*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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# 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

## 11. 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 <u>Molophilus</u> <u>ater</u> 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 <u>Juncus</u> <u>squarrosus</u>; the species is not found on bare peat, on redistributed peat where <u>Nardus</u> <u>stricta</u> is dominant, or on mineral soils with <u>Festuca</u> and <u>Agrostis</u> as co-dominants.

In previous ecological studies at Moor House, all areas with <u>Juncus</u> <u>squarrosus</u> as a dominant plant species have been considered as one habitat type. Recent studies by Welch (1964) have shown that <u>Juncus</u> <u>squarrosus</u> 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 <u>Juncus</u> <u>squarrosus</u>, than between two <u>Juncus</u> <u>squarrosus</u> communities. The use of <u>Juncus</u> <u>squarrosus</u> as one habitat type is undesirable. Though there is continuous variation between <u>Juncus</u> <u>squarrosus</u> 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 <u>Juncus squarrosus</u> 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 <u>Juncus squarrosus</u> noda were chosen as study areas, together with another site which is similar to a third nodum described by Welch, but where <u>Carex</u> spp. replace <u>Juncus squarrosus</u> 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 <u>Juncus squarrosus</u> 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 <u>Juncus squarrosus</u>. The Peaty Gley nodum is the most widespread at Moor House, and corresponds with the <u>Juncetum squarrosi sub-alpinum</u> 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

¼ Mile

A   Peaty Gley Site

B   Peaty Podsol Site

C   Carecetum Site
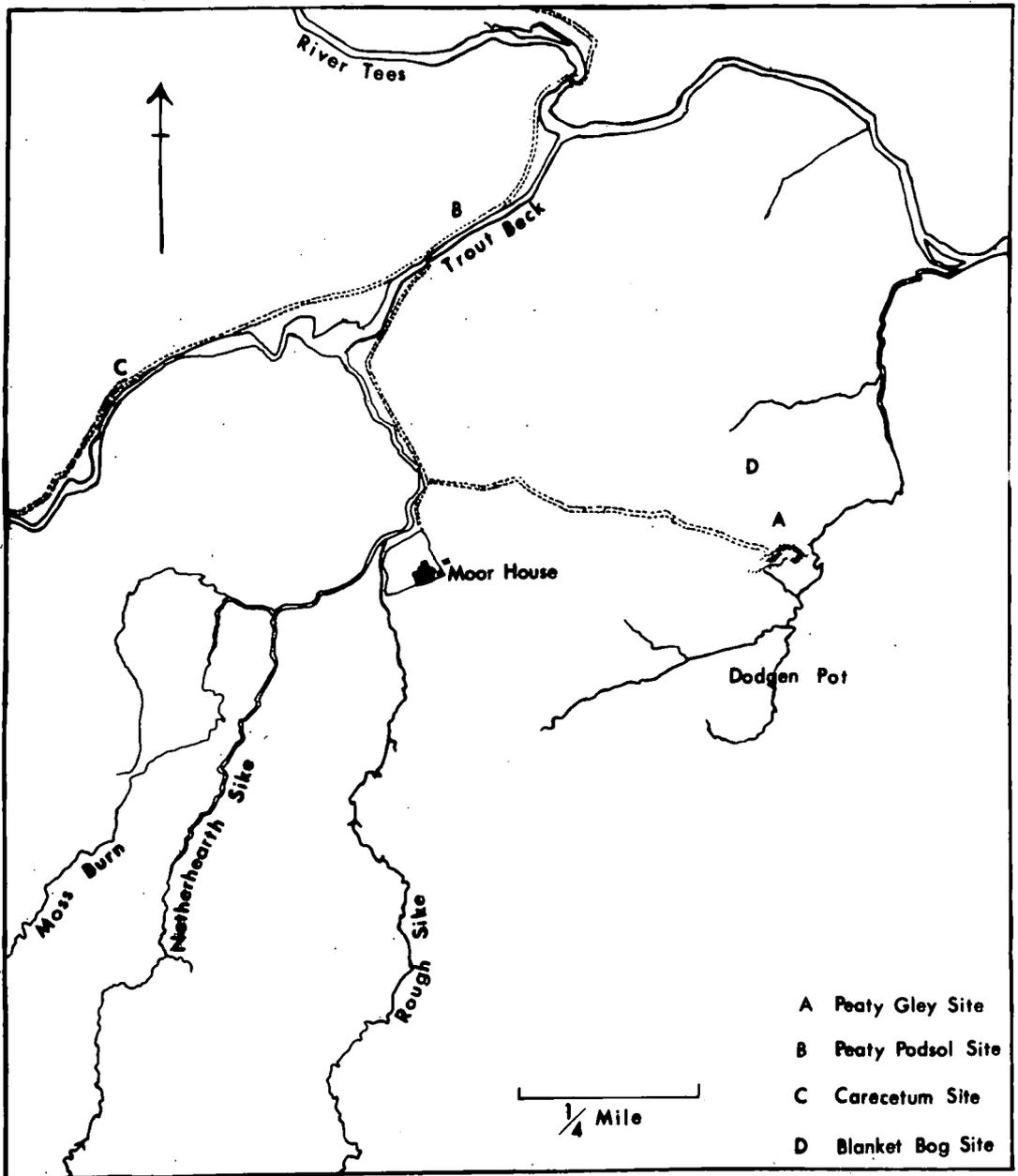
D   Blanket Bog Site

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 <u>Molophilus</u> <u>ater</u> 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.

FLEXIBLE HOSE

RUBBER CONNECTOR

PAXOLIN LID

CLAMP FOR LID

NYLON COLLECTING
BAG SUPPORTED ON
WIRE RING

METAL CYLINDER

RUBBER WASHER

FAN HOUSING

FAN OUTLET

O 2 4 CM.

12 VOLT MOTOR
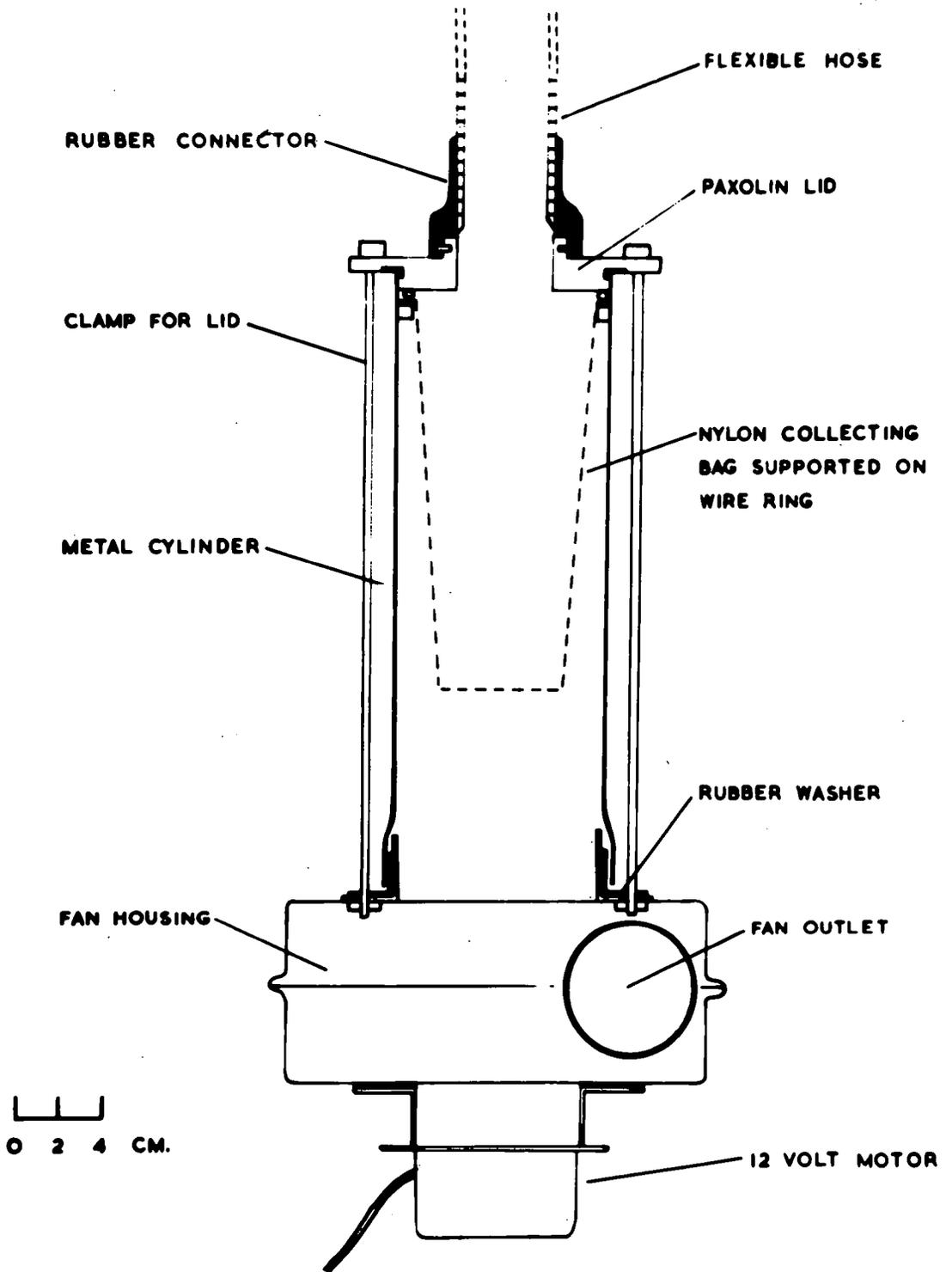
SECTIONAL DRAWING OF VACUUM EXTRACTOR

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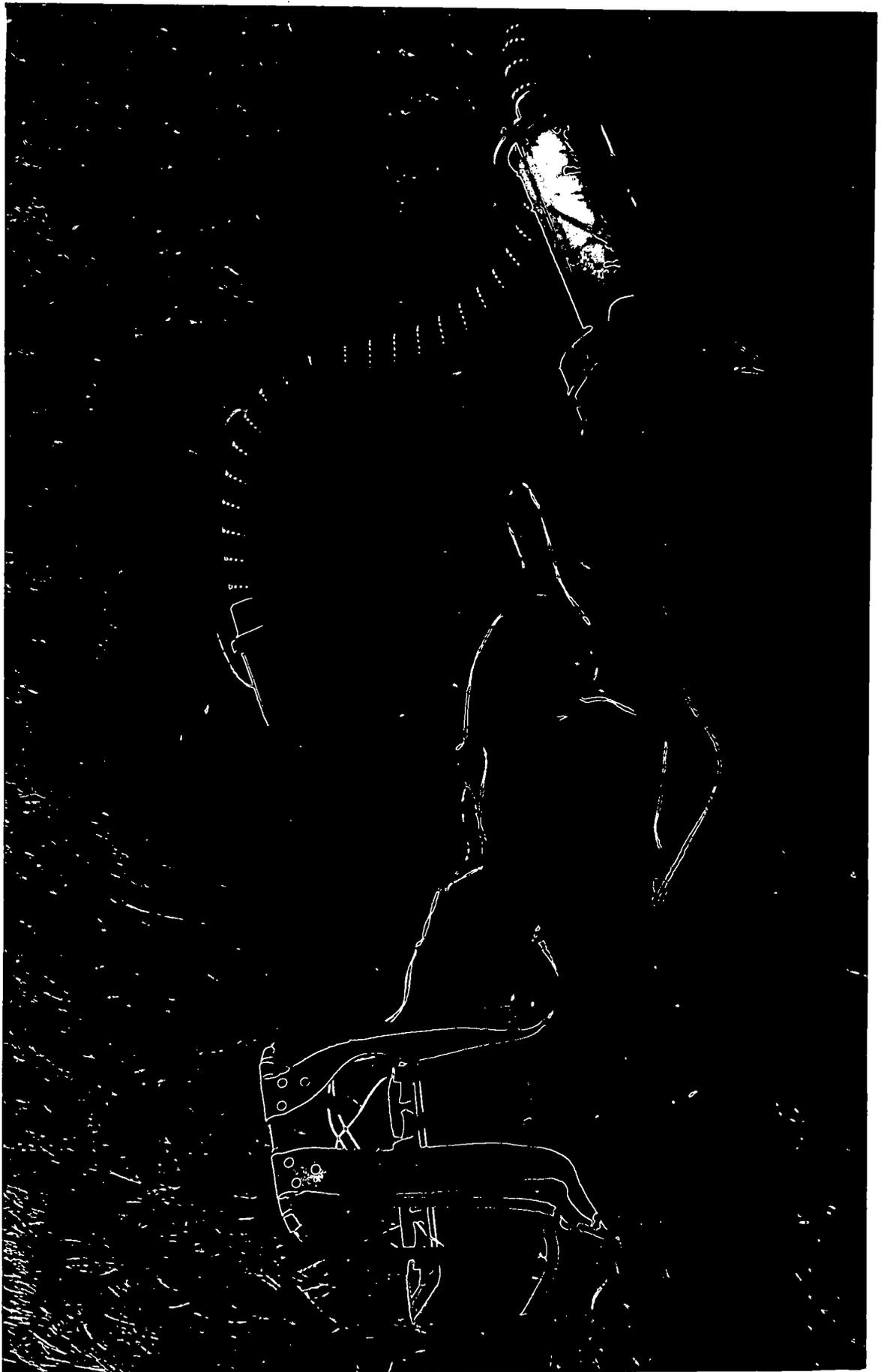
of diameter 3.5 centimetres.   Organisms and debris are
carried down the flexible hose into the metal cylinder.
The larger diameter of this cylinder, compared with that of
the nozzle, results in a radical fall in the air speed, and
organisms are collected in the nylon bag without damage.

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 over-hanging 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 <u>Molophilus</u>, 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 <u>Molophilus</u> 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 <u>Molophilus</u>, 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.
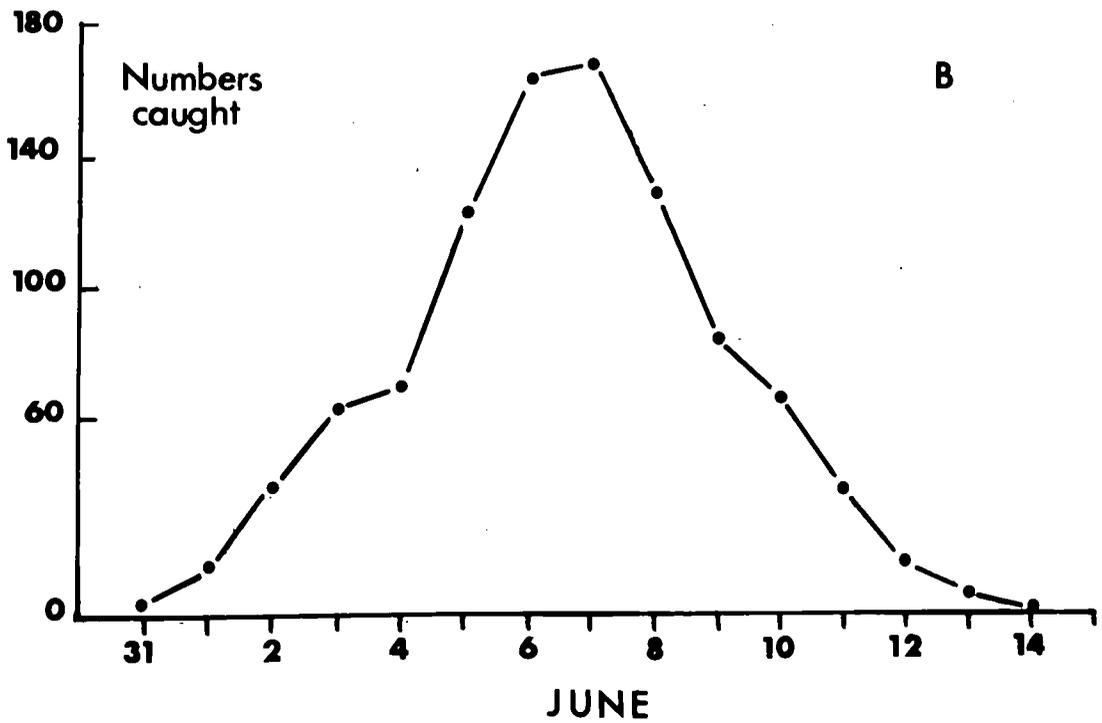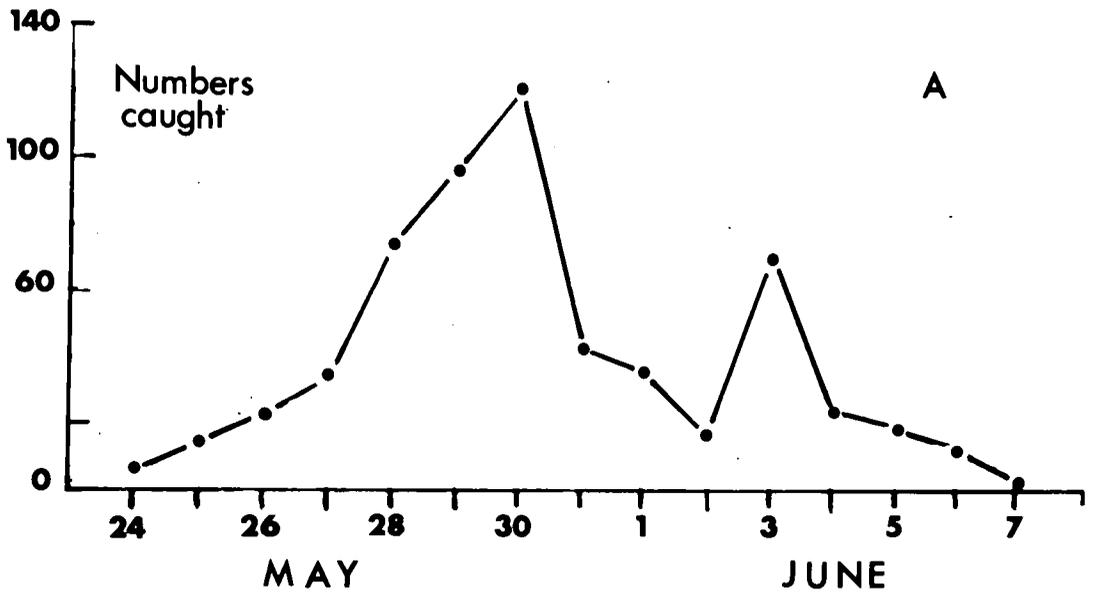
FIG. 4.  THE EMERGENCE PERIOD OF ADULTS

