Biological studies on the meadow pipit (anthus pratensis) and moorland tipulidae; members of a food chain

Coulson, John Cameron

Biological studies on the Meadow Pipit (*Anthus pratensis*) and moorland *Tipulidae* (Dipt.); members of a food chain

by

John Cameron Coulson.

Observations were made on 65 species of *Tipulidae* found on the Moor House Nature Conservancy Reserve, Westmorland, between 1953 and 1956.

The larval habitats were recorded and a study was made of the abundance and seasonal distribution of adults.

Particular attention was paid to the biology of two common species of *Tipulidae*, namely *Tipula subnodicornis* Zett. which lives on peat moors and *Tipula paludosa* Meigen which lived in mineral soils, while a comparison was made between the latter species and the closely related species, *Tipula oleracea*, Meigen.

A study of the egg production and mortality of the Meadow Pipit was carried out by means of ringing recoveries and nest record cards, particular attention being paid to the change in clutch size, nest mortality and time of breeding with an increase in altitude.

The Meadow Pipit was studied at Moor House and particular attention was paid to its food supply. A study was made of feeding areas and the food which was brought to the young.

It was concluded that the predation by the Meadow Pipit had little influence on the population of *T. subnodicornis* although this species and *T. paludosa* formed the major part of the food brought to the nestlings.

BIOLOGICAL STUDIES ON THE MEADOW PIPIT (ANTHUS PRATENSIS) AND MOORLAND TIPULIDAE; MEMBERS OF A FOOD CHAIN.

By

JOHN CAMERON COULSON

- being a thesis presented in candidature for the Degree of Doctor of Philosophy in the University of Durham, 1956.

The author wishes to express his thanks to Professor J.B. Cragg for his guidance and encouragement throughout the investigation, also to Dr. E.S. Page for advice on the application of suitable statistical techniques.

The author is indebted to the Durham Colleges and the Nature Conservancy for research studentships which have made this study possible.

Contents.

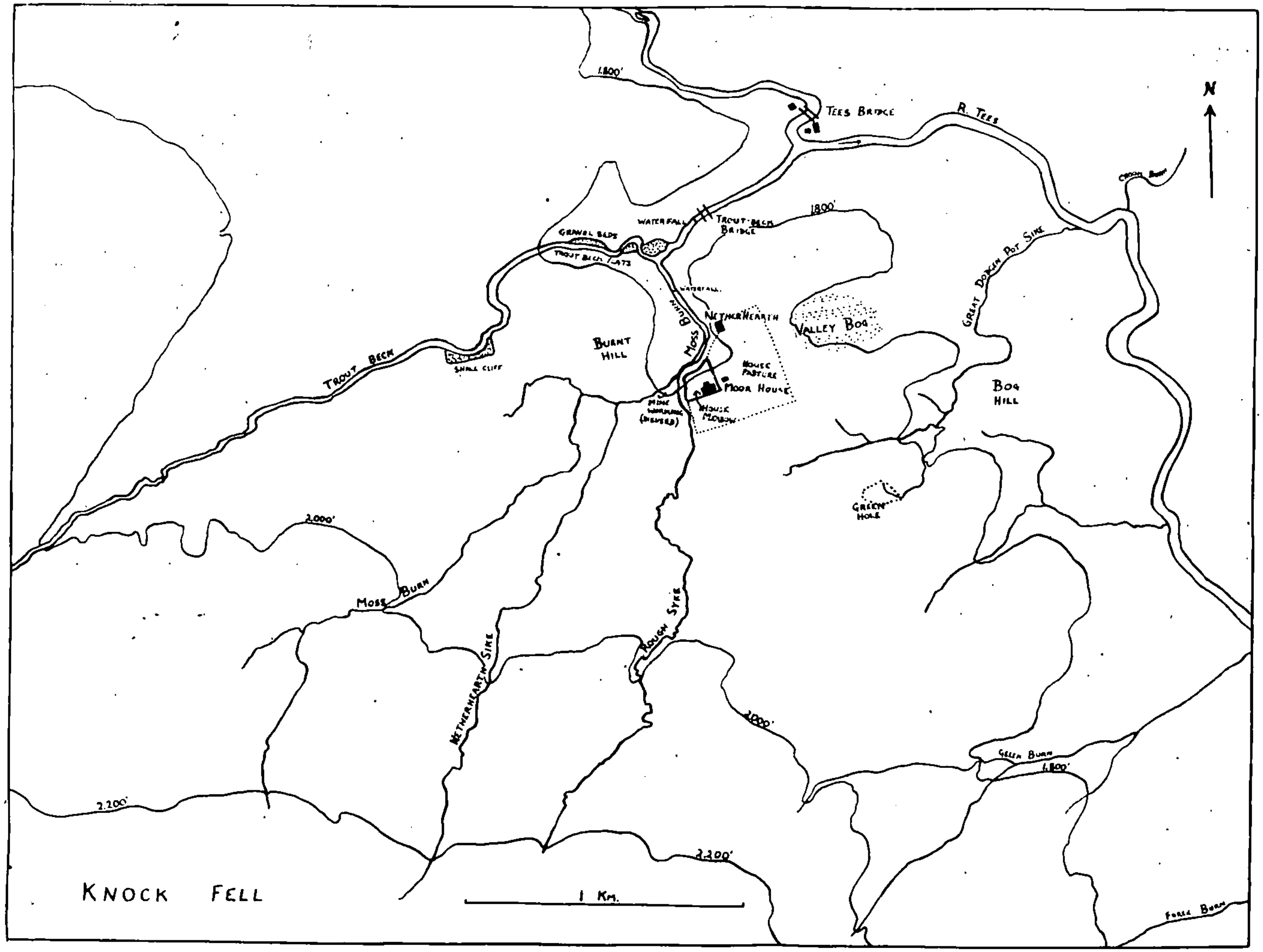
BIOLOGICAL STUDIES ON THE MEADOW PIPIT (*ANTHUS PRATENSIS* L.) AND MOORLAND *TIPULIDAE*; MEMBERS OF A FOOD CHAIN.

I Introduction.

Amongst the insects and birds inhabiting British moorlands, *Tipulidae* and Meadow Pipits are often the commonest representatives and in spite of this abundance, very little detailed biological information is available.

The investigations were carried out on the Moor House Nature Reserve, Westmorland between 1953 and 1956, an area where Campbell (1955) had shown the Meadow Pipit to be the commonest bird and where preliminary studies had shown that tipulids could be numerous.

It was hoped that as a result of the present studies it would prove possible to assess the rôle of tipulids and Meadow Pipits in the general ecology of this Reserve and particularly the relative importance of *Tipulidae* as food of the Meadow Pipit.


N
R. Tees
Tees Bridge
1800'
Trout Beck Bridge
Waterfall
Gravel Beds
Trout Beck Flats
Great Dodgen Pot Sike
Valley Bog
Netherhearth
House Pasture
Moor House
House Meadow
Burnt Hill
Moss Burn
Bog Hill
Green Hole
Trout Beck
Shale Cliff
2,000'
Moss Burn
Netherhearth Sike
Rough Syke
Gelia Burn
2,200'
Knock Fell
1 Km.

II Literature and taxonomy.

The classical study on the family Tipulidae is the work of Alexander (1920) and while this was confined to the taxonomy of the adults and larvae in the State of New York, it summarized much of the literature on the biology of the family.

The taxonomy of adult European Tipulidae had been well studied prior to this study and little difficulty arose in using the keys of Edwards (1938) and Coe (1951) while the incomplete keys of Mannheims (1940-53) were of assistance since they contained drawings of the male genetalia for the majority of species found in Europe.

The taxonomy of larvae of European Tipulidae has not been studied extensively and little has been published since the works of Beling (1879, 1886) (this work is not wholly satisfactory through the lack of illustrations). Oldham (1928) has described the larvae of Tipula paludosa and T. lateralis Meigen, while the larva of Phalacrocera replicata has been illustrated by Miall& Shelford (1897).

The ecology of the Tipulidae has not been studied extensively. Bodenheimer (1923, 1924) has made a study of Tipula oleracea but T. paludosa was confused with this species. Rennie (1916, 1917) studied the life history of *T. paludosa* and Barnes (1937) studied this species under laboratory conditions. White (1951) has studied *T. lateralis* in the laboratory and recorded that this species has four larval instars.

Cuthbertson (1926) described the larval habitats of a number of tipulids in Scotland but did not describe any of the larvae.

Barnes (1925) selected 16 habitats in Carnarvonshire and showed that the *Tipulidae* were most common in damp or wet habitats and Rogers (1933, 1942) came to similar conclusions from studies in Florida and Michigan, U.S.A.

The seasonal change in species and the nocturnal activity of certain *Tipulinae* has been studied at Rothamsted by means of a light trap (Pinchin & Anderson 1936; Robertson 1939) and they concluded that the nocturnal activity of *Tipula paludosa* was controlled by the daily minimum temperature. Recently, Hemmingsen (1952) has reviewed and described the oviposition of craneflies and suggested that the egg filament found in some of the *Tipulinae* is an adaptation to a wet environment.

III The study area.

The Moor House Nature Conservancy Reserve 80, Westmorland, of approximately 4,000 hectares, is situated on the north and east by the River Tees. The Reserve covers part of the Pennine scarp and dip slope, the western scarp slope being much steeper and drained better than the eastern, dip slope. Three major fells occur on the Reserve, Great Dun Fell (alt. 2,780 ft.), Little Dun Fell (2,761 ft.) and Knock Fell (2,604 ft.).

The River Tees is the major river on the Reserve with the smaller Moss Burn and Trout Beck as important tributaries. On the ~~eastern~~ western slopes, Crowdundle Beck and Knock Ore Gill are the larger streams.

The Geology of the area has been described by Dunham (1948) and it consists of stratified beds of sandstone, shales and limestones with occasional mineral veins and pockets. Drift has covered much of the bed rock and thus modified the soil structure.

Botanically, the Reserve can be divided into a number of arbitrary groups which tend to merge into one another. First there are the high slopes of the fells which are extensively erroded and where peat cover is absent or much reduced, *Nardus stricta* is the dominant plant. Secondly, there is the major part of the Reserve which is covered by a blanket of peat, between 2 and 3 metres deep and in some places even exceeding this depth. This blanket bog can be further divided into areas where erosion is taking place and areas where peat accumulation is actively taking place. The former area is characterised by peat hags surrounding areas of shallow, redeposited peat with little vegetation. The hags are well drained and a Calluna-Cladonia complex exists on the tops together with a little Eriophorum vaginatum L. The blanket bog moor, where growth of peat is taking place, is characterised by an abundance of Sphagnum sp. with a little Calluna and Eriophorum vaginatum. It must be stressed that all types of intermediates exist between these two types of vegetation. Thirdly, there are small areas where Eriophorum vaginatum is dominant and it is possible that these were caused by excessive grazing or burning (Pearsall 1950).

