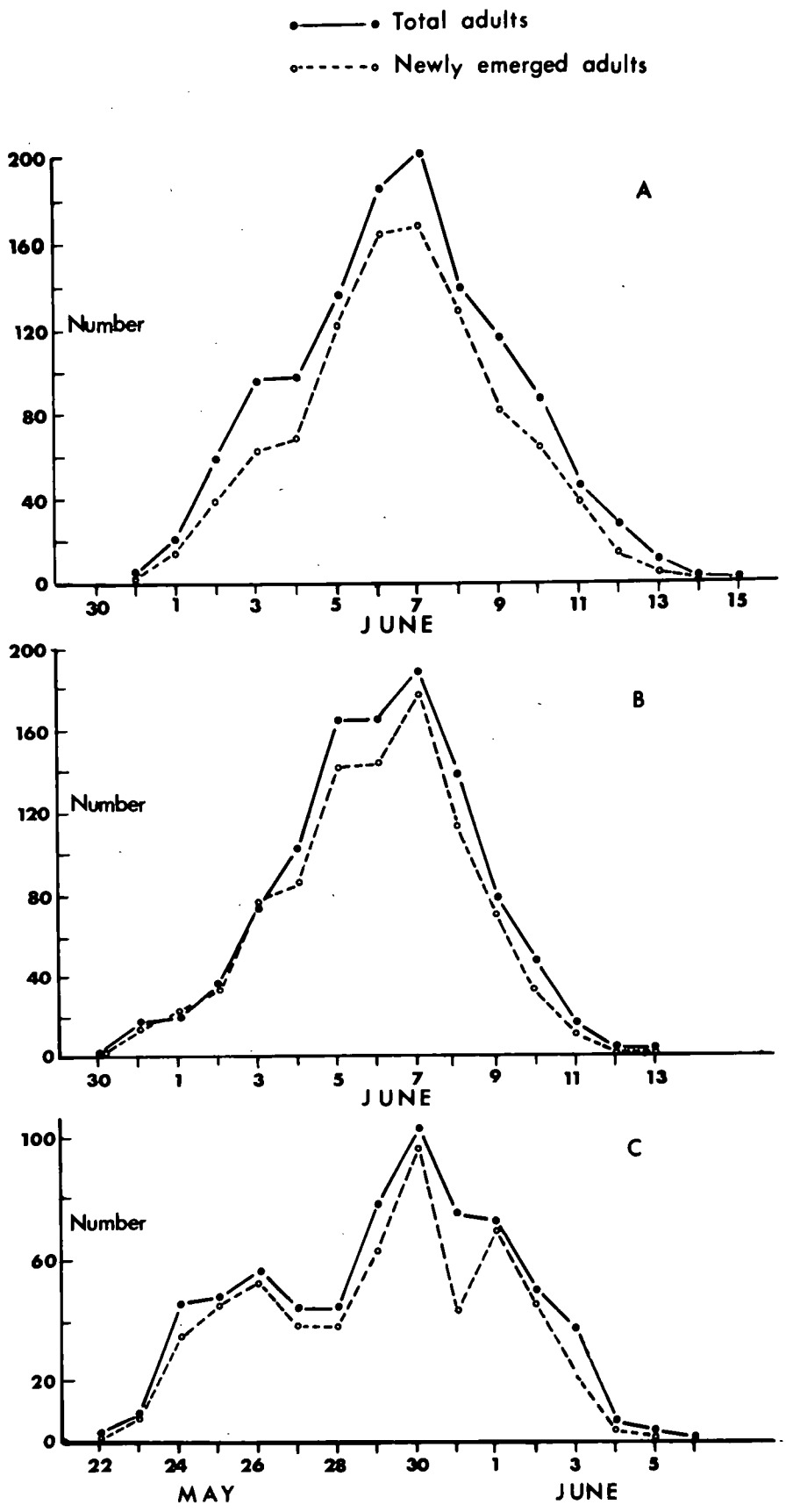

Total adults
Newly emerged adults
A
Number
200
160
120
80
40
0
30
1
3
5
7
9
11
13
15
JUNE
B
Number
200
160
120
80
40
0
30
1
3
5
7
9
11
13
JUNE
C
Number
100
60
20
0
22
24
26
28
30
1
3
5
MAY
JUNE

TABLE 16. THE AVERAGE DAILY ELIMINATION RATES OF ADULTS IN THE FIELD IN 1965, DERIVED FROM COMPARISON OF THE NUMBERS OF NEWLY EMERGED AND TOTAL ADULTS

	Males	Females	Total
PEATY GLEY SITE			
Total emergence	620	359	979
Total adults	824	414	1238
Average daily elimination rate	0.75	0.87	0.79
PEATY PODSOL SITE			
Total emergence	590	343	933
Total adults	698	363	1061
Average daily elimination rate	0.85	0.94	0.88
CARECETUM SITE			
Total emergence	354	211	565
Total adults	426	247	673
Average daily elimination rate	0.83	0.85	0.84
COMBINED DATA			
Total emergence	1564	913	2477
Total adults	1948	1024	2972
Average daily elimination rate	0.80	0.89	0.83

TABLE 17 MORTALITY OF NEWLY EMERGED ADULTS IN THE LABORATORY

Relative Humidity (%)	55	65	75
Number of adults introduced	50	50	50
Number alive after 24 hours	13	17	11
Mortality per day (%)	74	66	78

Saturated solutions of different salts (see Atalla & Hobart, 1964) were used to provide relative humidities between 55 and 75%. The temperature in the laboratory varied between 9 and 12°C. during the period of observation. At the three relative humidities used, mortality during the 24 hour observation period varied between 66 and 78% (Table 17). These are only slightly lower than the average elimination rates recorded under natural conditions.

It seems doubtful, therefore, that predation or parasitism can have any critical effect on a species where the functions of the adult phase, namely the propagation of the following generation, are completed within a day of an adult's emergence. Though there is a considerable literature on the enemies of adult crane-flies (e.g. Alexander, 1920; Hobby, 1931; Audcent, 1932; Rogers, 1942; Hughes, 1959), observation has failed to reveal any major predator

or parasite of the adult stage of Molophilus ater. Examination of over 200 adults showed no sign of either ecto- or endo-parasitism. Birds have not been observed to take adults, though the Committee of Inquiry on Grouse Disease (1911) reported that the species is an important food source for grouse chicks.

On only two occasions have entomophagous insects been noted as preying on adult Molophilus, namely the empid Platyptera borealis L. and the yellow dung fly Scopeuma stercorarium (L). Though the orb-web spiders are known to feed on Tipula subnodicornus (Cherrett, 1961) no information is available as to the extent, if any, of their predation on Molophilus. Frogs appear to include the species in their diet. Nineteen frogs collected on the sample sites contained 47 adults, together with a diverse range of other invertebrates. Though the densities of frogs at Moor House is not known, it seems unlikely that their influence on the adult stage of Molophilus is anything more than minimal. Thus, there is no evidence that biotic factors play any significant part in the low survival rate of adults of Molophilus ater; this appears to be an intrinsic characteristic of the species.

E. ACTIVITY

During 1965, detergent and sticky traps, the operation and dimensions of which have already been described, were used to provide information on the degree of activity of adults. On each of the three sites investigated, ten detergent and ten sticky traps were employed. These were arranged alternately at one metre intervals in an area measuring five metres by four metres. In Figures 10, 11, and 12, the numbers caught daily are compared with the numbers of adults removed from ten random samples, each of area 0.05 sq.m., using the vacuum extractor. The latter provides a measure of the potential population available for capture by detergent and sticky traps. The degree of activity on any one day may be expressed by the ratio of the number of captures by detergent and sticky traps compared with the numbers of adults actually present on each study area, recorded by vacuum sampling. This provides an "activity ratio", a measure of activity which is independent of density. Analysis of daily activity ratios with components of the weather, has produced no cogent explanation of the factors influencing the activity of adults. On several occasions widely differing "activity ratios" were recorded on different sites, and by the two trapping methods, on the same day.

On each of the sites it is noticeable that the activity ratio tends to be large both at the beginning and the end of the adult period, when the density of adults is low. In

FIG. 10. COMPARISON OF THE NUMBERS CAUGHT DAILY BY DETERGENT AND STICKY TRAPS WITH THE NUMBER RECORDED BY RANDOM SUCTION SAMPLING ON THE PEATY GLEY SITE IN 1965.

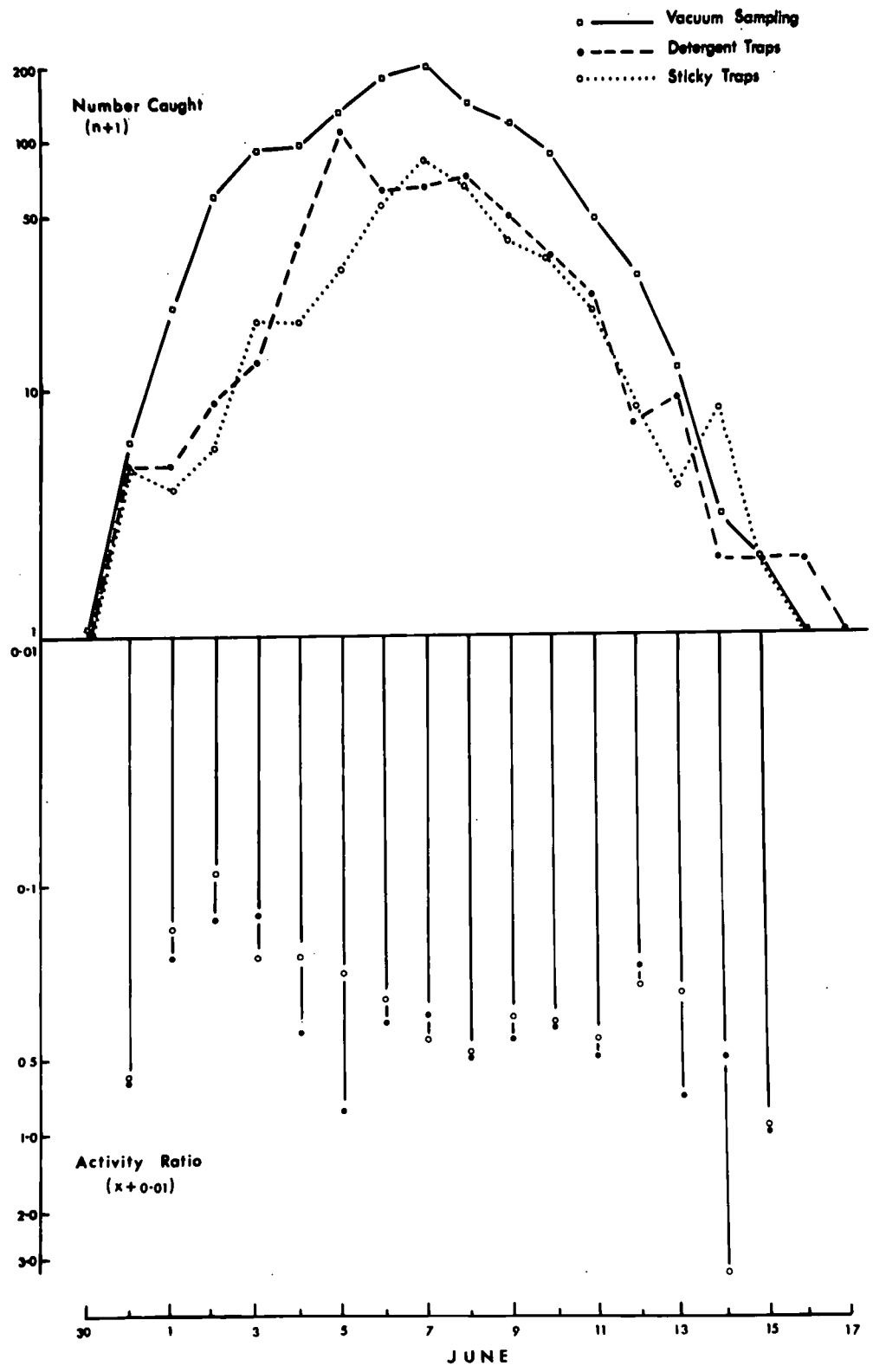

Vacuum Sampling
Detergent Traps
Sticky Traps
Number Caught
(n+1)
200
100
50
10
1
0·01
0·1
0·5
1·0
2·0
3·0
Activity Ratio
(x+0·01)
30
1
3
5
7
9
11
13
15
17
JUNE

FIG. 11. COMPARISON OF THE NUMBERS CAUGHT DAILY BY DETERGENT AND STICKY TRAPS WITH THE NUMBER RECORDED BY RANDOM SUCTION SAMPLING ON THE PEATY PODSOL SITE IN 1965.

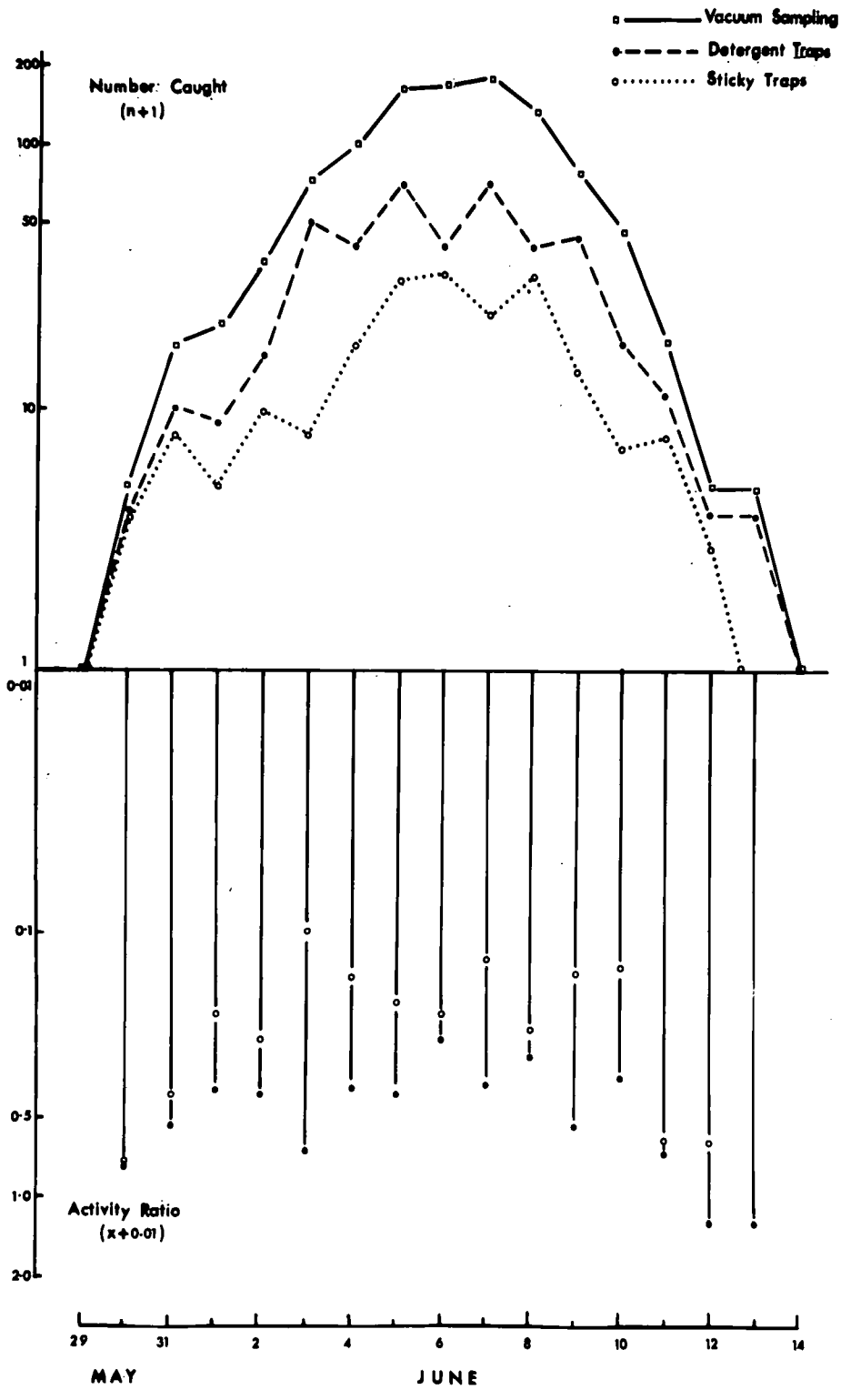
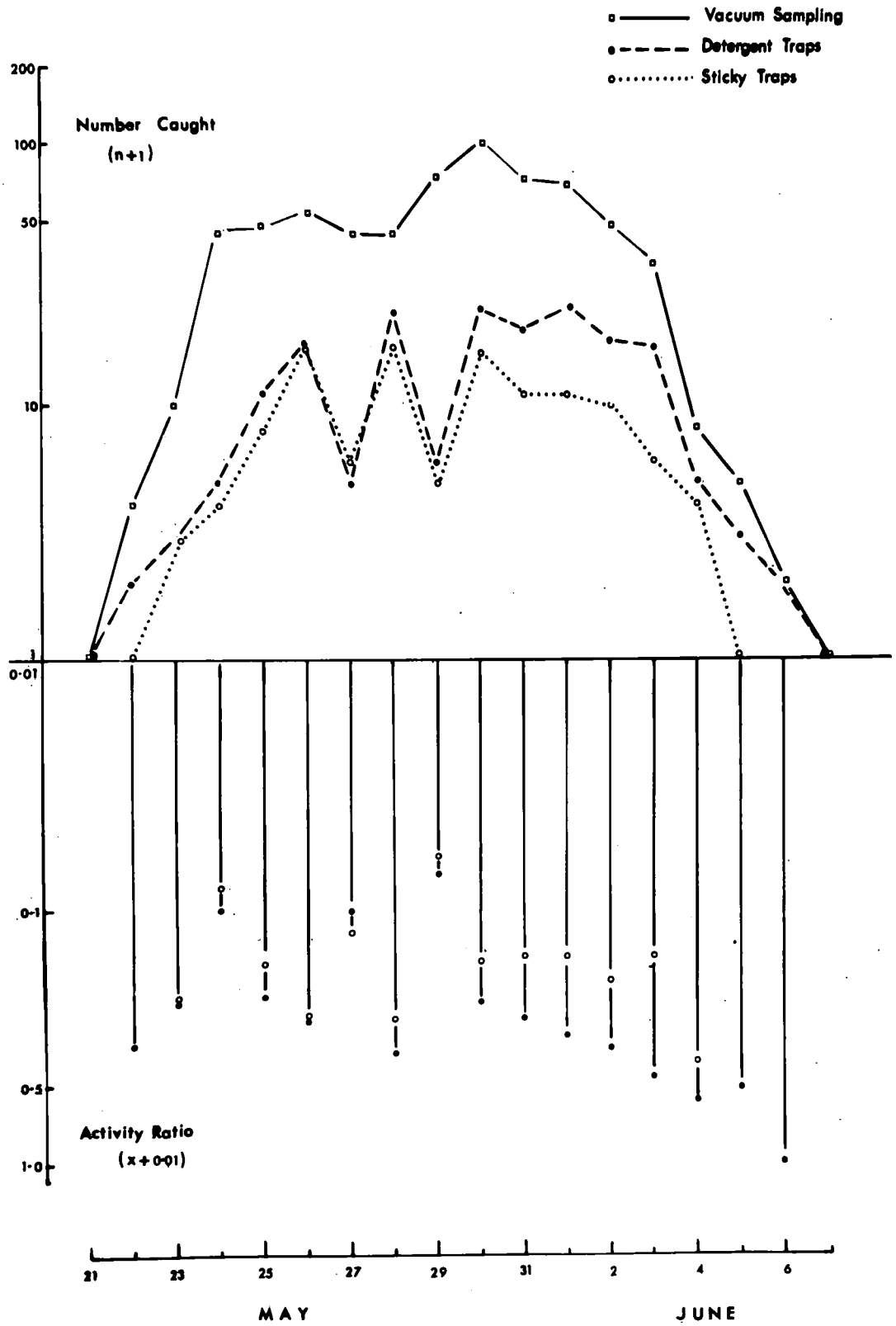

Vacuum Sampling
Detergent Traps
Sticky Traps
Number Caught
(n+1)
200
100
50
10
1
0·01
0·1
0·5
1·0
2·0
Activity Ratio
(x+0·01)
29
31
2
4
6
8
10
12
14
MAY
JUNE

FIG. 12. COMPARISON OF THE NUMBERS CAUGHT DAILY BY DETERGENT AND STICKY TRAPS WITH THE NUMBER RECORDED BY RANDOM SUCTION SAMPLING ON THE CARECETUM SITE IN 1965.


Vacuum Sampling
Detergent Traps
Sticky Traps
200
100
50
10
1
Number Caught
(n+1)
0·01
0·1
0·5
1·0
Activity Ratio
(x+0·01)
21
23
25
27
29
31
2
4
6
MAY
JUNE

Molophilus ater, a short-lived species which does not feed in its adult stage, it is essential that mating occurs a short time after emergence. Mating appears to be dependent on random wanderings within the herbage bringing individuals of each sex into actual physical contact. During the middle part of the adult period, when densities are large, the probability of individuals meeting is far greater than when densities are low. This is reflected in the higher activity ratios recorded at the extremes of the adult period, activity resulting from the greater difficulty of finding individuals of the opposite sex under these low densities.

To investigate both the range of movement of the species, and the extent to which activity is affected by the difficulty of finding an individual of the opposite sex, a series of experimental populations was set up on an area of Juncus moor lacking an indigenous population of the species. On 5 June 1966, nine circular areas of diameter twenty cm., spaced at five metre intervals, were marked out and surrounded by concentric rings, each ten cm. apart. At 10.00 hours G.M.T. thirty male adults were released at the centre of three of the circular areas, and thirty females at the centre of another three. Into each of the other three areas, fifteen males and fifteen females were released. These were introduced separately; they were not in copula.

TABLE 18. THE DISTANCE OF CAPTURE OF ADULTS FROM A CENTRAL AREA, TEN HOURS AFTER THEIR RELEASE

	RANGE OF MOVEMENT (cm.)					
	0	0-10	10-20	20-30	30-40	Number recovered
MALE ONLY REPLICATES 1	6	9	7	2	0	24
2	8	7	4	3	1	23
3	8	6	4	1	1	20
Total	22	22	15	6	2	67
%	33	33	22	9	3	
FEMALES ONLY REPLICATES 1	9	6	7	1	0	23
2	10	7	1	1	0	19
3	8	10	5	0	0	23
Total	27	23	13	2	0	65
%	42	35	20	3	0	
MALE + FEMALE REPLICATES 1	12	7	0	0	0	19
2	14	6	1	1	0	22
3	10	7	0	1	0	18
Total	36	20	1	2	0	59
%	61	34	2	3	0	

At 18.00 hours G.M.T., ten hours after release, adults were recovered using the vacuum extractor, and their distance of capture from the release point recorded (Table 18). For the replicates comprising males only, 66% of the number recovered were found within 10 cm. of the central area of release, for

the replicates comprising females only, 77% were recovered within 10 cm. of the area of release, but for the replicates comprising equal proportions of males and females 95% were found within this same area. Both for the male only replicates ($\chi^2 = 16.4$, d.f. = 1, $P < 0.001$), and the female only replicates ($\chi^2 = 8.1$, d.f. = 1, $P < 0.01$), the proportion of individuals recovered within 10 cm. of the release area is significantly less than for replicates comprising equal numbers of males and females, suggesting that the difficulty of finding an individual of the opposite sex is a major factor in determining the degree of activity in the species. For the replicates comprising one sex only, a smaller proportion of males were recovered within 10 cm. of the release area than were females, though this difference is not significant ($\chi^2 = 2.0$, d.f. = 1, $P > 0.1$).

Though it must be remembered that these results are a minimum estimate of the degree of activity, taking no account of random wanderings between the areas of release and recapture, they do suggest that the range of movement in adults is limited and that adults move only a short distance from where they emerge. The low activity of adults is emphasized by comparison of the total numbers caught by each detergent and sticky trap with the potential number of adults available for capture (Table 19). Since the detergent and sticky traps were arranged at one metre intervals, this potential population is considered as twice the total number of adults obtained by the random vacuum sampling

TABLE 19. THE PROPORTION OF THE POTENTIAL POPULATION CAUGHT BY EACH DETERGENT AND STICKY TRAP

Site	Peaty Gley	Peaty Podsol	Carecetum	Mean
Potential number of adults per sq.m.	2476	2122	1346	1981
Mean capture by each detergent trap	50.1	43.7	17.0	36.9
% of potential population in one sq.m. caught	2.0	2.1	1.3	1.9
Mean capture by each sticky trap	39.4	19.2	11.2	23.3
% of potential population in one sq.m. caught	1.6	0.9	0.8	1.2

of ten, 0.05 sq.m. samples per day. Combining the data for the three sampling sites in 1965, the percentage of the potential population captured by each detergent trap was 1.9% and by each sticky trap 1.2%.