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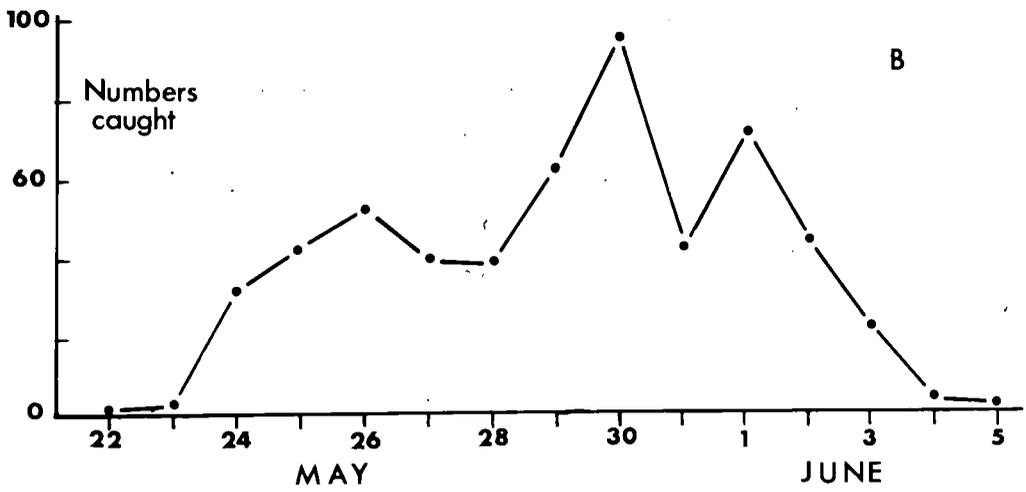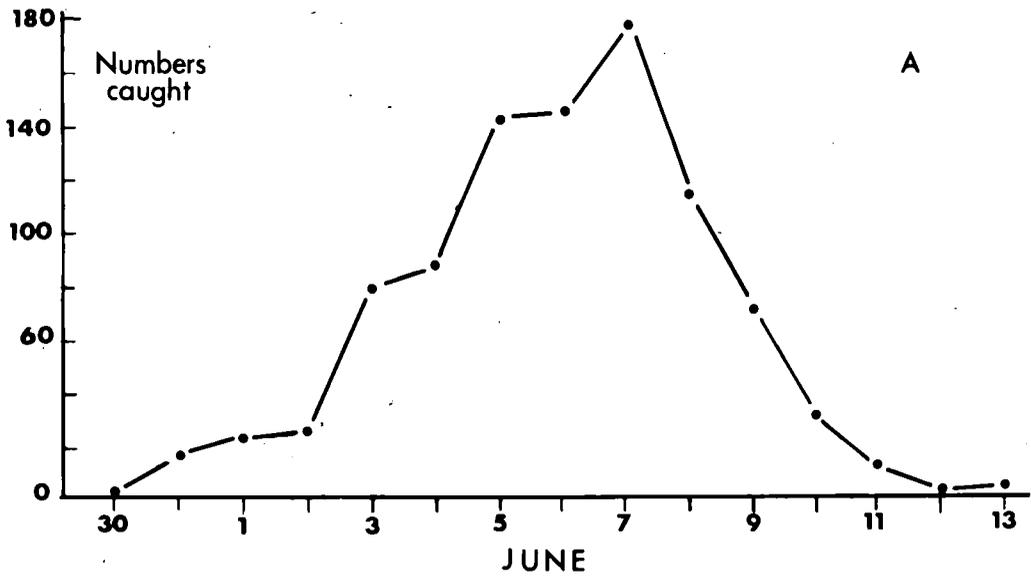
TABLE 6. DAILY DENSITY PER SQ.M. ($\pm$ S.E.) OF NEWLY EMERGED
ADULTS AT MOOR HOUSE

| | 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 <u>Molophilus</u> <u>ater</u>. 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% of

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 <u>Molophilus</u> <u>ater</u>, though it must be remembered that there is a large difference in size between <u>Molophilus</u> <u>ater</u> and <u>Tipula</u> 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 <u>Molophilus</u> <u>ater</u>; 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 <u>Coleophora</u> <u>alticolella</u> 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.
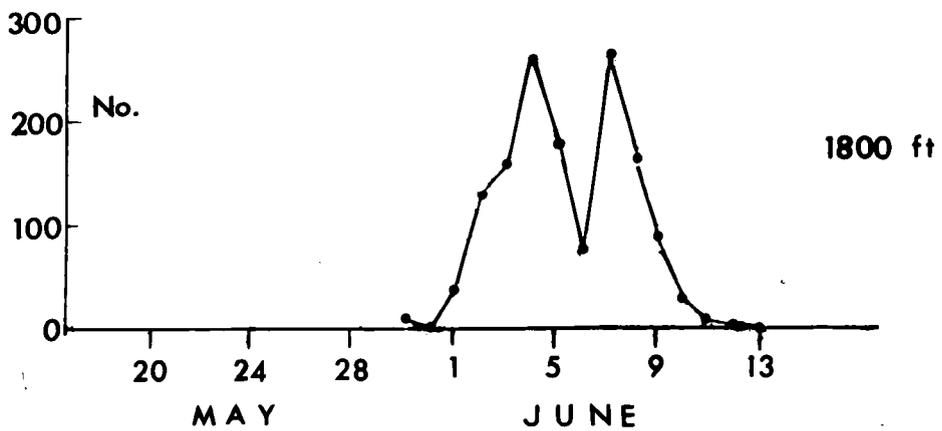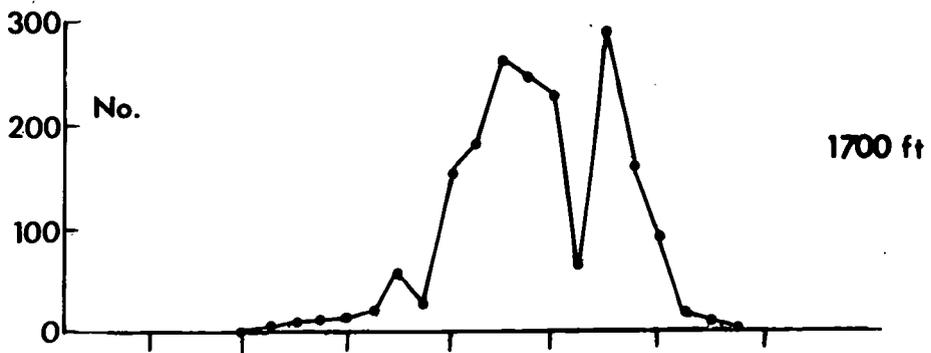
TABLE 10   DAILY DENSITY PER SQ. M. ($\pm$ S.E.) OF ADULTS ON

THE "EAST TRANSECT", 1965

Altitude (ft.)

| Date | 1500 | 1600 | 1700 | 1800 |
|---|---|---|---|---|
| 21 May | 50 $\pm$ 15.3 | 14 $\pm$ 5.7 | 0 | |
| 22 May | 82 $\pm$ 21.3 | 44 $\pm$ 13.2 | 0 | |
| 23 May | 40 $\pm$ 24.4 | 118 $\pm$ 39.7 | 0 | |
| 24 May | 178 $\pm$ 21.5 | 350 $\pm$ 51.2 | 4 $\pm$ 2.4 | |
| 25 May | 452 $\pm$ 61.3 | 604 $\pm$ 91.7 | 8 $\pm$ 4.2 | |
| 26 May | 556 $\pm$ 76.2 | 584 $\pm$ 35.4 | 24 $\pm$ 9.7 | |
| 27 May | 370 $\pm$ 40.0 | 612 $\pm$ 40.6 | 22 $\pm$ 6.6 | |
| 28 May | 258 $\pm$ 59.4 | 422 $\pm$ 55.1 | 28 $\pm$ 12.2 | 0 |
| 29 May | 378 $\pm$ 45.6 | 438 $\pm$ 52.2 | 50 $\pm$ 18.6 | 0 |
| 30 May | 438 $\pm$ 47.6 | 456 $\pm$ 55.1 | 130 $\pm$ 31.3 | 8 $\pm$ 4.2 |
| 31 May | 270 $\pm$ 35.4 | 418 $\pm$ 44.1 | 66 $\pm$ 18.4 | 0 |
| 1 June | 130 $\pm$ 26.4 | 370 $\pm$ 34.2 | 314 $\pm$ 31.4 | 108 $\pm$ 28.4 |
| 2 June | 166 $\pm$ 34.2 | 206 $\pm$ 20.2 | 374 $\pm$ 32.7 | 270 $\pm$ 25.0 |
| 3 June | 120 $\pm$ 21.9 | 212 $\pm$ 30.9 | 534 $\pm$ 53.8 | 322 $\pm$ 28.3 |
| 4 June | 26 $\pm$ 9.4 | 86 $\pm$ 19.2 | 512 $\pm$ 51.6 | 548 $\pm$ 72.4 |
| 5 June | 28 $\pm$ 8.6 | 54 $\pm$ 11.3 | 472 $\pm$ 39.4 | 368 $\pm$ 38.9 |
| 6 June | 6 $\pm$ 2.9 | 40 $\pm$ 9.4 | 148 $\pm$ 14.7 | 172 $\pm$ 22.8 |
| 7 June | 0 | 16 $\pm$ 6.8 | 588 $\pm$ 47.9 | 540 $\pm$ 38.1 |
| 8 June | 0 | 12 $\pm$ 4.2 | 334 $\pm$ 35.1 | 356 $\pm$ 26.8 |
| 9 June | | 0 | 204 $\pm$ 26.4 | 186 $\pm$ 17.4 |
| 10 June | | 0 | 52 $\pm$ 11.7 | 70 $\pm$ 17.3 |
| 11 June | | | 34 $\pm$ 8.3 | 28 $\pm$ 8.1 |
| 12 June | | | 0 | 4 $\pm$ 2.4 |
| 13 June | | | 0 | 2 $\pm$ 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.
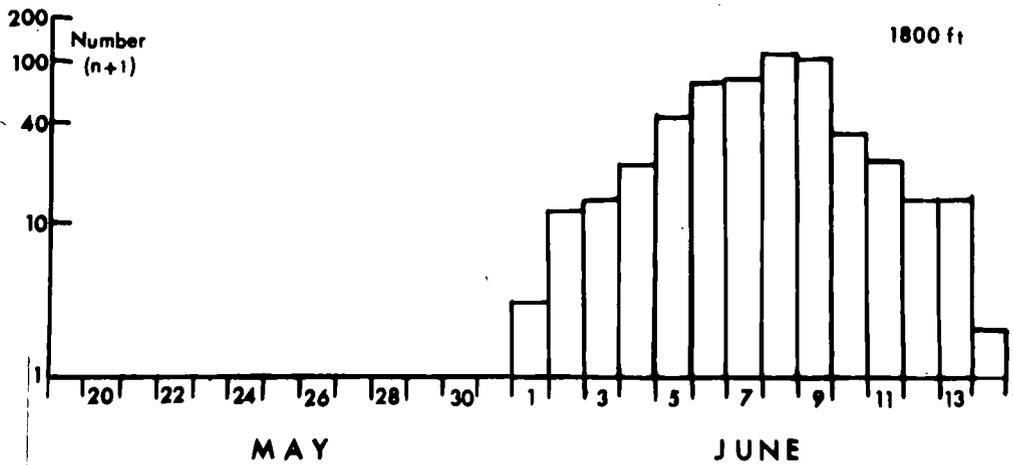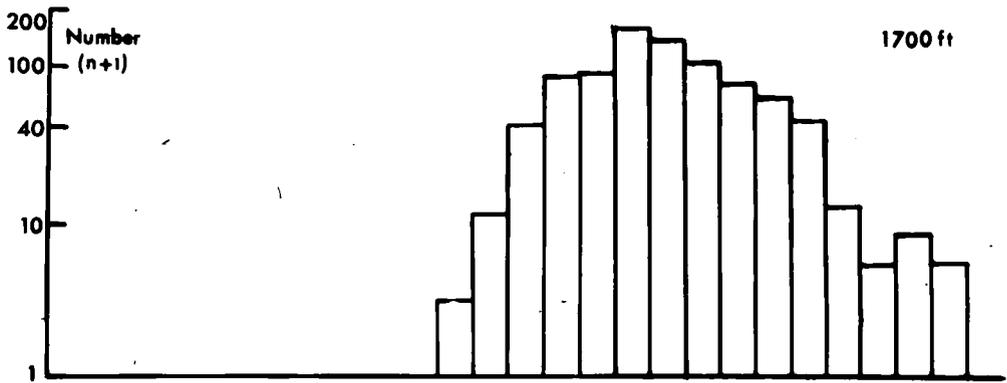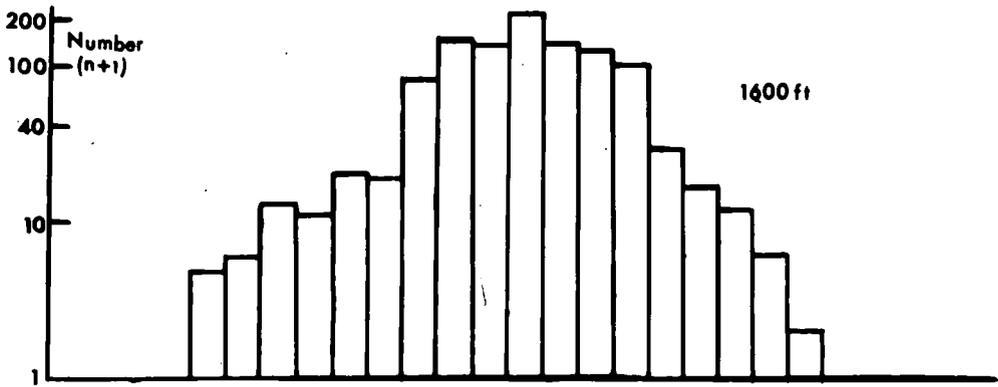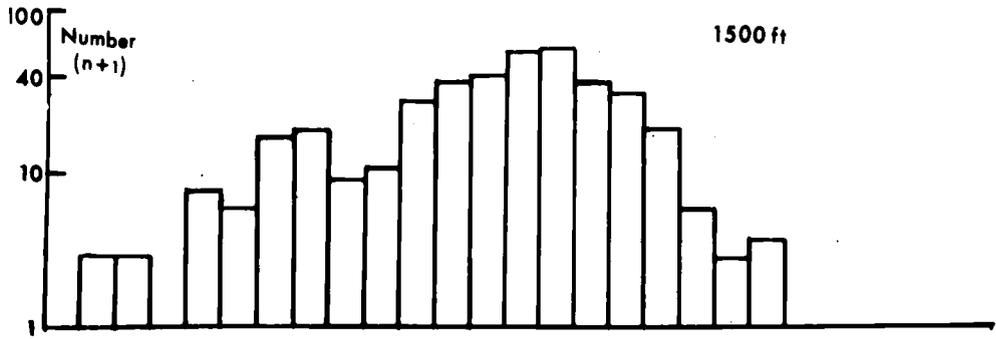
recorded in 1965. In both years emergence is delayed at higher altitudes, the peak emergences occurring 7 to 9 days later at 1800 ft. than at 1500 ft. Similar findings, that the seasonal occurrence is earlier at lower than at higher altitudes, have been recorded for Tipula lesnei Pierre in the Canary 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 | $\chi^2$ | P |
|---|---|---|---|---|---|
| Peaty Gley, 1964 | 429 | 177 | 70.1 | 104.8 | <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 $\chi^2$ 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 <u>Molophilus</u> 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

Estimated Number per sq.m. ($\pm$ S.E.)

| Site and Year | Instar 4 larvae | Adult emergences |
|---|---|---|
| Peaty Gley, 1964 | 1100 $\pm$ 143 | 1212 $\pm$ 87 |
| Peaty Gley, 1965 | 1866 $\pm$ 329 | 1958 $\pm$ 75 |
| Peaty Podsol, 1965 | 2040 $\pm$ 353 | 1866 $\pm$ 154 |
| Carecetum, 1965 | 933 $\pm$ 172 | 1130 $\pm$ 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
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.