Fourth, there are areas of shallow peat situated on the edges of the moor and these are often characterised by Juncus squarrosus L. Finally there are the areas completely devoid of peat. These areas consist of rock outcrops and alluvial terraces along the streams. Areas of grassland on top of limestone are infrequent and carry a typical calcicole flora. Most of the grassland is situated on top of drift and supports a less luxuriant flora.

The climate of Moor House has been studied by Manley (1936, 1943) and he came to the conclusion that the climate was sub-arctic, being similar to that of south Iceland at sea-level, with the exceptions at Moor House that the temperature and rainfall are a little higher and the duration of sunlight a little lower. He also estimated that the annual average rainfall at Moor House was 70 inches. Biologically, this value is of little use as much of the rain falls during Winter, late Autumn and early Spring when the moor is almost certainly saturated with water. As Pearsall (1950) has pointed out, the important factor is the duration of the periods when evaporation exceeds precipitation. Thus the rainfall data for 1953 and 1955 were almost equal for the whole year, but the total for the months of June, July, August and September was 27 inches and 15 inches in 1953 and 1955 respectively. This difference was most apparent in the amounts of drying out which occurred on the moor in these years.

IV The study of Tipulidae

1. Methods used in the study of *Tipulidae*.

1. Sampling for eggs and larvae.

The different sizes and numbers of eggs and larvae necessitated the use of different sized samples and extraction techniques. Circular samplers of 10 and 7.25 cm. diameter were used to estimate the numbers of final instar larvae, while samplers cutting 3.6 and 2.0 cm. diameter cores were used for estimating eggs and early stage larvae.

Samples containing large larvae were hand sorted and checked by washing through a series of graduated sieves. The error involved in hand sorting was always less than 10% and usually below 5% as indicated by the number of larvae recovered from the washing. Eggs and small larvae were recovered from samples by flotation in magnesium sulphate solution (S.G. 1.23). When the samples contained peat, only a small amount of material (1cc.) was sorted at one time and this was well dispersed in a bowl of magnesium sulphate solution.

2. Emergence traps.

In 1954, aluminium and perforated zinc emergence traps were used but the emergence from these traps was apparently numerically low and was much delayed.

Records of the temperature just below ground level taken inside and outside of the traps showed that under conditions of sunlight, the temperatures may be as much as 8-10°C greater outside of the traps, and even under overcast conditions, differences as large as 2°C were recorded. No differences were recorded between the minimum temperatures inside and outside of the traps. Thus these traps (Fig.I) appeared to cut down the daily, upper fluctuation of temperature and this may have accounted for the delay in emergence and also the small numbers that emerged.

In 1955, butter-muslin emergence traps were used (Fig.I) and these had virtually no insulating effect. Temperature readings in the soil inside and outside of the traps were similar. These traps consisted of a metal cylindrical base, covering .0625 sq. metre which was inserted into the ground for a depth of 8 cm. A butter-muslin cylinder was added to the base and supported by an iron wire rod bent into an inverted -U The free ends being placed into the ground. These traps failed to give satisfactory results as it was found that some of the females remained in the litter and were not collected.

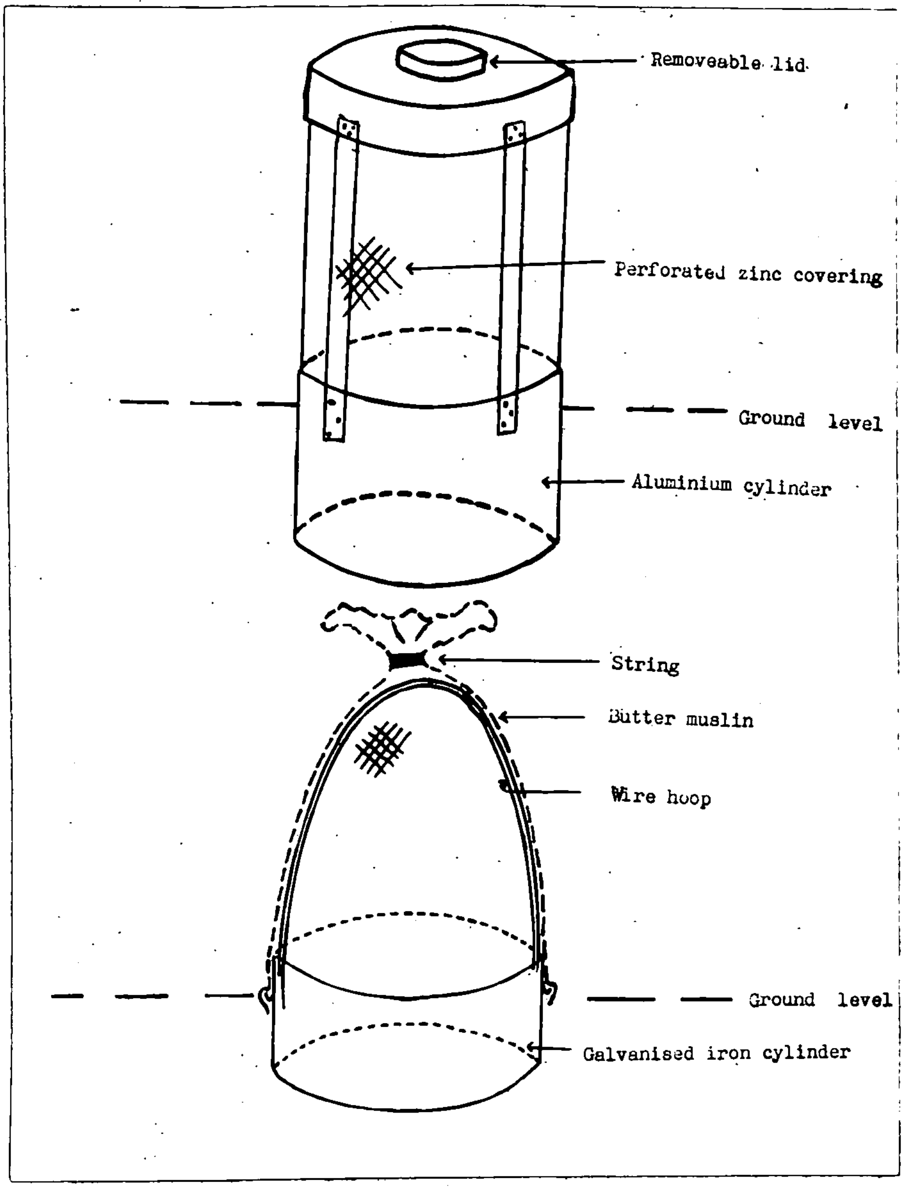


Fig. 1. Emergence traps used to estimate tipulid populations. See text.

3. Sticky traps.

The sticky traps consisted of aluminium cylinders of the type used by Broadbent (1948) and were 30cm tall and 12.7 cms. in diameter, each being covered by a celluloid sheet spread with "Stik-tite". Each trap was supported by means of a wooden stake sunk into the ground and protruding some 30cms. from the ground surface. The majority of adult tipulids could be identified without the need of removing them from the sheet but material which required microscopic examination was removed by dissolving the adhesive material in ethyl acetate.

4. Rearing adults from eggs and larvae.

Eggs and first instar larvae had to be kept covered with free water as they were very susceptible to dessication. Eggs were usually hatched by placing them on wet filter paper in Petri dishes, sufficient water being added to cover the eggs with a thin film. Even under these conditions, rarely more than 75% of the eggs hatched.

2. List of species of *Tipulidae* recorded from the Moor House Nature Reserve.

Family *Tipulidae*.

Sub-family *Tipulinae*.

1. *Dolichopeza albipes* Ström.
2. *Nephrotoma* (*Pales*) *submaculosa* Edwards.
3. *Tipula paludosa* Meigen.
4. *Tipula oleracea* Meigen.
5. *Tipula fusca* (= *czizeki*) Staeger.
6. *Tipula cheethami* Edwards.
7. *Tipula rufina* Meigen.
8. *Tipula alpium* Bergroth.
9. *Tipula staegeri* Nielson.
10. *Tipula marmorata* Meigen.
11. *Tipula subnodicornis* Zetterstedt.
12. *Tipula melanoceros* Schummel.
13. *Tipula pagana* Meigen.
14. *Tipula montium* Egger.
15. *Tipula coerulescens* Lackschewitz.
16. *Tipula variipennis* Meigen.
17. *Tipula gimmerthali* Lackschewitz.
18. *Tipula macrocera* Zetterstedt.
19. *Tipula vafra* Riedel.
20. *Tipula excisa* Schummel.

(*Prionocera turcica* Fabricius.)

Sub-family *Cylindrotominae*.

21. *Phalocrocera replicata* Linnaeus.

Sub-family *Limoniinae*.

22. *Limonia* (*L.*) *nubeculosa* Meigen.
23. *Limonia* (*L.*) *flavipes* Fabricius.
24. *Limonia* (*L.*) *dilutior* Edwards.
25. *Limonia* (*Rhiphidia*) *maculata* Meigen.
26. *Limonia* (*Dicranomyia*) *chorea* Meigen.
27. *Limonia* (*D.*) *mitis* Meigen.
28. *Limonia* (*D.*) *modesta* Meigen.
29. *Limonia* (*D.*) *autumnalis* Staeger.
30. *Limonia* (*D.*) *didyma* Meigen.
31. *Limonia* (*D.*) *morio* Fabricius.
32. *Limonia* (*D.*) *stylifera* Lackschewitz.

Tribe *Pediciini*.

33. *Pedicia rivosa* Linnaeus.
34. *Tricyphona schummeli* Edwards.
35. *Tricyphona immaculata* Meigen.
36. *Dicranota* (*Paradicranota*) *robusta* Lundstroem.
37. *Dicranota* (*P.*) *subtilis* Loew.
38. *Dicranota* (*P.*) *brevitarsis* Bergroth.

39. Dicranota (D.) bimaculata Schummel.

40. Dicranota (D.) guerini Zetterstedt.

41. Dicranota (Rhaphidiolabis) exclusa Walker.

Tribe Hexatomini.

42. Hexatoma bicolor Meigen.

43. Dactylolabis sexmaculata Macquart.

44. Limnophila (Phylidorea) meigeni Verrall.

45. Limnophila (P.) fulvonervosa Schummel.

46. Limnophila (P.) squalens Zetterstedt.

47. Limnophila (Idioptera) pulchella Meigen.

48. Limnophila (Elaeophila) trimaculata Meigen.

49. Limnophila (E.) mundata Loew.

50. Limnophila (L.) punctata Schrank.

51. Limnophila (L.) nemoralis Meigen.

var. separata Walker.

52. Limnophila (L.) nemoralis Meigen.

var. nemoralis Meigen.

Tribe Eriopterini.

53. Gonomyia (G.) dentata de Meijere.

54. Gonomyia (G.) conoviensis Barnes.

55. Rhabdomastix hilaris Edwards.

56. Platytoma cinerascens Meigen.

57. *Erioptera* (*E.*) *lutea* Meigen.

58. *Erioptera* (*E.*) *fuscipennis* Meigen.

59. *Erioptera* (*E.*) *trivialis* Meigen.