The captures by detergent and sticky traps suggest a significant difference in activity between the sexes. (Table 20). Comparison of the proportion of each sex recorded by random daily sampling using the vacuum extractor with the proportion of each

TABLE 20. COMPARISON OF THE NUMBERS OF EACH SEX CAUGHT BY DETERGENT AND STICKY TRAPS WITH THE NUMBERS RECORDED BY VACUUM SAMPLING, ON THREE SITES IN 1965

	Males	Females	Total	% Males	χ^2 (1 d.f.)	P
PEATY GLEY SITE						
Detergent traps	313	124	437	71.6	4.8	<0.05
Vacuum sampling	698	363	1061	65.8	15.5	<0.001
Sticky traps	154	38	192	80.2		
PEATY PODSOL SITE						
Detergent traps	351	150	501	70.1	2.0	>0.1
Vacuum sampling	824	414	1238	66.6	5.4	<0.05
Sticky traps	287	107	394	72.8		
CARECETUM SITES						
Detergent traps	123	47	170	72.4	4.9	<0.05
Vacuum sampling	426	247	673	63.3	27.8	<0.001
Sticky traps	99	13	112	88.4		
TOTAL						
Detergent traps	787	321	1108	71.0	11.0	<0.001
Vacuum sampling	1948	1024	2972	65.5	36.2	<0.001
Sticky traps	540	158	698	77.4		

The χ^2 value has been calculated on a null hypothesis that the sex ratio is the same as that given by vacuum sampling.

sex captured by detergent and sticky traps indicate that males are more active than females. Combining the results from three sites studied in 1965, for both detergent traps ($\chi^2 = 11.0$, d.f. = 1, $P<0.001$) and sticky traps ($\chi^2 = 36.2$, d.f. = 1, $P<0.001$) the proportion of males is significantly greater than the proportion of males recorded by vacuum sampling, this representing the population available for capture. It is not known whether this differential activity is due to an intrinsic difference in the capacity for movement between males and females, or whether the excess of males recorded by vacuum sampling requires that males undergo greater movement than females in order to come into contact with an individual of the opposite sex.

It is perhaps interesting to note that though both detergent and sticky traps indicate a greater activity for males than for females, there is a difference in the proportion of each sex captured by these two methods. For detergent traps 71.0% of the total number captured were males, but for sticky traps 77.4% of the total were males. These differences are significant ($\chi^2 = 8.8$, d.f. = 1, $P<0.01$).

Since captures by detergent traps are dependent on movement at ground level, whilst sticky traps are a measure of activity at all levels in the vegetation, the most probable explanation of this difference is that a greater proportion of male activity takes place in the higher strata of the vegetation than does female activity. This hypothesis seems to be confirmed

by the height of capture of individuals on sticky traps (Table 21).

TABLE 21. THE HEIGHT OF CAPTURE OF MALES AND FEMALES ON STICKY TRAPS IN 1965

	Height of capture			
	0 - 6 cm.	6 - 18 cm.	χ^2	P
Males - number	356	184		
%	66	34		
			12.0	<0.001
Females - number	127	31		
%	80	20		

Each sticky trap was divided into three, 6 cm. zones, and for each individual the sex and height of capture above ground level was recorded. Of the total males, 34% were recorded above 6 cm. from ground level; of the total females only 20% were captured above this level. The difference between the height of capture for males and females is significant ($\chi^2 = 12.0$, d.f. = 1, $P<0.001$). This indicates a difference in behaviour between males and females. Two possibilities suggest themselves. The difference may be due to the searching of females at ground level for suitable oviposition sites, or, since mating usually occurs in the upper levels of the vegetation, it may reflect the proportionally greater activity of males than females in bringing about contact between the sexes. The validity of these suggested behaviour differences between the sexes, and the precise explanation of why a larger proportion of males are caught by sticky traps than by detergent traps, must remain conjecture.

F. DIURNAL PERIODICITY OF EMERGENCE AND ACTIVITY

Though in many insect groups the diurnal rhythm of emergence from the pupa is well documented (e.g. Park, 1940; Lewis & Bletchley, 1943; Nielsen & Haeger, 1954; Harker, 1958), there is little known of the diurnal emergence rhythm for members of the brevi-palp crane-flies, or of the relationship between the emergence of adults and the daily pattern of activity.

Fifteen emergence traps, each enclosing an area of vegetation of 0.05 sq.m., were emptied of newly emerged adults at two-hour intervals throughout the day, on an area adjacent, and of similar vegetation, to the Peaty Gley site in 1965 (Fig. 13). The activity of both sexes was measured by recording the numbers of adults captured by forty detergent traps, which were again emptied at two-hour intervals. The pattern of activity is also shown in Fig. 13.

The well-defined diurnal patterns of emergence and activity are similar on each of the four days on which observations were made (8 June to 11 June inclusive), and no attempt has been made to correlate the minor daily differences in emergence and activity with the components of the weather. Such analysis requires more comprehensive data than it was possible to acquire in the present study. The main features of the weather over the four-day observation period are recorded in Table 22.

FIG. 13. THE NUMBERS OF EMERGENCES THROUGHOUT 24 HOUR PERIODS COMPARED TO ACTIVITY (RECORDED BY CAPTURES BY DETERGENT TRAPS).

A. 8th June 1965

B. 9th June 1965

C. 10th June 1965

D. 11th June 1965

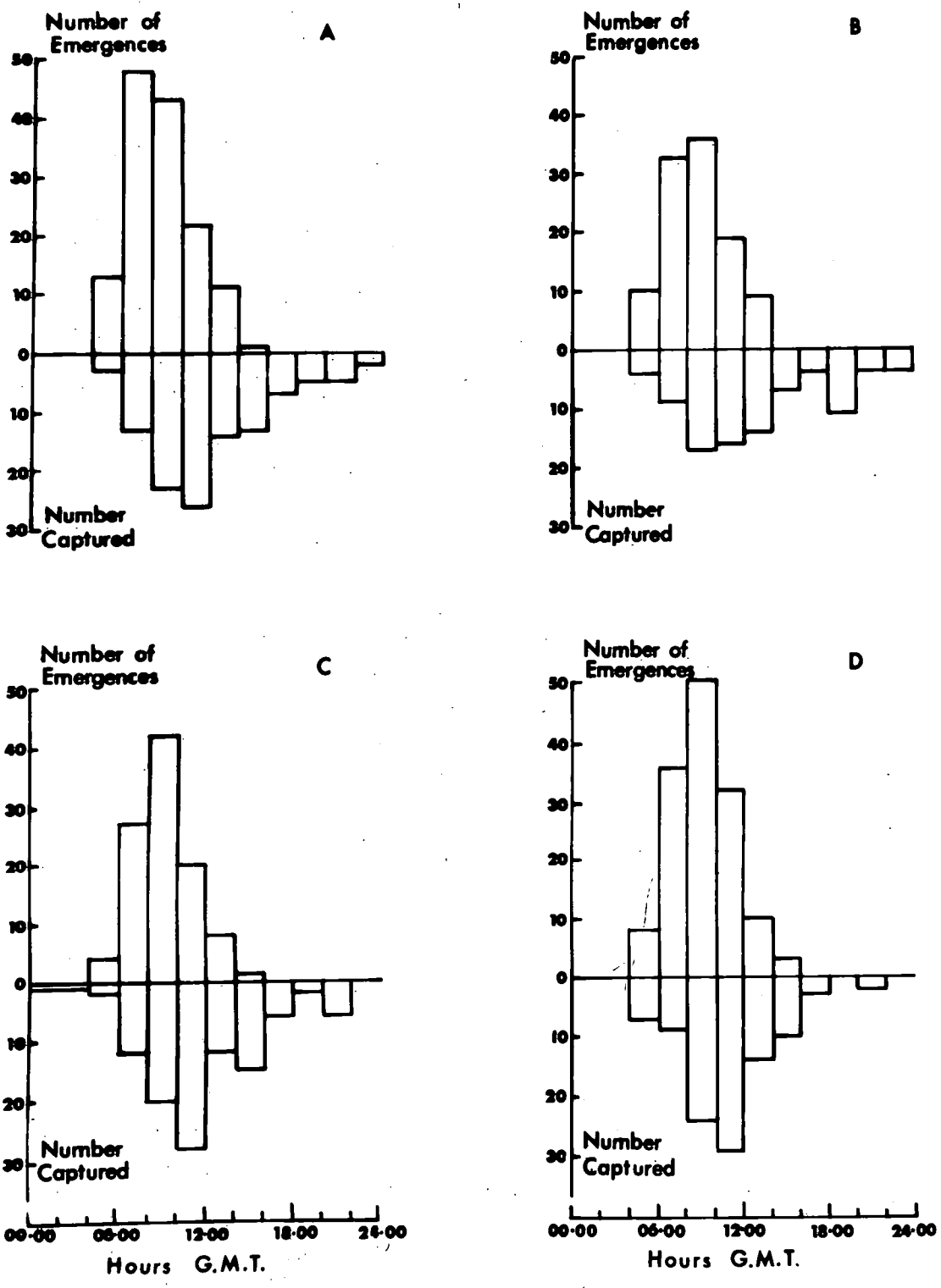

Number of Emergences
A
50
40
30
20
10
0
10
20
30
Number Captured
Number of Emergences
B
50
40
30
20
10
0
10
20
30
Number Captured
Number of Emergences
C
50
40
30
20
10
0
10
20
30
Number Captured
00·00
06·00
12·00
18·00
24·00
Hours G.M.T.
Number of Emergences
D
50
40
30
20
10
0
10
20
30
Number Captured
00·00
06·00
12·00
18·00
24·00
Hours G.M.T.

TABLE 22. METEOROLOGICAL CONDITIONS DURING THE FOUR DAY OBSERVATION PERIOD, TAKEN FROM THE MOOR HOUSE RECORDS

Date, 1965	8 June	9 June	10 June	11 June
Maximum temperature (^{o}F)	57.5	63.3	65.3	61.6
Minimum temperature (^{o}F)	43.2	40.3	42.3	41.5
Rainfall (inches)	Trace	Trace	0	0.15
Sunshine (hours)	3.0	13.8	9.0	3.2

There is a well-marked, unimodal rhythm of emergence. All emergences were recorded within 04.00 and 16.00 hours G.M.T. The combined results of the four-day observation period (Table 23) indicate that 85% of the daily emergence took place within a period of 6 hours, between 06.00 and 12.00 hours G.M.T., with a peak emergence, comprising 36% of the total, between 08.00 and 10.00 hours G.M.T. There is no evidence of a difference in the time of emergence between males and females. For example, over the four-day observation period, by 10.00 hours G.M.T., 73% of the total male and 72% of the total female emergence had taken place.

The diurnal pattern of activity, though slightly delayed and of longer duration, is closely associated with the pattern of emergence. Peak activity occurred between 10.00 and 12.00 hours G.M.T., during which period 25% of the daily total was recorded (Table 24).

TABLE 23. THE DIURNAL RHYTHM OF EMERGENCE OF ADULTS

Hours G.M.T.	Males		Females		Males & Females	
	No.	%	No.	%	No.	%
24.00 - 04.00	0	0	0	0	0	0
04.00 - 06.00	20	7.0	15	7.6	35	7.3
06.00 - 08.00	85	29.8	59	29.9	144	29.9
08.00 - 10.00	104	36.5	68	34.5	172	35.7
10.00 - 12.00	54	18.9	39	19.8	93	19.3
12.00 - 14.00	19	6.7	13	6.6	32	6.6
14.00 - 16.00	3	1.1	3	1.5	6	1.2
16.00 - 24.00	0	0	0	0	0	0
Total	285	100	197	100	482	100

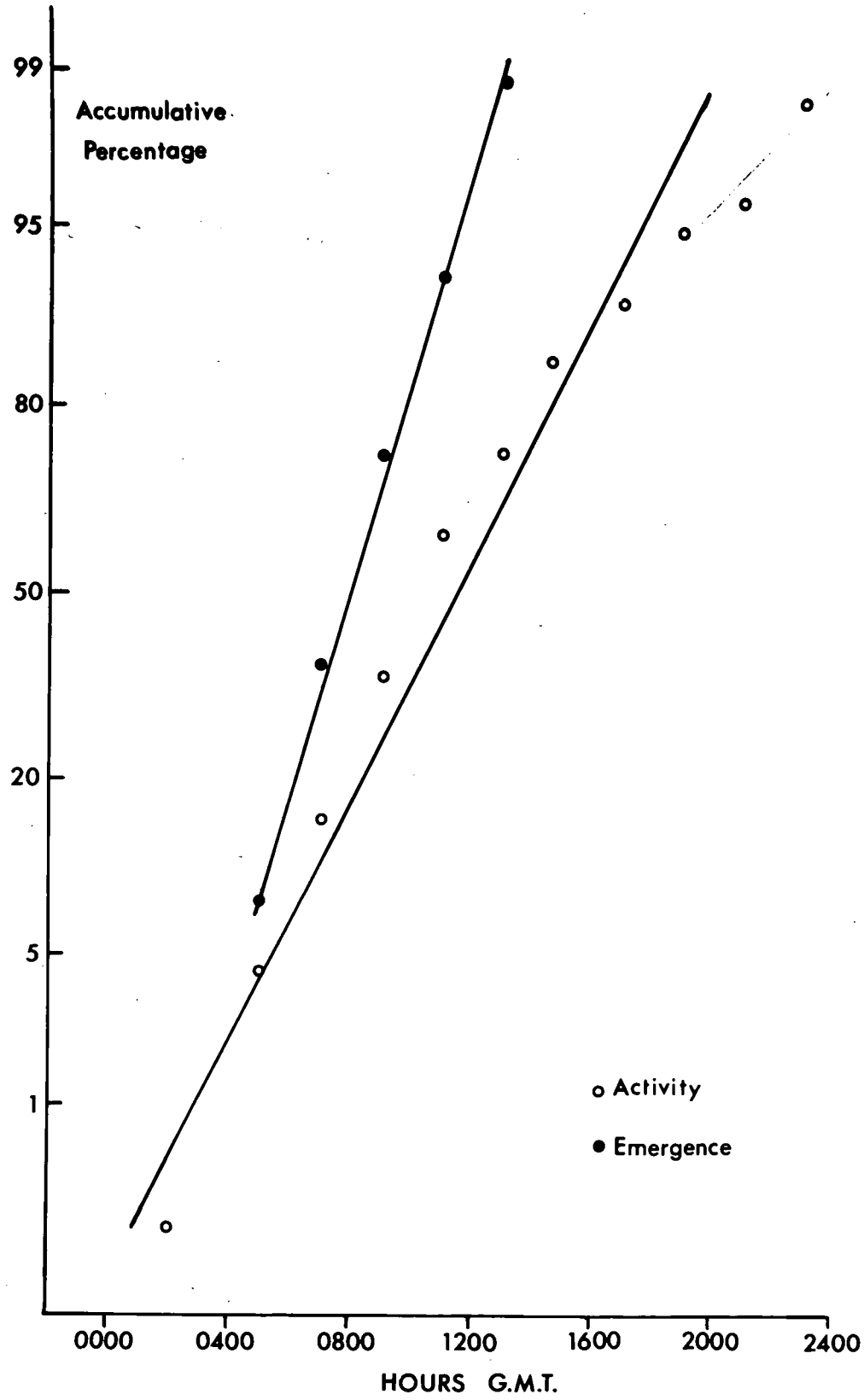
This compares with emergence, which reaches a peak between 08.00 and 10.00 hours G.M.T. Though adults were captured by detergent traps throughout the 24 hour period, 81% of the total capture was recorded within a 10 hour period, between 06.00 and 16.00 hours G.M.T. Within the same 10 hour period, 93% of the total emergence took place. There is no evidence of a difference in the time of activity between the sexes.

TABLE 24. THE DIURNAL RHYTHM OF ACTIVITY OF ADULTS

Hours G.M.T.	Males No.	Males %	Females No.	Females %	Males & Females No.	Males & Females %
00.00 - 04.00	1	0.4	0	0	1	0.2
04.00 - 06.00	10	3.9	6	4.1	16	4.0
06.00 - 08.00	29	11.2	14	9.7	43	10.7
08.00 - 10.00	53	20.5	31	21.4	84	20.8
10.00 - 12.00	65	25.2	34	23.4	99	24.6
12.00 - 14.00	37	14.3	17	11.7	54	13.4
14.00 - 16.00	25	9.7	20	13.8	45	11.2
16.00 - 18.00	12	4.7	8	5.5	20	5.0
18.00 - 20.00	11	4.3	7	4.8	18	4.5
20.00 - 22.00	11	4.3	6	4.1	17	4.2
22.00 - 24.00	4	1.6	2	1.4	6	1.5
Total	258	100	145	100	403	100

For both emergence and activity, probability curves have been fitted to periodicity samples (Fig. 14). The curve for emergence confirms that the emergence rhythm is unimodal, and that the total emergence takes place within a very short period of time, the extremes of emergence occurring within a period of approximately 10 hours.

FIG. 14. PROBABILITY CURVES FITTED TO EMERGENCE AND ACTIVITY PERIODICITY SAMPLES.


99
95
80
50
20
5
1
Accumulative
Percentage
o Activity
● Emergence
0000
0400
0800
1200
1600
2000
2400
HOURS G.M.T.

The curve for activity emphasises the longer time period during which individuals are active, compared with their period of emergence. Though the curve is a much less perfect single distribution than that recorded for emergence, there is no evidence of a bimodal periodicity in activity. There is, however, a small positive skewness in the distribution, due to the capture of limited numbers of individuals between 16.00 and 24.00 hours G.M.T., but this does not appear in any way significant and no transformation of the time co-ordinate has been made.

In Molophilus ater, the emergence rhythm appears to be the dominant factor influencing the time of activity. A similar close association between emergence and activity has been noted in other insect species where the adults are short-lived (e.g. Palmén, 1955; Morgan, 1956; Morgan & Waddell, 1961). This contrasts with certain long lived species where the daily periodicity of activity does not appear to be directly influenced by the initial emergence rhythm of the adult (see Lewis & Taylor, 1965).

It is perhaps interesting to note that in Molophilus, where the peaks of both emergence and activity occur within a short time of mid-day, the body colour of the adult is black. Lewis & Taylor (1965) found that night flying Nematocera were noticeably paler in colour than species whose flight activity took place during the daylight hours. These authors found a significant association between body colour and the light intensity at the time of maximum flight.

The precise significance of melanism in insects is uncertain. Kalmus (1941) suggested that dark colour in insects is associated with resistance to desiccation, but Wigglesworth (1948) denies this, stating that the impermeability of the cuticle is independent of its degree of sclerotisation. Dark body colouration may confer protection against the injurious effects of ultra violet radiation (Erhard, 1929), as well as assisting in the absorption of heat in direct sunshine (Buxton, 1924; Uvarov, 1948; Digby, 1955). Certainly, Mani (1962) found that insects were darker at high altitudes, where temperatures are lower and ultra violet radiation greater, than at lower altitudes.

Whether the dark body colour of Molophilus ater is an adaptation to high altitudes, and whether this is in any way correlated with the diurnal patterns of emergence and activity, remains conjecture. At Moor House, where the climate is severe and the crane-fly fauna well documented (Coulson, 1959), an interesting investigation would be the detailed comparison of body colour of crane fly species with different periodicities in emergence and activity.

G. BREEDING BIOLOGY

1. MATING

The eggs of Mollophilus ater are fully developed at the time of emergence of the adults, and mating takes place almost immediately after the emergence of the female. Mating pairs frequently involve females whose swollen abdomens are still soft and pale in colour. Though newly emerged females are quickly attended by at least one male, laboratory observations lend no support to the contention of Alexander (1919), that in certain crane-fly species male adults will position themselves adjacent to female pupae, waiting for the latter to emerge.

The habit of newly emerged, unattended females to crawl up to more elevated or exposed positions in the vegetation provokes the question whether this is in any way analogous to the swarming habits observed in certain Tipula spp. and in the Limoniini (Cuthbertson, 1926, 1929a; Rogers, 1933; Pierre, 1934). Though the precise significance of swarming in flies is a subject of great controversy (an admirable review of the topic is given by Haddow et al., 1961), it seems certain that swarms have evolved as mating devices, possibly to facilitate the meeting of the sexes. Downes (1958) has discussed the importance of fixed objects or markers in swarm formation, and comments that swarm formation does not necessarily involve any gregarious factor, but only an individual's reaction to a marker.

The movements of newly emerged females of Molophilus ater to elevated positions in the herbage, where they may be more easily found by searching males, is tentatively suggested as being analogous to swarming, behaviour which reduces the possibility that females might remain unfertilised throughout their very short adult phase.

The search of the male for the female in the upper levels of the vegetation appears to be completely random. Males are not attracted to crushed females, and laboratory experiments show no male directional movement towards newly emerged females imprisoned either in small net cages or in glass phials. In certain members of the Tipulidae (e.g. Dictenidia, Tanyptera, and Ctenophora spp.), the antennae exhibit sexual dimorphism, the male antennae being variously adorned with segmental processes, whilst in the female the antennae are more or less simple. Here the male antennae appear to be chemo-sensory organs, probably enabling the male to locate the female. In Molophilus ater, however, the antennae of the male and female are similar, and pairing of the sexes is apparently dependent upon physical contact, usually of the tarsi.

The mating attitude is typical of that in other crane-fly species; during copulation the two individuals face in opposite directions, the female usually hanging on to a plant stem or leaf in an upright vertical position with the male below. The average duration of mating is not known in

detail, but pairs have been observed to remain in copulation in the laboratory for periods up to 5 hours and in the field for periods up to 2 hours. There was no evidence of either sex feeding in the adult stage, either before or after mating. This is in accordance with most previous observations, records of adult feeding in Tipulidae being mainly confined to Geranomyia spp. (Knab, 1910; Rogers, 1926), where the elongated proboscis is adapted to extract nectar from tubular flowers.

2. OVIPOSITION

In Appendix II, the lengths of different body parts of males and females are compared. The figures given are the means of measurements made on 50 newly emerged males and 50 newly emerged females. The thorax and abdomen lengths are significantly greater for females, whilst the wings are slightly (though for the number measured, not significantly,) longer in females than in males. Similar differences in body size have been reported for other Tipulidae (Hemmingsen, 1956; Hemmingsen & Jensen, 1960); the difference is probably a function of egg production and oviposition in the female. The lengths of various leg components is significantly less for females than males, though there were no discernable differences in the thickness of appendages between the two sexes. Whether these observations are indicative of a difference in the intrinsic capacity for movement between the sexes (see Section III E), or whether it is connected with the method of oviposition of

the female (see Hemmingsen, 1952) is not known.

The mechanism of egg laying was studied in the laboratory, the thickness of herbage and the small size of individual Molophilus precluding observations being made in the field. Mating pairs involving newly emerged females were placed in "Petri" dishes containing a thin layer of peat and covered by inverted glass jars. Oviposition is superficial, only the cerci, and occasionally the last few abdominal segments, being inserted into the substrate. These observations appear to support the findings for Tipula spp. by Hemmingsen (1952), that oviposition is relatively superficial in species inhabiting moist biotopes, whilst deep borings are performed by species whose larvae live in substrates where the surface humidity is low. It seems probable that the depth of oviposition depends not, as might be supposed, on the nature of the substrate, but on the innate behaviour pattern of the species. There was no observable difference in the depth of penetration of the abdomen in cultures comprising several substrates (namely, peat, wet sand, dry sand, and sieved gley soil).

The use of agar gel as a substrate for oviposition provided information on the depth at which eggs are laid. Five fertilised females were introduced separately into glass tubes containing flat surfaced 2 cm. layers of agar gel. The tubes were inspected seven hours after the introduction of the females. The eggs were readily visible in the transparent

substrate; their distance from the surface of the substrate was recorded. Of the 185 eggs whose depth could be measured, 98 (53%) occurred within 5 mm. of the surface. All of the eggs were recorded within 1 cm. of the surface. Since the mean total length of the female abdomen in mm. is 2.66 ± 0.39 (± S.D.), these findings might appear to deprecate the observations that oviposition is superficial, that only the tip of the abdomen is inserted into the substrate. Several authors have commented on the high velocity at which crane-fly eggs are ejected from the female abdomen (e.g. Hemmingsen, 1952; Coulson, 1962). This phenomenon almost certainly accounts for the discrepancy between observations on the nature of oviposition and measurements of the depths of eggs laid in an agar substrate.

It was found difficult to investigate directly the depth at which eggs are laid under natural conditions. Hemmingsen (1952) and Coulson (1962) used saturated salt solutions to determine the numbers and distribution of eggs of Tipula spp. The use of similar flotation techniques proved unsuccessful for the eggs of Molophilus ater laid in peat, preventing estimation of egg densities in the field.

The depth at which eggs are laid under natural conditions was investigated by separating 6 cm. deep soil samples into 1 cm. vertical zones. Soil samples were taken during the middle part of the emergence period, before any eggs could have hatched.