$y = 102.94 - 4.97x$

$r = - 0.97$
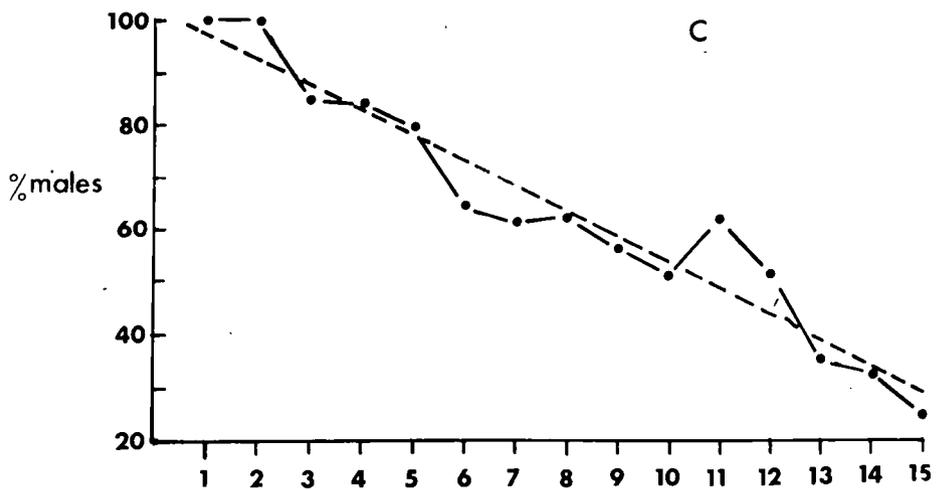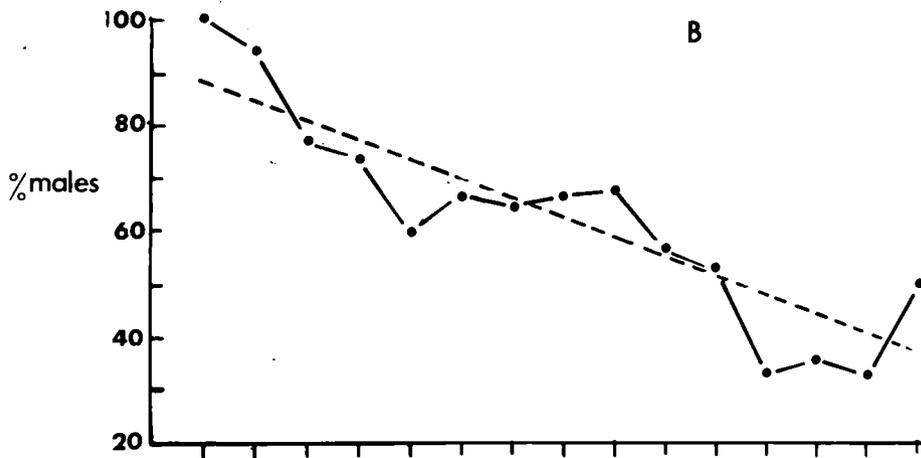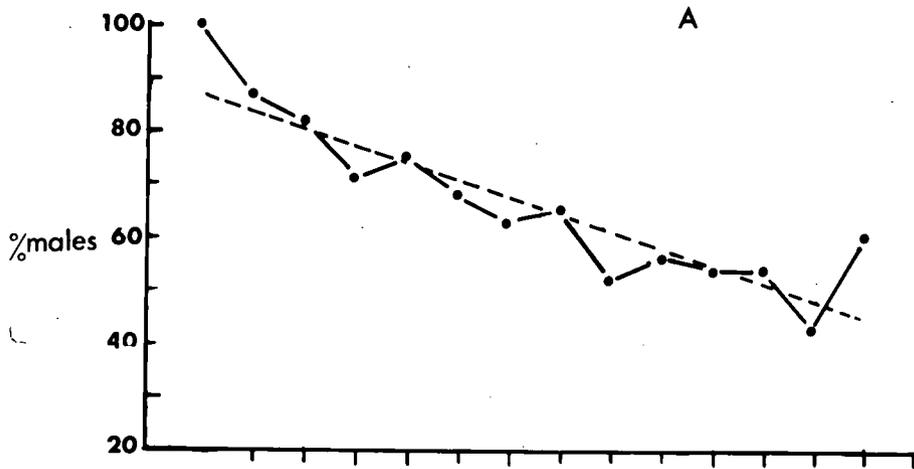
DAY OF EMERGENCE PERIOD

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.

$y = 88.48 - 3.42x$

$r = -0.89$
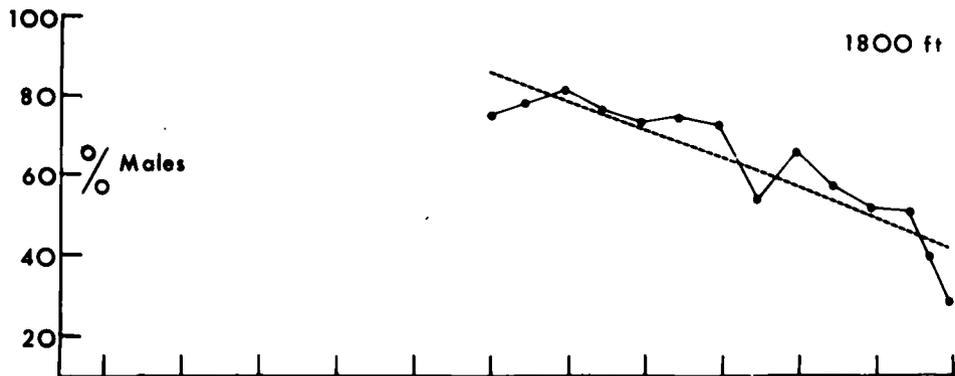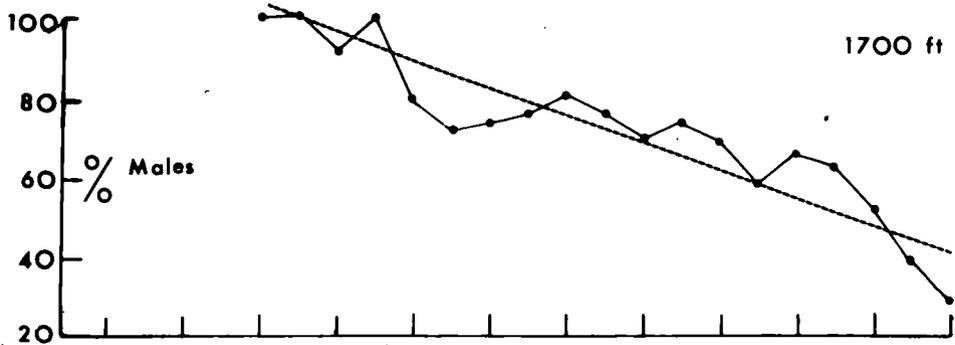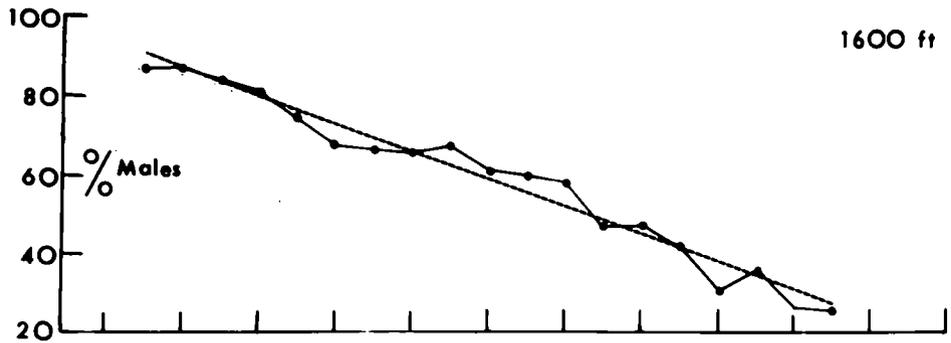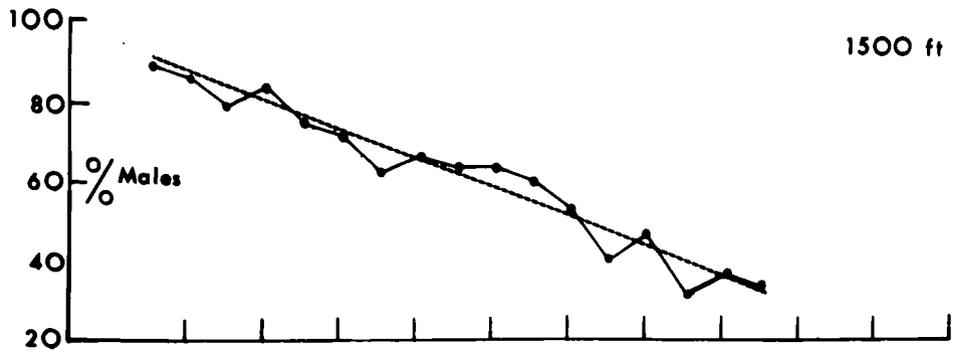
Similar observations, of a rise in the proportion of females in the population with time, have been reported for several members of the <u>Tipulidae</u> (e.g. Maercks, 1939; Hemmingsen, 1952; Hemmingsen & Jensen, 1957; Freeman, 1964). Though there is little discussion in these studies of male and female survival rates, it does seem probable that the males emerge slightly before the females. There has been no investigation in the <u>Tipulidae</u> 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. ($\pm$ S.E.)

| | Peaty Gley Site | Peaty Podsol Site | Carecetum Site |
|---|---|---|---|
| 22 May | | | 6 $\pm$ 4.0 |
| 23 May | | | 18 $\pm$ 7.7 |
| 24 May | | | 92 $\pm$ 17.8 |
| 25 May | | | 94 $\pm$ 20.4 |
| 26 May | | | 112 $\pm$ 21.0 |
| 27 May | | | 90 $\pm$ 15.8 |
| 28 May | 0 | 0 | 90 $\pm$ 16.3 |
| 29 May | 0 | 0 | 154 $\pm$ 31.2 |
| 30 May | 0 | 8 $\pm$ 4.2 | 206 $\pm$ 38.3 |
| 31 May | 10 $\pm$ 5.1 | 34 $\pm$ 9.4 | 148 $\pm$ 45.8 |
| 1 June | 42 $\pm$ 11.5 | 40 $\pm$ 9.4 | 144 $\pm$ 33.9 |
| 2 June | 120 $\pm$ 26.5 | 72 $\pm$ 18.2 | 98 $\pm$ 22.7 |
| 3 June | 192 $\pm$ 27.0 | 144 $\pm$ 19.0 | 70 $\pm$ 17.7 |
| 4 June | 194 $\pm$ 19.6 | 208 $\pm$ 18.6 | 14 $\pm$ 6.4 |
| 5 June | 274 $\pm$ 18.8 | 330 $\pm$ 33.5 | 8 $\pm$ 6.4 |
| 6 June | 370 $\pm$ 30.4 | 330 $\pm$ 19.8 | 2 $\pm$ 1.9 |
| 7 June | 404 $\pm$ 17.6 | 376 $\pm$ 26.9 | 0 |
| 8 June | 280 $\pm$ 18.3 | 278 $\pm$ 33.6 | 0 |
| 9 June | 236 $\pm$ 29.2 | 158 $\pm$ 16.8 | 0 |
| 10 June | 176 $\pm$ 13.8 | 94 $\pm$ 12.6 | |
| 11 June | 94 $\pm$ 15.2 | 34 $\pm$ 9.8 | |
| 12 June | 56 $\pm$ 8.4 | 6 $\pm$ 4.0 | |
| 13 June | 22 $\pm$ 7.7 | 6 $\pm$ 2.9 | |
| 14 June | 4 $\pm$ 2.5 | 0 | |
| 15 June | 2 $\pm$ 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
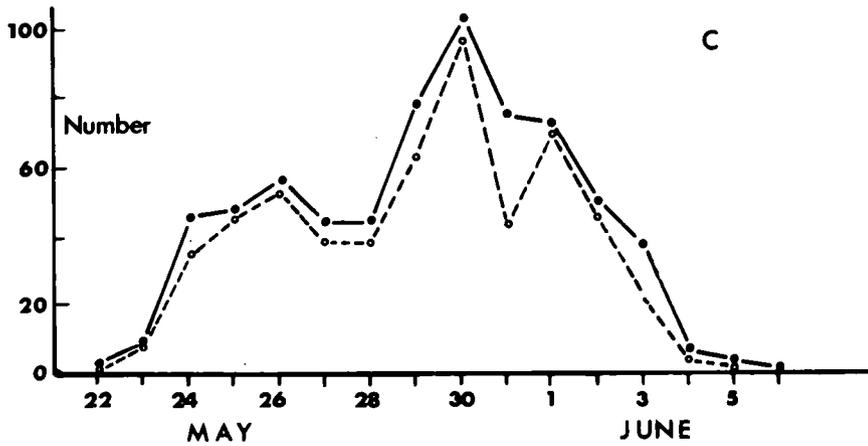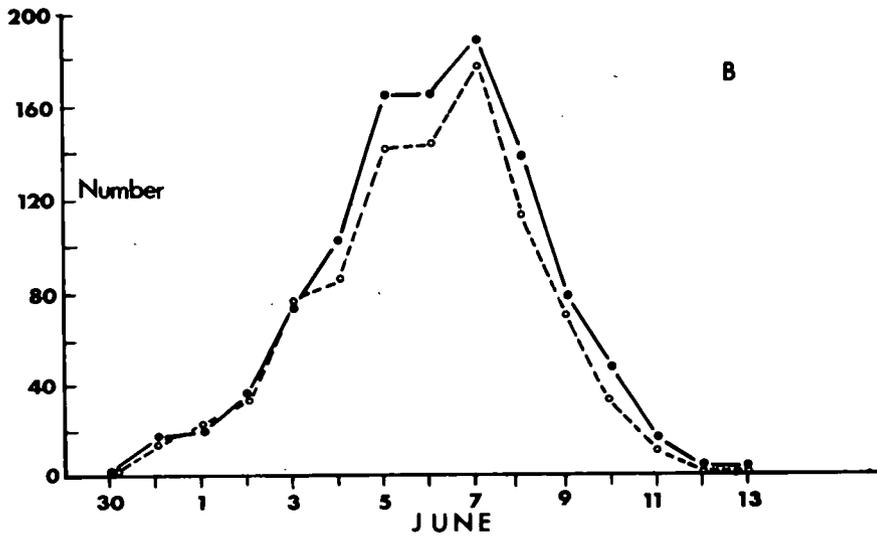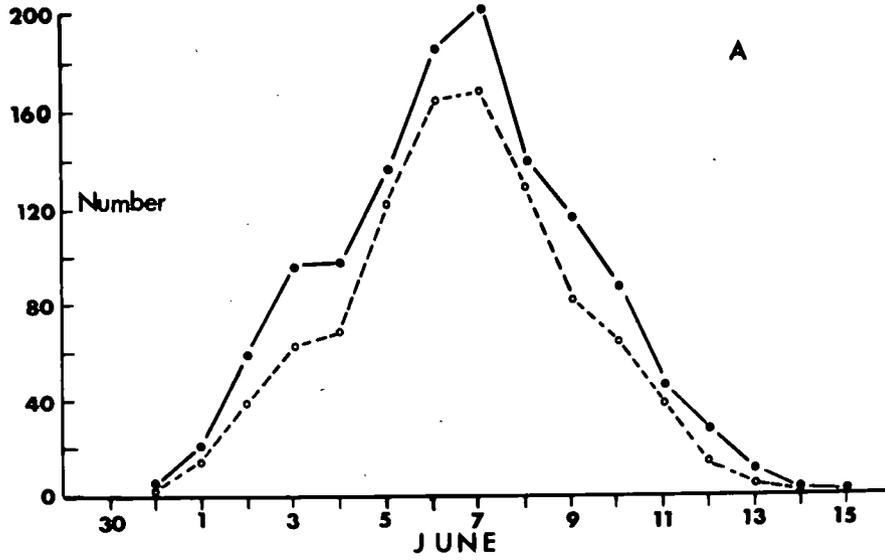
TABLE 16.   THE AVERAGE DAILY ELIMINATION RATES OF ADULTS IN
THE FIELD IN 1965, DERIVED FROM COMPARISON
OF THE NUMBERS OF NEWLY EMERGED AND
TOTAL ADULTS