60. *Erioptera* (*E.*) *diuturna* Walker.

61. *Erioptera* (*Symplecta*) *stictica* Meigen.

62. *Ormosia lineata* Macquart.

63. *Ormosia hederae* Curtis.

64. *Ormosia pseudosimilis* Lundstroem.

65. *Molophilus ater* Meigen.

66. *Molophilus griseus*? Meigen.

3. Geographical distribution of the British *Tipulidae*.

Sixty-six species of the family *Tipulidae* have been recorded from the Moor House Nature Reserve out of a total of 300 species on the British list, and in addition, one species (*Prionocera turcica*) has been recorded at over 1,500 ft. a.s.l. in Co. Durham.

The population at Moor House has two distinct components, those species which are confined to moorland and those which also occur at low altitudes. The latter group consists of typical alluvial living species such as *Tipula paludosa* and *Tipula variipennis* or mud inhabiting species, for example *Erioptera trivialis* and *Tricyphona immaculata*.

Of the 67 species recorded from the northern Pennines, 43 have been recorded from Norway or Sweden (Lackschewitz 1935) and 30 from France (Pierre 1924). Of the French records, only 15 were recorded from the Pyrenees and 4 from the French Alps. Some of these differences may have resulted from a scarcity of collectors and the analysis has been repeated on the more widely collected *Tipulinae*. This showed that 9 of the 20 species recorded from Moor House also occur in France, 6 being recorded from the Pyrenees and 2 from the Alps. On the other hand, 16 of the 20 species noted at Moor House occurred in north Scandinavia. Thus it would appear that the *Tipulidae* fauna of the northern Pennines has a closer affinity with that of Scandinavia than with the fauna of the Pyrenees or the French Alps. In addition, there are at least 5 tipulids which have been recorded from this country, but not from the Moor House area, which form part of the fauna of northern Scandinavia.

There are records of only 13 species of *Tipulidae* from Iceland (Nielson, Ringdahl & Tuxen 1954) and of these, no less than 10 have been recorded from the northern Pennines. None of the species noted at Moor House have been recorded from Greenland and, apparently, there are only two species common to Britain and Greenland.

4. Notes on the Tipulidae of Moor House Reserve.

1. Dolichopeza albipes

The adults were only found on the banks of Moss Burn (see map at front of thesis) but pupae were taken on the River Tees. The tarsus of the adults is elongated and hairy, apparently being modified for alighting on water. When the weak flying adults are disturbed, they escape by moving across the surface of the stream, using the wings for propulsion and the legs as floats.

Larvae were taken among mosses and liverworts on the bank of Moss Burn, immediately below the house. Audcent (1932) described the larval habitat as "moss on tree trunks" but Cuthbertson (1926) recorded the banks of streams.

2. Nephrotoma submaculosa

This species was common in the House Meadow in both 1952 and 1953 but was not taken on the Reserve in 1954, although an extensive search was made for larvae as well as adults. In 1955, 10 adults were taken on shingle with extensive grass cover beside the Tees, near Bog Hill. The complete disappearence of this species from House Meadow during one year cannot be explained.

3. *Tipula paludosa*

This species, like *Nephrotoma submaculosa*, was also very abundant in 1952 and 1953 but the population was noticeably reduced in 1954 and 1955. Adults of this species have been taken up to an altitude of 2,300 ft. on the Reserve. Barnes (1938) records this species up to 1,500 ft. in north Wales.

The larvae occur in alluvial soils and typical habitats are shown in Figs. 2 & 3.

4. *Tipula oleracea*

In 1955, five adults were taken (2 females in early July and 3 males in late September). It seems possible that this species, which is large and strong flying, may under suitable wind conditions fly from the lowlands of the Eden Valley. Its absence in 1953 and 1955 supports this conclusion.

5. *Tipula fusca*

A single specimen was captured at Netherhearth. This species has been recorded at over 1,000 ft. on the Pentland Hills, near Edinburgh and at 2,100 metres in the Alps (Brown 1947; Mannheims 1952).

6. *Tipula cheethami*

Only 7 specimens of this species were taken at Moor House. It was surprisingly rare although

Fig. 2. Grassland on top of limestone. Note Juncus effusus tufts used as shelter by T. paludosa.

Fig. 3. Alluvial grassland with tufts of Nardus stricta Larval habitat of T. paludosa and T. variipennis.

Audcent (1932) states that it is commonly found in moutainous areas on mossy rocks. Brown & Duncan (1951) recorded it as rare in the Solway area, taking only one specimen. Pupal cases which are found protruding from moss are frequently attributed to this species, but are equally likely to be _T. alpium_ or _T. marmorata_.

7. _Tipula rufina_

This species was usually taken in the close vicinity of the House. Mannheims (1951) and Brown & Duncan (1951) indicated that, unlike most members of this genus, this species has two generations per year, but it is doubtful if this is so at Moor House since all but one of the adults were collected in May. Data in Iceland suggested that this species usually has one generation a year (Nielsen, Ringdahl & Tuxen, 1954).

8. _Tipula alpium_

This is a common moorland tipulid, being closely associated with vertical surfaces such as peat hags and rocky sides of streams. The adults are frequently found in close association with such sites and probably find shelter on these surfaces during cold and rainy weather. Fig 4 shows a typical sheltering

Fig.4. Edge of a peat hag showing overhang used as a shelter by T. alpium.

Fig. 5. Bank of Moss Burn showing moss in which larvae of T. alpium and T. marmorata were found.

site on a peat hag. Since this is a species which does not have ripe eggs on emergence, it seems possible that this behaviour increases the chances of the females to survive until the eggs are ripened and laid.

Larvae have been collected from moss growing on the bank of Moss Burn (Fig. 5). A single larva has been taken from moss growing on the edge of a peat hag and it is suggested that this latter habitat may be an important one for the species on the moor.

9. Tipula staegeri

This species was somewhat local at Moor House, being numerous in only two localities, namely the lower end of Green Hole and where Rough Syke and Moss Burn meet. Most records of this species are from coniferous woodland, but this is probably due to lack of observations elsewhere since the larvae are associated with mosses.

10. Tipula marmorata

The adults were very local at Moor House but were found to be more common on a drier, shallow peat moor at Struan, Perthshire (alt. 1,500ft.) and it is interesting to note that mosses, the food plant of the larvae, were commoner on this moor than at Moor House.

The larvae have been taken in association with _T. alpium_ in moss growing on the bank of Moss Burn (Fig. 5). At lower altitudes, off the Moor House Reserve, larvae have been collected from moss growing on walls and under trees.

11. _Tipula subnodicornis_

This was the most abundant tipulid on the Reserve and occurred over most of the areas that were covered by peat. Audcent (1932) states that it is "plentiful only on bogs where cotton - grass (_Eriophorum vaginatum_ Linn.) grows". At Moor House large populations existed on cotton - grass areas but the largest populations were recorded from _Juncus squarrosus_ dominant areas (see page 91)

Typical larval habitats are shown in Figs. 6,7 and 8.

12. _Tipula melanoceros_

Two adults were bred from larvae obtained on House Hill in 1953 but no free living larvae or adults were taken in 1954. In 1955, this species was found abundantly over a small swampy area in the

Fig. 6. Juncus squarrosus moor, showing butter muslin type of emergence trap.

Fig. 7. View of Valley Bog, a Sphagnum Bog with Calluna and Eriophorum

Fig. 8 Raised Sphagnum bog with Calluna, Eriophorum and Cladonia. An area where peat growth is taking place

Fig.11 A small stream draining off limestone. Larval habitat of T. coerulescens.

House Pasture and less common in other areas where rain water tended to stand on top of peat. This habitat was, however, restricted and adult males were rarely taken more than a few feet away from the typical habitat which is illustrated in Fig. 9.

13. Tipula pagana

The typical form, in which the female is markedly short winged, occurred at Moor House. It was common but confined to alluvial areas. In 1955, the adults were noted to spread along the alluvial sides of Moss Burn and Rough Syke almost to the source and as far as the alluvial edge extended. Larvae have been collected from House Pasture, Green Burn , Moss Burn and Troutbeck Flats. Larvae were found in the habitat illustrated in Fig.2.

14. Tipula montium

Adults were recorded from the vicinity of three streams all of which drained off peat. Audcent (1932) recorded this as a late summer species, but it was almost entirely an early spring species at Moor House. The larvae of this species are aquatic and live in small streams with considerable vegetation such as that shown in Fig. 10.

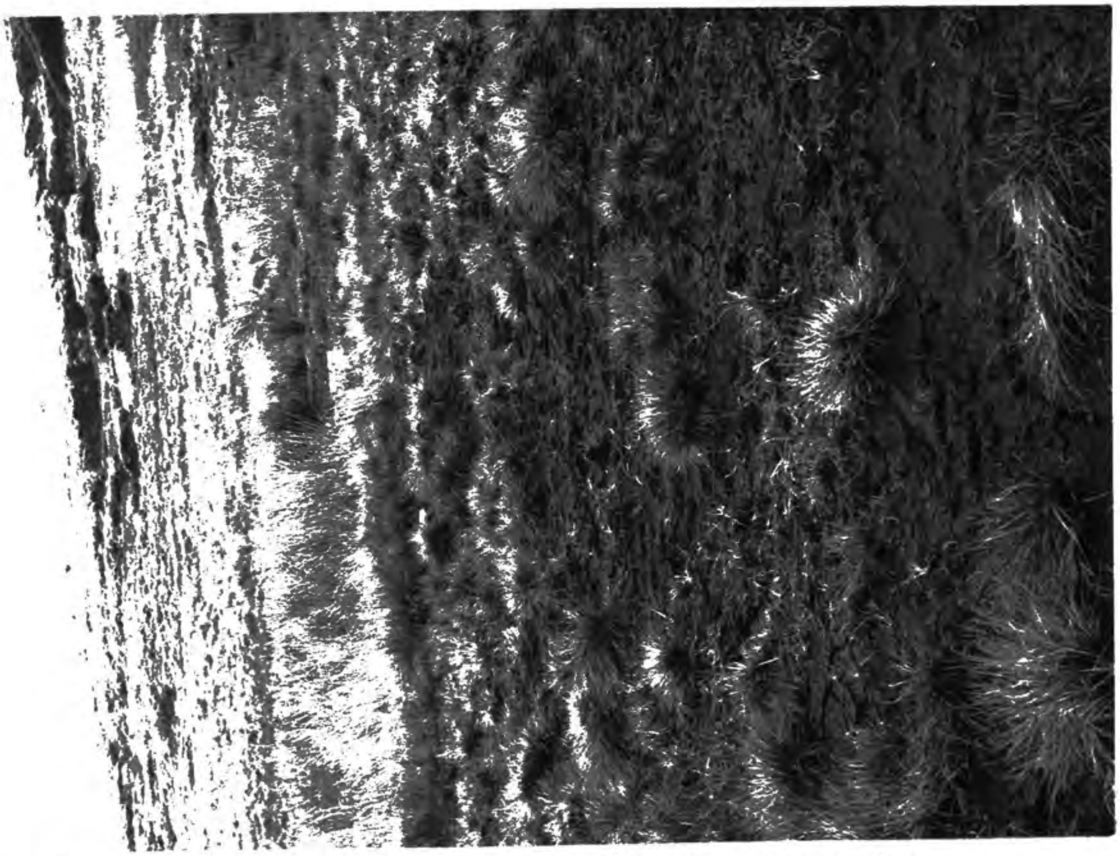


Fig. 9. swampy peat under dry conditions, note tufts of *Eriophorum* in foreground.