Each 1 cm. sub-sample was enclosed separately in a sealed polythene bag and kept moist at a temperature of 10°C. After five weeks each sub-sample was subjected to a wet funnel extraction, and the numbers of first instar larvae recovered from each vertical layer recorded (Table 25). The majority of eggs are laid within 1 cm. of the surface, confirming laboratory observations that oviposition is superficial. The presence of individuals below 1 cm. suggests that some adult females crawl into suitable cavities in the soil profile to deposit eggs. The eggs of crane-flies are extremely susceptible to mortality by desiccation (Maercks, 1939; Loughlin, 1948); the laying of eggs at depths below one centimetre could be of critical importance in preventing wholesale decimation of the population during the vulnerable egg stage in periods of extreme drought. Several authors have recorded large annual fluctuations in the numbers of certain crane-fly species, and have showed that high larval densities are related to high rainfall during the egg and first instar stages (Maercks, 1943; Coulson, 1962; Milne, Laughlin & Coggins, 1965). During the present study there was no year of relative drought at Moor House, and no large fluctuations were recorded in the density of populations of Molophilus ater from one year to another on any particular site.

TABLE 25. THE VERTICAL DISTRIBUTION OF FIRST INSTAR LARVAE, RECIVERED FROM SOIL SUB-SAMPLES TAKEN AT THE TIME OF EGG LAYING

Depth in centimetres	Number	Percentage
0-1	92	60
1-2	28	18
2-3	17	11
3-4	7	5
4-5	10	6
5-6	0	0
Total	154	100

There is some evidence that many of the probings of substrate by the abdomen do not result in an egg being deposited. Newly emerged females, which had been allowed to mate, were introduced to glass jars containing a thin layer of peat. The number of probings during a period of continuous observation was recorded, immediately after which the females were dissected and the number of eggs remaining in the abdomen was found. The most eggs recorded in any newly emerged female, prior to egg laying, is 110. If one supposes that each of the females used in the experiment contained initially this maximum number of eggs (110), subtraction from this figure of the number of eggs remaining in the abdomen after dissection gives an extremely liberal estimation of the number of eggs actually laid. For each individual observed, the number of probings or prickings exceed the number of eggs that could possibly have been laid (Table 26).

TABLE 26. COMPARISON OF THE NUMBER OF PROBINGS AND THE NUMBER OF EGGS LAID

Individual	A	B	C	D	E	F
Number of probings observed	240	174	195	350	408	278
Number of eggs remaining in abdomen (x)	34	63	52	22	14	43
Maximum number of eggs possibly laid (110 - x)	76	47	58	88	96	67

The precise explanation of these unproductive probings is not known. A certain amount of controversy (see Hemmingsen, 1952) exists over whether these abortive attempts at oviposition are a result of searching for suitable oviposition sites, or whether they are a form of "vacuum" or instinctive activity, movements of the cerci which occur independent of the presence of specific external stimuli, in this case the absence of a suitable substrate for oviposition. Though no information is available on the micro-distribution of where eggs of Molophilus are laid in the field, openings and closings of the cerci have certainly been observed for females enclosed in empty glass tubes, tubes lacking a suitable substrate for oviposition.

3. RATE OF EGG LAYING

At 08.00 hours G.M.T. on 5 June 1965, all adults were removed from an area adjacent to the Peaty Gley site. Mating pairs involving newly emerged adults were collected between 09.00 and 10.00 hours and placed in a number of open aluminium cylinders, similar to those used as emergence traps. These were positioned over an area of peat moor which did not support the species. Samples of adults were taken periodically using the vacuum extractor and the females killed rapidly by dropping them into ethyl acetate; this prevented more eggs being laid. The females were later dissected to determine the number of unlaid eggs (Table 27).

Few eggs are laid in the first two hours of the release of mating pairs, presumably because in the majority of cases mating had not been completed. This tends to confirm laboratory observations, already recorded, that individuals may remain in copulation for periods up to 5 hours.

After this, eggs are laid at a high rate, 70% being laid within 6 hours of the release of mating pairs, and between 6 to 8 hours of emergence. The initially high rate of egg laying gradually decreases as fewer eggs remain to be laid. These results resemble closely those recorded for another short-lived moorland crane-fly, Tipula subnodicornis (Coulson, 1962), where 90% of eggs were laid within 7 hours of the completion of mating.

TABLE 27. THE NUMBER OF EGGS FOUND IN FEMALES AT INTERVALS AFTER THE RELEASE OF MATING PAIRS INVOLVING NEWLY EMERGED ADULTS
MEANS CALCULATED FROM EXACT NUMBER OF EGGS FOUND

Time after release (hours)	Number of eggs in abdomen							Mean No. eggs	No. adults
	0	1-20	21-40	41-60	61-80	81-100	101-120		
0	0	0	0	2	25	18	1	79	46
2	0	2	1	0	19	15	0	72	37
4	3	12	1	2	10	12	1	48	41
6	11	13	3	2	8	3	0	24	40
9	22	17	0	1	2	0	0	11	42
12	25	11	1	0	1	0	0	4	38
22	24	11	2	0	0	0	0	4	37
24	21	8	0	0	0	0	0	3	29

For the results given above for Molophilus, perhaps worthy of comment is the fact that few females were recorded containing between 20 and 60 eggs, suggesting that for each individual once oviposition has started the majority of eggs are laid within a very short period of time.

4. DIURNAL EGG COMPOSITION

During the study on the diurnal rhythm of emergence and activity, numbers of females were collected periodically using a sweep net during 8, 9 and 10 June 1965. They were killed immediately and dissected later to determine the numbers of eggs contained by females at different times during the day (Table 28. Fig. 15). There were no appreciable differences in the egg composition of females taken at the same hour G.M.T.

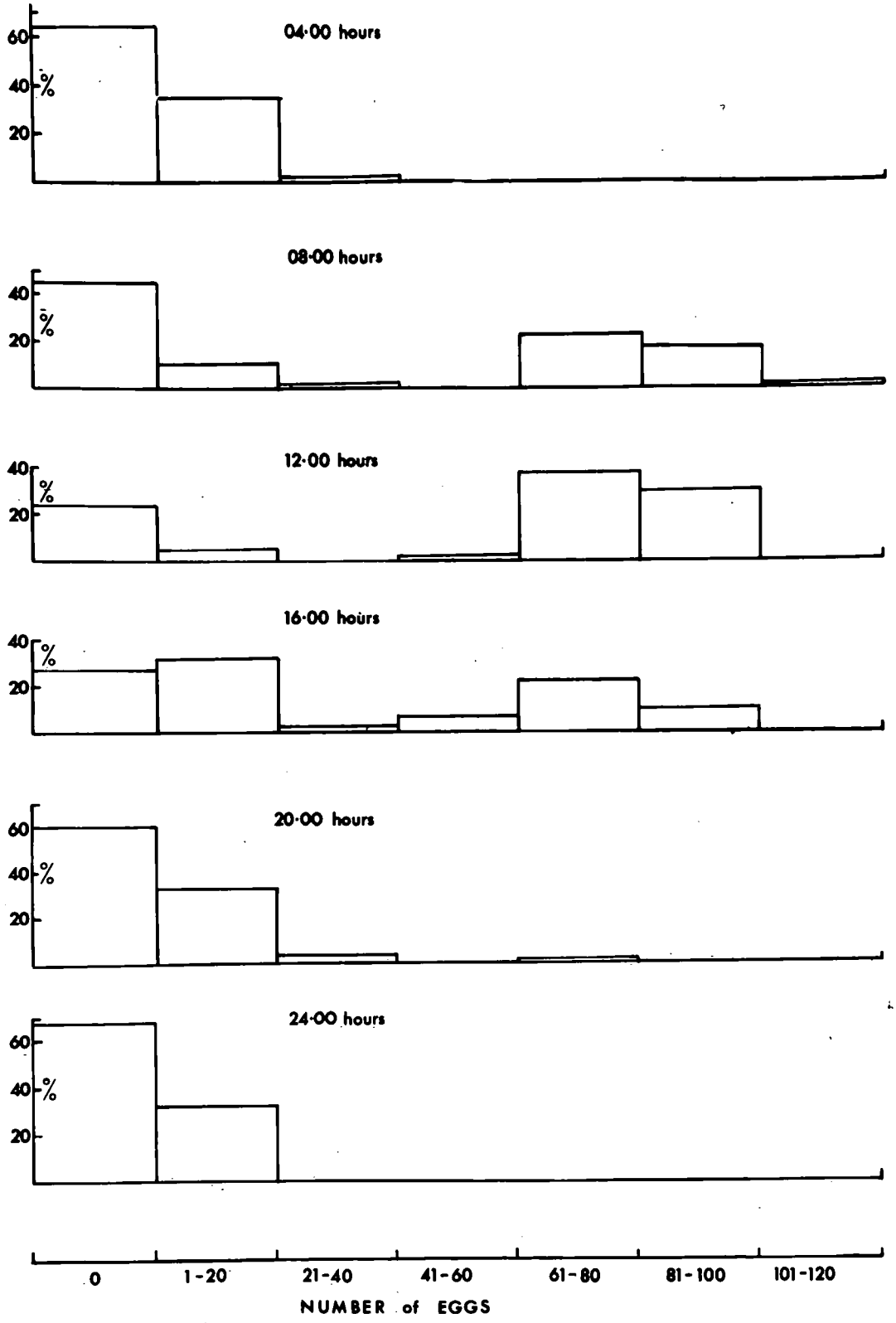
TABLE 28. EGG COMPOSITION OF FEMALES AT DIFFERENT TIMES DURING THE 24 HOUR PERIOD. MEANS CALCULATED FROM EXACT NUMBER OF EGGS FOUND

Time, hours G.M.T.	Number of eggs in abdomen							Mean No. eggs	No. adults
	0	1-20	21-40	41-60	61-80	81-100	101-120		
04.00	59	30	3	0	0	0	0	3.6	92
06.00	74	29	6	0	15	6	0	15.7	130
08.00	62	14	3	0	33	20	3	34.5	135
10.00	51	7	0	6	37	31	5	47.2	137
12.00	38	12	1	3	66	55	2	57.0	177
14.00	30	24	7	11	64	47	4	51.4	187
16.00	29	38	3	7	25	10	0	28.5	112
18.00	46	39	2	2	1	3	0	14.7	83
20.00	59	32	4	0	2	0	0	6.6	97
22.00	63	27	3	1	0	2	0	8.4	96
24.00	28	13	0	0	0	0	0	2.5	41

on the three days of collection; the results have therefore been composited.

The results add confirmation to the observations already recorded on the rate of egg laying of newly emerged females, and the diurnal rhythm of emergence of females. The mean number of eggs per female is only 3.6 at 04.00 hours G.M.T., when no female contained over 40 eggs. From 06.00 to 12.00 hours there is a gradual rise in the mean number of eggs per female with a rise in the proportion of females containing over 60 eggs. At 12.00 hours, 69% of the total females contained over 60 eggs, and the

FIG. 15. THE NUMBERS OF FEMALES CONTAINING DIFFERENT NUMBERS OF EGGS IN THE ABDOMEN AT DIFFERENT TIMES DURING THE 24 HOUR PERIOD.


04·00 hours
08·00 hours
12·00 hours
16·00 hours
20·00 hours
24·00 hours
60
40
20
%
0
1-20
21-40
41-60
61-80
81-100
101-120
NUMBER of EGGS

mean number of eggs was 57.0 per female. These results are in agreement with observations on the diurnal periodicity of emergence of adults, that on average over 80% of the total daily emergence takes place between 06.00 and 12.00 hours G.M.T.

After 14.00 hours there is a pronounced fall in the mean number of eggs per female. By 18.00 hours, the mean number was only 14.7 eggs per female, and only 5% of females taken at this time contained over 60 eggs, confirming the high rate at which eggs are laid and emphasizing the short time after emergence within which the functions of the adult phase are completed.

IV. THE EGG STAGE

The eggs of Molophilus ater, which are mature on emergence, are soft and whitish, and lack an egg filament. Within the long-palped crane-flies the egg filament appears to be an adaptation to oviposition in wet habitats, (Hemmingsen 1952), though they are not generally found in the brevi-palp crane-flies. The linear dimensions of the egg (in μ, $\pm$ S.E.) were determined by the measurement of 150 eggs dissected from 15 females. The mean length was 221 $\pm$ 9, the mean maximum breadth 134 $\pm$ 2. In some females up to 32 smaller eggs were found, between 80 and 100 μ in length. These were especially noticeable when the majority of normal sized eggs had been laid. The development and significance of these smaller eggs is not known, but it seems unlikely that these eggs are matured and laid before the death of the female.

The mean number of eggs per female was 78.0 $\pm$ 1.7 ($\pm$ S.E.), based on the dissection of 50 newly emerged females. It is perhaps interesting to record that the ovaries extend in part into the thorax. Sectioning of adults revealed that the thorax of certain females contained as many as 8 eggs. This is possibly an advantage conferred by the reduction in wing size, and the consequent release of thorax space taken up by wing muscles to other functions. This suggestion must remain tentative; its confirmation would entail a detailed comparison of the wing musculature and distribution of eggs between Molophilus ater

and other Mollophilus species.

Great difficulty was found in handling the eggs of the species. Not until June 1966 were any eggs, laid on agar plates, successfully reared. At 15°C the hatching time varied between 12 and 18 days, suggesting a development time of between 3 and 4 weeks in the field. Nothing is known of the causes of mortality during the egg phase. More sensitive and sophisticated techniques must be used to study such factors as infertility, resistance to desiccation and degree of predation and parasitism in the field. The egg stage proved to be the "bête noire" of the three year investigation.

V. THE LARVAL STAGE

A. METHODS

1. EXTRACTION OF LARVAE

a) THE EXTRACTION APPARATUS

An efficient extraction method is a basic requirement for any quantitative study on soil organisms. Comprehensive reviews of extraction methods for soil animals have recently been provided by Kevan (1962), Macfadyen (1962), Murphy (1962) and Southwood (1966). These methods may be conveniently divided into two main categories, dependent on the degree of participation of the animal in the extraction process. Dynamic methods involve movement of the organism out of its surrounding medium, in response to either attractant or repellent stimuli. In mechanical methods the organism's role is a passive one, separation being effected by sieving, flotation or sedimentation.

Several extraction methods have been used in the study of the larval stages of crane-flies. Coulson (1962) and Freeman (1962) successfully separated larvae of Tipula spp. by washing soil samples through a series of graded sieves. Mechanical methods are, however, unsuitable for use on relatively small organisms, as well as being laborious and time consuming.

Barnes (1941) used an emulsion of orthodichlorobenzene to bring leatherjackets to the surface of grassland turf. Unfortunately, this method is subject to seasonal variations in its efficiency (Milne, Coggins & Laughlin, 1958), as well

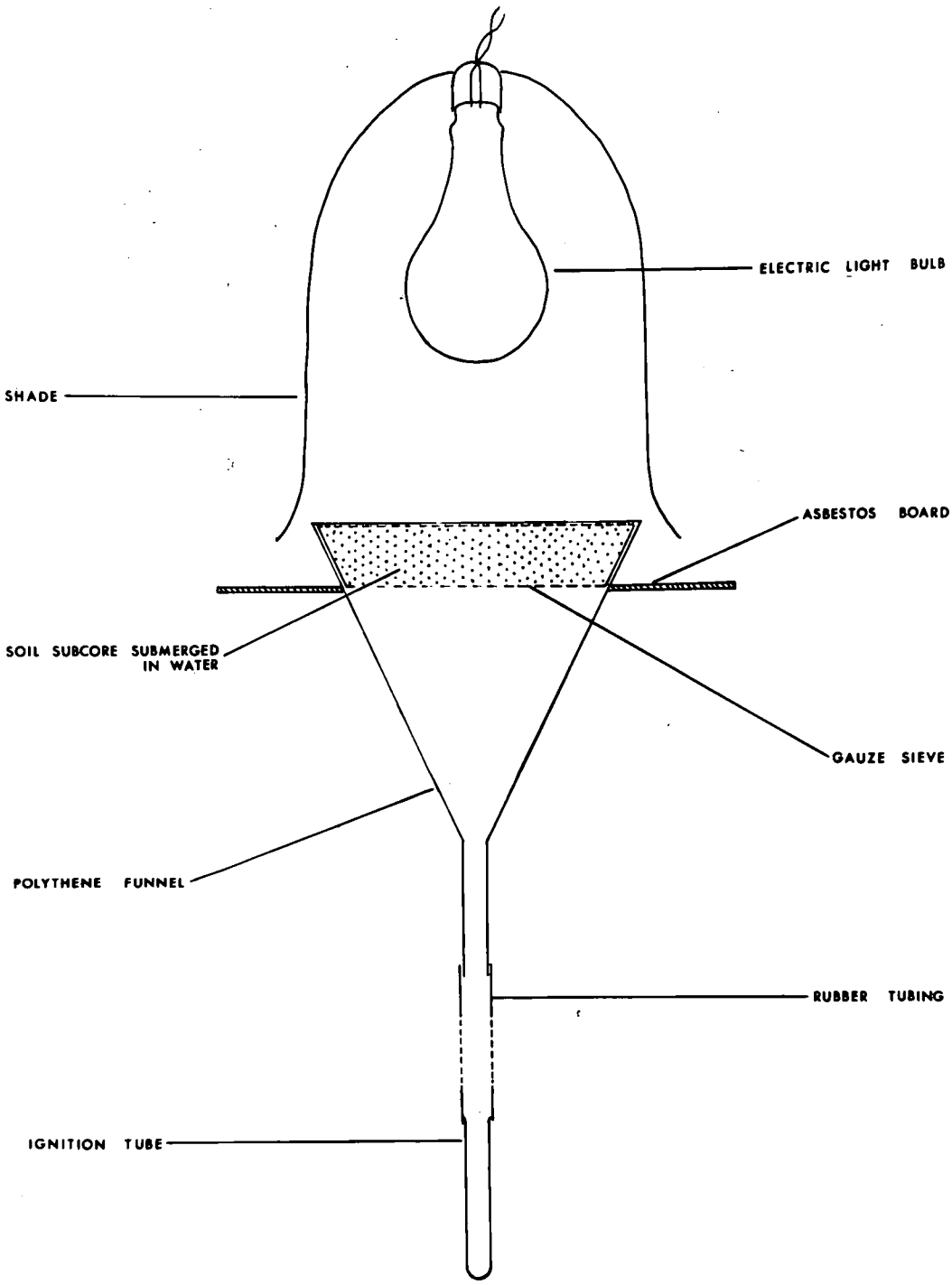
as being suitable only where there is adequate drainage; its use at Moor House, where the soils are frequently waterlogged, was discarded.

A dynamic hot water process for extracting the larvae of Tipula spp. has been developed by Milne, Coggins & Laughlin (1958). Larvae are driven from sample turves by gradually raising the temperature of a surrounding water bath. The method's main disadvantage is an operational one; continuous observation must be made throughout the extracting process and the larvae removed from the surface of the sample as soon as they appear.

Another type of dynamic extraction process was therefore employed, the wet funnel method developed by O'Connor (1955, 1962). In this technique, a modification of one devised by Baermann (1917), heat is applied to soil spread on a sieve submerged in a funnel filled with water. The animals move away from the heat source, downwards through the sieve and fall through the water to be collected in the funnel base. This particular technique was first employed by O'Connor in studies on enchytraeid worm populations in North Wales, though wet funnel methods have been used for extracting a variety of organisms in recent years, including Nematoda, Rotifera and Turbellaria.

The apparatus consists of a battery of 34 units, built according to the dimensions given by O'Connor (1955, 1962). Each unit (Fig. 16) comprises a polythene funnel (diameter 11 cm.),

FIG. 16. SECTIONAL DRAWING OF A SINGLE UNIT OF THE WET FUNNEL EXTRACTION APPARATUS.


ELECTRIC LIGHT BULB
SHADE
ASBESTOS BOARD
SOIL SUBCORE SUBMERGED IN WATER
GAUZE SIEVE
POLYTHENE FUNNEL
RUBBER TUBING
IGNITION TUBE

inserted in a hole (diameter 9 cm.) in an asbestos board, and in which rests a brass gauze sieve (diameter 9 cm., 10 mesh). To each funnel outlet is attached a piece of rubber tubing, the distal end of which is closed by an ignition tube. The heat source is an electric light bulb (60 W.), enclosed in a metal shade.

To avoid lateral temperature gradients the gap between the funnel and the shade was kept narrow and draughts reduced by enclosing the whole apparatus in a shield. The light bulbs and their shades are attached to a movable frame which is raised and lowered by means of a pulley system. The light bulbs are wired in parallel, and heating is controlled by a zenith Variac transformer (Type 100 M).

Several authors have commented on the importance of using only a thin layer of substrate in each funnel (e.g. Dinaburg, 1942; Peachey, 1962). Each sample unit (diameter 8 cm., depth 9 cm.) was therefore sub-divided horizontally into 1.5 centimetre layers, and each undisturbed sub-sample placed surface downwards on the sieve in the polythene funnel. The funnel was filled with water, completely submerging the sample of soil.

b) TEMPERATURE GRADIENT AND EMERGENCE OF LARVAE

O'Connor (1962) recommended a gradual increase in temperature during the extraction process. The heating of the funnel was increased gradually by increasing the current through

a variac, extraction being complete when the sample surface has reached a teperature of about 46°C. after 195 minutes (Table 29). After this time there is a temperature gradient of approximately 9°C between the surface and the base of the sub-sample, equivalent to 6°C per cm. The larvae move down the temperature gradient, emigrate from the sample and collect in the ignition tube; they may then be identified and counted.

In Table 29 are included the times of movement of larvae out of 40 samples, each of diameter 8 cm. and each sample divided into six, 1.5 cm. horizons. There is a single peak of movement out of samples, 65% of the total movement occurring between 75 and 120 minutes after the start of the extraction process. After 120 minutes, 87% of the total number emptied from ignition tubes had been recorded, and the entire movement was completed after 3 hours. Though there were slight differences in the time at which larvae leave different soil horizons and soil taken from different sampling areas, these were not significant and the results have therefore been composited.

TABLE 29. TEMPERATURE CHANGES, AND THE EMERGENCE OF LARVAE, DURING THE EXTRACTION PROCESS

Time from start of heating (minutes)	Variac reading (volts)	Soil temperature (°C) Surface	Base	Gradient (°C/cm.)	Number of larvae extracted	Percentage of total
0	90	16.0	16.0	0	0	0
15	90	22.4	18.2	2.8	0	0
30 *	105	26.6	21.8	3.2	1	0.3
45	105	29.4	24.0	3.6	11	2.8
60 *	120	31.0	25.2	4.1	28	7.2
75	120	32.2	25.8	4.3	49	12.6
90 *	135	33.8	27.4	4.3	85	21.9
105	135	34.8	28.0	4.5	91	23.5
120 *	150	36.0	29.0	4.7	74	19.1
135	150	38.6	31.4	4.8	32	8.2
150 *	165	40.0	32.4	5.1	12	3.1
165	165	42.2	34.0	5.5	4	1.0
180 *	180	44.0	35.6	5.6	1	0.3
195	180	45.6	36.8	5.9	0	0

* Variac reading changed

c) EFFICIENCY OF EXTRACTION PROCESS

The efficiency of extraction was estimated by sterilising samples of soil (diameter 8.0 cm. and 1.5 cm. deep) in an oven at 105°C for 24 hours. These sub-samples were soaked in water and stored separately in polythene bags at a temperature of 5°C for 7 days. They were then returned to the extraction room and a known number of larvae, which had been previously extracted

from soil samples, were introduced into each sub-sample. In most cases, ten larvae were introduced into each sub-sample. After 24 hours the sub-samples containing known numbers of larvae were then placed in the funnels, and subjected to the extraction procedure already described.

Comparison of the number of larvae extracted with the number introduced enabled estimates to be made of the efficiency of the extraction process (Table 30). For most of the larval period, from August to May and for instars 2, 3 and 4, the extraction efficiency was high, ranging between 89.2 and 97.1 per cent. Of the 700 larvae introduced on 5 occasions during this period the mean recovery rate was 94.6%, though it must be remembered that this is a maximum estimate of efficiency, relying as it does on the introduction of larvae into prepared, and somewhat artificial, samples of soil; it is improbable that the larvae take up a comparable micro-distribution to that which occurs under natural conditions. Hand sorting, using a muslin net, of soil samples from which larvae had been extracted failed to reveal more than the very occasional individual, and it seems likely that the estimates of efficiency obtained throughout most of the larval period satisfactorily reflect the true efficiency of the extraction process. This is confirmed by the close agreement between the estimated density of larvae immediately prior to pupation, and the estimated density of the total adult emergence (see Section III C). The estimated

TABLE 30. ESTIMATED EFFICIENCY OF THE WET FUNNEL EXTRACTION PROCESS

Date 1964 - 65	Instar composition	Number of larvae introduced	Number of larvae recovered	Percentage recovered
July	1	100	63	63.0
August	2-3	150	144	96.0
September	3-4	150	139	92.7
November	4	170	165	97.1
February	4	150	145	96.7
May	4	120	107	89.2

efficiency for instar one larvae taken in July was unsatisfactory. Of 100 individuals introduced, only 63 were recovered. Unfortunately, larger numbers of replicates could not be performed since the majority of larvae at this stage were already dead on collection from ignition tubes at the end of their initial extraction. It seems possible that some first instar larvae become inactive due to excess heat or lack of oxygen during the extraction process, and thus do not pass through the sieve, and into the ignition tubes. However, using a more sensitive heat gradient (the water surface reaching a temperature of 45°C after 8 hours) and shaking the funnel occasionally in order to increase the aeration, there was only a small rise in efficiency. Of 60 individuals introduced into sterilised soil samples, only 41 (68%) were recovered.