|  | 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$^{o}$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.
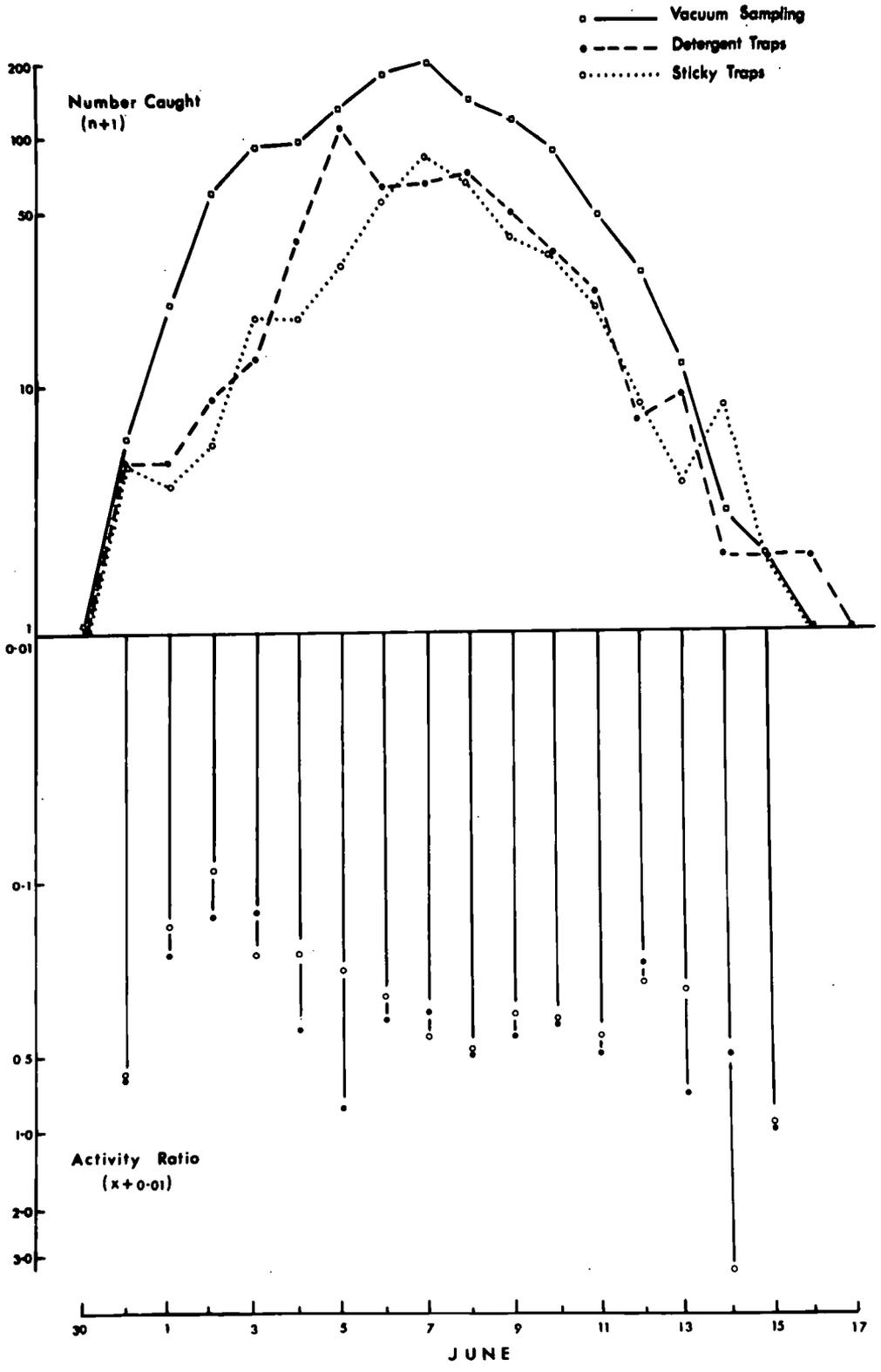
FIG. 11.  COMPARISON OF THE NUMBERS CAUGHT

DAILY BY DETERGENT AND STICKY TRAPS

WITH THE NUMBER RECORDED BY RANDOM

SUCTION SAMPLING ON THE PEATY PODSOL
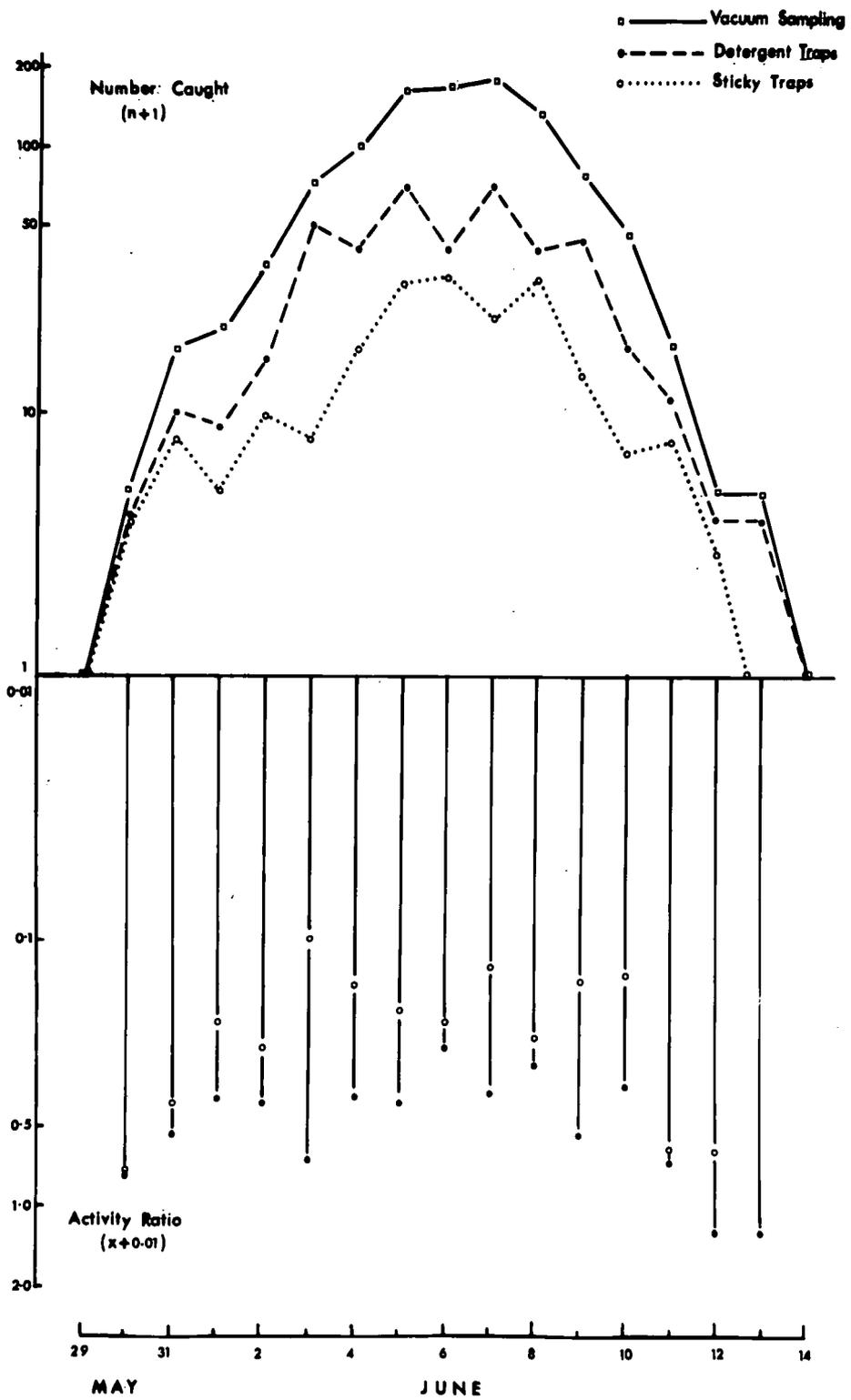
SITE IN 1965.

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.
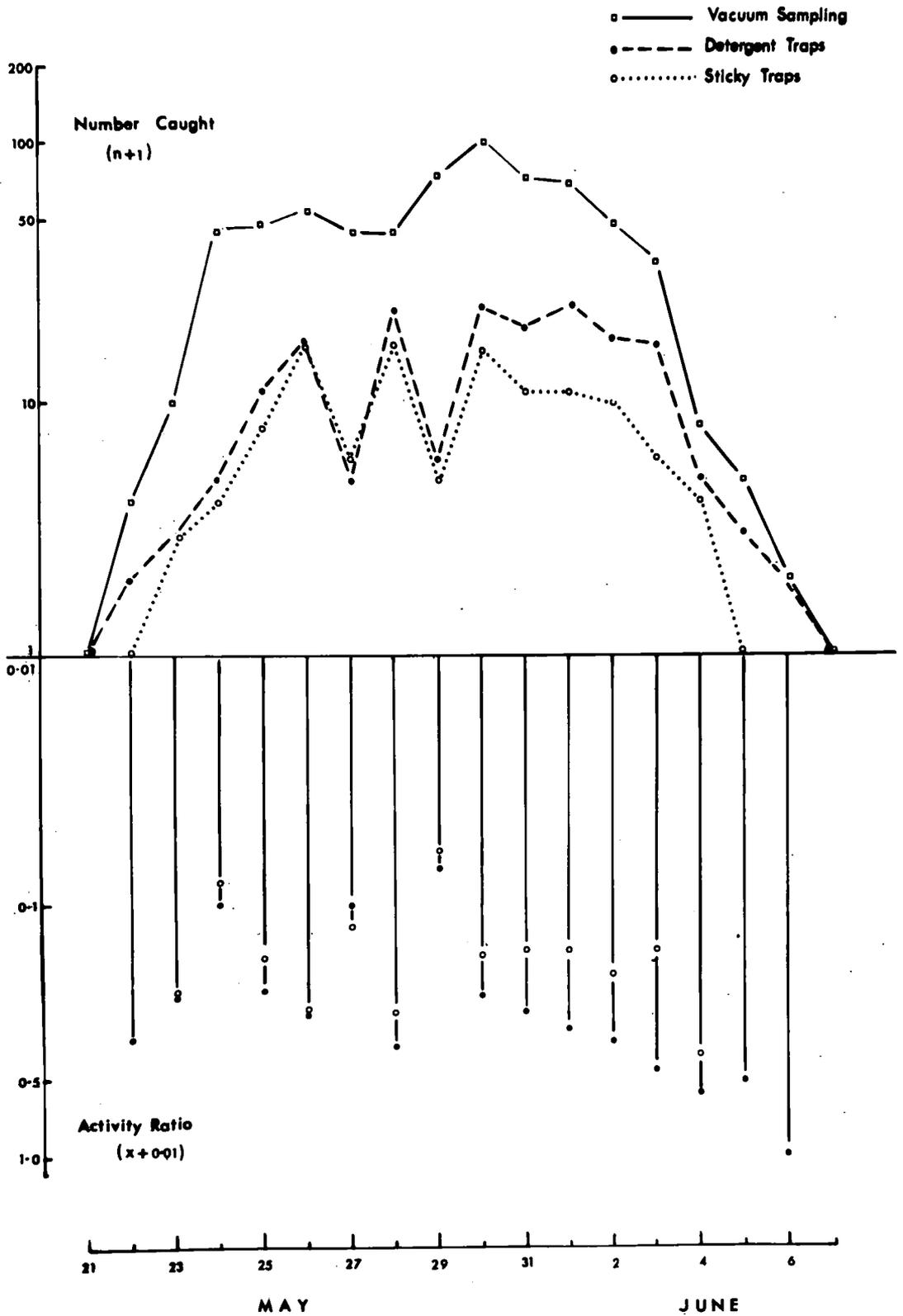
Molophilus ater, a short-lived species which does not feed in its adult stage, it is essential that mating occurs a short time after emergence. Mating appears to be dependent on random wanderings within the herbage bringing individuals of each sex into actual physical contact. During the middle part 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.) |  |  |  | Number recovered |
|---|---|---|---|---|---|---|
|  |  | 0 | 0-10 | 10-20 | 20-30 | 30-40 |  |
| 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 ($x^2 = 16.4$, 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 | $\chi^2$ (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 $\chi^2$ 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. | $\chi^2$ | 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
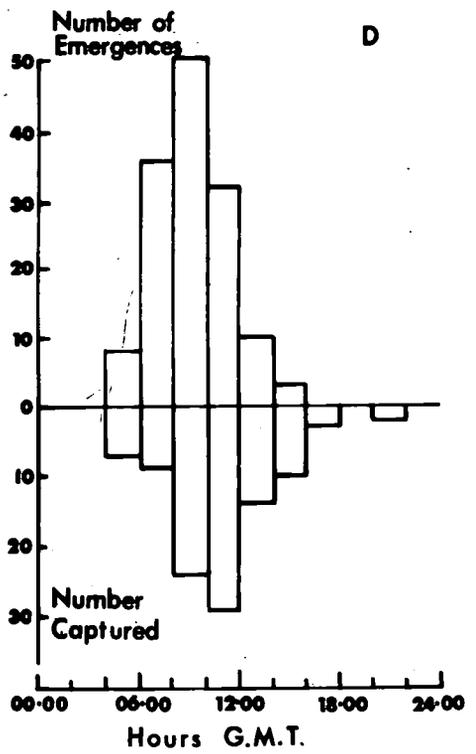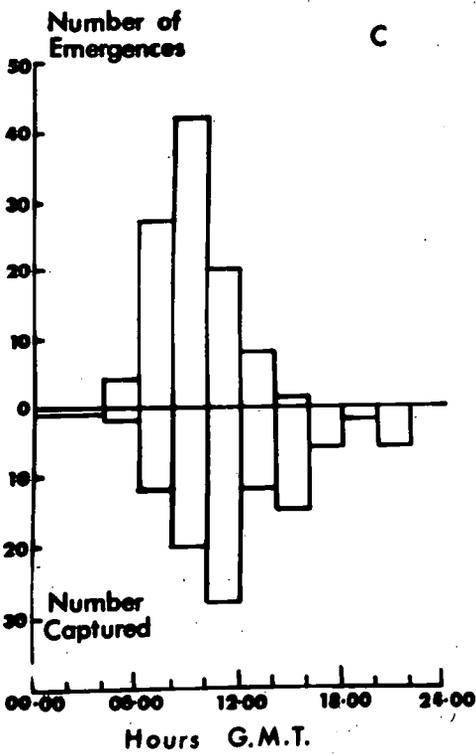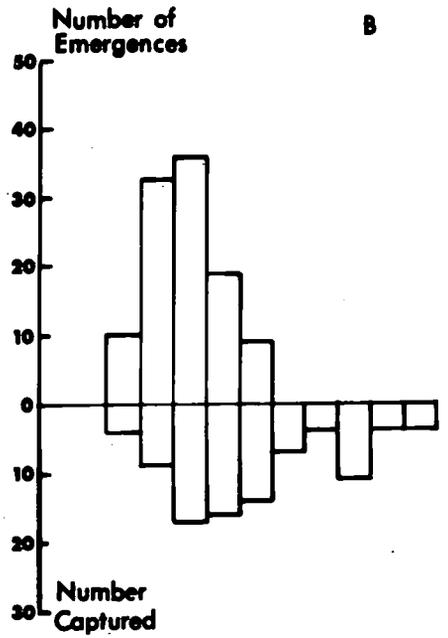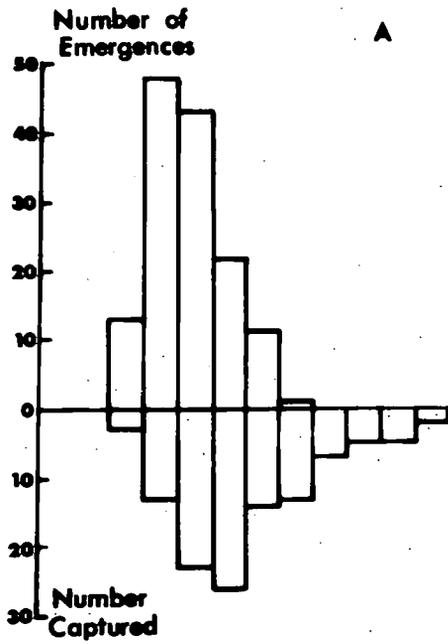
TABLE 22.    METEOROLOGICAL CONDITIONS DURING THE FOUR DAY
OBSERVATION PERIOD, TAKEN FROM THE MOOR HOUSE
RECORDS