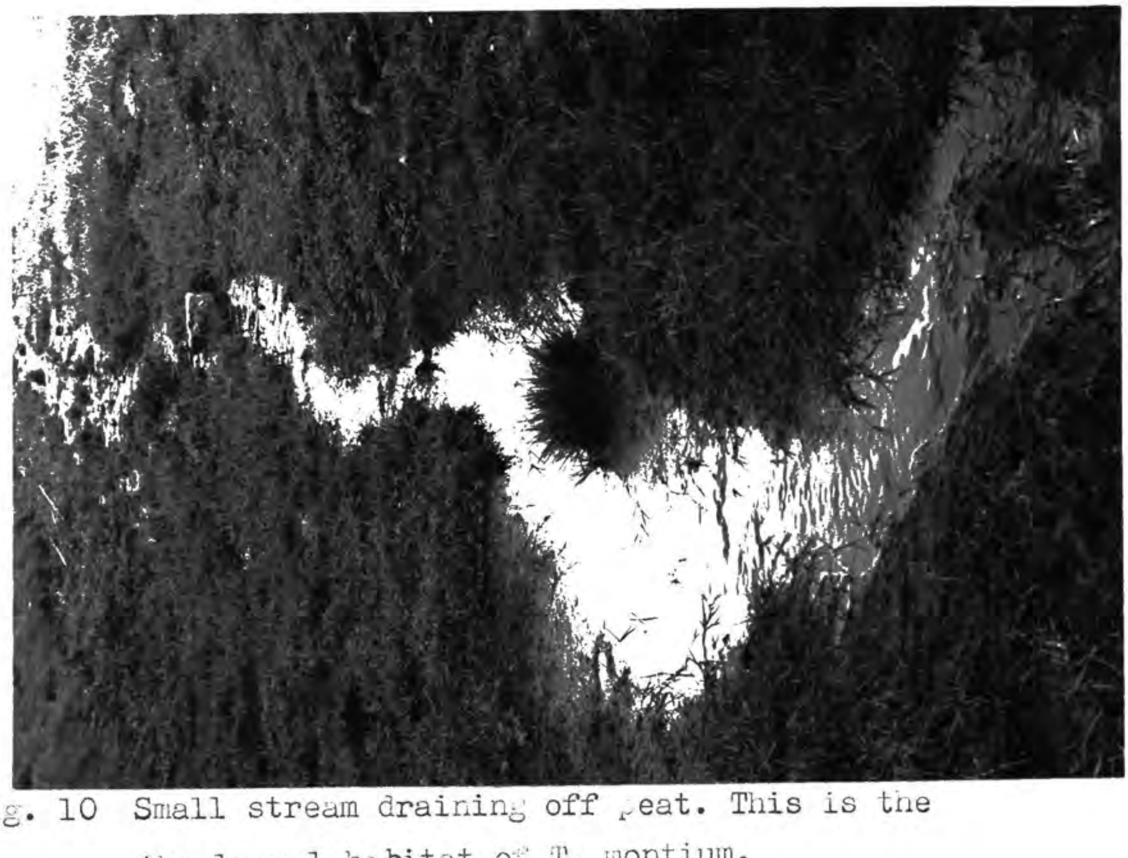


Fig. 10 Small stream draining off peat. This is the the larval habitat of *T. montium.*

15. *Tipula coerulescens*

This species is closely related to *T. montium*, both belonging to the *T. lateralis* group. The larvae are aquatic and live in small streams, similar to those used by *T. montium* but these two species have never been taken together by the same stream. The record of *T. coerulescens* from Moor House is the second locality record from England and the third from Great Britain. (The other records are- Austwick, Ingleborough district, Yorkshire and Aviemore, Inverness). Fig.11 shows a stream in which the larvae of this species were taken.

16. *Tipula variipennis*

Like *T. pagana*, this species occurred on alluvial areas but appeared more frequently on areas of poor shallow soil or soils with a small proportion of peat present.

17. *Tipula gimmerthali*

A single male specimen was taken on 8 October 1954 in the vicinity of Green Hole. Under field conditions the male appeared very similar to that of *T. pagana* which was abundant at this time and it was not until the material was examined in the laboratory that the species were separated. In October 1955, an extensive search was carried out which showed that this species was widely distributed, but local on the Moor House Reserve. Adult males (the females being sub-apterous) were never found far from flushes which appeared to be the larval habitat. Adults were only found on flushes on the edge of moor or on alluvial areas and never on *Sphagnum* flushes in which *T. macrocera* was found. This is the first record of *T. gimmerthali* from England, the only other record being that of Brown (1947) who recorded it at about 1,000 ft. near Edinburgh.

18. *Tipula macrocera*

This is a typical bog inhabiting species and adults have been taken on 6 different *Sphagnum* flushes on top of peat.

19. *Tipula vafra*

This species was taken commonly in late September on the moor between Bog Hill and Green Hole. This is the second locality record from England and the third from Great Britain, (other localities being Morayshire, Scotland and Austwick, Yorkshire).

20. *Tipula excisa*

This species was common on the upper part of the Reserve but occurred less frequently in the lower areas. It has been collected as low as 1,700ft. on the Reserve and at 1,500 ft. near Struan, Perthshire.

Larvae of this species have been taken on shingle at Trout Beck Flats and the area is shown in Fig. 12.

(*Prionocera turcica*

Adults of this species have not been taken on the Reserve but the larvae of this species have been collected from *Polytrichum commune* growing in the shallows of a reservoir alt, 550 ft. above Eggleston Burn (a tributary of the River Tees) Co. Durham.

21. *Phalocrocera replicata*

Adults and larvae of this species have been recorded from three ponds on the estate; all ponds concerned had an extensive growth of *Sphagnum* but many similar ponds contained no larvae. The closely related *Triogma trisulcata* Schummel, has not been recorded from the Reserve although Coe (1951) recorded it as "uncommon on bogs".

The following eight species were rare at Moor House.

22. *Limonia nubeculosa*

Fig. 12. Raised shingle bed; a habitat of T. excisa

Fig. 13. Wet organic soil on side of small stream.

23. Limonia flavipes

24. Limonia dilutior

25. Limonia maculata

26. Limonia chorea

27. Limonia mitis

28. Limonia modesta

29. Limonia autumnalis

30. Limonia didyma

This species was associated with mosses splashed or temporarily covered by stream water. Oviposition has been observed on moss at the waterfall on Trout Beck.

31. Limonia morio

Uncommon. Most of the material collected at Moor House was taken on alluvial terraces which contain occasional stands of Juncus effusus.

32. Limonia stylifera

This was also uncommon and had a similar distribution to the last. The Moor House records are the first from England but this species has been recorded from Perthshire, Scotalnd.

33. Pedicia rivosa

Adults of this large tipulid have been taken in July and August, 1953 but none have been recorded in 1954 or 1955.

The larvae of this species have been taken from Sphagnum flushes and also the mud and peat at the bottom of sink holes.

34. Tricyphona schummeli

Up to 1955, only two specimens were found but in 1955 it was more numerous and adults were taken commonly on the moor. Its habitat did not appear to differ from that of the following species, T. immaculata.

35. Tricyphona immaculata

This was a common peat inhabiting species. The captures on sticky traps (Fig.18) suggested that it had only one generation per year, although there was some indication of a very minor emergence in late September. Observations at Boldon Flats, Co. Durham suggested that at low altitudes this species had at least two generations per year.

The larvae are predatious and, judging from its numbers, its main food probably consists of Enchytraeidae and Collembola as there appeared to be few other animals available as food. Larval habitats are shown in Figs. 7,8 and 9.

36. Dicranota robusta

Adults were taken on the rocky edge of Trout Beck in 1955. The wings are markedly reduced in both sexes and they are incapable of flight. Because of their small size and lack of flight, they were very easily overlooked and were only found as a result of a chance fall which disturbed the adults from under a stone. This is the second locality record for this species in Great Britain, having already been recorded from the river Goyt, above Taxal, Derbyshire. Elsewhere it is known only from Finland and Latvia (Edwards 1939).

The larvae, like all other members of this genus, are probably aquatic.

37. Dicranota subtilis

Only two specimens were taken (Moss Burn).

38. Dicranota brevitarsis

This species was also uncommon and only three specimens were obtained. The apparent rarity of these species may be explained in the limited collections made on the stream side shingle.

39. Dicranota bimaculata

The habitat of this species and of the next (D. guerini) appear to be similar to those of T. montium and T. coerulescens, namely small streams with much vegetation.

40. Dicranota guerini

Adults were taken commonly in 1955. This is the second locality record from England, and the other record was from Austwick, Yorkshire. Coe (1951) gave three localities from Scotland.

41. Dicranota exclusa

This species was locally common on the edges of streams, particularly Moss Burn. Females were observed ovipositing in the clay bank of a stream, about 1 cm. above the water level. This is the first English record but the species has been recorded from Scotland and Wales.

42. Hexatoma bicolor

One specimen of this tipulid was obtained in July, 1953, near Trout Beck Flats. No specimens were obtained in 1954 but in 1955, a number of adults were taken in the stretch of river from the Tees bridge to Force Burn.

43. Dactylolabis sexmaculata

A single specimen taken.

44. Limnophila meigeni

A peat inhabiting species, common in 1953 and 1954 but more scarce in 1955. The larva of this species is figured by Nielsen, Ringdahl and Tuxen (1954) and

and lived in shallow peat soils. It's larva is probably predatious.

45. Limnophila fulvonervosa

This species was closely associated with Juncus effusus in Sphagnum flushes and was never taken away from the former plant. Many adults were seen from the flush between Bog Hill and the House.

46. Limnophila squalens

Although Edwards (1938) recorded it as common on peat bogs, only a few specimens of this species were taken at Moor House and they were confined to the vicinity of water that trickled over peat silt.

47. Limnophila pulchella

An uncommon tipulid, but this was due to some extent to the fact that the male was small and the female was sub-apterous. The adults were usually taken on Calluna-Eriophorum moor with exposed peat. This species was recorded by C.A. Cheetham from the bog moors near Austwick, Yorkshire.

48. Limnophila trimaculata

Adults were recorded from the vicinity of Green Hole and Rough Syke, but were never common.

49. Limnophila mundata

This species was not taken in 1953 and in 1954 a single specimen was taken from peat hags bordering Rough Syke. In 1955, this species was taken abundantly, especially along the sides of streams. At sunset, swarms of this species were encountered over the banks of the streams.