2. SAMPLING

Morris (1955) and Cochran (1963) have both drawn attention to the importance of selecting the most suitable sample unit size, and the total number of sample units taken, in any quantitative sampling programme. Preliminary sampling using a core borer of surface area 0.001 sq.m. yielded numbers in the order of 0 to 4 per sample unit. This was considered too low a yield, and a larger borer of surface area 0.005 sq.m. was constructed to provide a reasonable balance between the variance and the cost. The borer, attached to a handle, comprised a brass cylinder 15 cm. high with a cutting edge of diameter 8.0 cm. Samples were taken to a depth of 9 cm., preliminary sampling indicating that the majority of larvae occur within 3 cm. of the soil surface, and that only a small number occur between 6 to 9 cm. of the surface.

Initially 30 sample units were taken each month from two different areas, but when the number of study areas was increased to four in July 1964, it was found impossible to continue taking 30 sample units of this size from each area. Rather than sample fewer areas, or sample the same number of areas less often, it was decided to reduce the number of sample units taken by half, to fifteen. This made little appreciable difference to the mean or to the variance of the populations investigated. (Table 31).

TABLE 31. EFFECT OF REDUCING THE NUMBER OF SAMPLE UNITS TAKEN FROM 30 TO 15 ON THE MEANS AND CONFIDENCE LIMITS OF LARVAE ON THE PEATY GLEY SITE IN 1964

	12 Aug.	21 Sept.	14 Oct.	4 Nov.
Mean of 15 units	11.73	12.13	11.20	11.13
S.E. of 15 units	1.98	2.05	1.73	1.51
Mean of 30 units	11.23	11.43	11.97	12.20
S.E. of 30 units	1.44	1.29	1.29	1.20
Difference of means	0.50	0.70	0.77	1.07
S.E. of difference	2.45	2.42	2.16	1.93

Samples were taken without bias in a stratified random manner (see Yates & Finney, 1942; Healy, 1962); each sampling area was divided into equal sized sub-divisions and one sample taken randomly from each sub-division.

Each 9 cm. deep sample unit was divided into six, 1.5 cm. horizontal layers; on return to the laboratory, each sub-sample was stored separately at a temperature of 5°C, approximating to soil temperatures recorded at Moor House. Since the temperature of the extraction room varied between 14 and 18°C, the samples were gradually warmed to this temperature over a 24 hour period prior to extraction.

B. THE LARVAL INSTARS

1. INTRODUCTION

Several hypotheses have been purported regarding the growth of insects. Dyar's Law (Dyar, 1890) was based on the observation that the head capsule width of lepidopterous larvae increases in a geometric progression at each moult by a factor, usually 1.4, which is constant for each species. A similar pattern has been found in many other groups and for linear measurements of many cuticular structures (e.g. Kettle, 1948; Hale, 1965). The rate of growth is not, however, always constant. According to Calvert (1929), Forbes (1934) and Beck (1950) the increase from the first to the second instar is greater, and that from the penultimate to the last instar less than that for other moults.

Information on the number of larval instars of Tipulidae is scarce in the published literature. Many references merely discuss the first or final larval stages, and do not indicate the number of instars involved (e.g. Barnes, 1937; Chiswell, 1955). The evidence available, and this is restricted almost entirely to the Tipulinae, suggests that four is the usual number of instars (Hennig, 1950; Brauns, 1954). Coulson (1956), measuring the maximum diameter of spiracular discs, found the larval phase to comprise 4 instars in six species of crane-flies. Similar findings have been reported by White (1951) for Tipula lateralis Meigen, and by Byers (1961) for members of the genus

Dolichopeza. Several other authors have found no indication of a fifth instar in the Tipulidae (De Jong, 1925; Sellke, 1936; Hemmingsen, 1959). One exception to this general rule is Phalacrocera replicata Linnaeus, which Alexander (1920) quotes as having at least 8, and possibly 10, instar stages. There has been no recent confirmation of this. No reference has been found indicating the number of instars in any member of the Eriopterini, the tribe which includes the genus Molophilus.

2. DETERMINATION OF INSTARS

The generalised crane-fly capsule, such as is typical of the Tipulinae, is formed of three rigid plates, a fronto-clypeus and two side pieces or lateralia. A rather more specialised condition is found in Molophilus spp. and other members of the Eriopterini. Here, the rigid part of the head capsule is reduced to six rods, two dorsal, two lateral and two ventral. In this dissected type of head capsule, the dorsal and lateral rods unite anteriorly and are joined to a strong bridge, providing a fulcrum for the upper mouthparts, just behind the base of the labrum.

Two head capsule characters were found to provide a satisfactory basis for the evaluation of larval instars, namely the length of the dorsal rod and the width of the dorsal bridge. The latter character is, in fact, the maximum width of the head capsule, and will be referred to as such in the following account. A third character investigated was the spiracular disc. Following

Coulson (1956), the maximum diameter of the spiracular disc was measured, as the shape of the disc tended to change from a circular form in the early instars to a more oval form in the later instar stages.

Frequency distribution histograms of each of the characters measured show the existence of 4 clearly defined size groups (Fig. 17), indicating that Molophilus ater has 4 larval instars. There was no dimorphism in the fourth instar for any of the characters measured. Freeman (1964) was able to estimate the sex ratio of the final instar larvae of Tipula luna by analysis of polymodal frequency distributions of the length of head capsules; similar analysis for Molophilus ater proved unfruitful.

The ratios of the mean for each character from one instar to the next are compared in Table 32, and are sufficiently regular to show a geometric increase in size at each moult. Though the rate of increase for measurements on the length of the dorsal rod is greater between first and second instars than between succeeding instars, there is no evidence of a similar trend in the other two characters measured. Measurements on Molophilus lend no support to the statement of Beck (1950) that "the supposed constant factor is not actually constant but tends to decline in succeeding instars".

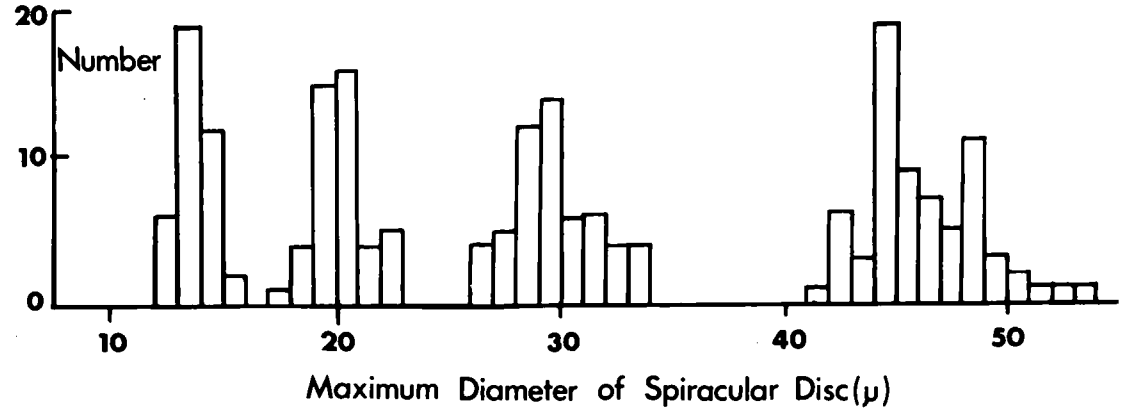
Logarithmic transformation of any data suspected of showing a geometric progression should result in a linear relationship. In Fig. 18, the logarithm of the mean of each character is plotted against the 4 instars. For each character a straight

FIG. 17. FREQUENCY DISTRIBUTION HISTOGRAMS OF THE LARVAL INSTARS.

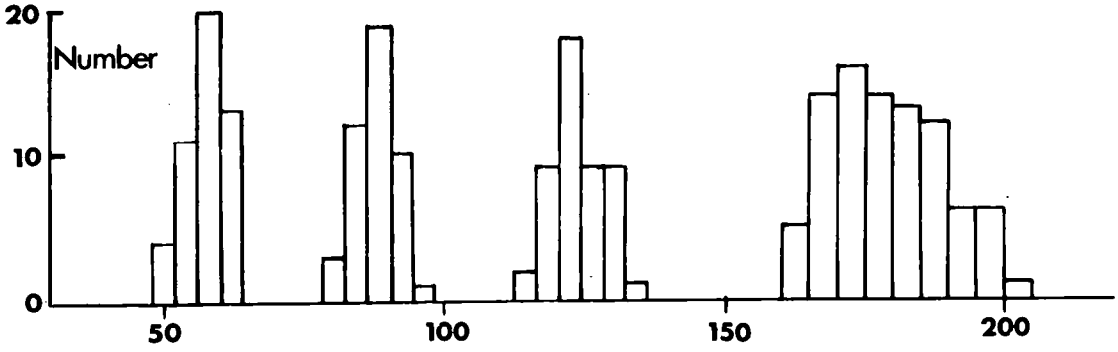
a) Maximum diameter of spiracular disc

b) Maximum width of head capsule

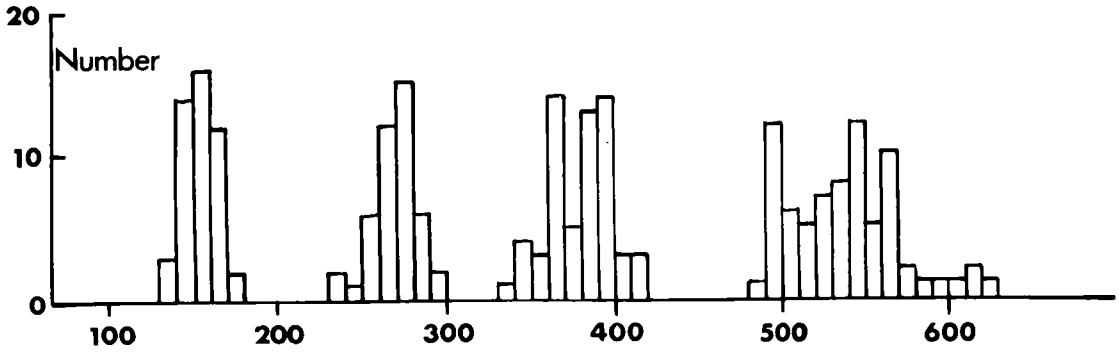
c) Length of dorsal rod of head capsule



Maximum Diameter of Spiracular Disc(μ)



Maximum Width of Head Capsule (μ)



Length of Dorsal Rod (μ)

TABLE 32. MEASUREMENTS OF CHARACTERS USED IN EVALUATION OF INSTARS, AND RATES OF INCREASE, OF MOLOPHILUS ATER

	Instars			
	1	2	3	4
MAXIMUM DIAMETER OF SPIRACULAR DISC				
Number measured	39	45	57	69
Mean (μ)	13.8	20.1	29.3	45.9
Standard deviation	0.75	1.12	1.87	2.58
Rate of increase		1.46	1.46	1.57
MAXIMUM WIDTH OF HEAD CAPSULE				
Number measured	48	45	49	87
Mean (μ)	58.0	87.6	122.4	178.4
Standard deviation	1.72	2.83	4.32	10.20
Rate of increase		1.51	1.40	1.46
LENGTH OF DORSAL ROD				
Number measured	47	44	59	74
Mean (μ)	156.9	269.6	378.6	536.7
Standard deviation	6.66	13.15	18.99	32.09
Rate of increase		1.72	1.40	1.42

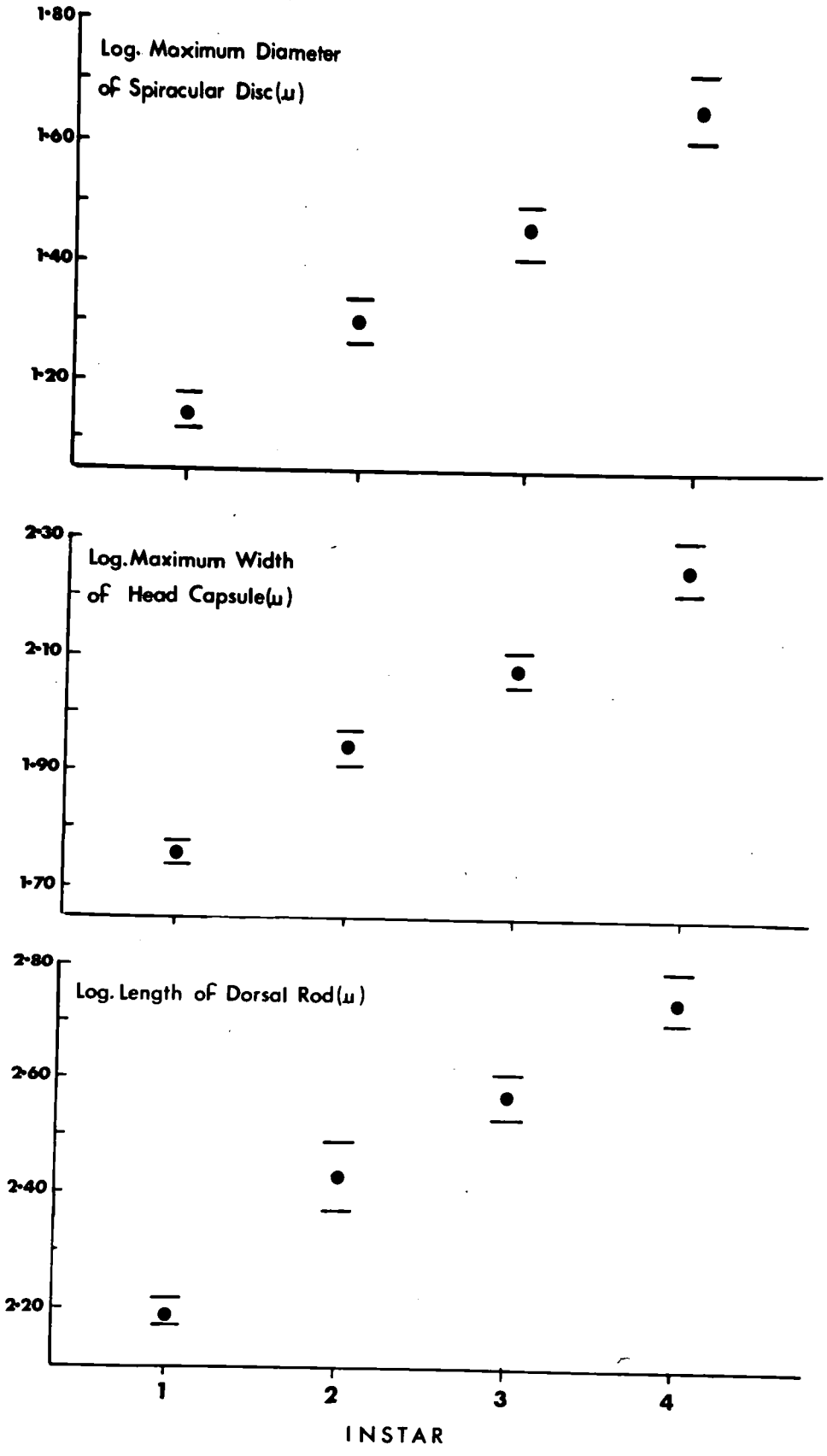
line is obtained and Dyar's Rule supported. The resulting straight line relationship indicates that it is unlikely that another instar exists between the 4 postulated. The possibility that a larval stadium may have been missed at either end of the series has been eliminated. Measurements of head capsule widths within the egg, and of cast larval head

FIG. 18. THE LOGARITHM OF THE MEANS OF THREE LARVAL CHARACTERS, PLOTTED AGAINST THE INSTAR NUMBER. THE OBSERVED EXTREME VALUES FOR EACH MEAN ARE SHOWN.

a) Maximum diameter of spiracular disc

b) Maximum width of head capsule

c) Length of dorsal rod of head capsule


1·80
Log. Maximum Diameter
of Spiracular Disc(μ)
1·60
1·40
1·20
2·30
Log. Maximum Width
of Head Capsule(μ)
2·10
1·90
1·70
2·80
Log. Length of Dorsal Rod(μ)
2·60
2·40
2·20
1
2
3
4
INSTAR

capsules found in culture after pupation, show close agreement with the measurements obtained for instars 1 and 4 respectively.

3. DURATION OF INSTARS

The method used to calculate the duration of instars was that of Gabbutt (1959). For each sampling date, the percentage instar composition of a random sub-sample of extracted larvae was found, and a mean value for the maximum width of the head capsule determined (Table 33). This mean value for any sampling date is a function of the proportion of instars present in the population, and the growth processes taking place will be reflected by changes in the mean. By plotting the mean against time, interpolation from the resulting sigmoid curve of the values for the mean maximum width of head capsule for successive instars will indicate the time lapse between those instars (Fig. 19). Unfortunately this technique has certain limitations. It cannot delimit the duration of the first instar stage, nor, in the present study, indicate precisely the change from the third to fourth instar; a different sampling date would have altered the shape of the upper part of the curve. The analysis does, however, indicate that the second instar stage lasts for about 4 weeks, and that the entire population is in the final instar stage by the beginning of November.

The proportion of instar 1 larvae recorded in the samples for July and August is almost certainly lower than the true proportion in the field. The efficiency of extraction for the

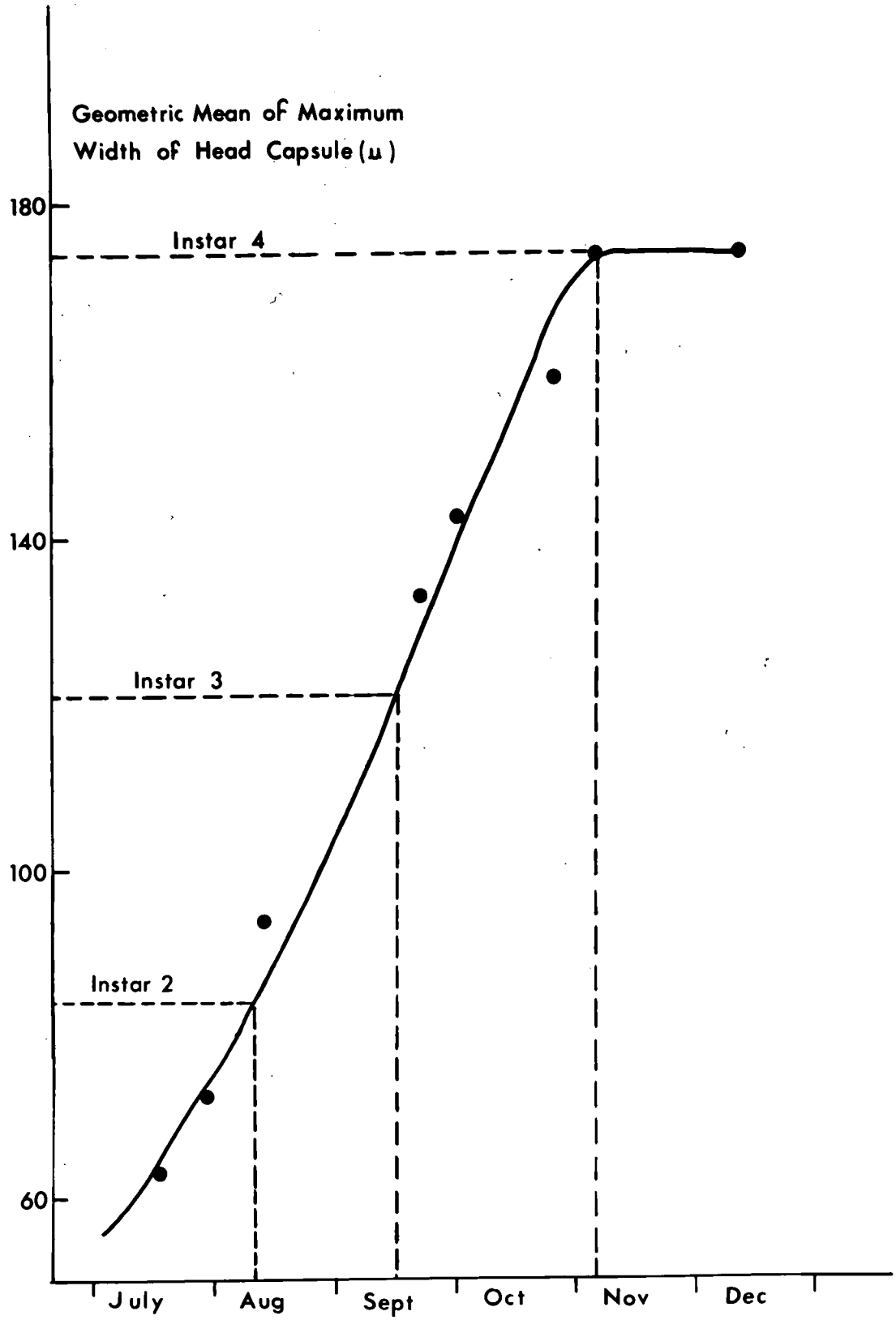
TABLE 33. PERCENTAGE INSTAR COMPOSITION ON DIFFERENT SAMPLING DATES

Date 1964	% Instar 1	2	3	4	Geometric Mean of maximum width of head capsule (μ)	Number measured
16 July	85.5	3.6	0	10.9	66	55
28 July	56.0	32.0	2.0	10.0	75	50
12 August	11.1	64.8	13.0	11.1	94	54
21 September	0	4.3	63.0	32.7	136	46
30 September			58.6	41.4	145	58
14 October			33.9	66.1	159	56
4 November				100.0	178	45
10 December				100.0	178	53
6 May 1965				100.0	178	50

first instar is lower than for succeeding instars (see Section VA), but no correction has been made in the data presented here. Perhaps surprising is the presence of a significant proportion of instar 4 in the samples for 16 July, when there was complete absence of instar 3. Though this proportion is inflated, due to the previously mentioned low extraction efficiency for instar 1, measurements of head widths and detailed investigation of the anatomy and morphology leave no doubt that these individuals are instar 4 larvae of Molophilus ater. It was thought that these individuals might be the larvae of Erioptera spp. or Ormosia pseudosimilis Lundstroem, species which are closely related to Molophilus ater which occur in similar habitats to the latter at

FIG. 19. THE DURATION OF INSTARS ON THE PEATY GLEY SITE IN 1964.

Each point represents the geometric mean of the maximum head width of the population on each sampling date. The projected horizontal lines are the means of the maximum head capsule width of instars two to four.


Geometric Mean of Maximum
Width of Head Capsule (μ)
180
140
100
60
Instar 4
Instar 3
Instar 2
July
Aug
Sept
Oct
Nov
Dec

Moor House (Coulson, 1959). The spiracular discs of these two genera show differences from Molophilus spp. (see Alexander, 1920); examinations of the spiracular discs clearly showed that these larvae are not those of Erioptera or Ormosia spp., but are larvae of Molophilus ater. Attempts to induce these individuals to pupate in the laboratory were not successful. They were cultured on agar plates of the type used by Springett (1964), but they died after 3 to 4 weeks. There was no apparent reason for their death.

Cuthbertson (1929b) included Molophilus ater in a group of species with a wide seasonal distribution, occurring from May to September with probably more than one emergence period per year. It is not clear by this whether Cuthbertson believes the species to be bivoltine under certain environmental conditions. Detergent traps were kept in position from July to October on all the sites under investigation but there was no evidence of a second period of emergence for the species at Moor House. Whether these individuals, whose development seems retarded in some way, might produce a second emergence period at lower altitude must remain conjecture.

Within the Tipulidae, there is a limited literature on the influence of altitude on the timing and number of emergence periods. One rather surprising relationship between altitude and the timing of emergence is that of Tipula paludosa. At Rothamsted, the adults reached maximum abundance in September

(Barnes, 1937; Robertson, 1939), whilst at higher altitudes at Moor House the peak emergence occurred some six weeks earlier, during late July and early August (Coulson, 1962). As yet there is no explanation for these results.

The effects of altitude on the number of emergence periods is slightly better documented. At Moor House, Limnophila meigeni Verral, Limnophila pulchella Meigen and Pedicia rivosa Linnaeus are each characterised by one emergence period per year (Coulson, 1956), whilst in the New Forest there are two distinct periods of emergence for these species (Freeman, 1962). Again, Brown & Duncan (1949) indicate that Tipula rufina Meigen has two generations per year, whilst data for Moor House (Coulson, 1956), and for Iceland (Nielson, Ringdahl and Tuxen, 1954), suggests that at these locations the species is univoltine. Tricyphona immaculata Meigen has two periods of emergence at lowland altitudes (Freeman, 1962), but at high altitude at Moor House the second emergence period is very poorly represented (Coulson, 1956).