| Date, 1965 | 8 June | 9 June | 10 June | 11 June |
|---|---|---|---|---|
| Maximum temperature (°F) | 57.5 | 63.3 | 65.3 | 61.6 |
| Minimum temperature (°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 No. | % | Females No. | % | Males & Females 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. | % | Females No. | % | Males & Females No. | % |
|---|---|---|---|---|---|---|
| 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.
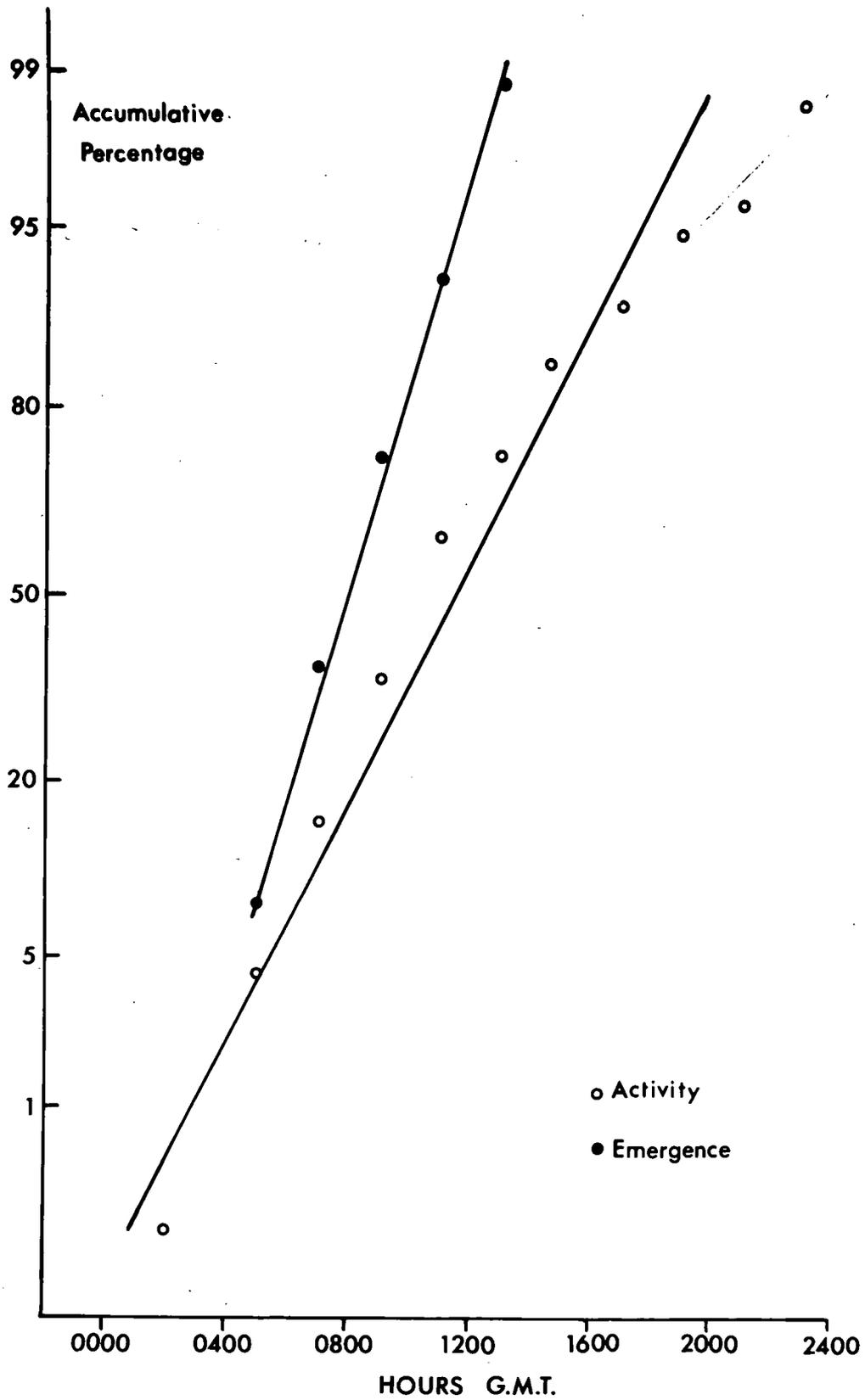
The curve for activity emphasises the longer time period during which individuals are active, compared with their period of emergence. Though the curve is a much less perfect single distribution than that recorded for emergence, there is no evidence of a bimodal periodicity in activity. There is, however, 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 <u>Molophilus</u> <u>ater</u> 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 <u>Tipulidae</u> (e.g. <u>Dictenidia</u>, <u>Tanyptera</u>, and <u>Ctenophora</u> 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 <u>Molophilus</u> <u>ater</u>, 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$^{\circ}$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 intro-
duced 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 ob-
served, 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
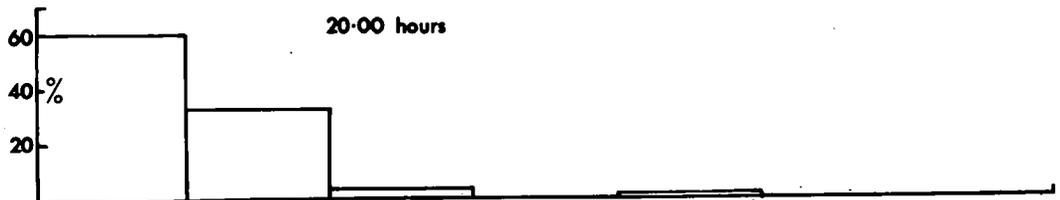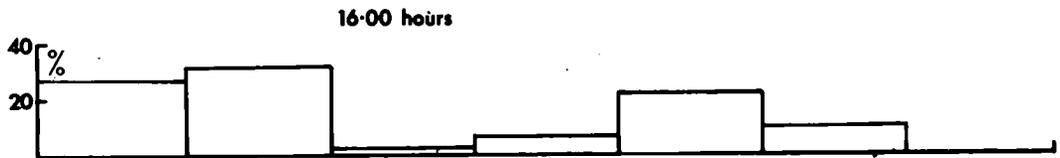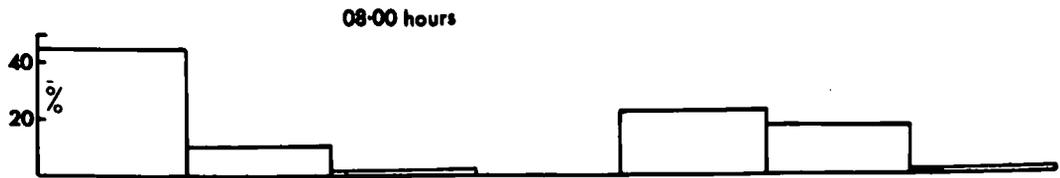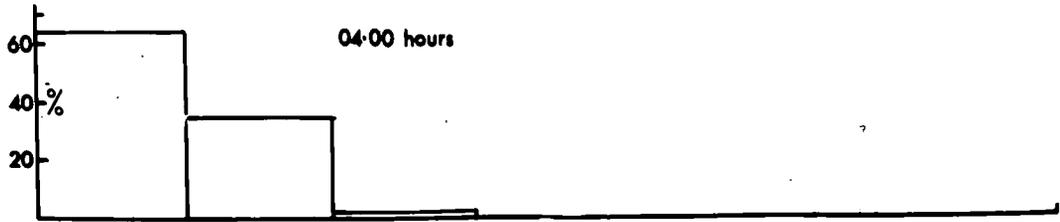
NUMBER of EGGS

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 $\mu$, $\pm$ 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 $\mu$ 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 <u>Mollophilus</u> 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$^{o}$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
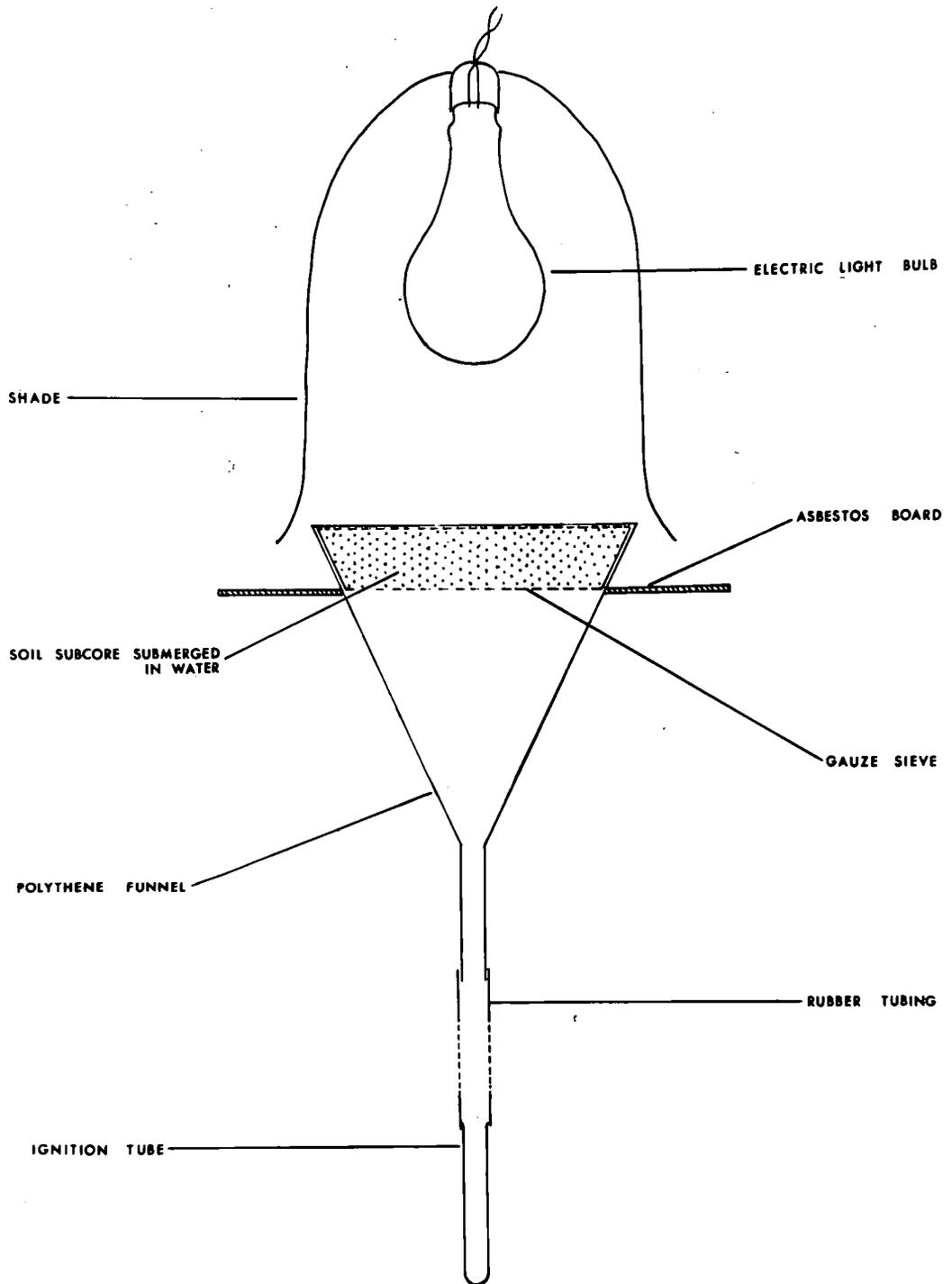
IGNITION TUBE

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 $46^{\circ}$C. after 195 minutes

(Table 29). After this time there is a temperature gradient

of approximately $9^{\circ}$C between the surface and the base of the

sub-sample, equivalent to $6^{\circ}$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 diff-

erences 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 ($^o$C) Surface | Base | Gradient ($^o$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$^o$C for 24 hours.   These sub-samples were soaked in water and stored separately in polythene bags at a temperature of 5$^o$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 $45^{\circ}C$ 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 $5^{\circ}C$, approximating to soil temperatures recorded at Moor House. Since the temperature of the extraction room varied between 14 and $18^{\circ}C$, 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 <u>MOLOPHILUS</u> <u>ATER</u>

|  | Instars | | | |
|---|---|---|---|---|
|  | 1 | 2 | 3 | 4 |
| **MAXIMUM DIAMETER OF SPIRACULAR DISC** | | | | |
| Number measured | 39 | 45 | 57 | 69 |
| Mean ($\mu$) | 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 ($\mu$) | 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 ($\mu$) | 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

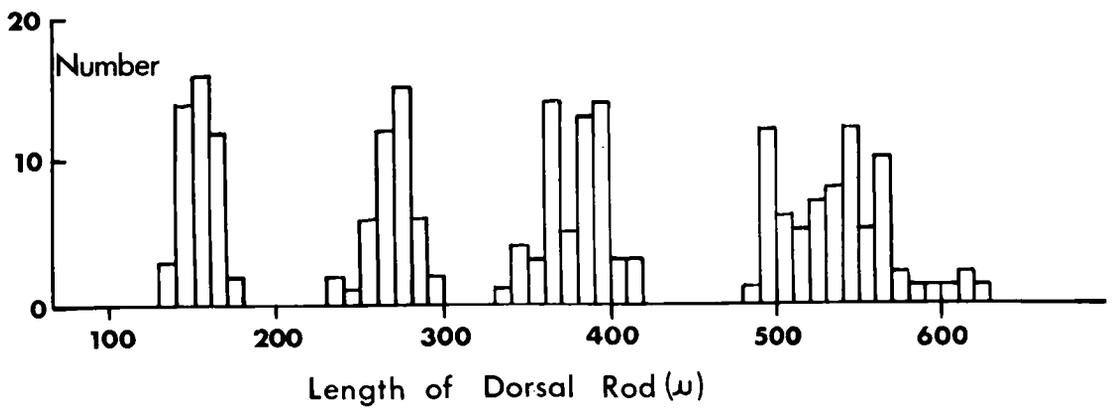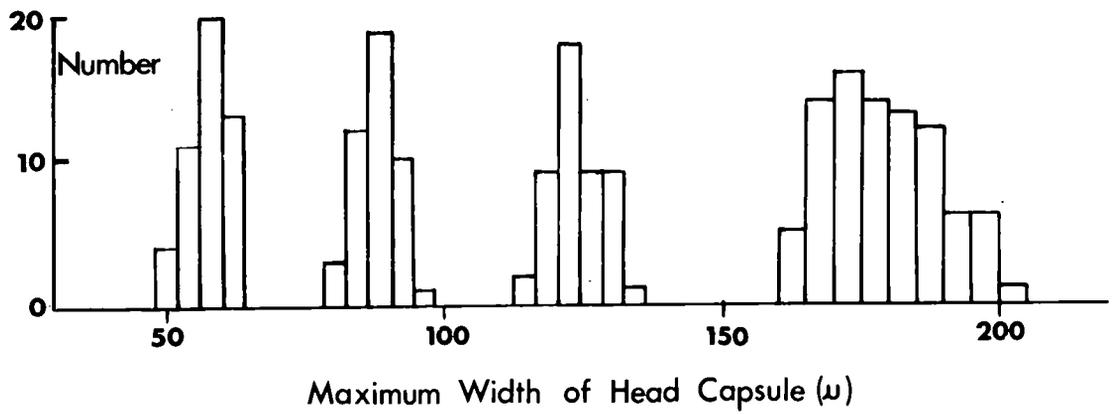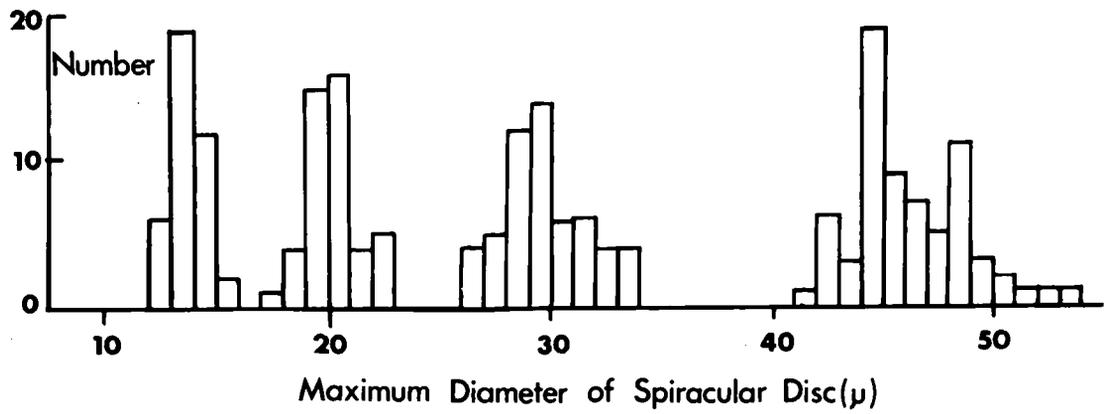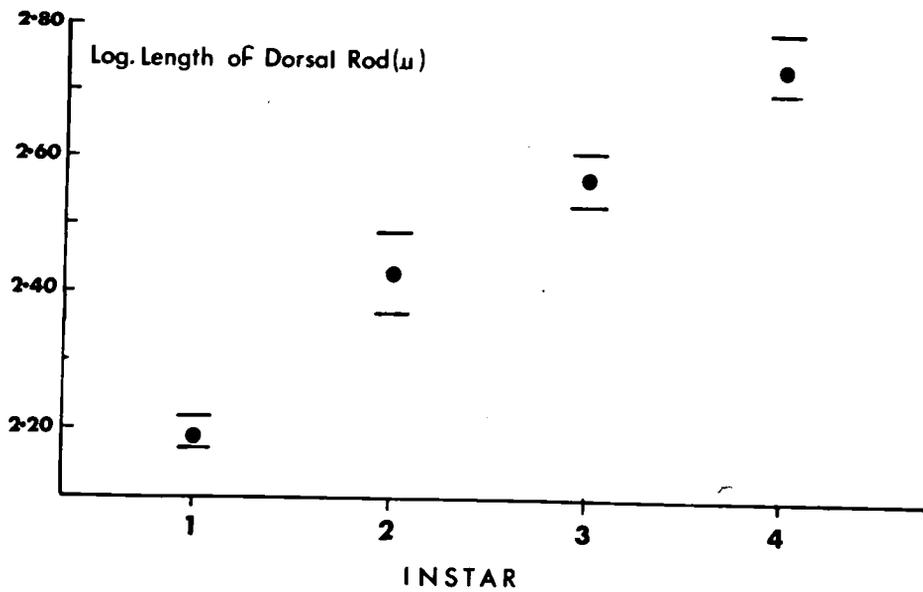Log. Maximum Diameter of Spiracular Disc($\mu$)

Log. Maximum Width of Head Capsule($\mu$)