50. Limnophila punctata

This species was associated with the type of habitat occupied by Tipula coerulescens, that is, small streams with a rich flora.

51. Limnophila nemoralis var. nemoralis

This is the typical form of the species and is referred to as L. nemoralis "A". This variety was confined to areas of Juncus effusus growing on alluvial soils and was not so abundant at Moor House as the type "B".

52. Limnophila nemoralis var. separata

Referred to as L. nemoralis "B" in future. This variety is generally distributed in the hilly districts of northern Britain and it is also recorded from Finland (Edwards, 1938). It was common on the moor and was one of the three species noted to swarm on the Reserve. This species was also associated with peat hags and adults swarmed over and rested on the hags.

The larval habitat is probably in the exposed peat underneath hags, but larvae have not been found. These so called varieties can be separated on the following characters:-

	Variety "A"	Variety "B"
Size.	Larger, wing 7-10 mm.	Smaller, wing 5-7 mm.
Colour.	Dark, greyish.	Light, yellow-brown.
Antennae.	All segments dark.	Base yellowish.
Wing.	Broad, distinct angle on hind margin near 2A.	Tending to be narrow, and no angle on hind margin.
Legs.	Femur dark tipped.	Femur light brown.

The male genetalia of the two forms did not seem to differ.

Data in Fig.15 show that the flying period of the adults of these forms were different, although adults of both forms had been taken within 50 metres of each other on the same day. These differences suggested that two species were present. The fact that the male genetalia did not differ need not be an obstacle, since Edwards (1938) admitted _L. adjuncta_ Walker as a distinct species although the male genetalia did not differ from L. nemoralis. It is therefore interesting that Edwards (1938) says of the variety separata "it is possibly to be regarded as specifically distinct from nemoralis ".

53. Gonomyia dentata

This species was common on the moor in 1953 but none were taken in 1954, and only a few specimens were taken in 1955.

54. Gonomyia conoviensis

A single male specimen was taken from the road side drainage ditch near Trout Beck Bridge in 1955.

55. Rhabdomastix hilaris

Three specimens of this species were obtained on the shingle beds, near to where Crook Burn enters the Tees. This was the first record of this species in England and was previously recorded from Perth and Inverness.

56. Platytoma cinerascens

Six specimens were taken, all during 1955 from various localities.

57. Erioptera lutea

Adults were taken by the side of a small stream, immediately below the House. In this habitat, adults were taken frequently.

58. *Erioptera fuscipennis*

This species was only taken during 1955. Adults were found frequently on the silt at sides of small ponds and streams. This was also the habitat of *E. trivialis* which was invariably the more common.

59. *Erioptera trivialis*

This was a common species especially in 1955.

The larval habitat appeared to be silt and very wet peat (Fig. 9) and appeared to be more wide spread than the last species. Cuthbertson (1926) recorded both *E. fuscipennis* and *E. trivialis* from mud in marshes.

60. *Erioptera diuturna*

This late Autumn species was very similar to *E. trivialis* and occurred in similar habitats. The wings were distinctly narrower than in the previous species.

61. *Erioptera stitica*

A single female specimen was taken at Netherhearth in 1954.

62. *Ormosia lineata*

A single specimen was taken near Moss Burn in October, 1954. It was found commonly around the wall of the House in Spring.

63. _Ormosia hederae_.

This species was taken commonly in 1955, mainly because its larval habitat was discovered. This was the moss, grass and liverwort community found at the base of rocky outcrops.

64. _Ormosia pseudosimilis_

A common species that inhabited _Calluna_ and _Juncus_ squarrosus moor. Although fully winged, this species rarely flew and was usually observed crawling over the vegetation.

65. _Molophilus ater_

A common Spring species in which both sexes are sub-apterous. This and the previous species inhabited similar habitats and are amongst the smallest tipulids found in this country.

66. _Molophilus griseus_?

A single female specimen, belonging to the genus _Molophilus_ and probably this species was obtained in October, 1954.

Of the total of 66 species recorded from this Reserve, 2 species were recorded for the second time in Great Britain and 3 species for the third time. Further, 3 species were recorded from England for the first time and 4 species recorded for the second time.

5. <u>Larval habitat on the Moor House Reserve.</u>

It was rare to find an adult tipulid far away from its larval habitat and if numbers of adults were taken in a particular habitat, it was fairly certain that this was the larval habitat. This was often confirmed by the breeding out of larvae or alternatively by finding adults emerging or egg laying. Fig. 14 shows the distribution of larval habitats on the Moor House Reserve divided into 17 arbitary groups. Many of these could have been expanded e.g. "moss on banks of streams" or "small streams with vegetation" could have been sub-divided into many groups.

It is obvious from Fig. 14 that the species were most abundant in the wet habitats and fewer species were found on the better drained areas, such as limestone outcrops, moss growing on rocks and raised shingle beds. No attempt has been made to analyse the data into species per habitat, as has already been stated, some of these were very arbitary in their definition.

Fig. 14 also gives some indication of the abundance of the species in the various habitats. This data is based on both larvae and adult collections, an X indicating the larval habitat and C a larval

Fig. 14. Distribution of larval habitiats at Moor House.

"x" indicates a larval habitat

"C" indicates a habitat in which larvae are frequent.

	Swift rocky streams	Small streams with vegetation	Peat pools	Pools on alluvial soils	Sphagnum bog	Sphagnum flush	Alluvial flush	Calluna-Sphagnum moor	Eriophorum moor	Juncus sqarrosus moor	Calluna-Cladonia moor	Vegetation below rock outcrops	Alluvial grassland	Limestone grassland	Moss by stream banks	Mosses on rocks	Raised shingle beds
1. Dolichopeza albipes															x		
2. Pales submaculosa													x				
3. Tipula paludosa													C	C			
6. Tipula cheethami																x	
7. Tipula rufina																x	
8. Tipula alpium															x	x	
9. Tipula staegeri															x	x	
10. Tipula marmorata															x	x	
11. Tipula subnodicornis					x			C	C	C	x						
12. Tipula melanoceros			x														
13. Tipula pagana													C	x			
14. Tipula montium		C															
15. Tipula coerulescens		C															
16. Tipula variipennis													C	x			
17. Tipula gimmerthali							C										
18. Tipula macrocera						C											
20. Tipula excisa																	C
21. Phalacrocera replicata				x													
25. Limonia didyma															x		
30. Limonia morio													x	x			
33. Pedicia rivosa					x	x											
34. Tricyphona schummeli								x		x							
35. Tricyphona immaculata					x			C	C	C	x						
36. Dicranota robusta	x																
37. Dicranota subtilis	x																
38. Dicranota brevitarsis	x																
39. Dicranota bimmaculata	x	C															
40. Dicranota guerini	x	C															
41. Dicranota exclusa	x																
42. Hexatoma bicolor	x																
44. Limnophila meigeni								x		C							
47. Limnophila pulchella								x	x								
49. Limnophila mundata	x																
51. Limnophila nemoralis "B"								C	x								
52. Limnophila nemoralis "A"													x				
57. Erioptera lutea		x															
58. Erioptera fascipennis		x		x													
59. Erioptera trivialis		C					x	x		C							
60. Erioptera diuturna							x	x		x							
62. Ormosia lineata												x					
63. Ormosia hederae												C					
64. Ormosia pseudosimilis								x		C							
65. Molophilus ater								x		C							

← FREE WATER →← WET →← DAMP →← DRY →

habitat where the species has been recorded as common or abundant. Species not recorded on the list were too rare for their habitat to be discovered.

6. Duration of adults and duration of pupation.

Adult tipulids live only for a few days so that the duration of adults of any species gives a measure of the duration of pupation within the species. For example, if the adults are found for two weeks then the larvae of this species must have entered pupation within a similar period.

The duration of adults of different species taken at Moor House between July 1953 and December 1955 are shown in Fig. 15. The emergences in different years were similar and do not extend the period excessively. It is interesting to note that the adults of most species were recorded over a period of less than 8 weeks and that the period of abundance was much shorter.

Table I shows the period of occurrence of adults belonging to 21 species which were common at Moor House. There was a marked indication that the Summer species, which reached the peak of emergence in July or August, were present for a longer period than those which occurred during Spring and Autumn; the duration being twice as long during July and August. These differences may have resulted from the pupation of the species being spread over a

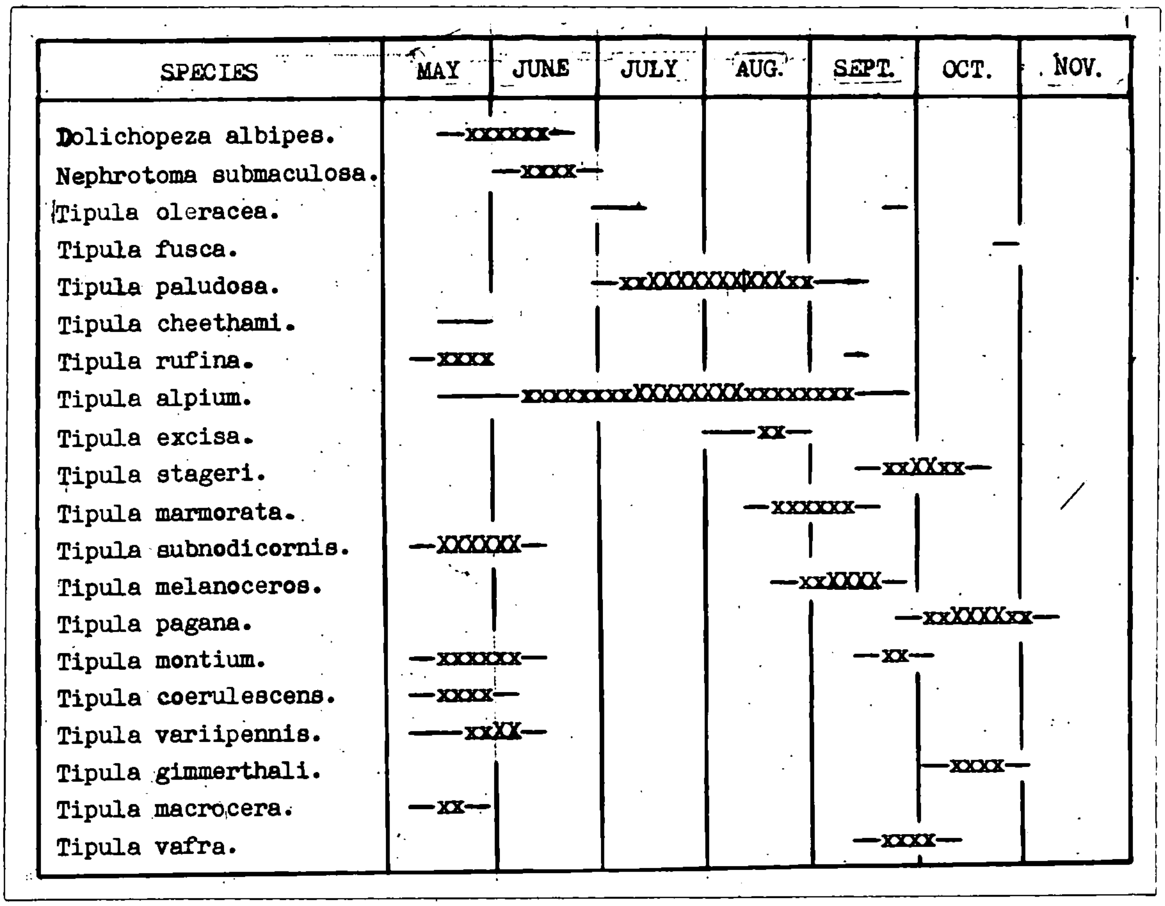


Fig. 15. The duration of adults at Moor House

In the figure above and on the following page

--- indicates that at least one adult was taken in the week

xx indicates that 4 to 10 adults were taken in the week

XX indicates that more than 10 adults were taken in the week.