There is no comparable information available for Molophilus ater. In Appendix III, particulars of adult specimens in the British Museum collection are given. For all specimens the dates and approximate locations of capture were listed, but only in isolated cases was the exact altitude of capture recorded. Adults were caught at dates ranging from 18 April to 27 July, but whether the species has two emergence periods at certain localities must remain conjecture. Studies on the emergence periods at

lowland altitudes, in conjunction with experimental work on those individuals which fail to pupate at Moor House, and remain as instar 4 during July, would prove a worthy topic for further investigation.

C. HORIZONTAL DISTRIBUTION

Aggregated distributions have been recorded for many animal groups living in the soil. Individuals forming these non-random distributions are affected by two antagonistic influences; a tendency to disperse in order to secure an adequate living space, and an opposing tendency to gregariousness induced by the ecological heterogeneity of the soil, and the consequent presence of micro-habitats which may be particularly favourable to the species.

Several methods have been used to evaluate the spatial distribution of soil organisms. One approach is that of Hughes (1962) who used a tie-line sampling technique to estimate the number and mean radius of animal aggregations. Another approach is that of complete enumeration of all organisms living in a certain predescribed area, and the subsequent mapping and analysis of the numbers found (see Salt and Hollick, 1946; Nielson, 1954; O'Connor, 1957). The disadvantage of this method is that it entails destruction of the habitat. A third approach, and that used in the present study, is the analysis of results obtained from random sampling. In this technique, which suffers in comparison with the two other methods described, in that aggregation is considered as a statistical rather than a biological phenomenon, the spatial distribution of organisms is determined by comparison of sample counts with a Poisson series. In a Poisson distribution, animals are distributed completely at

random, and it is supposed that there is no influence of one organism on another, and that the presence of one animal in a sampling unit makes no difference to the probability of finding others. In a Poisson distribution, the variance and the mean should always be exactly equal.

Blackman (1942) used this ratio of the variance to the mean to evaluate the presence or absence of non-randomness in a population. The ratio, known as the coefficient of dispersion, may be written:-

$$\frac{\Sigma(x - \bar{x})^2}{\bar{x}(n-1)} \quad \text{or} \quad \frac{V}{\bar{x}}$$

where x = number per sample unit

and $\bar{x}$ = mean number per sample

Any population not describing a Poisson or random distribution will be indicated by departures in this ratio from unity. Aggregations will be indicated by a ratio greater than unity, and a regular distribution by a ratio less than unity. The departure from unity was considered by Blackman (1942) to be significant at the 5% level of probability if the value was greater or less than unity by two standard errors.

Two standard errors are equal to:-

$$2\sqrt{\frac{2N}{(N-1)^2}}$$

where N = number of sample units taken

Bartlett[1] (in Greig-Smith, 1952) has provided a more correct estimation of this value, namely:

$$\sqrt{\frac{2}{(N-1)}}$$

Fifteen sample units were taken oneach sampling date, so that using this standard, the ratio of variance to mean may be considered to depart significantly from unity if it exceeds 1.76 or falls below 0.24.

The coefficients of dispersion for larvae on three sites during 1964-65 are presented in Table 34. For each series of samples, the coefficients of dispersion were significantly different from unity, indicating that the distribution of larvae was aggregated. Several authors have been able to correlate changes in the degree of aggregation with different stages in the life history of animals (e.g. Salt & Hollick, 1946; Milne, 1964; Whittaker, 1965), but the coefficients of dispersion presented for Molophilus ater provide no evidence of any change in spatial distribution during the larval phase of the species.

Taylor (1961, 1965) has expressed the relationship between the variance and the mean as:-

$$V = a\ \bar{x}^{b}$$

where a and b are constants; a is largely a sampling factor and b a true index of aggregation in the species. Using the trans-

TABLE 34. THE COEFFICIENTS OF DISPERSION OF LARVAE ON THREE SITES IN 1964-65

Date	Coefficient of Dispersion		
	Peaty Gley Site	Peaty Podsol Site	Carecetum Site
16 July	5.0	4.3	6.4
12 August	5.3	3.4	4.1
21 September	5.2	6.0	4.2
14 October	4.0	3.4	3.0
4 November	3.1	1.8	5.5
10 December	2.2	5.4	3.2
25 February	4.3	3.2	3.2
30 March	3.0	4.1	3.9
26 April	3.9	4.3	2.8
6 May	4.4	4.6	2.4

formation $z = x^{0.6}$ (see Healy & Taylor, 1962), the combined sampling results from three sites during the 1964-65 larval period were found to have the values $\underline{a}$ = 1.70 and $\underline{b}$ = 2.07. Taylor (1961) gives values of $\underline{b}$ ranging from 0.7 to 3.1.

Skellam (1952) and Greig-Smith (1964) have commented that coefficients of dispersion are dependent upon the size of the sample unit. This criticism is only justified, however, if an absolute measure of aggregation is required. Its use is perfectly valid to indicate the presence of aggregation, and to demonstrate differences in the degree of aggregation between different groups of samples of the same sample unit size. As Greig-Smith (1952) has pointed out, for any population there

exists an optimum sample unit size for detecting aggregation; sample units may be either too large or too small to indicate the presence of aggregation within a population. In certain cases, a given sample size may indicate that a population is distributed randomly, following a Poisson expectation, but this may not necessarily reflect the true state of affairs within a population. However, if a particular sample size detects aggregation, this is a real phenomenon and aggregation exists within the population.

A second criticism of the use of the coefficient of dispersion for demonstrating non-randomness in a population is that of Clapham (1936), that it is dependent on the sample mean. Sample counts have therefore been compared to the negative binomial distribution (see Anscombe, 1950; Bliss, 1958). One parameter of this distribution is the exponent $\underline{k}$, which provides a measure of the degree of clumping or aggregation in a population and which is considered by Cassie (1962) to be relatively independent of the mean. This parameter is an inverse measure of aggregation and becomes large as the distribution approaches the Poisson form.

Though the value of $\underline{k}$ may be determined by several methods (e.g. Bliss & Owen, 1958; Debauche, 1962; Katti & Gurland, 1962), the best possible of $\underline{k}$ is extremely tiresome to compute, and Healy (1962) suggests that an adequate estimation may be obtained from:-

$$k = \frac{\bar{x}^2}{V - \bar{x}}$$

In Fig. 20, the values of $\underline{k}$ have been plotted against the corresponding coefficients of dispersion. The values of $\underline{k}$ for the sampling data obtained during 1964-65 range between 1.12 and 5.46. Though there is a good deal of scatter, there is a relationship between these two measures of the degree of aggregation in the population, the coefficient of dispersion becoming smaller, and the value of $\underline{k}$ larger, as the distribution approaches the Poisson form.

The nature of aggregation may be readily appreciated by comparison of the sampling unit frequency found with that expected if the distribution described a Poisson form. There is no significant change in larval density throughout the larval period (see Section VII); the sampling unit frequencies for each sampling date on each site have therefore been combined. For 150 sample units, comprising 15 samples taken on each of 10 occasions during the 1964-65 larval period, the mean number of larvae per sample unit was 10.37 for the Peaty Gley site, 10.57 for the Peaty Podsol site and 6.33 for the Carecetum site. In Table 35, the expected Poisson distributions for these means are compared with the observed frequency distributions. On each site, the aggregated larval distribution is shown by the low number of observed unit values near the mean, and the relatively high number of values near the extremes of the distribution compared with the Poisson distribution.

FIG. 20. THE RELATIONSHIP BETWEEN THE COEFFICIENT OF DISPERSION (V/M) AND THE PARAMETER OF THE NEGATIVE BINOMIAL DISTRIBUTION K, FOR THE RESULTS OBTAINED DURING THE 1964-65 LARVAL PERIOD.

The regressions for the results for the three sites are as follows:-

Carecetum site:- $y = 3.93 - 0.41x$

$r = -0.82$

Peaty Podsol site:- $y = 7.40 - 0.92x$

$r = -0.88$

Peaty Gley site:- $y = 7.70 - 0.95x$

$r = 0.89$

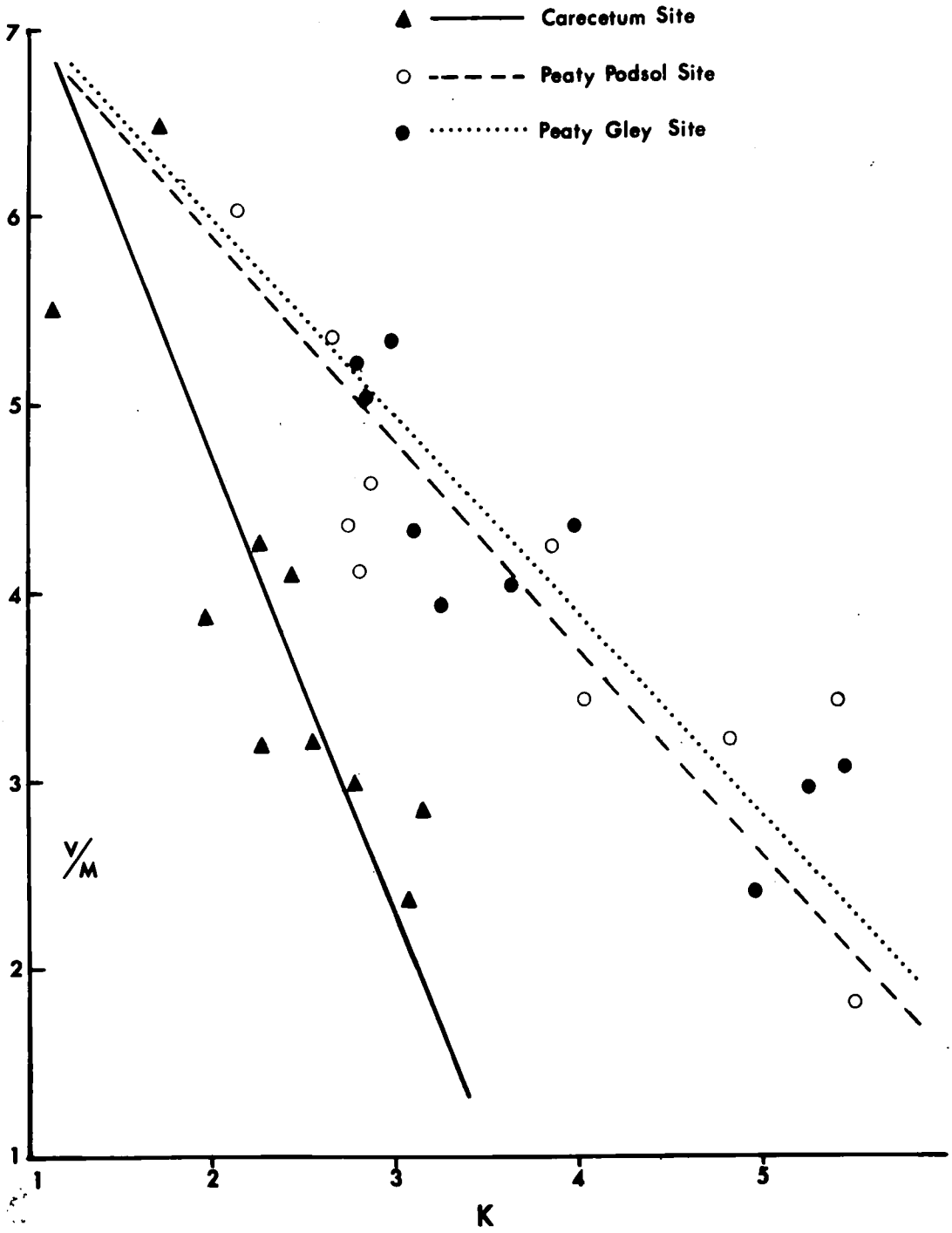

Carecetum Site
Peaty Podsol Site
Peaty Gley Site
7
6
5
4
3
2
1
V/M
1
2
3
4
5
K

TABLE 35. OBSERVED FREQUENCY DISTRIBUTIONS OF LARVAE ON THREE SITES DURING THE LARVAL PERIOD 1964-65, AND FITTED POISSON DISTRIBUTIONS

PEATY GLEY SITE			PEATY PODSOL SITE			CARECETUM SITE		
No. per sampling unit	Sampling unit frequency	Expected frequency	No. per sampling unit	Sampling unit frequency	Expected frequency	No. per sampling unit	Sampling unit frequency	Expected frequency
0	4	0.01	0	2	0.01	0	5	0.28
1	3	0.05	1	5	0.04	1	14	1.72
2	6	0.25	2	7	0.17	2	19	5.36
3	9	0.87	3	7	0.73	3	18	11.30
4	11	2.27	4	5	2.00	4	17	17.85
5	8	4.70	5	11	4.24	5	13	22.31
6	8	8.12	6	10	7.24	6	9	23.20
7	7	12.03	7	9	11.26	7	9	20.97
8	13	15.60	8	12	14.91	8	5	16.35
9	10	17.97	9	9	17.50	9	4	11.33
10	7	18.63	10	10	18.50	10	8	7.17
11	7	17.57	11	5	17.67	11	5	4.07
12	4	15.18	12	9	15.64	12	4	2.12
13	9	12.14	13	4	12.71	13	6	1.05
14	5	9.00	14	10	9.61	14+	14	4.92
15	8	6.21	15	7	6.76			
16	8	4.03	16	6	4.43			
17	6	2.45	17	6	2.77			
18+	17	2.92	18+	16	3.81			
TOTAL	150	150.00		150	150.00		150	150.00

Throughout the sampling period the dominant plant species of each sample was recorded, but the number of larvae extracted from individual sample units did not reveal any consistent differences which could be attributed to differences in plant species. Spatial distribution of larvae could not therefore be correlated with the heterogeneity of vegetation, at least not by using random sample units of the size taken (0.005 sq.m.). The larval stages of Molophilus ater have been shown to be aggregated in their distribution, but the biological reasons for this phenomenon must remain mere hypotheses. More sensitive sampling techniques, allied to studies on the grouping of eggs and the micro-distribution of larvae in relation to physical, chemical and biotic components of the environment, are required if progress is to be made on the precise factors which control the spatial distribution of not only the larvae of Molophilus ater but of other soil organisms whose distribution is aggregated.

D. VERTICAL DISTRIBUTION

Soil samples were taken to a depth of 9 cm. and divided immediately into 6 layers, each 1.5 cm. deep. During 1964-65, samples were taken monthly on three sites throughout the larval phase of the species, with the exception of February 1965 when adverse climatic conditions isolated the Moor House Reserve.

The vertical distribution of larvae has been presented as the number extracted from three strata; from 0-3 cm., from 3-6 cm. and from 6-9 cm. On the Peaty Gley and Peaty Podsol sites, the 3 cm. horizon coincides almost exactly with the boundary between the upper vegetation and decomposition layer, and a lower layer consisting of peat permeated by plant roots. On the Carecetum nodum the vegetation is less dense, decomposing material is consequently less and the above-mentioned boundary occurs at approximately the two cm. level.

The majority of larvae were extracted from the 0-3 cm. layer (Table 36). Combining the data for the three sites, 73.4% of the total number were recovered from this stratum. A similar concentration in the upper soil levels has been observed for many micro-arthropods (e.g. Macfadyen, 1952; Murphy, 1953; Wallwork, 1959; Dhillon & Gibson, 1962). This distribution seems to be largely due to the concentration of plant remains near the surface, though waterlogging of the substrate is a probable contributory factor. At Moor House, peaty areas are perpetually waterlogged below about 3 cm.,

TABLE 36. VERTICAL DISTRIBUTION OF LARVAE ON THREE SITES DURING THE LARVAL PHASE 1964-65. ON EACH SITE THE TOTAL NUMBER WERE EXTRACTED FROM 150 SAMPLE UNITS

	0-3 cm.		3-6 cm.		6-9 cm.	
Site	No.	%	No.	%	No.	%
Peaty Gley	1180	71.3	353	21.3	121	7.3
Peaty Podsol	1171	73.1	321	20.0	110	6.9
Carecetum	736	77.6	180	19.0	33	3.5
Total	3087	73.4	854	20.3	264	6.3

except during periods of extreme drought, such as the summer of 1955 (Coulson, 1962). Saturated peat increases the difficulties of living at lower levels in the soil, difficulties of low oxygen tension and lack of living space; certainly micro-arthropods appear to congregate where the pore spaces are largest (Elton & Miller, 1954; Murphy, 1955) and Haarløv (1955, 1960) has correlated reduction in pore size with increasing soil depth.

Though for each site the majority of larvae were extracted from the 0-3 cm. layer, a greater proportion of larvae were extracted from this layer on the Carecetum site (77.6%) than on the Peaty Gley (71.3%) and the Peaty Podsol (73.1%) sites. The differences are significant at the 1% ($\chi^2 = 11.6$, d.f. = 1, $P < 0.01$) and the 5% ($\chi^2 = 6.3$, d.f. = 1, $P < 0.05$) levels of significance respectively. It is not known whether this

difference in distribution is due to the less dense plant and decomposition on the Carecetum site, compared with the other two sites, or whether it is due to such factors as possible differences in pore size and degrees of oxygen exchange. There is no significant difference in the proportion of larvae recorded from the 0-3 cm. horizon between the Peaty Gley and Peaty Podsol sites ($\chi^2 = 1.3$, d.f. = 1, $P>0.2$).

In Fig. 21, the numbers of larvae extracted from each stratum are expressed as a percentage of the total number extracted on each sampling date for the Peaty Gley site in 1963-64, and for this site and two others in 1964-65. There is a pronounced increase in the percentage of larvae found below 3 cm. during the winter months. Combining the data for the three sites in 1965, 59.7% and 67.7% of the total number were extracted below the 3 cm. horizon in February and March respectively. There appears to be a downward movement from the surface layers, where the eggs are laid, in the winter months, and an upward movement in spring in preparation for pupation.

The seasonal variation in the percentage of larvae recovered from each stratum cannot be attributed to a differential mortality occurring in one of the sample layers. Though a full discussion of seasonal changes in the density of larvae is witheld until a succeeding section, there does appear to be no large mortality during the larval stage. In Table 37, the total number of larvae extracted, and the number extracted from each stratum, are given

FIG. 21. THE PERCENTAGE VERTICAL DISTRIBUTION OF LARVAE.

A. Peaty Gley site, 1963-64

B. Peaty Gley site, 1964-65

C. Peaty Podsol site, 1964-65

D. Carecetum site, 1964-65

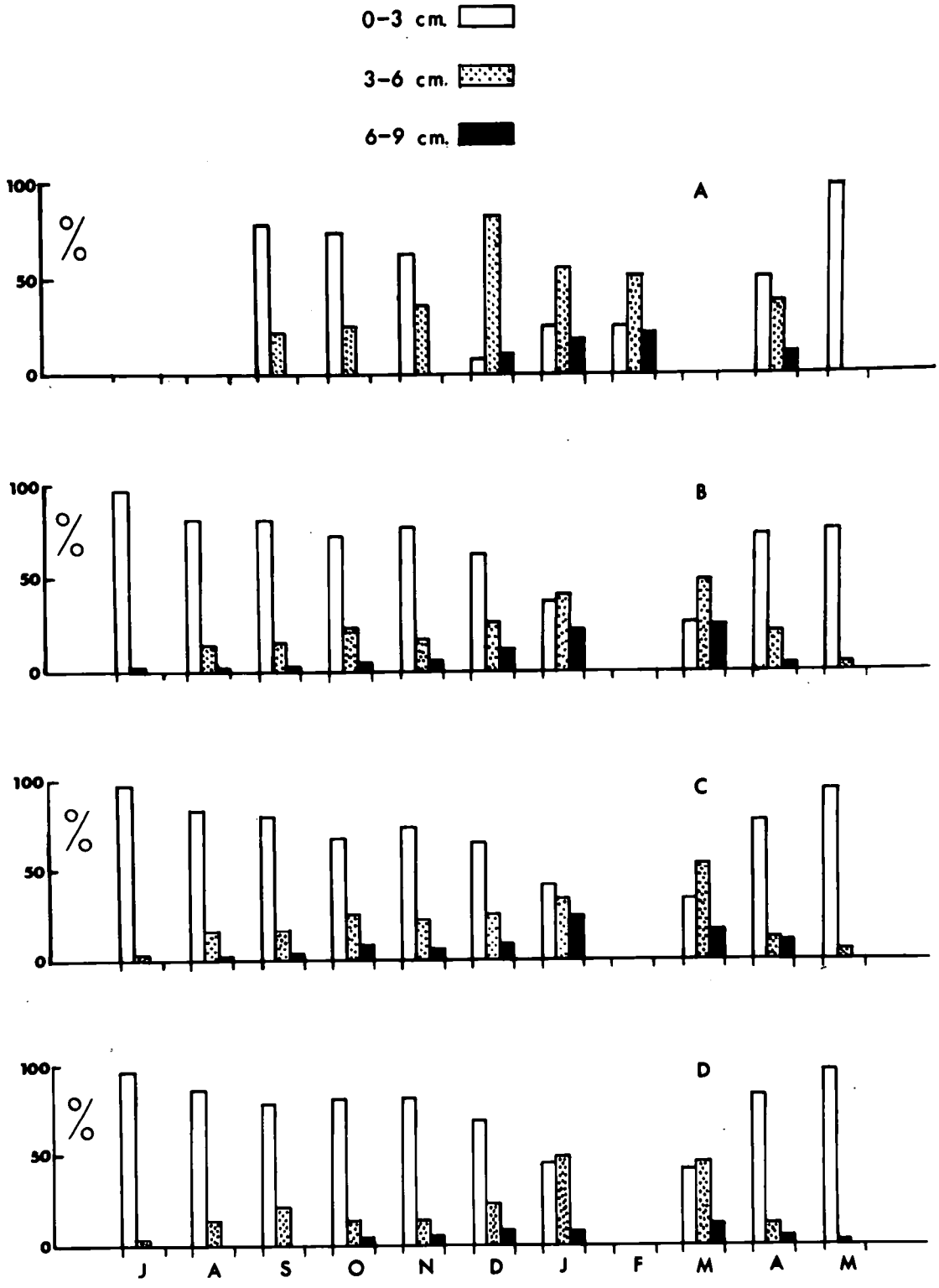

0-3 cm.
3-6 cm.
6-9 cm.
100
50
0
%
A
B
C
D
J
A
S
O
N
D
J
F
M
A
M

TABLE 37. VERTICAL DISTRIBUTION OF LARVAE ON THE PEATY PODSOL SITE. ON EACH SAMPLING DATE, 15 SAMPLE UNITS WERE TAKEN.

Date 1964-65	0-3 cm.		3-6 cm.		6-9 cm.		
	No.	%	No.	%	No.	%	Total
16 July	187	98	4	2	0	0	191
12 August	168	84	30	15	1	1	199
21 Sept.	130	81	26	16	5	3	161
14 Oct.	101	68	37	25	11	7	149
4 Nov.	107	74	30	21	8	6	145
10 Dec.	115	66	46	26	13	7	174
25 February	68	42	56	34	39	24	163
30 March	43	33	67	52	20	15	130
26 April	107	78	17	12	13	9	137
6 May	145	95	8	5	0	0	153

for the Peaty Podsol site in 1964-65. The same number of sample units were taken on each sampling date, and it is evident that the seasonal change in vertical distribution is due to movement by larvae and not to differential mortality.

Several authors have reported seasonal changes in the vertical distribution of micro-arthropods, which may be attributed to such causes as the drying out or flooding of the upper soil layers, or to adverse surface temperatures (Strickland, 1947; Macfadyen, 1952; Belfield, 1956; Peachey, 1963). In the present study a probable explanation of the downward movement of larvae in winter is the low surface temperatures recorded during this period. Perhaps illuminating are the results obtained on

the Peaty Gley site during the 1963-64 larval generation. On 16 December, only 7% of the total larvae were from the 0-3 cm. layer, which was frozen on this date, compared with 6 November when 64% of the total was extracted from this layer, which was unfrozen. The percentage had risen to 26% on 11 January when this 0-3 cm. horizon was again unfrozen. These changes in the percentages recovered from the 0-3 cm. stratum do not appear to be due to differential mortality; there is no significant change in larval densities recorded in November, December and January. The density per sq.m. ($\pm$ S.E.) was 1133 $\pm$ 329 on 6 November, 1165 $\pm$ 292 on 16 December and 1000 $\pm$ 197 on 11 January.

Though these observations may tend to suggest that the annual downward movement is attributable to unfavourable surface temperatures, this cannot be stated with any surety. Until information is available on the degree of dispersion of larvae from the surface where eggs are laid, on whether there is a diurnal vertical movement, and the factors and soil conditions which influence the distribution of larvae, the seasonal changes in vertical distribution can be reported but explanations of the phenomenon must remain uncertain.

E. THE LARVA AND ITS ENVIRONMENT

1. FEEDING

Immediately after extraction, larvae were placed in clean tubes containing distilled water, but examination of faeces produced failed to distinguish any plant cells. It seems likely that larvae do not feed directly on plant tissue, but only after this has been partially broken down by soil decomposers. Soil particles were present in faeces, but the extent to which micro-fauna and micro-flora are assimilated from imbibed soil is not known. Cultures comprising isolated strains of moorland algae, bacteria and fungi were set up, and larvae introduced which had been starved for 10 days to allow the gut to empty. In most cases larvae failed to survive more than a few days after their introduction into cultures. On removal, the guts of all the larvae examined were still empty; there was no evidence of larvae feeding on any of the culture media. The precise food requirements of the species remain problematic; the extent to which larvae feed on mor humus, or whether their food is more specific, requires further investigation.