Log. Length of Dorsal Rod($\mu$)
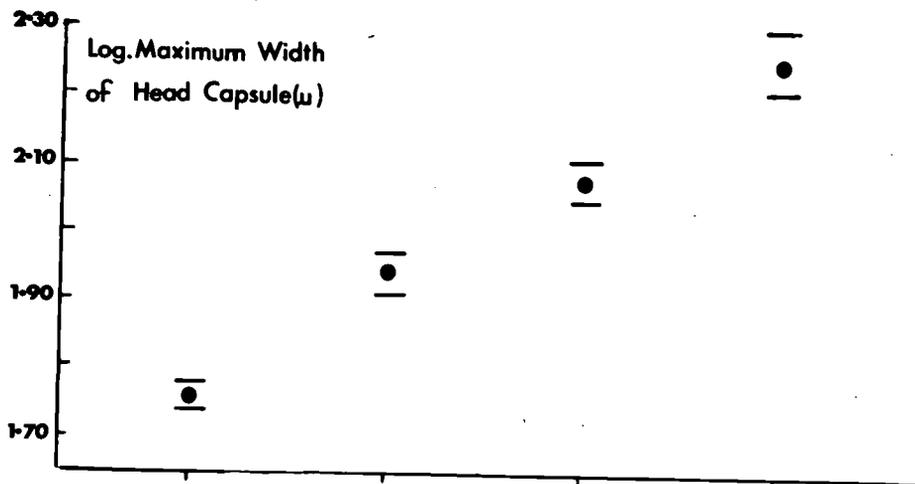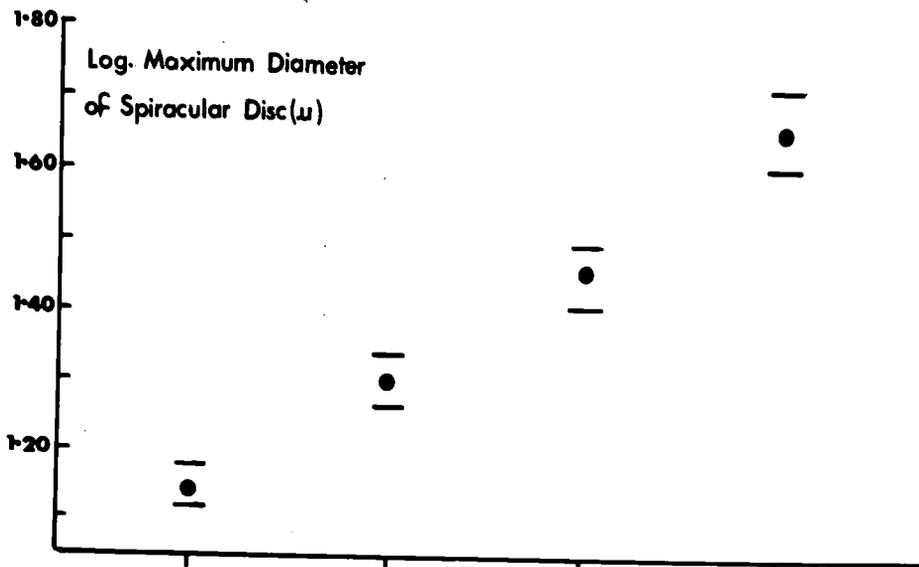
INSTAR

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 | | | | Geometric Mean of maximum width of head capsule (μ) | Number measured |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | | |
| 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 ($\mu$)

Instar 4

Instar 3

Instar 2

180

140

100

60

July    Aug    Sept    Oct    Nov    Dec
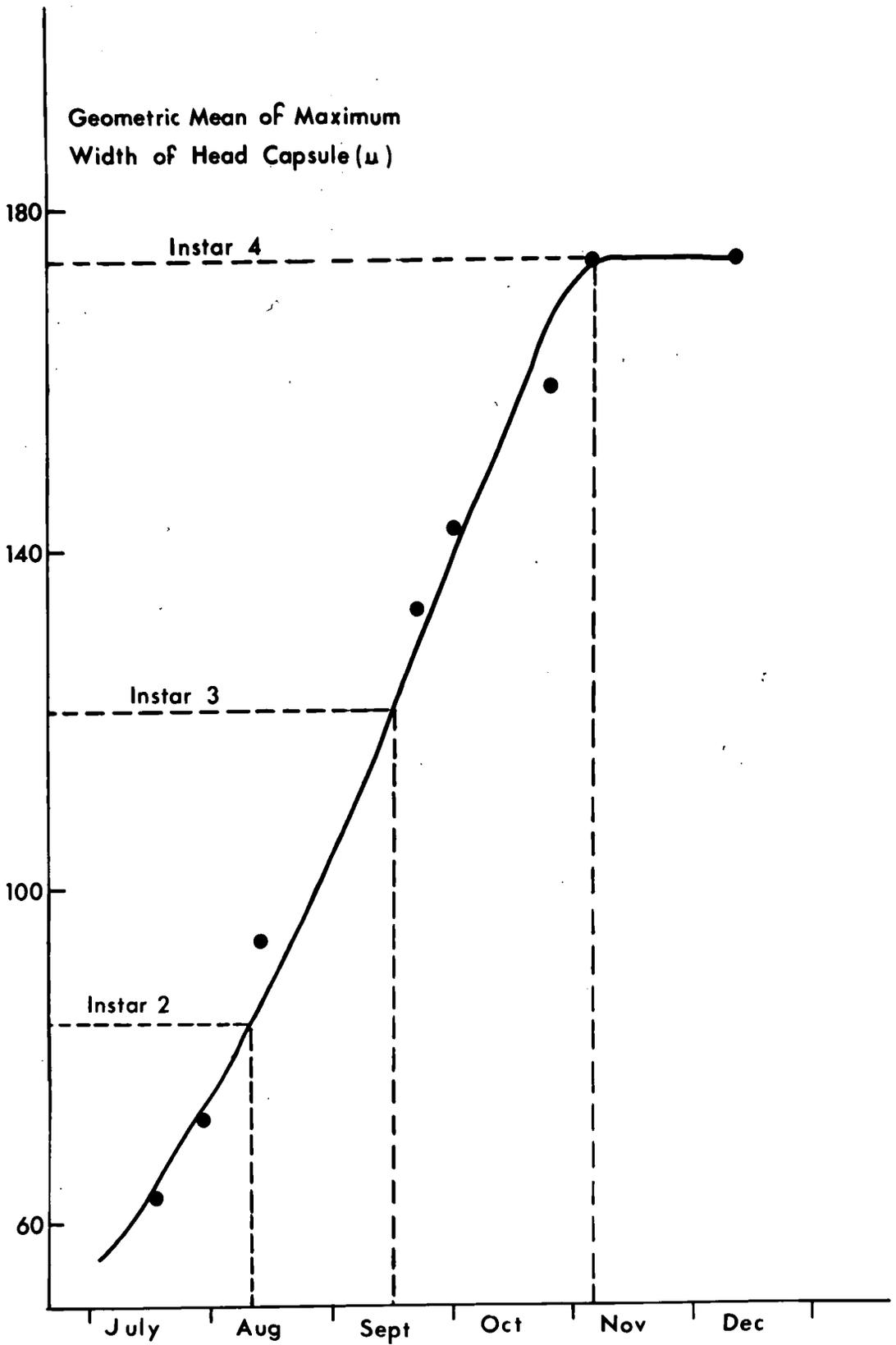
Moor House (Coulson, 1959). The spiracular discs of these

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:-

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

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:-

$$2\sqrt{\frac{2N}{(N-1)^2}} \quad \text{where N = number of sample units taken}$$

Bartlett (in Greig-Smith, 1952) has provided a more correct

estimation of this value, namely:

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

Fifteen sample units were taken on each 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-

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 k have been plotted against the corresponding coefficients of dispersion. The values of 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 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:-   $y = 7.70 - 0.95x$

$r = 0.89$
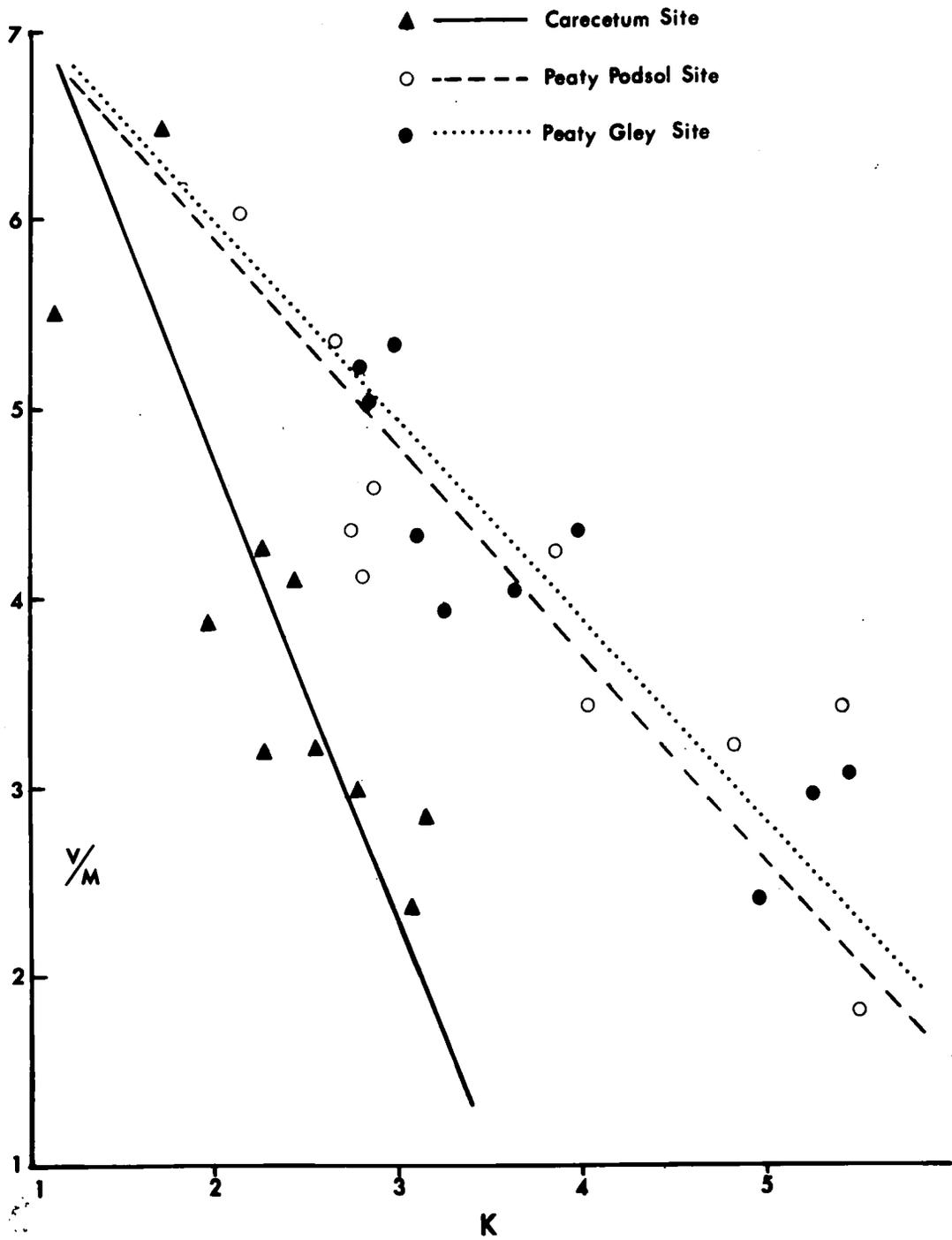
TABLE 35.  OBSERVED FREQUENCY DISTRIBUTIONS OF LARVAE ON THREE SITES DURING THE LARVAL

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 heterogen*e*ity of vegetation, at least not by using random sample units of the size taken (0.005 sq.m.). The larval stages of <u>Molophilus</u> <u>ater</u> 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 <u>Molophilus</u> <u>ater</u> 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

| Site | 0-3 cm. | | 3-6 cm. | | 6-9 cm. | |
|---|---|---|---|---|---|---|
| | 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 Haarløve (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
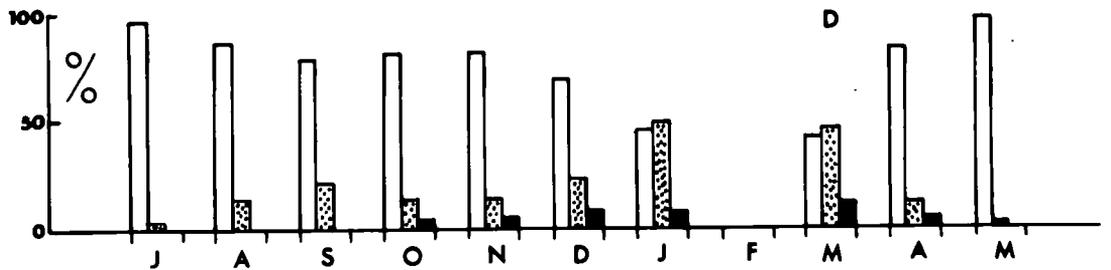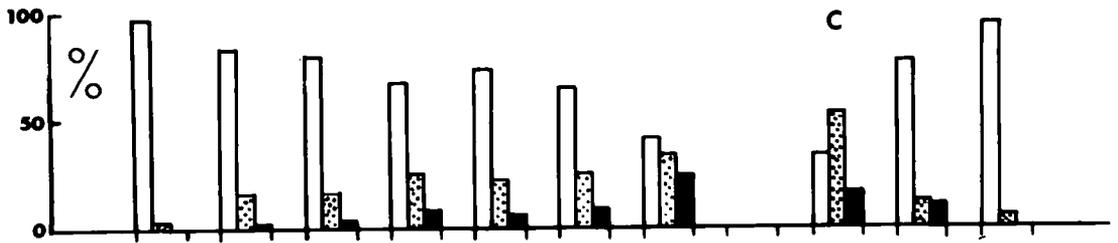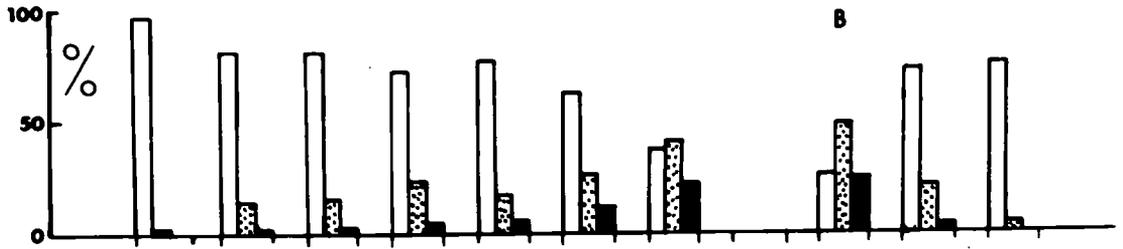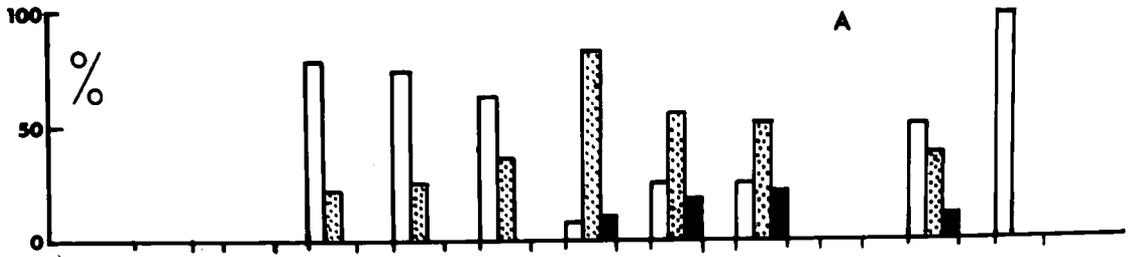
TABLE 37.    VERTICAL DISTRIBUTION OF LARVAE ON THE PEATY

PODSOL SITE.    ON EACH SAMPLING DATE, 15 SAMPLE

UNITS WERE TAKEN.

| Date 1964-65 | o-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 $5^{\circ}C$, 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 $1.23 \pm 0.06$ mg. ($\pm$ S.E.) to $1.46 \pm 0.05$ 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., $\pm$ 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 $\pm$ 287 |
| Juncus squarrosus | Troutbeck | 15 | 1733 $\pm$ 308 |
| Carex spp. | Troutbeck | 15 | 1187 $\pm$ 211 |
| Eriophorum vaginatum | Pasture | 15 | 1040 $\pm$ 164 |
| Juncus squarrosus | Moss Burn | 15 | 813 $\pm$ 175 |
| Blanket Bog | Bog Hill | 15 | 373 $\pm$ 78 |
| Blanket Bog | Burnt Hill | 15 | 147 $\pm$ 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 transf-
erred 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 $20^{o}C$, the pupal period
lasted 5.2 days, but at $10^{o}C$, 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 $6.9^{o}C$; 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, | Number | Mean duration of pupal stage in days ($\pm$ S.E.) Males | Number | Females | $t$ |
|---|---|---|---|---|---|
| 10 | 17 | 10.56 $\pm$ 0.34 | 15 | 10.74 $\pm$ 0.27 | 0.42 |
| 15 | 38 | 7.57 $\pm$ 0.19 | 32 | 7.72 $\pm$ 0.12 | 0.65 |
| 20 | 22 | 5.11 $\pm$ 0.20 | 20 | 5.21 $\pm$ 0.18 | 0.41 |
| 23 | 16 | 4.43 $\pm$ 0.17 | 13 | 4.38 $\pm$ 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 <u>Tipula oleracea</u> (Laughlin, 1960) and for

the culicid <u>Aedes aegypti</u> 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 temper-

ature 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 <u>Tipula oleracea</u> by reference to male and female growth

curves, which differ significantly from each other. Though

detailed studies on the growth of individual larvae of <u>Molophilus</u>

<u>ater</u> 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.