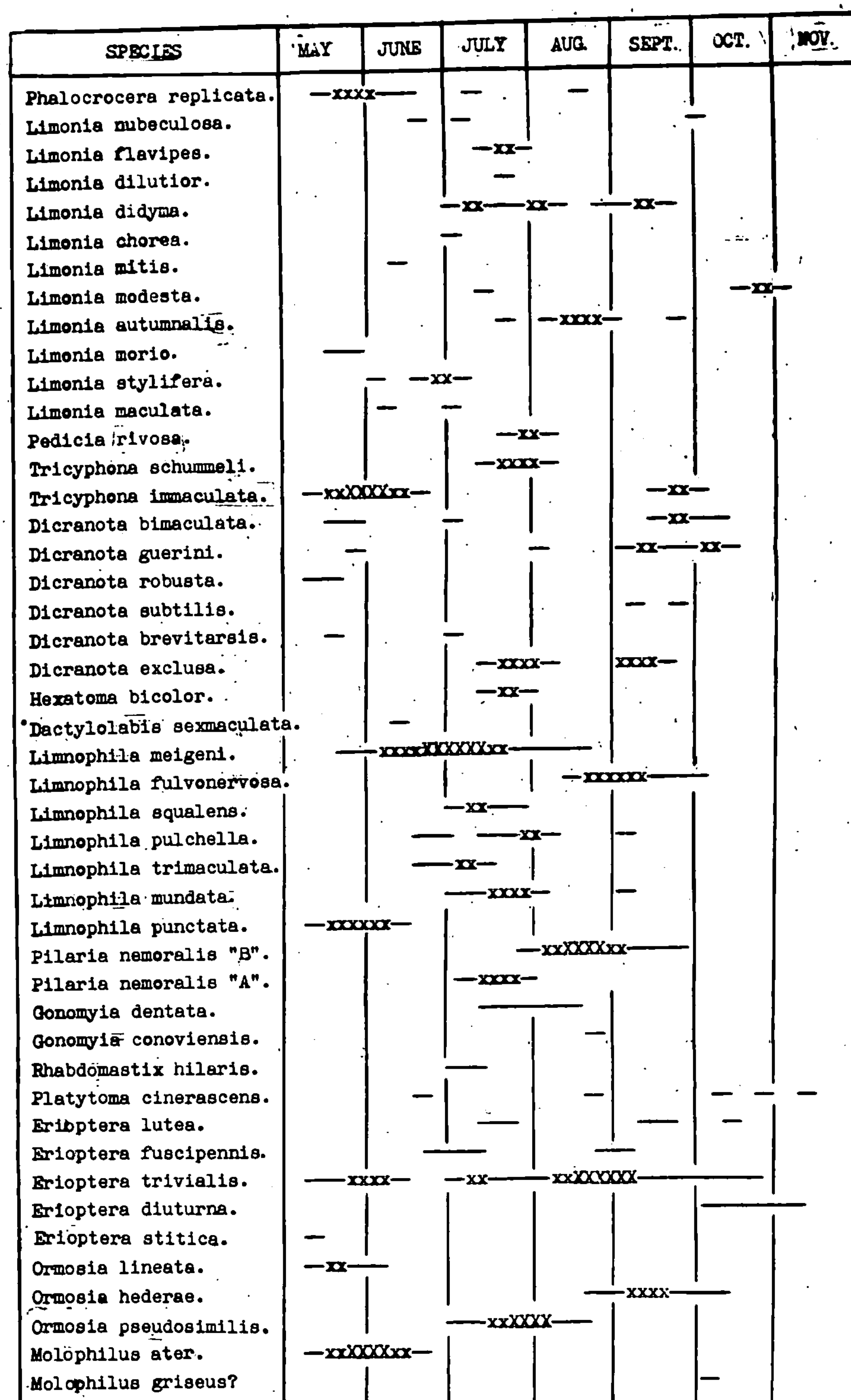

SPECIES
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
Phalocrocera replicata.
Limonia nubeculosa.
Limonia flavipes.
Limonia dilutior.
Limonia didyma.
Limonia chorea.
Limonia mitis.
Limonia modesta.
Limonia autumnalis.
Limonia morio.
Limonia stylifera.
Limonia maculata.
Pedicia rivosa.
Tricyphona schummeli.
Tricyphona immaculata.
Dicranota bimaculata.
Dicranota guerini.
Dicranota robusta.
Dicranota subtilis.
Dicranota brevitarsis.
Dicranota exclusa.
Hexatoma bicolor.
Dactylolabis sexmaculata.
Limnophila meigeni.
Limnophila fulvonervosa.
Limnophila squalens.
Limnophila pulchella.
Limnophila trimaculata.
Limnophila mundata.
Limnophila punctata.
Pilaria nemoralis "B".
Pilaria nemoralis "A".
Gonomyia dentata.
Gonomyia conoviensis.
Rhabdomastix hilaris.
Platytoma cinerascens.
Erioptera lutea.
Erioptera fuscipennis.
Erioptera trivialis.
Erioptera diuturna.
Erioptera stitica.
Ormosia lineata.
Ormosia hederae.
Ormosia pseudosimilis.
Molophilus ater.
Molophilus griseus?

Fig. 15 cont.

Table I

The period of occurence of adults according to the time of year

I Species in which the peak of emergence occurred in May or June

Species	Duration (weeks)
Tipula variipennis	5
Tipula subnodicornis	6
Tipula monium	5
Tipula coerulescens	4
Tipula macrocera	3
Tricyphona immaculata	6
Molophilus ater	6
Average	5.0 weeks

II Species in which the peak of emergence occurred in July or August

Tipula paludosa	10
Tipula alpium	16
Tricyphona schummeli	4
Limnophila meigeni	13
Limnophila nemoralis "A"	9
Erioptera trivialis	14
Ormosia pseudosimilis	7
Average	10.4 weeks

Table I cont.

III Species in which the peak of emergence occurred in September or October

Species	Duration (weeks)
Tipula stageri	5
Tipula marmorata	6
Tipula melanoceros	6
Tipula pagana	6
Tipula gimmerthali	4
Tipula vafra	4
Ormosia hederae	8
Average	5.6 weeks

greater number of days during the summer.

Larvae of Tipula subnodicornis and T. variipennis, which were collected in late March, pupated within two weeks of being brought into the laboratory. There can be little doubt that the time of pupation of these Spring emerging species is controlled by the rise in temperature which occurs in the Spring. On the other hand, larvae, of Tipula marmorata which were collected and brought into the laboratory in late March, emerged at the same time as larvae in the field (i.e. in late August and early September) despite the fact that the temperature in the laboratory was higher. Crisp & Lloyd (1954) also failed to shorten the life cycle by keeping Molophilus cinereifrons de Meijere, M. curvatus Tonnoir and M. griseus Meigen under laboratory conditions.

Tipula pagana was studied as a typical late Autumn species and in the three years 1953, 1954 and 1955, the onset of emergence occurred during the last three days in September and appeared to have been completed within a further 15 days. The similarity and the shortness of the emergence period in these years suggested that the larvae do not pupate when they have become fully developed, but wait for the presence of some particular conditions.

The data suggest that the factor or factors controlling the onset of pupation were more decisive during the Spring and Autumn than in the Summer.

7. The seasonal distribution of Tipulidae

A quantitative study of the seasonal distribution and abundance of tipulids was carried out in 1954 and 1955. In 1954, sticky traps were errected on three areas, a deep peat moor with *Calluna-Sphagnum-Eriophorum* complex, a shallow peat moor dominated by *Juncus squarrosus* and an alluvial grassland area with a certain amount of limestone drift. In 1955, observations were discontinued on the deep peat area but continued on the remaining two areas.

Johnson (1950) studied the effectiveness of sticky traps, suction traps and tow nets in capturing airborne insects and came to the conclusion that while the suction trap was the most effective means of sampling aphid populations, sticky traps captures of insects over ¼ inch long and *Diptera* smaller than ¼ inch long were greater. He did not examine the effectiveness of these traps for *Diptera* larger than ¼ inch long.

Sticky traps give a measure of activity, but if the insects captured are grouped into long enough periods, then they also give a comparative measure of abundance. Figs. 16 shows the captures