2. RESISTANCE TO SUBMERSION AND STARVATION

Larvae were immersed in three one-litre beakers which were filled with water. Each beaker was kept at a temperature of $5^{o}C$, and for one hour each day an aerator was used to re-introduce oxygen into each beaker. Of 30 larvae introduced, 27 were still alive

after 10 days. A similar number of larvae were immersed in beakers in which the water had been previously boiled and which was covered by a layer of paraffin. Out of 30 larvae, nine were dead after 24 hours and 26 after 72 hours. Thus, lack of oxygen results in the death of larvae within a short time period, suggesting a possible contributory factor why larvae are concentrated in the 0-3 cm. soil horizon in the field for most of the larval phase. At lower levels the peat is almost permanently water-logged, and the oxygen tension consequently low.

Though no detailed study has been made on the effect of starvation on larval development, the fact that out of 30 larvae kept in aerated water at 5°C, 27 (90%) were still alive after 10 days suggests that larvae are able to survive long periods without feeding. Larvae have in fact been kept alive for periods up to one month without food in Petri dishes containing just sufficient water to allow the spiracular discs to reach the water surface. This ability to survive long periods without feeding is probably reflected in the small amount of growth recorded for larvae in the field between November and February (see Section VIII). During this period the mean weight per larva rose from 1.23 ± 0.06 mg. (± S.E.) to 1.46 ± 0.05 mg., an increase of only 16%; it is evident that during this winter period, metabolic activity is low.

3. PARASITES AND PREDATORS

Examination of many hundreds of larvae failed to reveal any sign of either internal or external parasitism. The carnivorous larvae of Tricyphona immaculata Mg. have been observed to eat larvae of Molophilus ater in the laboratory, but if enchytraeid worms were included in cultures, the larvae of Molophilus were not attacked. It seems unlikely that predation by Tricyphona larvae has any large effect on mortality in the field. There was no evidence that any vertebrate used the larval stage as a food source; as Coulson (1956) has commented in reference to Tipula subnodicornis, another crane-fly with a very similar life cycle to that of Molophilus ater at Moor House, the moor is virtually deserted of birds during the lengthy final instar stage. The absence of any major predator or parasite is reflected in the low mortality recorded for most of the larval period (see Section VII).

4. DISTRIBUTION OF LARVAE

Considerable differences in larval densities were found on different vegetation sites at Moor House. In Table 38, densities of final instar larvae are recorded for soil samples taken during March and April 1965. The highest densities were found on peaty areas dominated by Juncus squarrosus, the lowest on Blanket Bog. No larvae were extracted from soil samples taken from limestone grassland areas dominated by Agrostis and Festuca, from bare peat areas or from well leached mineral soils or redistributed peat

TABLE 38. ESTIMATED DENSITIES (NUMBER PER SQ.M., ± S.E.) OF FINAL INSTAR LARVAE ON DIFFERENT VEGETATION SITES DURING MARCH AND APRIL 1965

Vegetation Type	Locality	No.of samples	Density
Juncus squarrosus	Bog End	15	2093 ± 287
Juncus squarrosus	Troutbeck	15	1733 ± 308
Carex spp.	Troutbeck	15	1187 ± 211
Eriophorum vaginatum	Pasture	15	1040 ± 164
Juncus squarrosus	Moss Burn	15	813 ± 175
Blanket Bog	Bog Hill	15	373 ± 78
Blanket Bog	Burnt Hill	15	147 ± 51
Nardus stricta	Moss Burn	15	0
Agrostis/Festuca	Rough Sike	15	0
Bare peat	Burnt Hill	15	0

areas dominated by Nardus stricta. Comparable findings of considerable differences in site densities have been recorded for Tipula subnodicornis by Coulson (1962); the significance of this "habitat mosaic" of distribution of the species will be discussed in a later section.

VI. THE PUPAL STAGE

1. DURATION OF PUPAL PERIOD

Larvae extracted from soil samples taken during late April and early May were introduced on to agar plates similar to those used by Springett (1964). On pupation, individuals were transferred and kept separately on pieces of damp filter paper in glass phials. The cultures were inspected two or three times a day, and the time from the onset of pupation to emergence at different temperatures recorded (Table 39). At 20°C, the pupal period lasted 5.2 days, but at 10°C, a temperature more similar to that recorded in the field during May, the pupal period was 10.6 days. At each temperature, there was no difference between the duration of male and female pupal periods in the laboratory.

The duration of the pupal period under natural conditions is less easy to determine. The average mean daily temperature for May, when pupation takes place, over the 13 year period 1952-65 was 6.9°C; interpolation from results obtained in the laboratory suggests the pupal period in the field to be in the order of 14 to 17 days. This estimate seems to be confirmed by observations made during 1964. Soil samples taken on the Peaty Gley site indicated a sudden drop in the larval population from 1100 $\pm$ 143 per sq.m. on April 29 to 260 $\pm$ 86 per sq.m. on 13 May, suggesting that approximately 75% of the population had pupated by the latter date. Studies on the adult population showed that 75% had emerged by 1 June; the duration of the pupal stage in the

TABLE 39. THE EFFECT OF TEMPERATURE ON THE DURATION OF THE PUPAL STAGE IN THE LABORATORY

Temp. °C,	Mean duration of pupal stage in days (± S.E.)				
	Number	Males	Number	Females	t
10	17	10.56 ± 0.34	15	10.74 ± 0.27	0.42
15	38	7.57 ± 0.19	32	7.72 ± 0.12	0.65
20	22	5.11 ± 0.20	20	5.21 ± 0.18	0.41
23	16	4.43 ± 0.17	13	4.38 ± 0.12	0.19

field may be taken as about 19 days.

Alexander (1920) lists the duration of pupal existence for over 40 crane-fly species. Though the accuracy of many of the observations may be questioned, and though no mention is made of temperature, the duration of the pupal stage is remarkably constant throughout the group, averaging from 6 to 8 days. Alexander attributes a pupal period of about a week for Molophilus hirtipennis O.S.; the longer pupal period recorded in the field for Molophilus ater is probably due to the sub-arctic nature of the climate at Moor House. Coulson (1962) reports that Tipula subnodicornis, another common cranefly at Moor House, has a pupal period of about 4 weeks.

2. SEX RATIO AND MORTALITY

Of the 872 individuals which pupated in the laboratory, 480 were males and 392 females, giving a sex ratio of 55% males (Table 40). This sex ratio is significantly different from

TABLE 40. THE SEX RATIO AND MORTALITY OF INDIVIDUALS WHICH PUPATE IN THE LABORATORY

	Males	Females	Total
Number of pupae	480	392	872
Number of emergences	187	148	335
Mortality (%)	61.0	62.2	61.6

unity ($\chi^2 = 8.9$, d.f. = 1, $P<0.01$).

Mortality during the pupal period in the laboratory was high (61.6%), though there was no evidence of a differential mortality between the sexes. ($\chi^2 = 0.08$, d.f. = 1, $P>0.9$).

3. ONSET OF PUPATION IN THE LABORATORY

Though the pupal period is of similar duration for males and females, it appears that males pupate earlier than females (Table 41). For cultures comprising larvae taken from different localities on different dates, and kept at constant but different temperatures, the males pupate about one day earlier than females. Of the five examples given, three are significant at the 5% level, the other two at the 10% level. Combining the data for the five cultures, males pupate significantly earlier than females ($t = 5.0$, d.f. = 4, $P<0.01$). Thus the earlier recruitment of males into the adult population, recorded earlier, is due to the slightly shorter period of larval development in the male compared with the female, and not to any difference in the duration of the pupal period. A similar earlier pupation for males than females has

been observed for Tipula oleracea (Laughlin, 1960) and for the culicid Aedes aegypti L. (Christophers, 1960).

For each culture, all individuals pupate within a short time period. For example, for culture 'a', 95% of the total males pupate within 6 days, and 95% of the total females within 8 days. Similarly, for culture 'b', 95% of both males and females pupate within 5 days. Since these cultures were kept at a temperature of 15°C, and the average mean temperature in the field during the pupal period is approximately 7°C, the results recorded in the laboratory closely parallel the highly synchronised pattern of emergence in the field, where 95% of the total emergence takes place within a period of 10 to 12 days.

Laughlin (1960) was able to determine the sex of last instar larvae of Tipula oleracea by reference to male and female growth curves, which differ significantly from each other. Though detailed studies on the growth of individual larvae of Molophilus ater were not made, subjective observations in the laboratory suggested that male pupae developed from the smaller last instar larvae, female pupae from the larger larvae.

In 1966, larvae were extracted from soil samples taken in early May, weighed immediately after extraction and kept separately on agar plates in glass phials. The phials were inspected daily, and, on pupation, individuals were weighed and the sex recorded. In Fig. 22, the relationship between larval weight and the weight and sex of the pupae are shown; it is evident that the smaller

FIG. 22. THE RELATIONSHIP BETWEEN LARVAL WEIGHT AND THE WEIGHT AND SEX OF PUPAE.

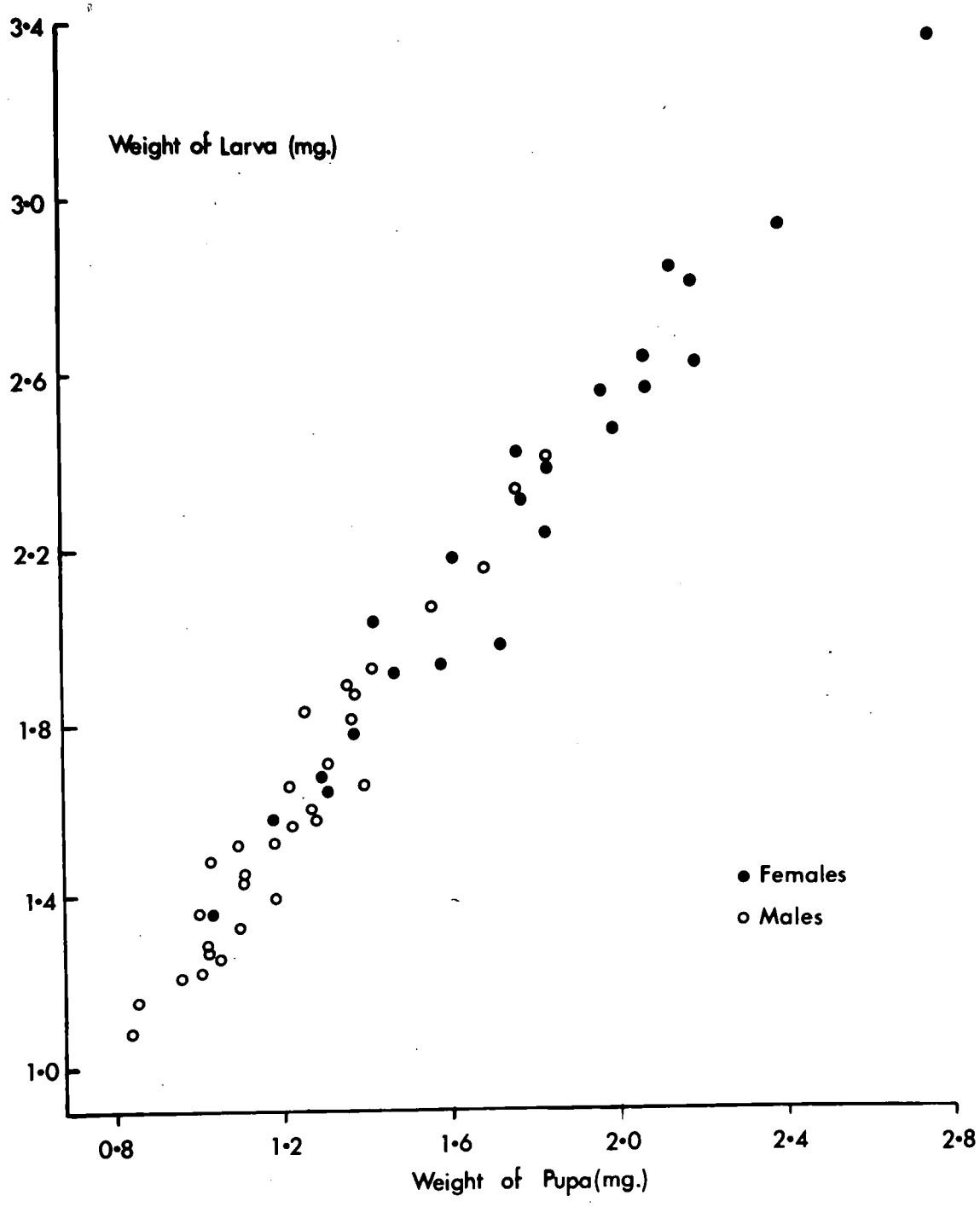

3·4
3·0
2·6
2·2
1·8
1·4
1·0
Weight of Larva (mg.)
0·8
1·2
1·6
2·0
2·4
2·8
Weight of Pupa(mg.)
● Females
○ Males

TABLE 41. THE ONSET OF PUPATION IN THE LABORATORY

Culture	Temp. °C.	Mean number of days before pupation (± S.E.) Males	Females	d.f.	t	P
a	15	12.58 ± 0.27	13.59 ± 0.39	82	2.13	<0.05
b	15	7.07 ± 0.31	8.13 ± 0.33	28	2.32	<0.05
c	15	13.09 ± 0.42	14.17 ± 0.43	62	1.80	<0.1
d	20	6.11 ± 0.30	7.00 ± 0.39	92	1.79	<0.1
e	20	8.28 ± 0.53	9.88 ± 0.45	20	2.29	<0.05

larvae tend to produce male pupae, and vice-versa. The mean weight of larvae pupating into males was 1.60 ± 0.34 mg. (± S.D.), the mean weight of larvae pupating into females was 2.27 ± 0.47 mg. The mean weight of male and female pupae was 1.22 ± 0.24 and 1.77 ± 0.41 mg. respectively. These differences between males and females are significant (Table 42).

TABLE 42. COMPARISON OF THE WEIGHTS OF POTENTIAL MALE AND FEMALE LARVAE, AND OF MALE AND FEMALE PUPAE

	Mean weight in mg. (± S.E.) Larvae	Pupae	Percentage loss of weight on pupation	Number
Males	1.60 ± 0.06	1.22 ± 0.04	23.7	30
Females	2.27 ± 0.10	1.77 ± 0.08	22.0	23
t	4.98	5.80		
P.	< 0.001	< 0.001		

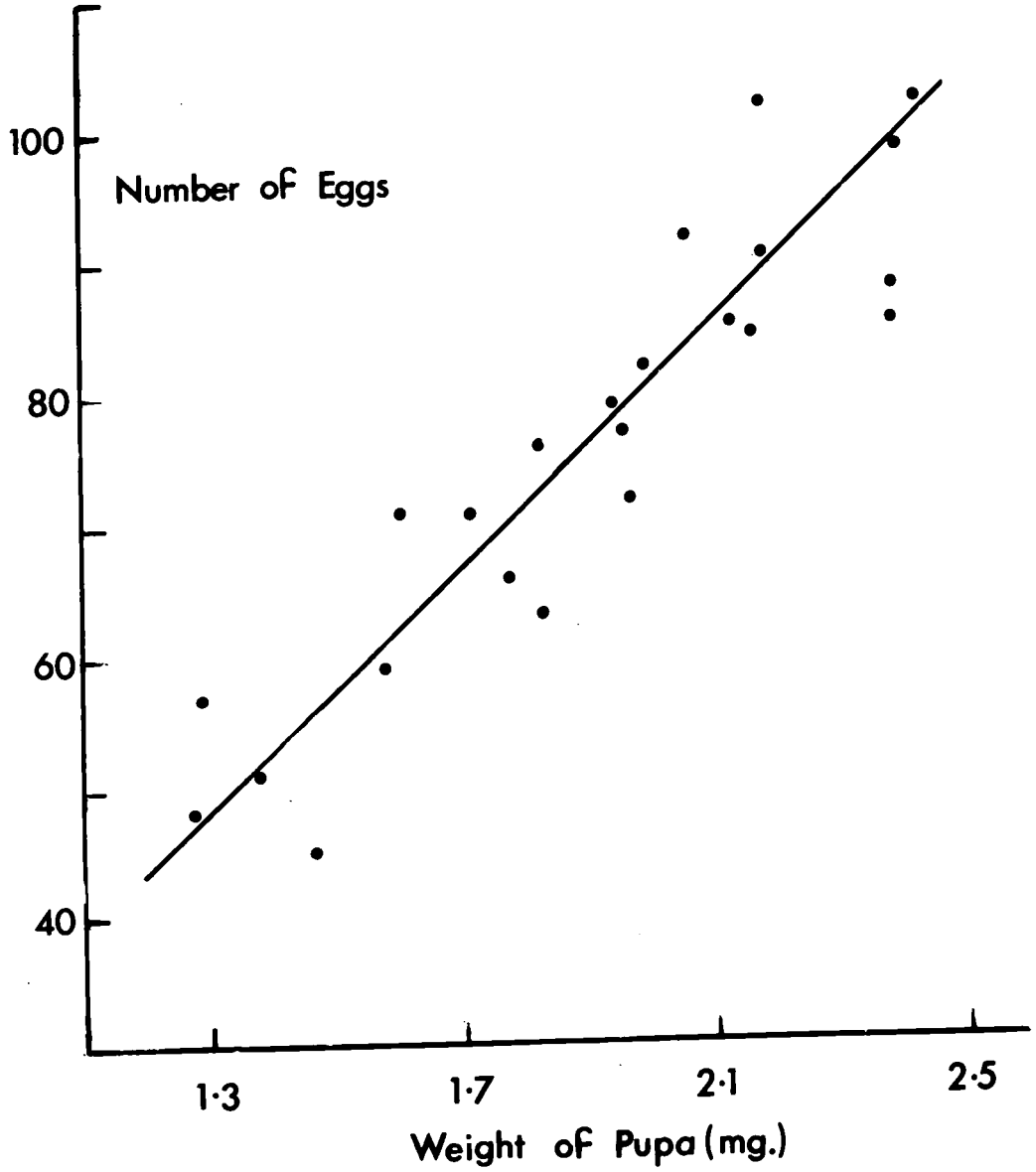
4. FECUNDITY

Dissection of newly emerged females, both taken in the field and reared in the laboratory, revealed a considerable variability in the fecundity of individual adults, the number of eggs ranging from 45 to 110 per female. This variation in fecundity proved to be related to pupal weight, which has been shown to be closely dependent on the larval weight. Immediately on pupation, females were weighed and on emergence dissected. Thus, for each female the weight of its pupa and its fecundity were known. The relation is shown in Fig. 23. On average, fecundity increases by 4 to 5 eggs with an increase of 0.1 mg. in the pupal weight.

FIG. 23. THE RELATIONSHIP BETWEEN PUPAL WEIGHT AND ADULT FECUNDITY.

The regression is :-

$$y = 46.3x - 11.9$$


100
80
60
40
Number of Eggs
1·3
1·7
2·1
2·5
Weight of Pupa (mg.)

VII. POPULATION STUDY

1. SEASONAL VARIATION IN NUMBERS

The life cycle of Molophilus ater, the components of which have been described previously, is represented diagrammatically in Fig. 24. The species is univoltine, producing only one generation each year. The egg stage and the first three instars are each completed in approximately 4 weeks. The overwintering larval stage, the fourth instar, lasts from November to early May, a period of about 30 weeks. There was no evidence of a diapause during this, or in fact,in any other stage. Larvae taken from the field during winter pupated earlier when kept at higher temperatures in the laboratory. The three week pupal phase gives way to adult emergence in early June, which is completed within a short period of about two weeks.

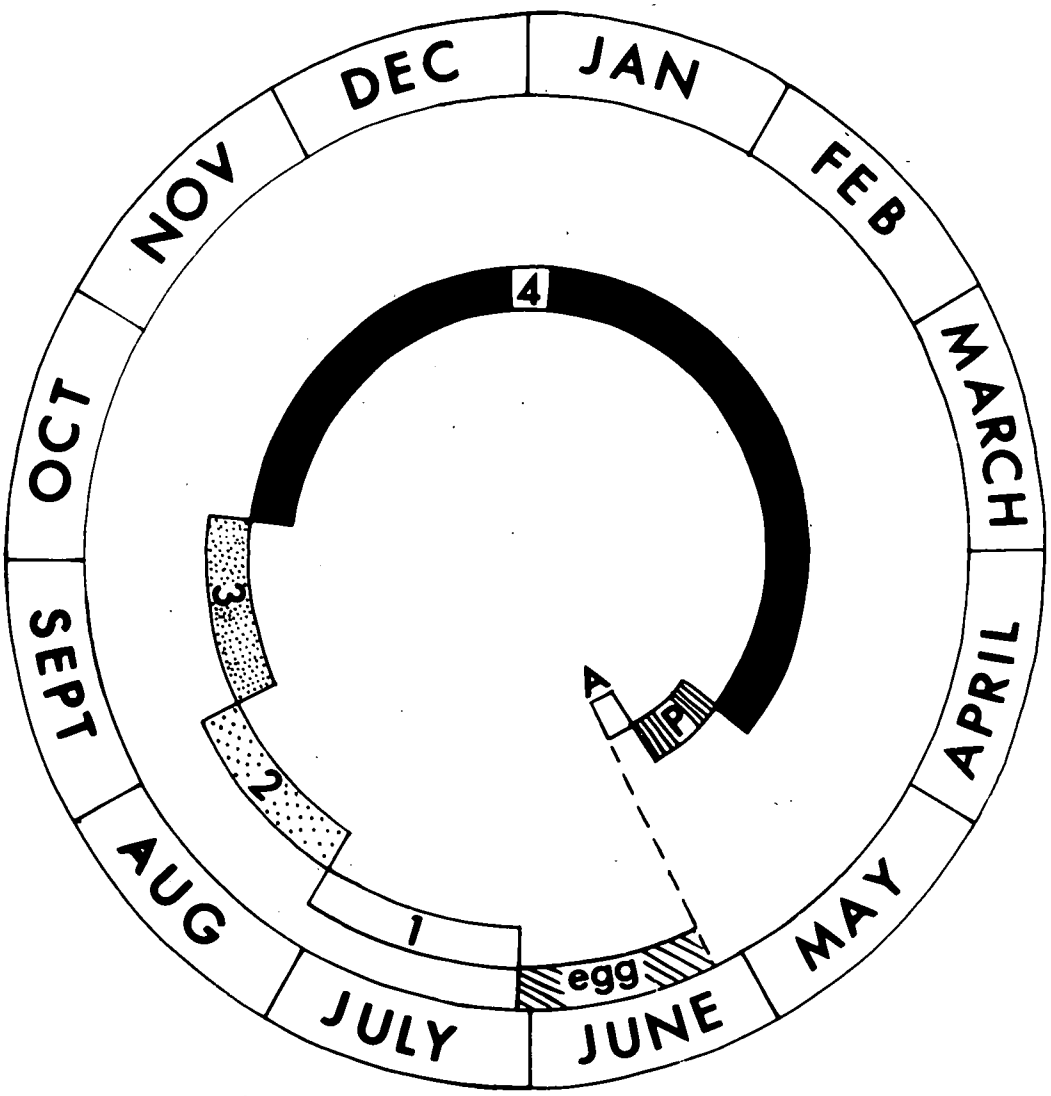
The extraction of larvae from monthly soil samples using the wet funnel process enabled estimates to be made of density throughout the larval period. The wet funnel extraction was found to have an efficiency of 95% for most of the larval period, for instars 2 to 4 and for larvae extracted between August and May. Only during the first instar stage was the efficiency considered unsatisfactory, estimated at only 63% for larvae taken during July (see Section V A). Where the adult emergence was investigated, knowing the mean number of eggs per female, estimates could be made of the density of eggs laid on each site.

FIG. 24. THE LIFE CYCLE OF MOLOPHILUS ATER.

1-4, larval instars

P, pupa

A, adult


DEC
JAN
FEB
MARCH
APRIL
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
4
3
2
1
egg
A
P

The density estimates for the Peaty Gley site are shown in Fig. 25, for the Peaty Podsol site in Fig. 26, and for the Carecetum site in Fig. 27. For soil samples taken during July, both the densities estimated from the actual number of larvae extracted, and the corrected densities are shown.

On each site there was a very high mortality in the egg, and to a lesser degree in the first instar stages. On the Peaty Gley site in 1964, mortality during the egg stage was approximately 88%; in 1965, egg mortality on the same site was even higher, estimated as 92%. On the Peaty Podsol and Carecetum sites in 1965, egg mortality was estimated as 92 and 91% respectively. These figures are included in the life tables presented in Table 43, though it must be remembered that all these estimates of egg mortality include any mortality of first instar larvae which occurs before the first sampling of these larvae in July.