Weight of Larva (mg.)

Weight of Pupa (mg.)
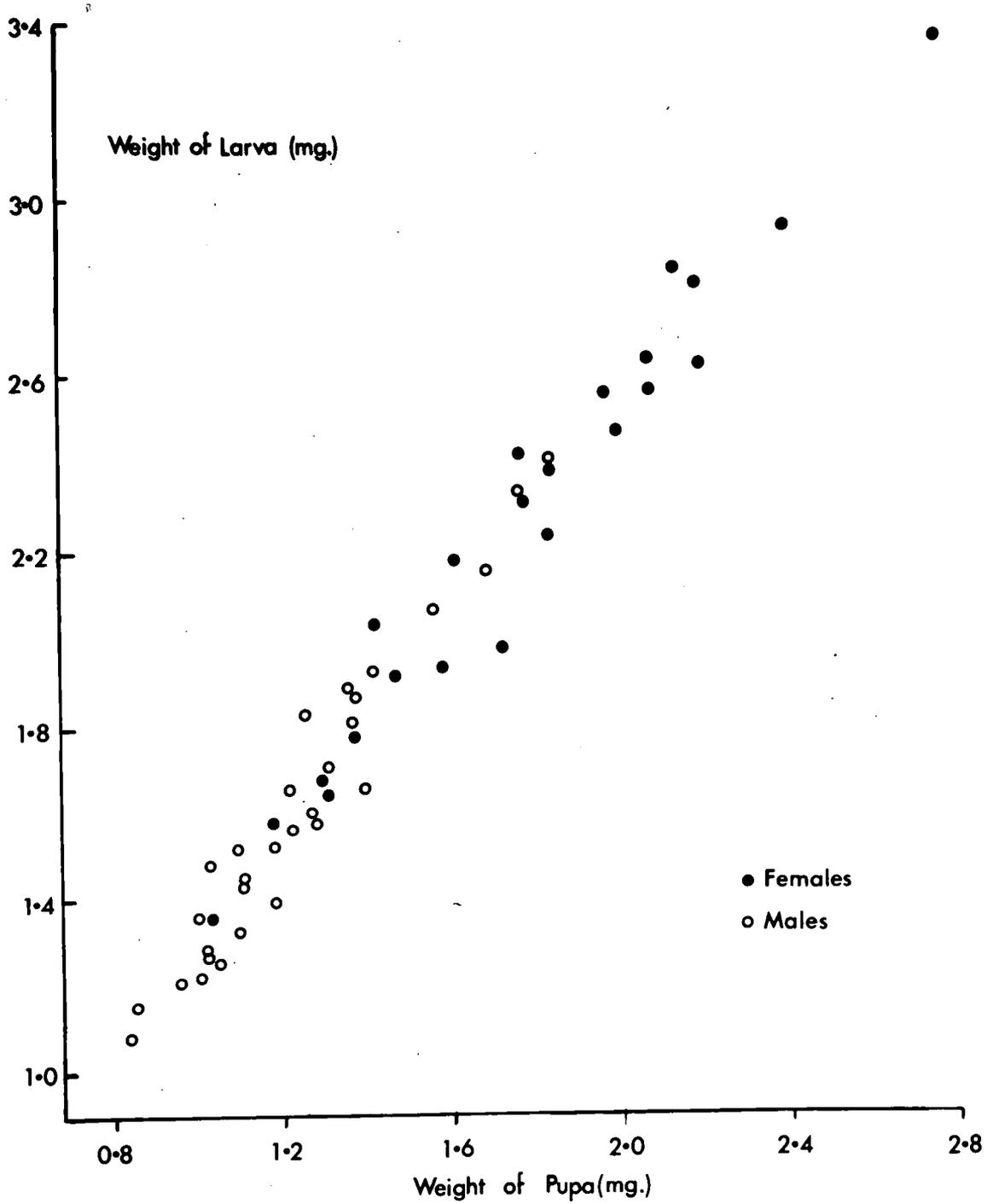
● Females
○ Males

TABLE 41.    THE ONSET OF PUPATION IN THE LABORATORY

| Culture | Temp. $^\circ$C. | Mean number of days before pupation ($\pm$ S.E.) | | d.f. | t | P |
|---------|------|----------|----------|------|------|--------|
| | | Males | Females | | | |
| a | 15 | 12.58 $\pm$ 0.27 | 13.59 $\pm$ 0.39 | 82 | 2.13 | <0.05 |
| b | 15 | 7.07 $\pm$ 0.31 | 8.13 $\pm$ 0.33 | 28 | 2.32 | <0.05 |
| c | 15 | 13.09 $\pm$ 0.42 | 14.17 $\pm$ 0.43 | 62 | 1.80 | <0.1 |
| d | 20 | 6.11 $\pm$ 0.30 | 7.00 $\pm$ 0.39 | 92 | 1.79 | <0.1 |
| e | 20 | 8.28 $\pm$ 0.53 | 9.88 $\pm$ 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 $\pm$ 0.34 mg. ($\pm$ S.D.),
the mean weight of larvae pupating into females was 2.27 $\pm$ 0.47 mg.
The mean weight of male and female pupae was 1.22 $\pm$ 0.24 and
1.77 $\pm$ 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. ($\pm$ S.E.) | | Percentage loss of weight on pupation | Number |
|---------|----------|----------|----------|--------|
| | Larvae | Pupae | | |
| Males | 1.60 $\pm$ 0.06 | 1.22 $\pm$ 0.04 | 23.7 | 30 |
| Females | 2.27 $\pm$ 0.10 | 1.77 $\pm$ 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 :-

$$y = 46.3x - 11.9$$

Number of Eggs

Weight of Pupa (mg.)
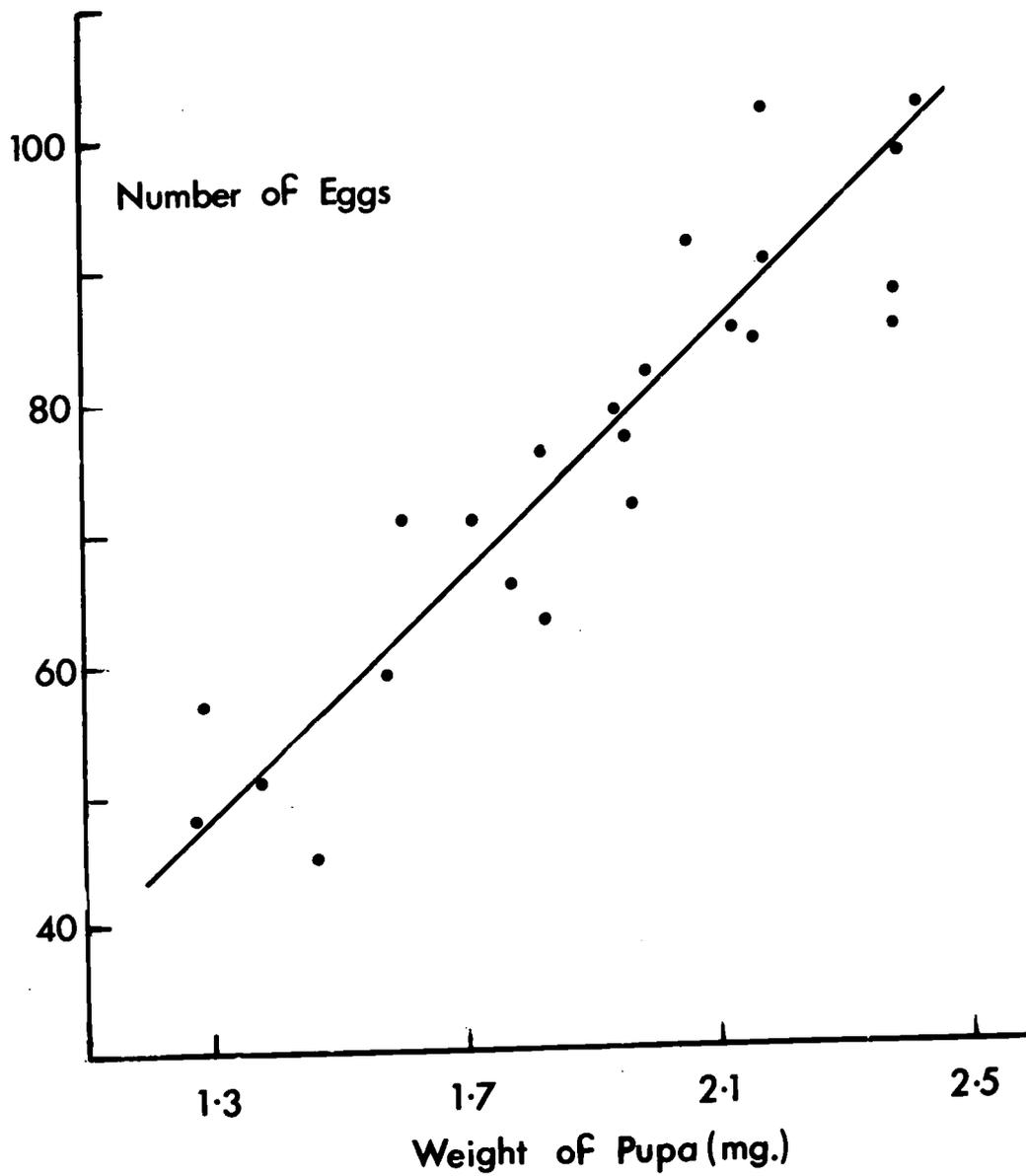
# VII.  POPULATION STUDY

## 1.  SEASONAL VARIATION IN NUMBERS

The life cycle of <u>Molophilus</u> <u>ater</u>, 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 over-wintering 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 <u>MOLOPHILUS</u> <u>ATER</u>.

1-4, larval instars

P, pupa

A, adult

123.
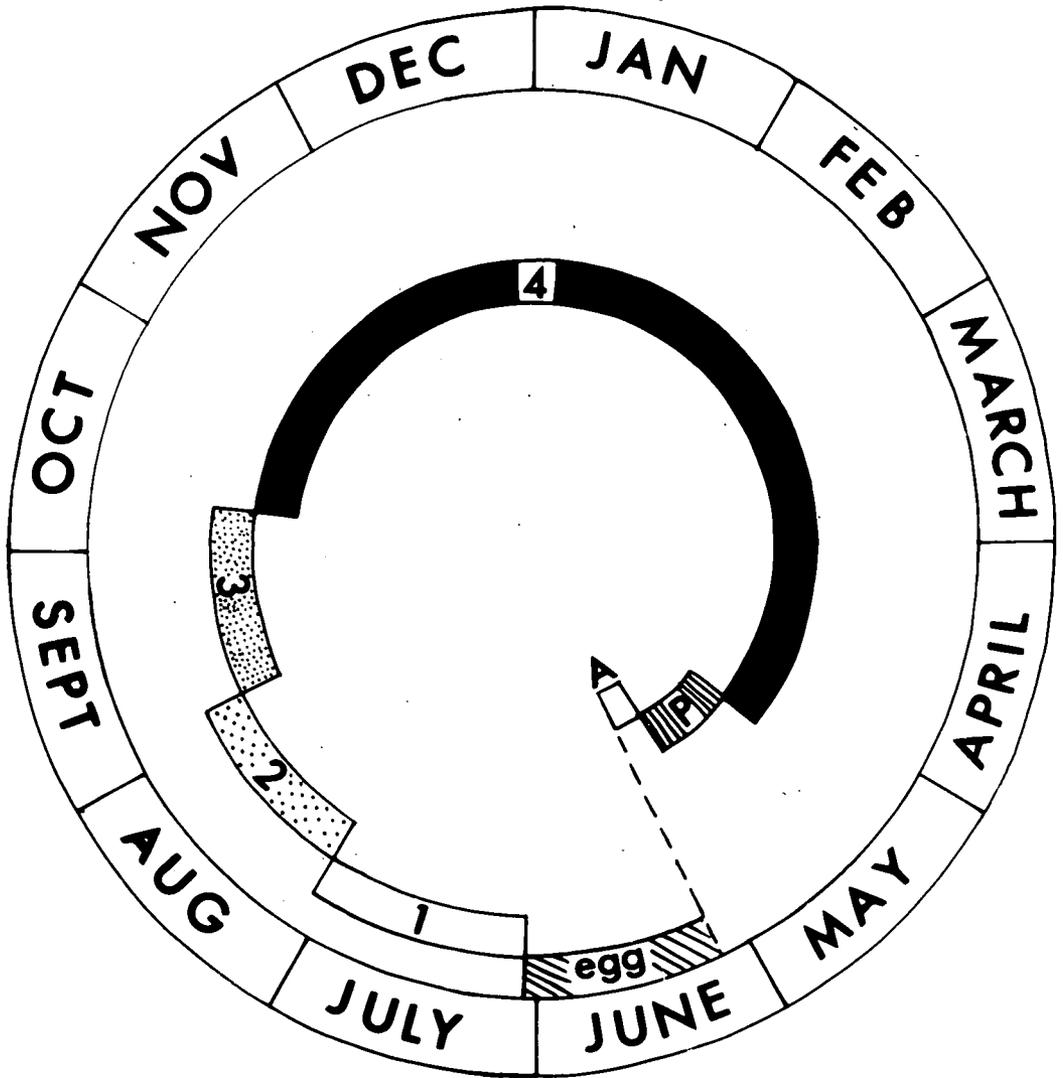
The density estimates for the Peaty Gley site are shown in
Fig. 25, for the Peaty Podsol site in Fig. 26, and for the
Carecetum site in Fig. 27. For soil samples taken during July,
both the densities estimated from the actual number of larvae
extracted, and the corrected densities are shown.

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. ($\pm$ 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
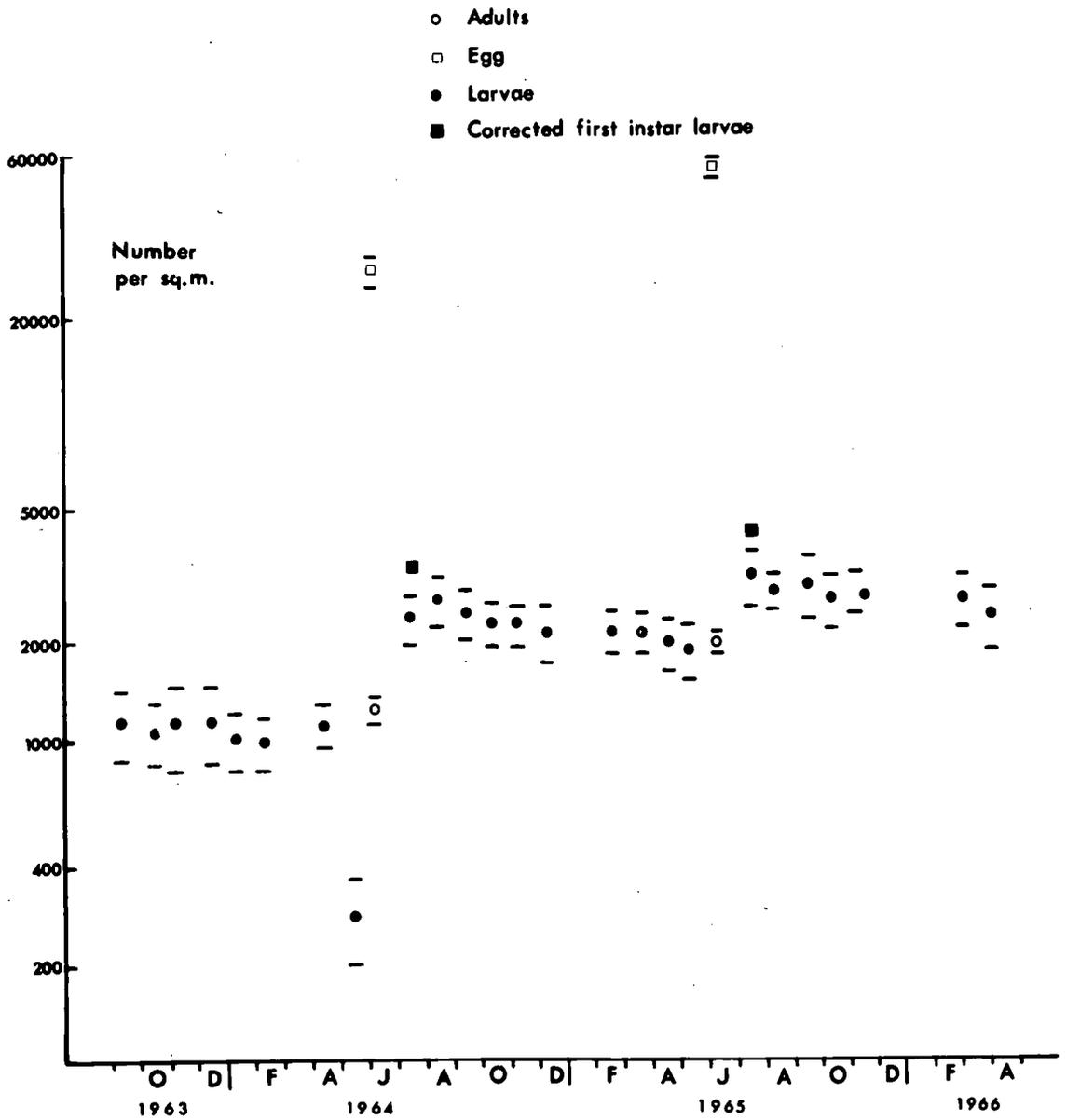
FIG. 26.  THE DENSITY PER SQ.M. ($\pm$ S.E.) ON THE

PEATY PODSOL SITE, 1964-66.