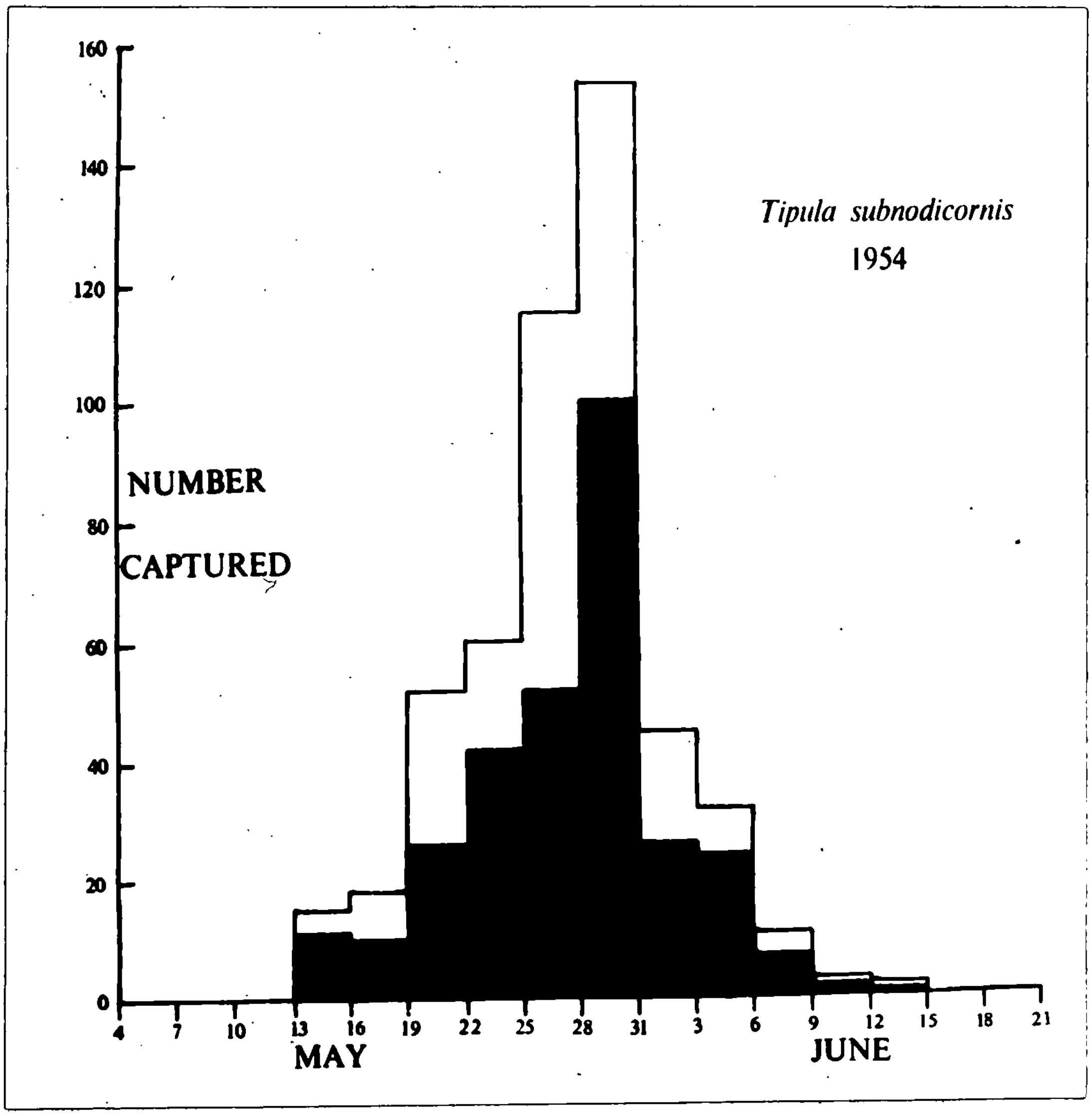


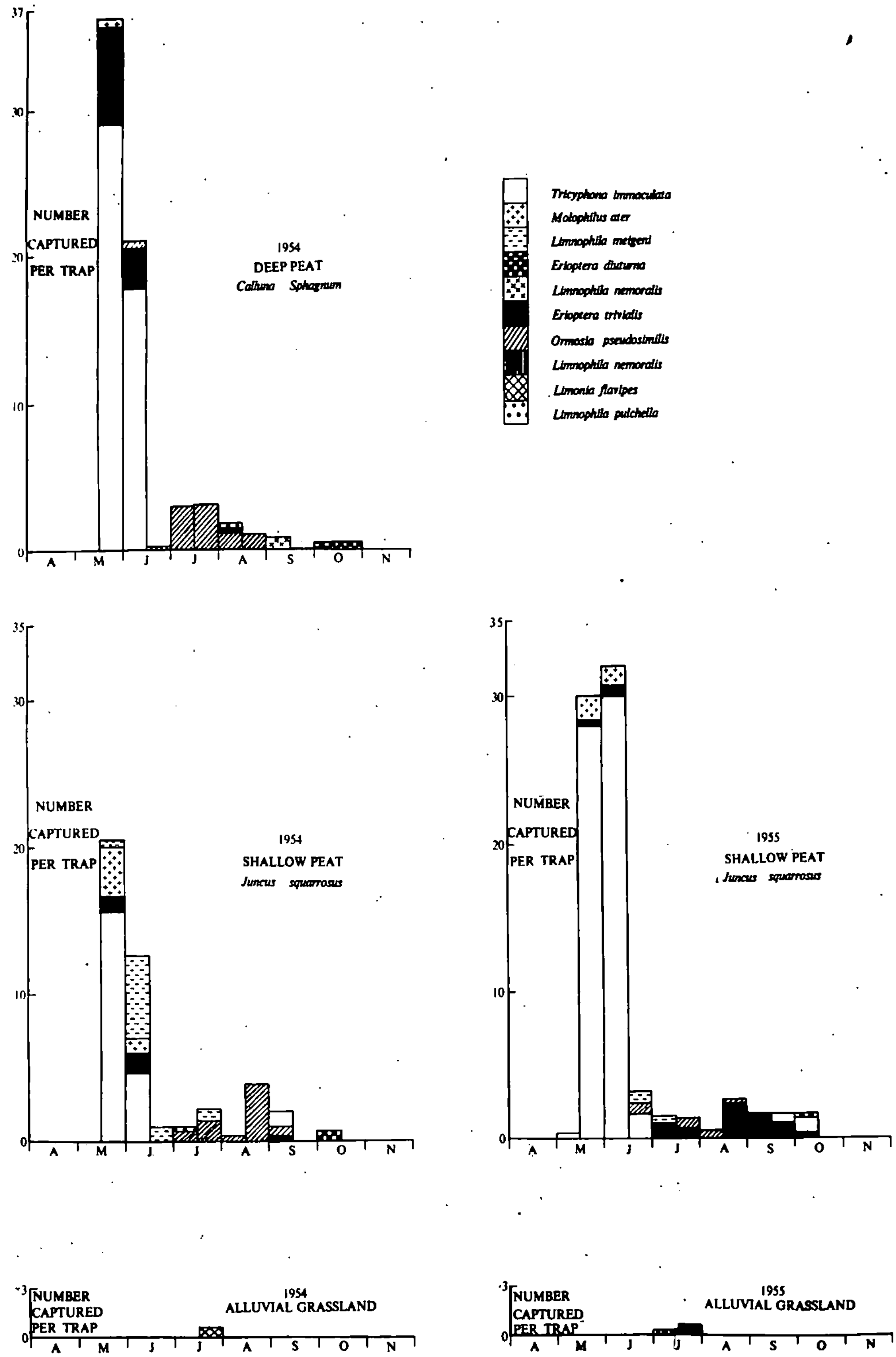
Fig. 16. The captures of Tipula subnodicornis on sticky traps, 1954. The white histogram represents total captures while the black histogram is the capture of males.

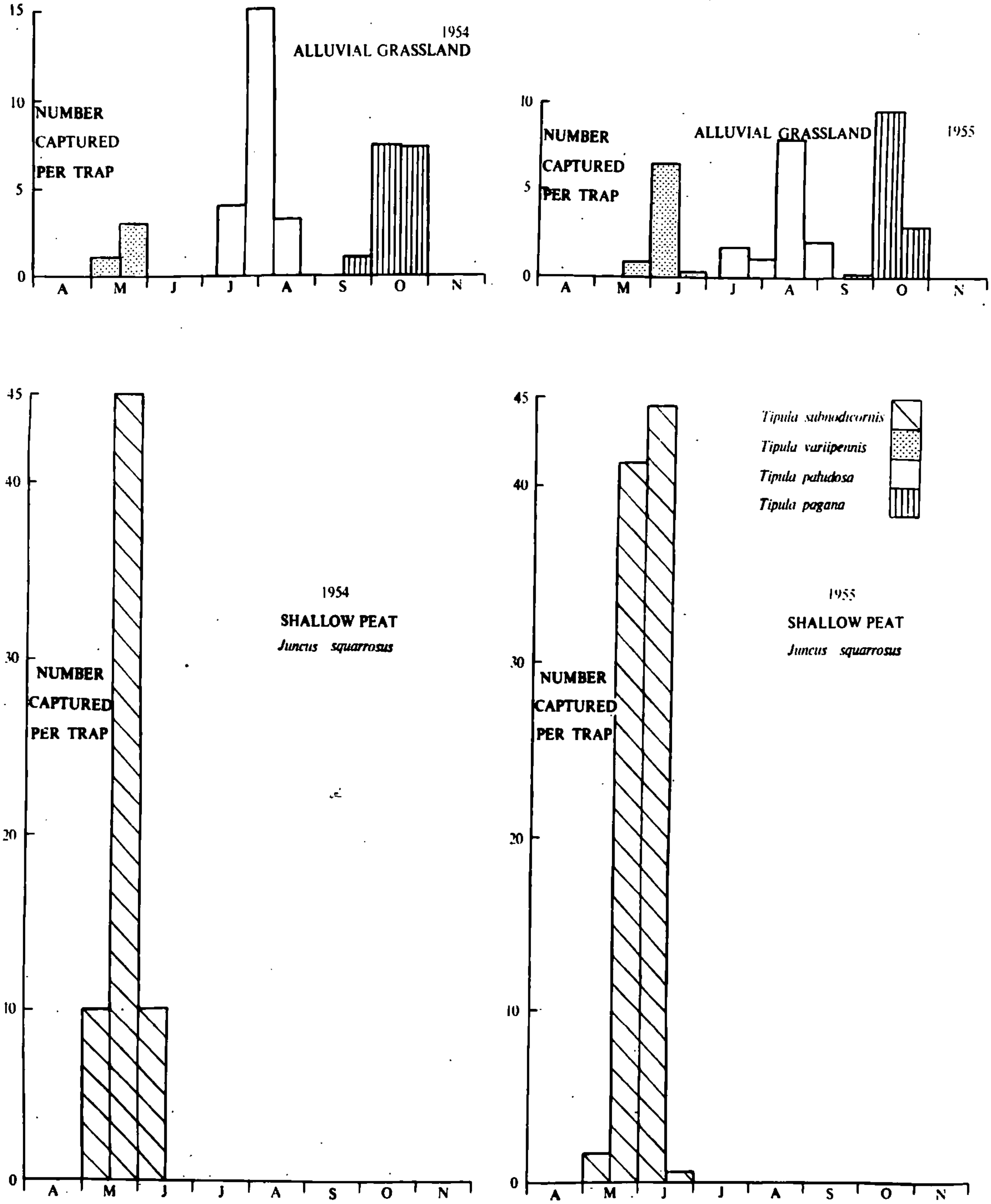
of *Tipula subnodicornis* in 1954 grouped into 3 day periods. The smooth distribution indicated that captures grouped into as short a period as three days give a good representation of abundance. It is also worth noting the short duration of adults in this area, the first and last adult having been taken within 33 days.

The long-palped craneflies (*Tipulinae*) were larger and apparently more active than the short-palped craneflies (remaining groups) and these have been considered separately.

The captures per trap, grouped into fortnightly periods, are shown in Figs. 17a & 17b. The genus *Tipula* produced only one peak on the moor, this being caused by *Tipula subnodicornis* in late May and early June. However, on the alluvial area, three peaks were observed, one in late May and early June, one in July and August and one in October, caused by the presence of *Tipula variipennis*, *T. paludosa* and *T. pagana* respectively. The numbers of animals involved in the emergence of the last two mentioned species were approximately equal. However, *T. paludosa* was more than twice the weight of *T. pagana* and therefore involved a greater turn over of

Figs. 17a& 17b. The captures of long-palped crane-flies (<u>Tipulinae</u>) and short palped crane-flies on six sticky-traps situated in each habitat.