Similar findings of a large mortality in the egg and first instar stages have been reported for other crane-fly species, and several authors have related excessive mortality to desiccation during these stages (Rennie, 1917; Rogers, 1942; Coulson, 1962; Milne, Coggins & Loughlin, 1965). Great difficulty was experienced in handling the eggs of Molophilus ater. Eggs laid on moist filter paper did not hatch, and not until June 1966, when females were induced to deposit their eggs on agar plates, were any eggs successfully reared. Even under these conditions, egg mortality was over 80%. The extent to which this high mortality is due to

FIG. 25. THE DENSITY PER SQ.M. (± S.E.)
ON THE PEATY GLEY SITE, 1963-66.

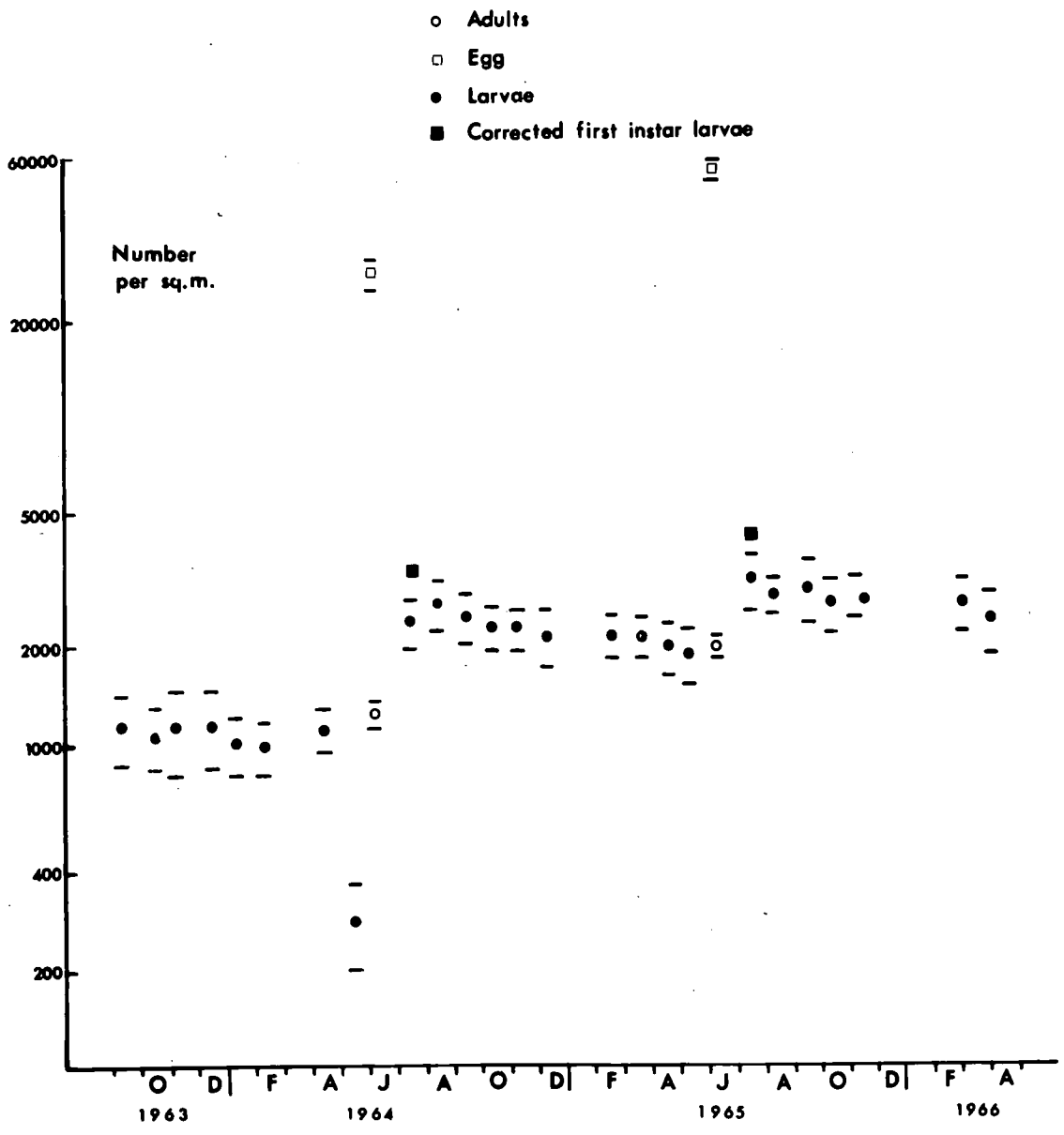

o Adults
□ Egg
● Larvae
■ Corrected first instar larvae
Number
per sq.m.
60000
20000
5000
2000
1000
400
200
O
D
F
A
J
A
O
D
F
A
J
A
O
D
F
A
1963
1964
1965
1966

FIG. 26. THE DENSITY PER SQ.M. (± S.E.) ON THE PEATY PODSOL SITE, 1964-66.

FIG. 27. THE DENSITY PER SQ.M. (± S.E.) ON THE CARECETUM SITE, 1964-66.

Key as on Fig. 26.

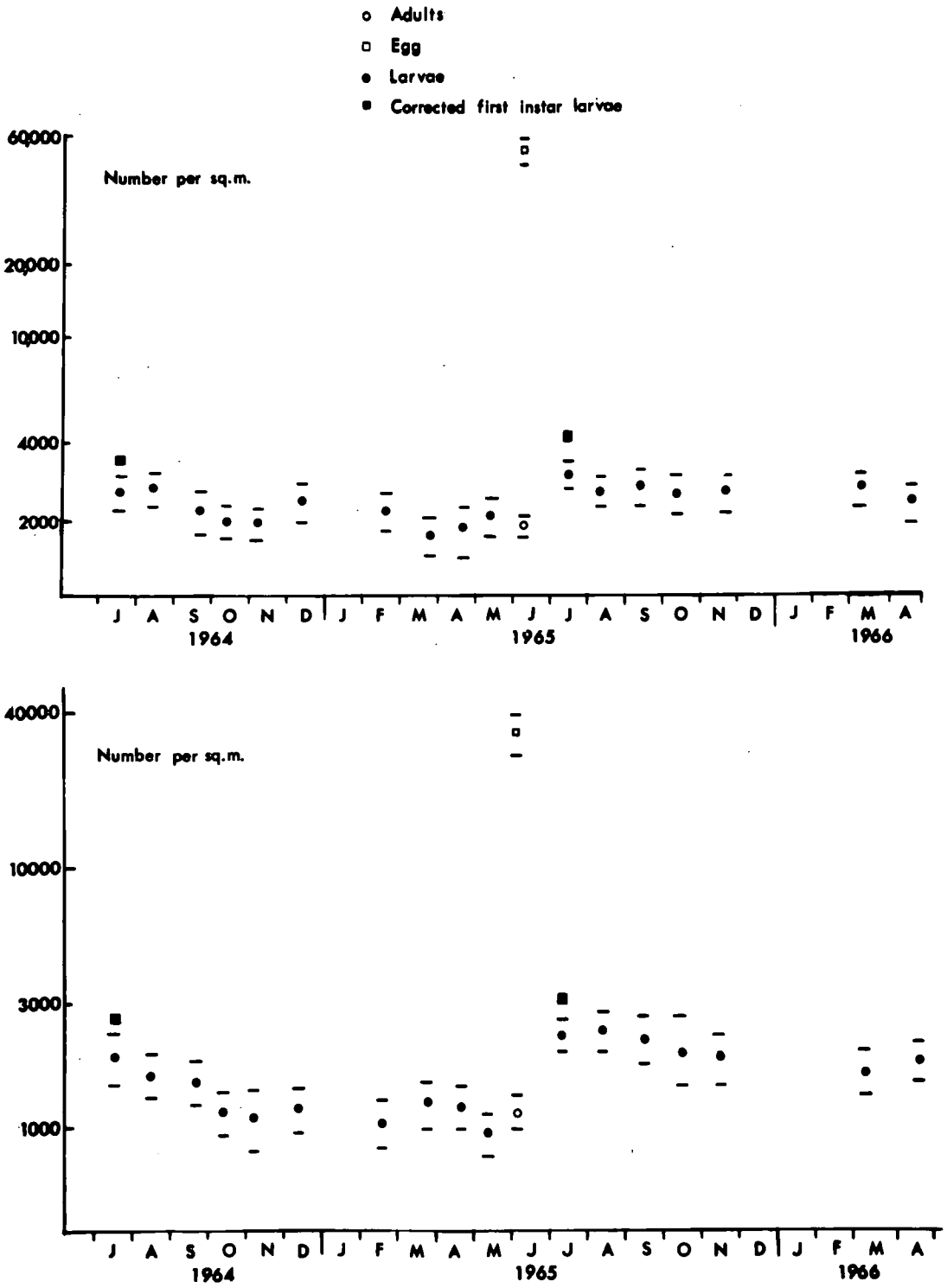

o Adults
□ Egg
● Larvae
■ Corrected first instar larvae
60000
20000
10000
4000
2000
Number per sq.m.
J A S O N D J F M A M J J A S O N D J F M A
1964
1965
1966
40000
10000
3000
1000
Number per sq.m.
J A S O N D J F M A M J J A S O N D J F M A
1964
1965
1966

TABLE 43. LIFE TABLES OF MOLOPHILUS ATER

x Age interval		l_x No. alive at beginning of x	d_x No. dying during x	100 q_x d_x as percentage of l_x
PEATY GLEY SITE 1964-65				
June	(eggs)	27612	24397	88
July	(instar 1)	3215	548	17
August	(instar 2)	2667	240	9
September	(instar 3)	2427	187	8
October	(instar 3-4)	2240	108	5
December	(instar 4)	2132	39	2
March	(instar 4)	2093	135	6
June	(adults)	1958	1958	100
PEATY GLEY SITE 1965-66				
June	(eggs)	56000	51670	92
July	(instar 1)	4330	1370	32
September	(instar 3)	2960	160	5
November	(instar 4)	2800	440	16
April	(instar 4)	2360		
PEATY PODSOL SITE 1965-66				
June	(eggs)	53500	49400	92
July	(instar 1)	4100	1450	35
September	(instar 3)	2650	100	4
November	(instar 4)	2550	230	10
April	(instar 4)	2320		
CARECETUM SITE 1965-66				
June	(eggs)	32920	29850	91
July	(instar 1)	3070	920	30
September	(instar 3)	2150	320	15
November	(instar 4)	1830	100	5
April	(instar 4)	1730		

experimental conditions or to infertility is not known. The size of eggs, and the difficulty of separating them from the substate, precluded any study of mortality under natural conditions. The high egg mortality of the species may be reported, but the factors causing this mortality remain uncertain. After the first instar stage, on no site was there evidence of a significant change in density throughout the larval period. (The decrease in larval density on the Peaty Gley site in 1964, from 1100 ± 143 per sq.m. on 29 April to 260 ± 86 per sq.m. on 13 May, does not indicate a sudden mortality, but rather that the majority of larvae had pupated by the latter date). The absence of any real seasonal trend in the density of larvae was confirmed by analysis of variance on the data for the Peaty Gley site during the 1964-65 larval phase (Table 44). This indicated that the sample strata were responsible for a greater source of variation than sampling occasions.

Deevey (1947) and Slobodkin (1962) have drawn attention to different types of survivorship curves, the slope of these curves describing the distribution of mortality with age in different animal species. The results presented for Molophilus ater agree with the survivorship curve type IV of Slobodkin, and of curve type III of Deevey. Here, mortality acts most heavily on the younger stages, after which mortality remains at a very low level.

TABLE 44. ANALYSIS OF VARIANCE OF SAMPLING RESULTS FROM THE PEATY GLEY SITE DURING THE 1964-65 LARVAL PERIOD. FIFTEEN SAMPLES WERE TAKEN ON EACH OF TEN OCCASIONS FROM JULY 1964 TO MAY 1965.

Source of Variation	Sum of Squares	d.f.	Mean Square	F
Sampling occasion (date)	185	9	20.6	0.378
Sampling strata (position)	7607	140	54.3	
Total	7792	149		

2. CHANGES IN DENSITY FROM YEAR TO YEAR

In Table 45, the densities of eggs and larvae are given, where available, for the entire study period. The figures for first instar larvae are corrected densities, allowance having been made for relative inefficiency of the extraction process for this instar stage. The fourth instar densities recorded are the mean densities of the results obtained from the three sampling occasions prior to pupation. All densities are given to the nearest 100 per sq. m.

On each site, there is no marked fluctuation in the numbers of final instar larvae from year to year. Coulson (1962) reported that in 1955 Tipula subnodicornis became virtually extinct on an area of Juncus sqarrosus moor. No second instar larvae were

TABLE 45. THE DENSITIES PER SQ.M. OF EGG AND LARVAL POPULATIONS OF *MOLOPHILUS ATER* AT MOOR HOUSE

Site and Year	Eggs	Larvae	
		1st instar	4th instar
PEATY GLEY			
1963-64	-	-	1000
1964-65	27600	3200	2000
1965-66	56000	4300	2600
PEATY PODSOL			
1964-65	-	3500	1900
1965-66	53500	4100	2500
CARECETUM			
1964-65	-	2500	1100
1965-66	32900	3100	1700
BLANKET BOG	-	-	
1964-65	-	-	400
1965-66	-	-	300

recorded in 1955, compared with a density of 1300 per sq.m. at the same stage in the previous year. This collapse in 1955 was brought about by the dry conditions during June, July and August of that year. During these months the peat surface became dry and powdery, only 9.9 in. (25.1 cm.) of rain being recorded, compared with 22.8 in. (57.9 cm.) in the same three month period in 1954. During the present study period, in no year did the peat become noticeably dry. The rainfall during

June, July and August was similar in each of the three years; in 1963 the rainfall during this period was 19.5 in. (49.5 cm.), in 1964, 15.5 in. (39.4 cm.) and in 1965, 18.5 in. (47.0 cm.). Perhaps significantly, the population of Molophilus ater remained relatively constant throughout the study period. It would be interesting to investigate the effect of a summer drought on the numbers and distribution of Molophilus ater. Such a study would reveal much information on the factors which are important in the regulation of the species; unfortunately, the necessary climatic conditions did not occur during the present study.

VIII. GROWTH AND BIOMASS

The growth of larvae under field conditions was investigated during the larval phase of 1964-65 on the Peaty Gley site. Sub-samples were taken from the total larvae extracted on each sampling date. Individuals were weighed on an electro-magnetic balance, after being first washed in clean water and then gently rolled on filter paper to remove surface moisture. The weights of individual larvae are recorded in Fig. 28, and the mean weight per individual in Fig. 29.

Growth was rapid from August to November, the mean weight increasing from 0.311 $\pm$ 0.08 mg. (1 S.E.) to 1.23 $\pm$ 0.06 mg. during this period. There is little growth during the winter months, between November and March, but there is evidence of a slight increase in the growth rate in the spring, the mean weight increasing from 1.51 $\pm$ 0.04 mg. in March to 1.93 $\pm$ 0.09 mg. immediately prior to pupation in May. There is an increase in the range of weights recorded during April and May, which has been attributed in the previous section to differential growth of male and female larvae.

In August, the distribution of individual weights is characterised by a large number of larvae of weight less than 0.2 mg., and a small tail of larvae whose weight ranges between 0.5 and 1.7 mg. The presence of these latter individuals confirm the composition of instars recorded during July and August, that the development of a small number of animals is retarded and they fail to pupate at the same time as the majority of their generation (see Section V B).

FIG. 28. THE WEIGHTS OF INDIVIDUAL LARVAE FROM THE PEATY GLEY SITE, 1964-65.

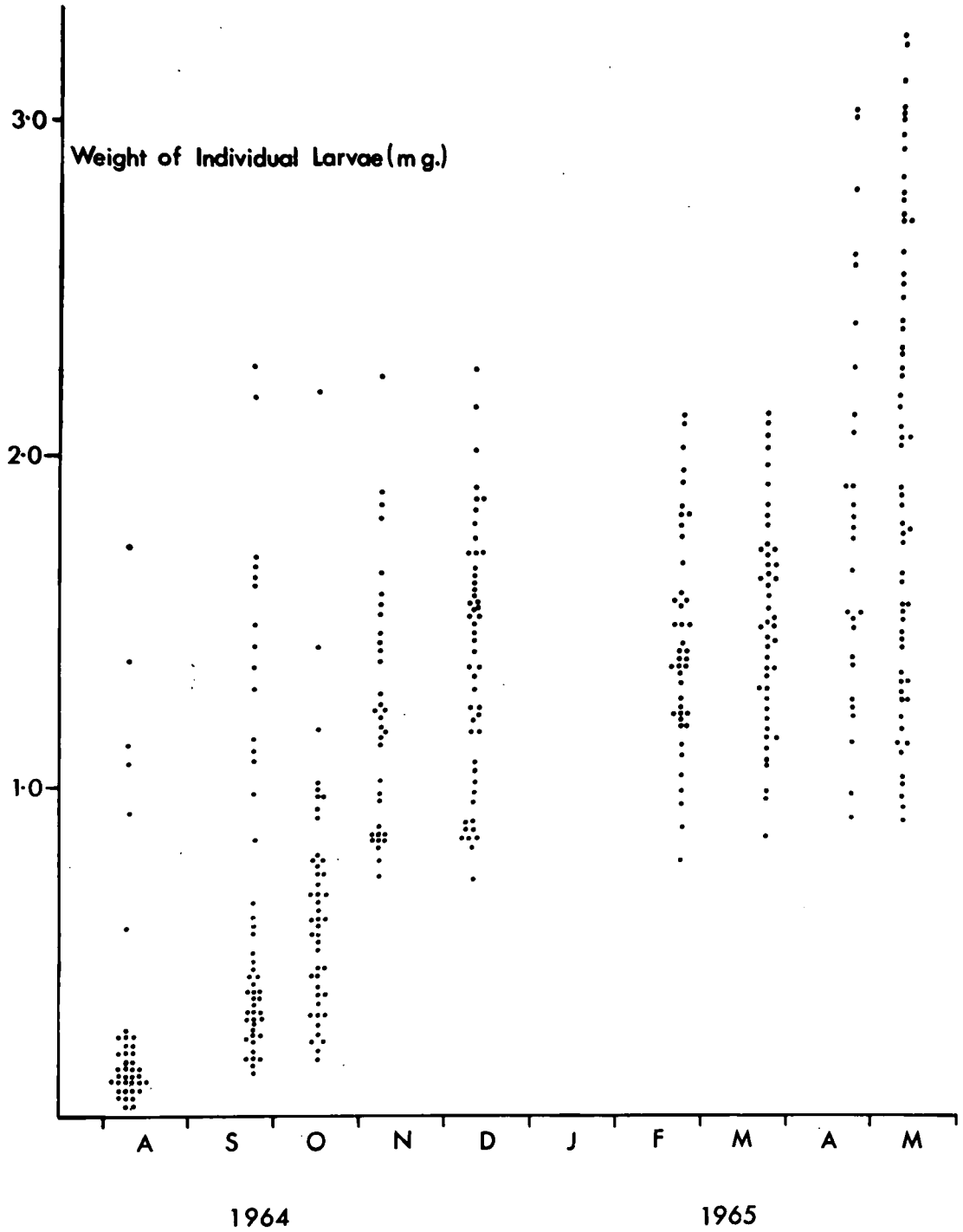
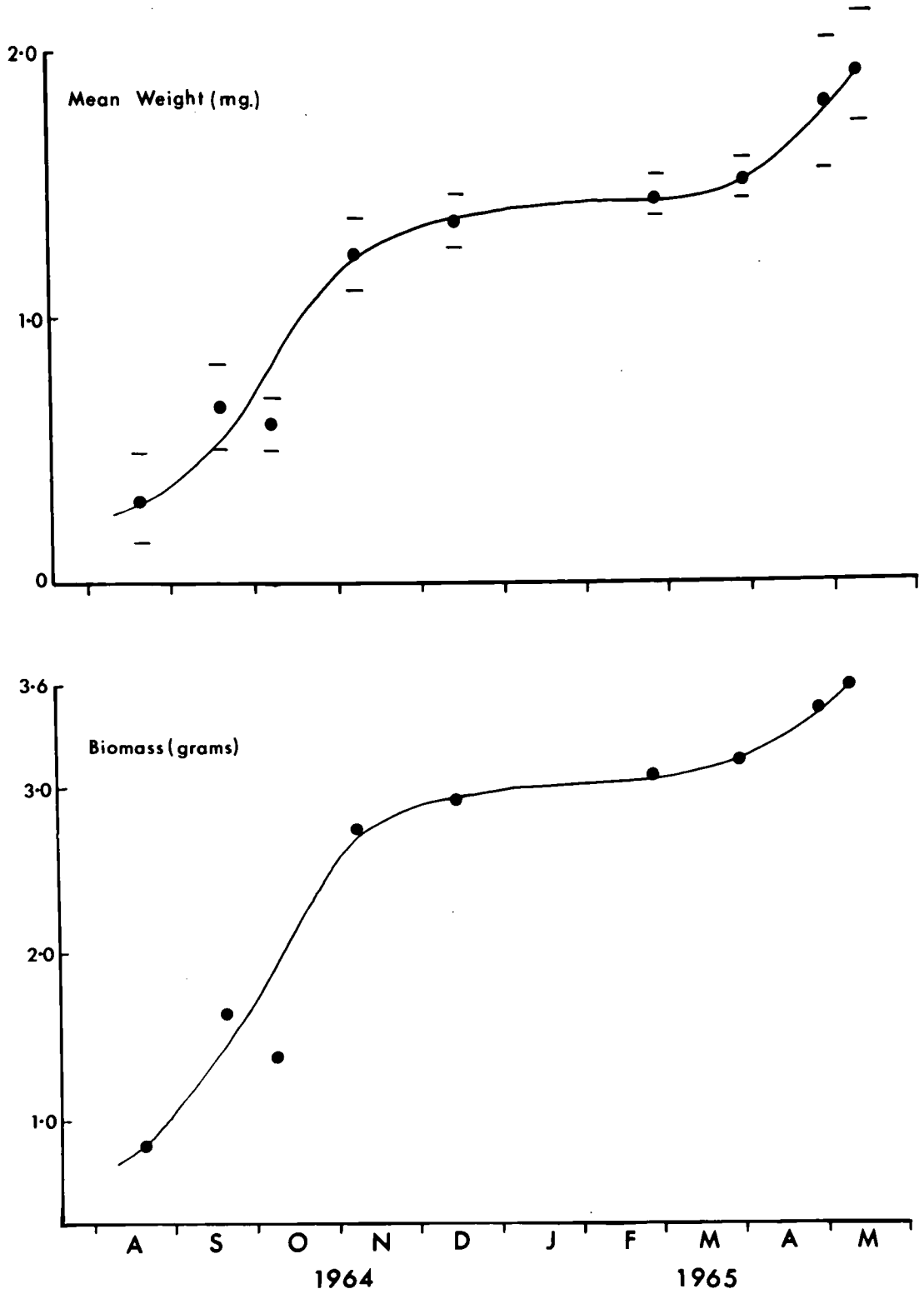

3·0
2·0
1·0
Weight of Individual Larvae (m g.)
A
S
O
N
D
J
F
M
A
M
1964
1965

FIG. 29. GROWTH CURVE OF LARVAE ON THE PEATY GLEY SITE, 1964-65.

FIG. 30. ESTIMATED BIOMASS PER SQ.M. OF LARVAE ON THE PEATY GLEY SITE, 1964-65.


2·0
Mean Weight (mg.)
1·0
0
3·6
Biomass (grams)
3·0
2·0
1·0
A
S
O
N
D
J
F
M
A
M
1964
1965

The skew in the distribution of individual weights is continued in the figures for September, but in October the majority of these larvae over 1.0 mg. in weight have presumably died, there being no evidence of an autumn emergence of adults at Moor House. This results in the lowering of the mean weight obtained in October compared with September, the majority of larvae showing an expected degree of growth compared with individuals taken in the previous month.

The estimated biomass per sq.m. of larvae on the Peaty Gley site during 1964-65 is shown in Fig. 30. The close similarity between the curves for biomass and mean weight per individual is indicative of the low mortality which occurs during the larval period, seasonal studies revealing no significant change in density throughout the larval stage. The loss of larval biomass during this period is probably minimal, though no measure has been made of the weight of cuticle lost at the change from one instar to another.

The major part of mortality occurs during the egg phase. On the Peaty Gley site in 1964-65, the mortality during this stage accounted for nearly 90% of the total estimated number of eggs laid. The small size of eggs precluded any measurements of weight being made; instead, the volume of the average egg size was calculated, assuming the egg to be a perfect ellipsoid. Estimation of the total volume of eggs laid could therefore be made, and, by taking their specific gravity to equal unity, an

approximation of mass determined. The loss of biomass during the egg stage was estimated to be only in the order of 0.05 grams per sq.m. on the Peaty Gley site during June and July 1964.

Direct loss of biomass to the ecosystem would appear to be concentrated during May and June, during the metamorphosis from last instar larvae to the pupal and adult stages, and the ultimate death of individual adults. This loss is probably in the order of 3.6 grams per sq.m., the larval biomass recorded in early May, immediately prior to pupation; the biomass passed on to the following generation, as eggs, by females in June was estimated to be only 0.11 grams per sq.m.