FIG. 27.  THE DENSITY PER SQ.M. ($\pm$ S.E.) ON THE

CARECETUM SITE, 1964-66.

Key as on Fig. 26.

o   Adults
□   Egg
●   Larvae
■   Corrected first instar larvae

Number per sq.m.

60000

20000

10000

4000

2000

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

Number per sq.m.

40000

10000

3000

1000

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
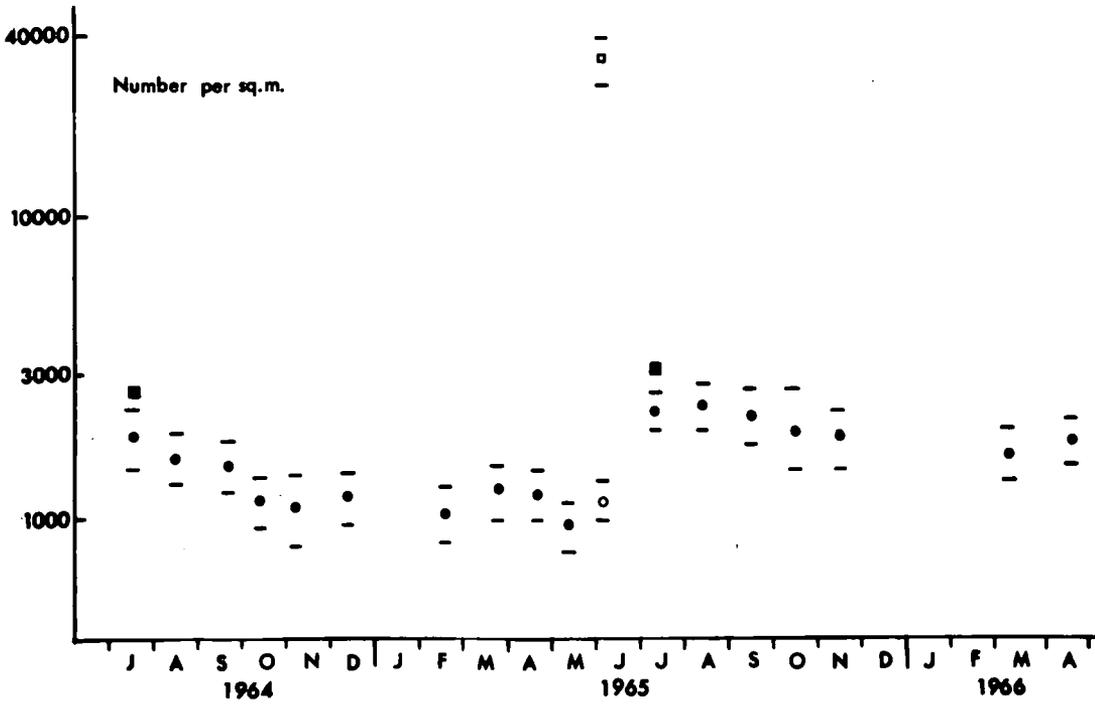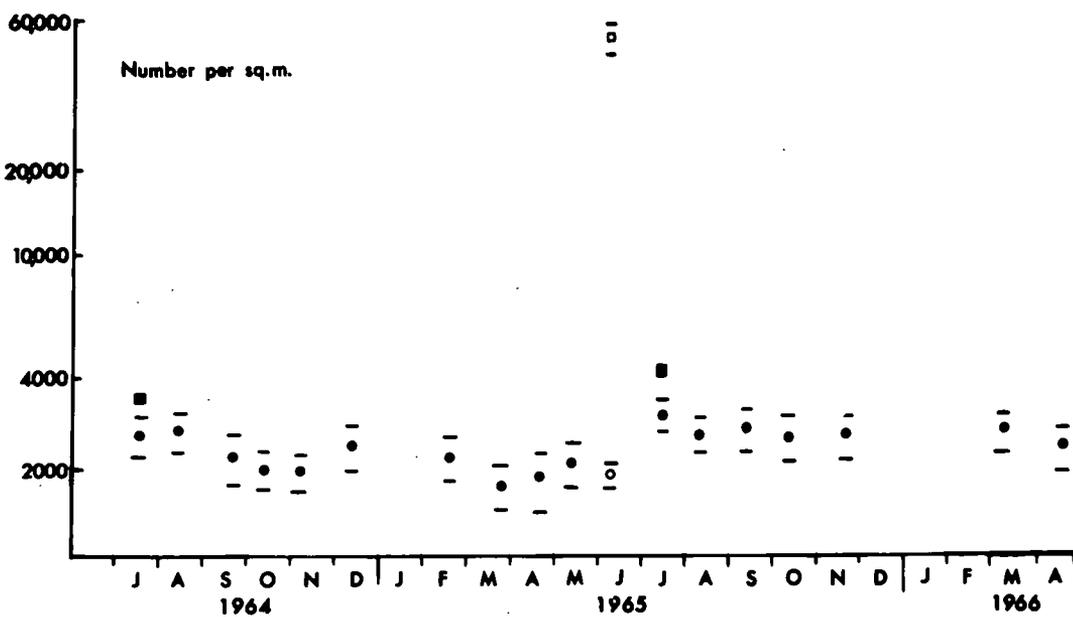
TABLE 43.    LIFE TABLES OF <u>MOLOPHILUS</u> <u>ATER</u>

| x.<br>Age interval | | $l_x$<br>No. alive at<br>beginning of<br>x | $d_x$<br>No. dying<br>during<br>x | $100\ q_x$<br>$d_x$ as percent-<br>age 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 $\pm$ 143 per sq.m.
on 29 April to 260 $\pm$ 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 <u>MOLOPHILUS</u> <u>ATER</u> AT MOOR HOUSE

|  |  | Larvae | |
| --- | --- | --- | --- |
| Site and Year | Eggs | 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.

129.

## 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 character-ised 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.

Weight of Individual Larvae (m g.)
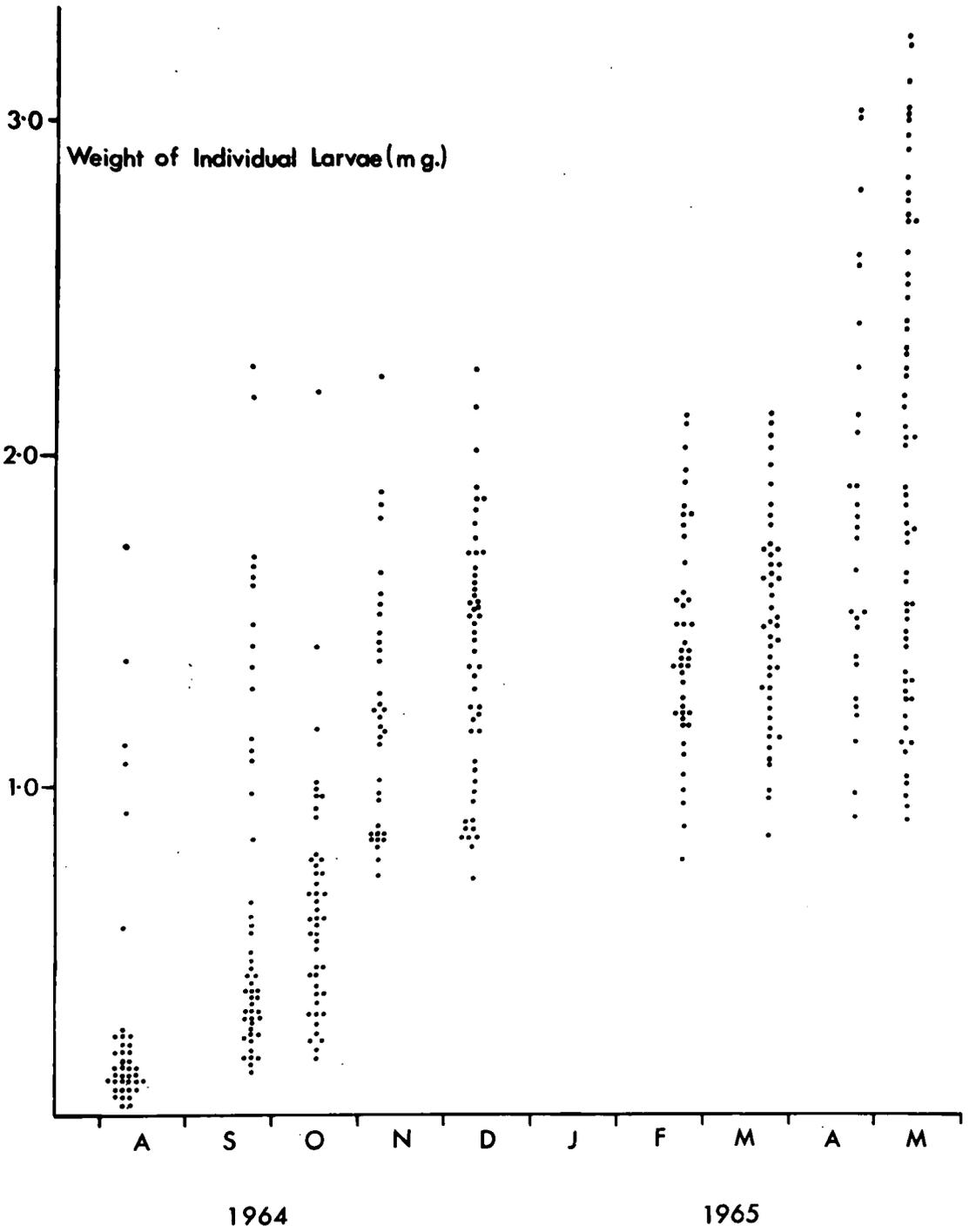
FIG. 29. GROWTH CURVE OF LARVAE ON THE

PEATY GLEY SITE, 1964-65.

FIG. 30. ESTIMATED BIOMASS PER SQ.M. OF LARVAE

ON THE PEATY GLEY SITE, 1964-65.
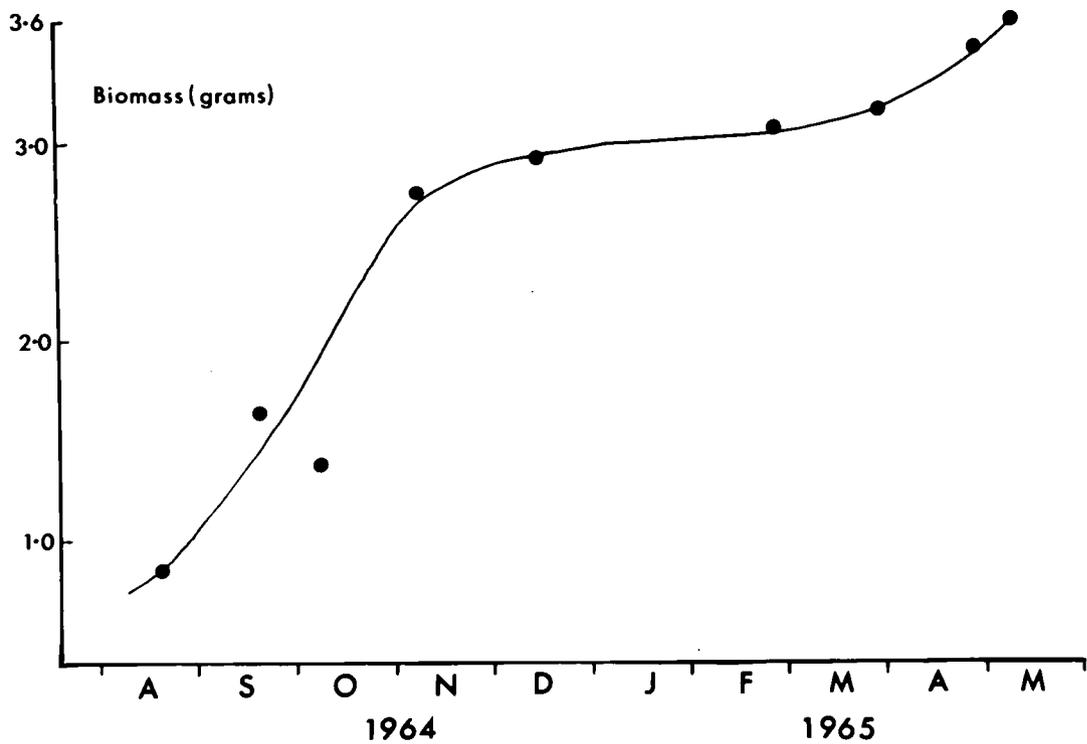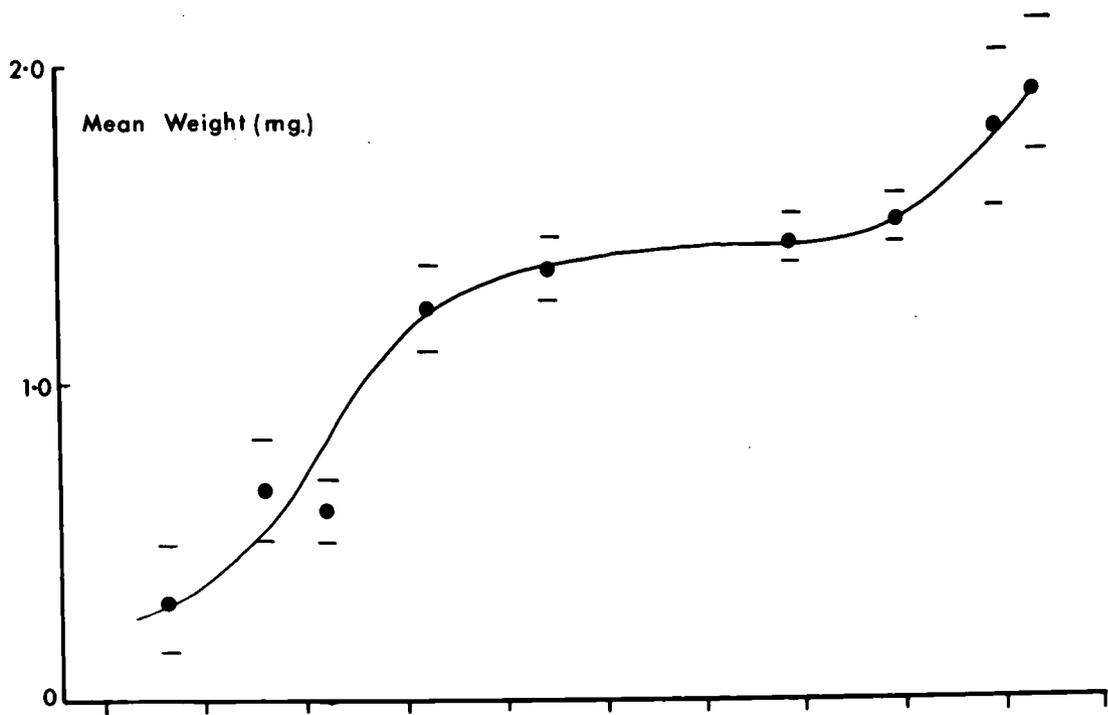
The skew in the distribution of individual weights is continued in the figures for September, but in October the majority of these larvae over 1.0 mg. in weight have presumably died, there being no evidence of an autumn emergence of adults at Moor House. This results in the lowering of the mean weight 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 main-
tained, 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 en-

countered, 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.

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 invest-
igated 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
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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 | | 1l | 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 | 1l |
| 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.   DOMIN 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., $\pm$ 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 $\pm$ 0.03 | 1.78 $\pm$ 0.03 | 1.72 | < 0.1 |
| Thorax | 0.87 $\pm$ 0.01 | 0.90 $\pm$ 0.01 | 2.08 | < 0.05 |
| Abdomen | 2.11 $\pm$ 0.09 | 2.66 $\pm$ 0.07 | 4.74 | < 0.001 |
| Femur 1 | 1.92 $\pm$ 0.03 | 1.34 $\pm$ 0.02 | 14.75 | < 0.001 |
| Tibia 1 | 1.95 $\pm$ 0.03 | 1.38 $\pm$ 0.03 | 14.31 | < 0.001 |
| Femur 2 | 1.35 $\pm$ 0.02 | 1.03 $\pm$ 0.04 | 7.27 | < 0.001 |
| Tibia 2 | 1.39 $\pm$ 0.02 | 1.02 $\pm$ 0.02 | 13.59 | < 0.001 |
| Femur 3 | 2.11 $\pm$ 0.03 | 1.71 $\pm$ 0.02 | 9.92 | < 0.001 |
| Tibia 3 | 2.02 $\pm$ 0.03 | 1.61 $\pm$ 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, Aberdeen-shire (c. 1500 ft.) | 26 July 1951 | R.L. Coe |