Cragg (1961), summarizing and discussing results obtained in studies on a number of animal groups at Moor House, quotes a total live biomass of between 45 and 78 grams per sq.m. on the Peaty Gley site. At their maximum of 3.6 grams per sq.m. (equivalent to approximately 1 gram dry weight per sq.m.), the larvae of Molophilus ater account for between 4.6 to 8.0% of the total biomass on this site, though the total crane-fly biomass may comprise nearly 30% of the total biomass (see Cragg, 1961). The figure for Molophilus is, however, of little value, given as it is in vacuuo. The exact role and importance of the species in the moorland ecosystem will remain unknown until detailed and co-ordinated studies are made of such factors as respiratory, assimilation and metabolic rates, not only of the larvae of Molophilus ater, but of other organisms representative of moorland soils.

IX. GENERAL DISCUSSION

The ramifications in the various views of the way in which the size of animal populations is regulated are almost as numerous as the laboratory and field studies on which these hypotheses are based. The influences comprising the environment of an animal have long been divided into biotic factors, factors involving other organisms or influences deriving from other organisms, and abiotic factors such as those of substrate and climate. The relative importance of biotic and abiotic factors in determining the densities of populations has been, and remains, a major issue of debate and controversy.

Howard & Fiske (1911) were perhaps the first workers to appreciate the mechanisms by which mortality factors control the densities of animals. Up to this time, different mortality factors had been recognised, but had been considered as mere contributors to total mortality and not as factors which could control densities. Howard & Fiske proposed that there were two types of mortality factors, one destroying a constant proportion of the population independent of density ("catastrophic factors"), and the other destroying a percentage that increases as density increases("facultative factors"). Since this classification depends on the relationship between mortality and density, these two groups of factors may be more conveniently designated as "density independent" and "density dependent" mortality factors respectively (Smith, 1935).

The writings of Thompson (1929, 1939, 1956) and Nicholson (1954a, 1954b, 1957, 1958) represent divergent views on the importance of these two groups of factors. Thompson believes that the primary factors controlling the abundance of animals are extrinsic, that they are primarily climatic and edaphic in nature and that populations are not "self-governed". For Thompson the "balance of nature", which may be taken as the maintenance of a more or less fluctuating population density within definable upper and lower limits, is a balance in the environment. The favourability or otherwise of the environment for a given species determines whether its population increases or decreases.

Thompson's views are a corollary to those of Andrewartha & Birch (1954) who argue that distribution and abundance are two aspects of the same problem. Within the distribution of animal species there may be favourable zones where a high density is maintained, but near the limits of the distribution there may be marginal zones which are sometimes habited, and sometimes not, and which are characterised by low numbers of individuals. Thus, distribution and abundance change together in a changing environment.

Nicholson (1954a), whilst recognising diversity and fluctuation in the environment, emphasises the role of biotic factors and presumes the environment to be relatively stable, or at least not disturbing. He writes that "any species automatically adjusts its density in different places, and in the same place at different times, in relation to the prevailing environmental

conditions, and it maintains a state of stability under all conditions which are not inherently intolerable". Nicholson (1954b) believes that the heterogeneity of habitats does not inconvenience organisms to any extent, and maintains that "most species are well adapted to cope with such fragmentation". These adaptations, in Nicholson's view, enable animals to occupy all favourable habitats, and in these habitats populations are controlled by density dependent factors; as density increases, density induced factors operate to check the increase. These arguments antedate those of Klomp (1962), who states that "the regulation of the density of animal populations by density independent weather factors as such is clearly an impossibility".

The two theories on the mechanisms controlling populations may appear contradictory, but they are not irreconcilable nor are they mutually exclusive. As Varley (1963) has pointed out, the disagreement may be largely attributable to differences in definition and emphasis. One difference seems to revolve on the meaning of the word "control". By control, Nicholson means regulation or government, whereas Thompson (1956) uses the word to refer to the fact that "no organism increases without limit". The essential disagreement, however, between the two schools of thought revolves about the ability of a species to thrive under different degrees of fluctuating environmental conditions. This ability to thrive involves the specific properties of the species, properties not only of the individual but also of the group or population.

(The term population is considered as that defined by Richards (1961); namely, "all those individuals of a species whose lives are sufficiently integrated to have an influence on one another"). Huffaker & Messenger (1964) have written in length on the influence of environment on populations. "To the degree that changes in the environmental conditions are sufficiently limited that the population is capable of fully compensating for changes in the stresses encountered, such change is unimportant to balance. With somewhat more violent change in the physical conditions of the environment, there will commonly occur a shift from the one balancing mechanism, with its characteristic equilibrium position, to other distinct mechanisms acting at either higher or lower equilibrium densities. Finally, the extrinsic environment may fluctuate so greatly that the ability of the population to compensate for varying stresses is no longer effective in maintaining any characteristic equilibria. At this time, states of balance or trends towards balance occur only momentarily, and imbalance is the rule". Thus the most cogent argument against Nicholson's views is that they lose much of significance in widely fluctuating environments. The correlation of changes in population density with changes in environmental conditions has led many authors to suggest that populations may be controlled for long periods without density dependent mechanisms being involved (e.g. Birch, 1957; Milne, 1957; Reynoldson, 1957; Cragg, 1961).

Cragg (1961), in his review of ecological studies at Moor House, doubts whether regulation of numbers, in the sense of restricted fluctuations in numbers from adult generation to adult generation, is important in a harsh environment where the extinction of local populations is a frequent occurrence, and where there are often violent local fluctuations in abundance. The information presented for Molophilus ater is the result of 3 years' study, and as such any discussion must be acknowledged as being tentative and in no way dogmatic. The species was characterised by a remarkable constancy in numbers and distribution from generation to generation throughout the study period. On no site was there a major fluctuation in population size. There was in fact an increase in density on each of the three major sites investigated; for example, on the Peaty Gley site the density (per sq.m.) of final instar larvae was approximately 1000 in 1964, 2000 in 1965 and 2600 in 1966.

It is necessary to ask which factors determine the population size of Molophilus ater in any one year. Coulson (1962) found that a period of low rainfall during the egg and first instar stages of Tipula subnodicornis in 1955 resulted in large changes in the numbers and distribution of that species at Moor House. A similar relationship between low rainfall and low survival of these stages has been reported for other Tipula species (Maercks, 1943; Milne, Laughlin & Coggins, 1965). In each year of the study period the rainfall at Moor House during June, July and

August, the months during which the susceptible egg and first instar stages are completed, was high; in no year did the peat become dry and powdery, as occurred in 1955 with such catastrophic effects on populations of Tipula subnodicornis (Coulson, 1962).

It is interesting to note that after the drought in 1955 Tipula subnodicornis became extinct on an area of Juncus squarrosus moor which had previously supported high densities of the species, whilst the numbers on an area of Sphagnum bog, which supported low densities, did not change significantly. These habitats, supporting low densities, may therefore ensure the maintenance of species in unfavourable years when local populations become extinct. As Cragg (1961) has written, "a species not too specific in its larval requirements has a better chance of survival under the markedly fluctuating conditions associated with high moorlands". Molophilus ater inhabits a variety of habitats at Moor House; during the final instar stage in 1965 densities ranging from 150 to 2100 per sq.m. were recorded. The significance of this "habitat mosaic" to the survival of the species during unfavourable years must remain conjecture. One consequence of studies of such limited duration as the present one is that variables whose influence on the population one wants to study cannot be artificially induced, nor can their occurrence be predicted.

The highly synchronised life cycle of Molophilus ater is characterised by a long larval feeding stage and a non-feeding adult phase, the functions of which, namely mating and egg

laying, are completed within a day of emergence. If the average estimate of the adult sex ratio is correct, and taking the mean number of eggs per female as 78, then approximately 1 out of every 27 eggs (3.7%) must survive throughout the life cycle for the population to remain static. (If the true adult sex ratio was equality, this percentage would be 2.6). For the Peaty Gley site, 7.4% of the estimated number of eggs laid in 1964 survived to the fourth instar stage immediately prior to pupation; in 1965, 4.2% of the eggs laid survived to the same stage. Similar survival rates were recorded on the Peaty Podsol (4.3) and Carecetum (5.3%) sites for eggs laid in 1965. These survival percentages are all slightly higher that those estimated for populations to remain static; consequently the densities on each of the sites show an increase throughout the study period.

It is unlikely that mortality factors are in any way important to the short adult stage and, with the exception of the early first instar, there is no marked reduction in densities throughout the larval and pupal stages. Most of the mortality in any generation occurs in the egg, and to a lesser extent in the first instar, stage. On the Peaty Gley site in 1964, the estimated egg mortality accounted for 88% of the total mortality throughout the generation of 93%. In 1965, egg mortalities on the three sites investigated varied between 91 and 92%. Morris (1959) considers that there are two types of factors which

determine the abundance of animal populations. The first category includes factors which cause a relatively constant mortality from year to year and which therefore cannot induce large changes in population densities. The second group of factors ("key factors") include those which cause a variable mortality and which are largely responsible for changes in population size. During the present study period, there was no evidence of Morris's "key factors" acting in any part of the life cycle in any year, densities on each site showing no marked fluctuation. Morris's other class of factors seem to operate during the egg and early first instar stages, estimated mortality during this period remaining constant at between 88 and 92%. There was no evidence that mortality acted in a density dependent manner during this period. On the Peaty Gley site, egg mortality in 1964 was 88% and in 1965 92%, even though the egg population in 1965 was over twice that estimated in the previous year.

delete

Bess (1945) and Morris (1957) consider that variations in mortality due to factors acting in the early stages of insect life cycles are relatively less important, as regards the elimination of the surplus individuals, than are similar variations due to late acting factors. There was no evidence of a compensatory mechanism acting at any stage in the life cycle of Molophilus ater. Densities showed no significant change throughout the long larval period, mortality between the corrected first instar and final instar densities accounting for only 3 to 5% of the total mortality

throughout the life cycle. Mortality during the larval stage was apparently independent of density. For example, on the Peaty Gley site, 54% of a certain stage of first instar larvae in 1964 (corrected density 3500 per sq.m.) survived to the final instar stage immediately prior to pupation; in the following year the equivalent percentage for a certain stage of first instar larvae of corrected density 4100 per sq.m. was 61%.

Several studies at Moor House have showed how violent climatic fluctuations result in marked variations in the distribution and abundance of animal species, but there is no evidence on whether density dependent factors begin to operate if populations are allowed by chance, for example if the environment is favourable over a number of years, to increase. The favourability of the climate during the study period, and the absence of marked density fluctuations, provokes the question which mechanisms in fact are regulating the numbers of the species, regulation in the sense that densities remain within certain upper and lower levels. The crucial, and unanswerable, question in the present context is what would happen to populations of Molophilus ater if the climate continued to remain favourable over a succession of years. The susceptible phase, even in favourable years, of Molophilus ater, as with other crane-fly species, is the egg and first instar stages. It is well documented that these stages are extremely vulnerable to desiccation and that catastrophic reductions in population

size occur in years of low rainfall, but the cause of the high mortality recorded in years with a high rainfall is less perfectly understood. Infertility and desiccation are probably major factors, but the importance of predation and parasitism is not known. Though no major enemy has been found during any part of the life cycle of Molophilus, personal observation on catches by detergent traps and the fauna extracted from soil samples suggests that there are considerable numbers of Chalcids and other parasitic Hymenoptera at Moor House. The bionomics and feeding habits of these organisms are not known, and their importance in "regulating" the abundance of other species during a succession of favourable years has not been investigated.

The present study shows that the major mortality occurs in the egg and first instar stages. Any density dependent mortality would have to work on these stages, there being no evidence of any marked mortality during other parts of the life cycle. A small number of favourable years resulted in an increase in the size of populations of Molophilus ater, but there was no evidence that mortality in the egg and first stages increased appreciably with increase in density; it seems likely that mortality factors did not act in a density dependent manner. Studies on the effect of unfavourable conditions on the abundance and distribution of the species, and the precise mortality factors which operate during unfavourable periods, are necessary to elucidate the problem of how the size of populations are determined.

SUMMARY

1. A study of the brevi-palp crane-fly Molophilus ater Mg. was made on the Moor House Nature Reserve, Westmorland, from 1963 to 1966.

2. Molophilus ater is univoltine, producing only one generation each year. The egg and the first 3 instar stages are each completed in about 4 weeks. The over-wintering 4th instar lasts from November to early May, a period of about 30 weeks. The three week pupal phase gives way to a well-defined and highly synchronised adult emergence period in late May – early June.

3. The adults of both sexes are flightless, and densities of both newly emerged and total adults were estimated by means of a portable vacuum extractor. Sticky traps and detergent traps were used to provide relative estimates of population size; both these methods were shown to accurately reflect the pattern and duration of the emergence period.

4. The entire population, comprising densities between 1000 and 2000 per sq.m., emerge within a period of about 15 days, the middle two-thirds emerging within 5 to 7 days. On each site, between 16 and 20% of the total adult emergence occurred on a single day. With increasing altitude, the time of emergence is delayed, and there is a narrowing in the duration of the adult period.

5. A preponderance of males was recorded both for individuals which pupate in the laboratory and for adult emergences.

6. There is well-defined trend towards a decrease in the proportion of males as the emergence period progresses. This earlier recruitment of males is shown to be due to the slightly shorter period of larval development for males than for females, and not to any difference in the duration of the pupal stage.

7. The adult mortality was very high. The average daily elimination rate was 80% for males and 88% for females. It does not appear that biotic factors are important contributors to this low survival rate; laboratory experiments suggest that this is an intrinsic characteristic of the species.

8. The range of movement of adults was shown to be limited; it is suggested that the difficulty of finding an individual of the opposite sex is a major factor in determining the degree of activity of the species. A greater proportion of male activity takes place in the higher levels of the vegetation than does female activity.

9. There is a well-defined, unimodal, diurnal pattern of emergence, nearly 90% of the total daily emergence taking place between dawn and 12.00 hours. The diurnal pattern of activity, though slightly delayed and of longer duration, is closely associated with the pattern of emergence.

10. Mating took place immediately after emergence, and 70% of eggs were laid within 6 to 8 hours of emergence. The great majority are laid within 1 cm of the soil surface.

11. Eggs, which are mature on emergence of the female, lack an egg filament. There is probably only one batch of eggs, with the number of eggs per female ranging from 45 to 110. The variation in fecundity of females was shown to be related to pupal weight.

12. Larvae were extracted from soil samples using a wet funnel process.

13. The existence of 4 larval instars was shown, based on measurements of three larval characters. There was no dimorphism in the 4th instar for any of the characters measured.

14. Evidence is given that a small number of individuals fail to pupate in May, but remain in the 4th instar stage from July to September. Their fate is not known, there being no evidence of a second emergence period at Moor House.

15. Larvae are aggregated in their distribution, but there was no evidence of any change in the spatial distribution during the larval period.

16. Like many soil organisms, larvae are concentrated largely in the surface layers of the soil. There was an increase in the proportion of larvae found below 3 cm. during the winter months. This was not due to a differential

mortality occurring in any of the sample layers, but was attributed to a downward movement of larvae, possibly to escape unfavourable surface temperatures.

17. It seems likely that larvae do not feed directly on plant tissue, but only after this has been partially broken down by soil decomposers.

18. Growth of larvae is rapid from August to September. Little growth occurs between November and March, but there is evidence of a slight increase in growth during the spring. The increase in the range of weights recorded during April and May is attributed to differential growth of male and female larvae; the smaller larvae give rise to male pupae, and vice-versa.

19. The contribution of species biomass to the ecosystem is concentrated during the metamorphosis from the 4th instar larvae to the pupal and adult stages. On the Peaty Gley site in 1965 this contribution was in the order of 3.6 grams per sq.m., the larval biomass recorded in early May immediately prior to pupation. Larvae were estimated to account for between 4.6 to 8.0% of the total biomass on the Peaty Gley site.

20. The species occupies a variety of habitats at Moor House, and considerable differences in site densities were recorded. During April and May 1965, larval densities ranging from 150 to 2000 per sq.m. were recorded on different sites.

21. There was a rise in species density on each site investigated throughout the study period. For example, on the Peaty Gley site, the density per sq.m. of final instar larvae was approximately 1000 in 1964, 2000 in 1965 and 2600 in 1966. This rise in population size is probably related to the favourable conditions which occurred each year during the susceptible egg and first instar stages.

22. The major mortality occurs in the egg and, to a lesser extent, the first instar stages. Egg mortality on different sites and in different years was estimated to vary between 88 and 92%, but there was no evidence that mortality factors during this stage acted in a density dependent manner. A compensatory mortality at other stages of the life cycle has not been demonstrated, there being no significant change in density throughout the long larval phase. ~~It seems likely that non-density dependent~~ factors are responsible for most of the mortality recorded, but a precise evaluation of the factors determining population size requires an investigation of the result of unfavourable conditions on the abundance and distribution of the species, allied to studies on the factors causing high egg mortality even in favourable years.

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APPENDIX I. THE VEGETATION OF SAMPLE SITES

On each of the four sites at Moor House, the major features of the vegetation have been described. The cover values shown in the accompanying tables are according to the Domin scale, namely:

10	cover about 100%
9	cover greater than 75%
8	cover 50-75%
7	cover 33-50%
6	cover 25-33%
5	abundant, cover about 20%
4	abundant, cover about 5%
3	scattered, cover small
2	very scattered, cover small
1	scarce, cover small
x	isolated, cover small

The quadrat size used was 50 cm. by 50 cm. (0.25 sq.m.)

Species nomenclature is from :-

flowering plants - Clapham, A.R., Tutin, T.G. and Warburg, E.F. (1962). Flora of the British Isles. Cambridge.

mosses - Watson, E.V. (1955) British Mosses and Liverworts. Cambridge.

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lichens - Watson, W. (1953). Census Catalogue of British Lichens. Cambridge.

TABLE A1. DOMIN SCALE VALUES FOR THE PEATY GLEY SITE (AFTER WELCH, 1964).

Quadrat Number	1	2	3	4	5	6	7	8	9	10
Carex nigra	3	4	4		4		3	3	3	2
Deschampsia flexuosa	4	4	2	4	2	3	4	4	4	3
Eriophorum angustifolium	2	2	1	2	1	2	2		2	1
Eriophorum vaginatum			x	3		5	1			3
Festuca ovina	3	4	3	3	5	3	5	2	4	2
Juncus squarrosus	6	7	8	7	7	6	6	8	7	8
Potentilla erecta			1					1		
Aulacomnium palustre	2	3	2	2	1	4	3	3		1
Plagiothecium undulatum	1			1		1	1	3		
Pleurozium schreberi	1									
Polytrichum commune	5	4	4	4	1	4	4	2	2	2
Rhytidiadelphus loreus	1	1		1		2				
Rhytidiadelphus squarrosus							4	1		
Spagnum cuspidatum				1						
Calypogeia trichomanis	2	1	1	2	1	2		1	1	
Leptoscyphus anomala						1				
Lophocolea bidentata	2	2	2	2	1	2	1	2	3	2
Lophozia floerkii					1					
Ptilidium ciliare	3	4	5	4	4	3	3		2	3

TABLE A2. DOMIN SCALE VALUES FOR THE PEATY PODSOL SITE.

Quadrat Number	1	2	3	4	5
Agrostis canina		1		1	1
Agrostis tenuis	2	2	3	1	
Anthoxanthum odoratum	1	1	2		
Carex nigra			1	2	
Deschampsia flexuosa	4	2	2	4	3
Festuca ovina	4	4	6	5	6
Juncus squarrosus	5	5	7	6	4
Luzula campestris	2	2	2	2	1
Nardus stricta	5	6		4	4
Galium saxatile	2	1	2	1	1
Potentilla erecta	2			1	
Aulacomnium palustre	1			1	
Hylocomnium splendens			1		
Hypnum cupressiforme	2	2	2	1	1
Plagiothecium undulatum			1		
Pleurozium schreberi	1	2	1	1	1
Polytrichum commune	4	5	4	2	2
Rhytidiadelphus squarrosus	2	1	2	2	2
Calypogeia trichomanis	1			1	1
Lophocolea bidentata	1	1	1	1	1
Lophozia floerkii				1	
Ptilidium ciliare		1		1	1

TABLE A3. DOMIN SCALE VALUES FOR THE CARECETUM FLUSHED PEAT ("CARECETUM") SITE

Quadrat Number	1	2	3	4	5
Agrostis tenuis	2	2	2	3	2
Anthoxanthum odoratum	1			2	
Carex demissa	3	5	2	1	3
Carex flacea	2	1	2		2
Carex nigra	1	2	3	2	1
Carex panicea	4	2	2	2	2
Carex pulicaris	2	5		1	
Eriophorum angustifolium		1			
Festuca ovina	4	4	4	4	3
Festuca rubra				1	
Juncus squarrosus				2	
Luzula campestris	1	1		1	1
Nardus stricta	5	4		5	3
Cerastum holosteoides	1			1	
Equisetum palustrae	1	1			1
Galium saxatile	1		1		
Pontentilla erecta	1	1	1	1	1
Prunella vulgaris		1			
Ranunculus repens			1		
Taraxacum officinalae			1		1
Trifolium repens	1	1	2	2	2
Vida palustris	2		1		
Aulacomnium palustre	2				1
Hylocomnium splendens	2		1		
Mnium hornum	1			1	
Mnium punctatum		1	4	1	1
Rhytidiadelphus squarrosus	2	1	1		1
Lophocolea bidentata	2	1		1	
Pellia epiphylla		1	1		

TABLE A4. BOMIN SCALE VALUES FOR THE BLANKET BOG SITE. (AFTER WELCH, 1964).

Quadrat Number	1	2	3	4	5	6	7	8	9
Carex nigra							1	1	
Deschampsia flexuosa	2	1		1		2	1	2	1
Eriophorum angustifolium	1	1	2	1	2	1	3	2	2
Eriophorum vaginatum	6	4	5	4	2	5	4	7	4
Empetrum nigrum			2	2		1	1		x
Festuca ovina					2				
Juncus squarrosus	4	3	4	6	6	2	2	3	1
Luzula campestris								1	
Calluna vulgaris	6	8	8	6	7	5	8	6	7
Aulacomnium palustre				2				2	
Hypnum cupressiforme									1
Plagiothecium undulatum	2		2	2	5	2			
Pleurozium schreberi	1	4	2			3	2	2	1
Polytrichum commune	x	1	2	4	3	5	4	3	1
Rhytidiadelphus loreus	1	2	2	2	1	1	2		
Rhytidiadelphus squarrosus	1				1			1	
Spagnum plumulosum	4	4	4	2	3	2	4	5	7
Calypogeia trichomanis	2	2	3	2	2	1	2	2	
Lepidozia reptans			1						
Lophocolea bidentata	2	1	1		2	1	1		
Lophozia floerkii				2					
Lophozia venticosa			1						
Ptilidium ciliare		1	1	1	1	2	1		

APPENDIX II. LINEAR MEASUREMENTS OF ADULTS.

The lengths of different body parts (in mm., ± S.E.) given below are the means of measurements made on 50 newly emerged males and 50 newly emerged females.

Body Part	Male	Female	t	P
Wing	1.71 ± 0.03	1.78 ± 0.03	1.72	<0.1
Thorax	0.87 ± 0.01	0.90 ± 0.01	2.08	<0.05
Abdomen	2.11 ± 0.09	2.66 ± 0.07	4.74	<0.001
Femur 1	1.92 ± 0.03	1.34 ± 0.02	14.75	<0.001
Tibia 1	1.95 ± 0.03	1.38 ± 0.03	14.31	<0.001
Femur 2	1.35 ± 0.02	1.03 ± 0.04	7.27	<0.001
Tibia 2	1.39 ± 0.02	1.02 ± 0.02	13.59	<0.001
Femur 3	2.11 ± 0.03	1.71 ± 0.02	9.92	<0.001
Tibia 3	2.02 ± 0.03	1.61 ± 0.02	11.01	<0.001

APPENDIX III. OCCURRENCE OF ADULTS IN GREAT BRITAIN

The data presented below were extracted from adult specimens in The Natural History Museum, London.

Locality	Date of Capture	Authority
Torbury, New Forest	18 April 1905	F.C. Adams
Mull, Argyll	26 April 1912	H. St. J.K. Donisthorpe
Barmouth, Merioneth	3 May 1902	Lt. Col. Yerbury
Helensburgh, Dumbarton	9 May 1903	F.C. Adams
Austwick, Yorks.	9 May 1921	F.W. Edwards
Bonhill, Dumbarton	16 May 1908	J.J. King
Taw Head, Devon	2 June 1920	F.W. Edwards
Scarfell	5 June 1965	A.M. Hutson
Hilnshaw, Kirkstone Pass (c. 1800 ft.)	6 June 1941	D.S. Himmins
Snowdon	8 June 1887	Verall Bequest
Glen Lochay (500-1500 ft.)	8 June 1932	F.W. Edwards
Ranngoch	27 June 1917	J.J. King
Inverness	30 June 1933	R.L. Coe
Inverness, Loch Avon (c. 2500 ft.)	4 July 1951	R.L. Coe
Loch Collater, Aberdeenshire (c. 1500 ft.)	26 July 1951	R.L. Coe