Tricyphona immaculata
Molophilus ater
Limnophila meigeni
Erioptera diuturna
Limnophila nemoralis
Erioptera trivialis
Ormosia pseudosimilis
Limnophila nemoralis
Limonia flavipes
Limnophila pulchella
NUMBER CAPTURED PER TRAP
1954
DEEP PEAT
Calluna Sphagnum
1954
SHALLOW PEAT
Juncus squarrosus
1955
SHALLOW PEAT
Juncus squarrosus
1954
ALLUVIAL GRASSLAND
1955
ALLUVIAL GRASSLAND
A M J J A S O N


1954
ALLUVIAL GRASSLAND
NUMBER
CAPTURED
PER TRAP
15
10
5
0
A
M
J
J
A
S
O
N
ALLUVIAL GRASSLAND
1955
NUMBER
CAPTURED
PER TRAP
10
5
0
A
M
J
J
A
S
O
N
1954
SHALLOW PEAT
Juncus squarrosus
NUMBER
CAPTURED
PER TRAP
45
40
30
20
10
0
A
M
J
J
A
S
O
N
1955
SHALLOW PEAT
Juncus squarrosus
NUMBER
CAPTURED
PER TRAP
45
40
30
20
10
0
A
M
J
J
A
S
O
N
Tipula subnodicornis
Tipula variipennis
Tipula paludosa
Tipula pagana

material in each season.

Like the genus Tipula, the short-palped crane-flies also formed a marked peak in numbers on the moor in late May and early June. This peak was almost entirely caused by the abundance of Tricyphona immaculata and similar results were obtained in both years.

The short-plaped craneflies were absent on the alluvial areas and only four specimens belonging to two species were taken.

In 1954 a comparison was made between the area of deep boggy peat and that of shallow peat. The general form of emergence and numbers of species were similar, the main difference being that Erioptera trivialis was more common on the deep peat area.

Thus there were marked differences between the numbers and time of abundance of tipulids on the peat and alluvial areas, the former having one major peak of emergence whilst the alluvial area had three peaks of much less magnitude, spread throughout the season.

8. Egg filament in Tipulinae

Hemmingsen (1952) postulated that the egg filament, which was found in many of the Tipulinae, was a means of anchoring the egg in the substratum selected by the females and was an adaptation to a wet environment. He showed that this filament was extensive amongst the Tipulinae and that closely related species could differ in that one possessed the filament while the other lacked it.

Data were collected from material obtained at Moor House to determine if this conclusion applied there. Table II shows the species which were examined

Table II

Species examined for the presence of an egg filament

Filament present.	
Dolichopeza albipes	Tipula pagana
Tipula oleracea	T. coerulescens
T. montium	T. alpium
T. marmorata	T. rufina
T. macrocera	T. staegeri
T. vafra	T. melanoceros
T. gimmerthali	
+ T. solistialis	+ T. fulvipennis
+ T. lateralis	+ T. maxima
+ T. luna	+ Prionocera turcica
Filament absent.	
Tipula paludosa	Tipula subnodicornis
T. variipennis	T. excisa
+ Nephrotoma maculata	

+ denotes that species absent from Moor House.

for the presence of an egg filament and it includes some species not recorded from Moor House. The Table shows that 13 species had an egg filament while only 4 species lacked it at Moor House. This is a larger proportion of species possessing this filament than the data given by Hemmingsen (1952) for Danish species (13 with and 11 without an egg filament) and this may support Hemmingsen's belief that the filament is related to a wet environment. Tipula subnodicornis is a marked exception to this contention and it lays eggs in much wetter habitats than T. pagana. Furthermore, many of the moss inhabiting species have relatively dry habitats and this is certainly the case of many larval habitats of T. marmorata and T. alpium and possibly T. staegeri.

9. Development of eggs.

The dissection of newly emerged females have shown that certain species emerge with the eggs fully developed, while a few species appear to emerge with immature eggs. Evidence has also been obtained that certain species may lay their first batch of ripe eggs and then develop a second batch. This latter development is more difficult to prove than the first. Evidence was obtained from Tipula paludosa that newly emerged females had fully developed eggs and also very small ova in ovaries measuring 2 mm. and also by finding females with one or two ripe eggs and many half developed eggs. The time taken to develop the second batch of eggs has not been measured.

Table III

The egg development of Tipulinae

I Species emerging with ripe eggs	
Tipula paludosa	Tipula oleracea
T. subnodicornis	T. montium
T. coerulescens	T. pagana
T. variipennis	T. marmorata
T. gimmerthali	T. excisa
T. melanoceros	T. macrocera

II Species emerging with unripe eggs	
Tipula alpium	Tipula rufina
+ Nephrotoma maculata	+ T. luna
+ Tipula maxima	

Table III cont.

III Species which redevelop eggs
Tipula paludosa + T. fulvipennis ?

+ denoted that the species did not occur at Moor House.

Table III shows that the majority of species which were recorded at Moor House emerged from the pupa with ripe eggs. Numerous scattered observations indicated that most of the species which emerged with ripe eggs laid their eggs very rapidly after emergence (see section on Tipula paludosa and and T. subnodicornis), the adults not living very long.

It is interesting to note that Tipula alpium and T. rufina which rested on vertical surfaces such as peat hags and rock faces and presumably obtained some protection from such places, emerged with unripe eggs.

How many?

10. A key to the larvae of some moorland Tipulinae

This key is based almost exclusively on the structure of the posterior end of the larvae, particularly the ammount of chitinisation on the spiracular lobes and the shape of the anal gills. Fig. 18a shows the position of the strctures used in the key.

This key can be used with greatest success on the final instar larvae but second and third instar larvae can also be identified. First instar larvae differ markedly from those subsequent but those illustrated in Fig. 18b suggest that they may differ sufficiently to be separated into species.

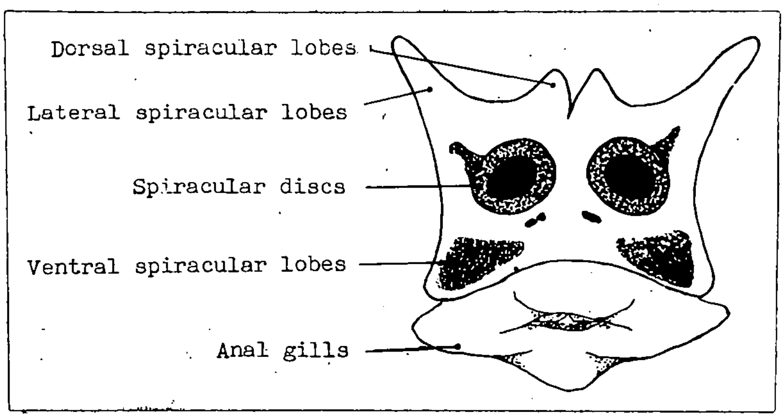


Fig. 18a Posterior end of tipulid larvae showing taxonomic characters.

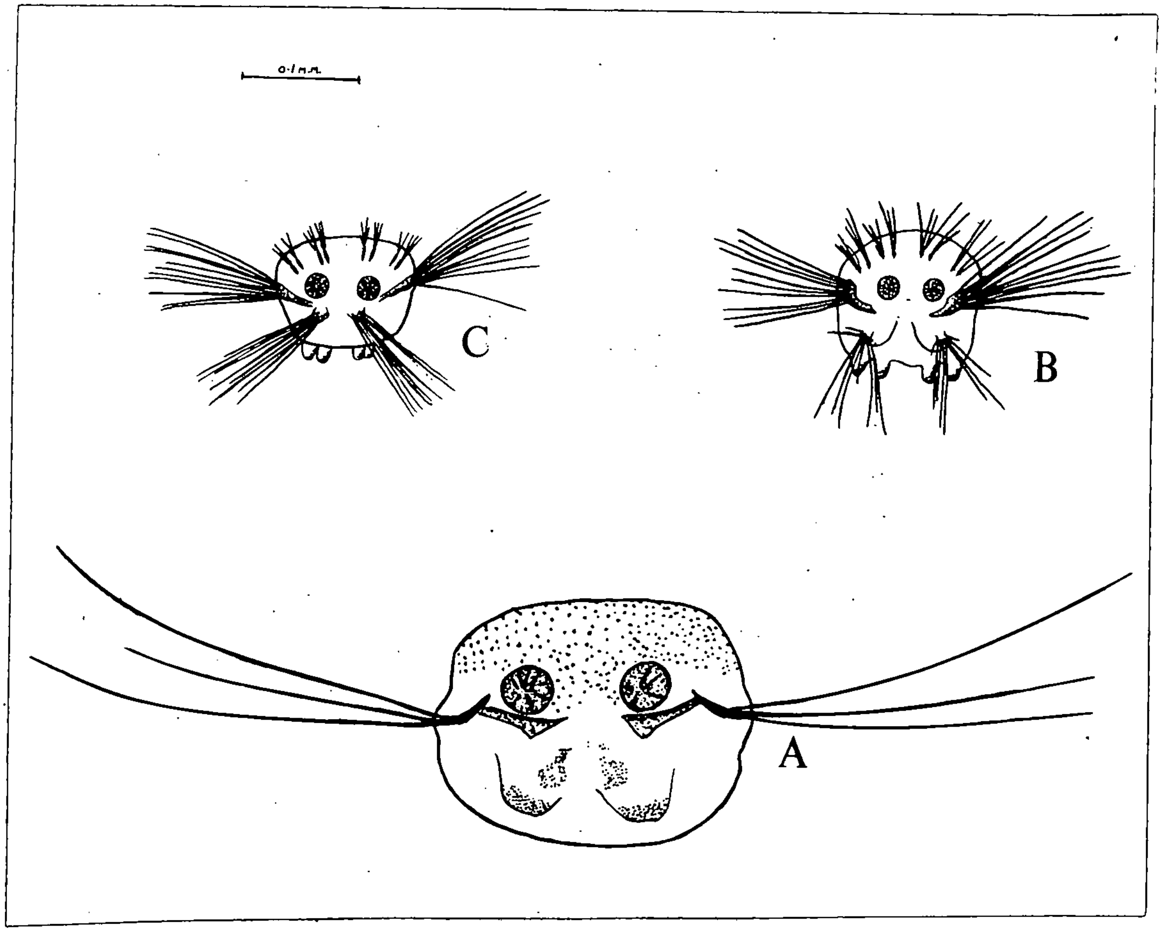


Fig. 18b. The posterior end of first instar larvae.

A. Tipula variipennis B. T. subnodicornis

C. Tipula marmorata

The larvae used in the key following, had been killed by dropping them into boiling water (this extended them) and were preserved in 4% formalin.

Key

1a. The six spiracular lobes very long; of equal length and equidistant from each other. Each lobe darkened on outer edges and with long hairs (this last character should be examined under water). Anal gills consisting of 6 long, thin tubes. (Fig. 19 C.)

PRIONOCERA TURCICA

Larvae aquatic, living in vegetation on edge of ponds and streams.

1b. The six spiracular lobes not equidistant or of equal length. Hairs, if present, short. 2.

2a. Dorsal and lateral spiracular lobes long and pointed, with black, chitinous tips. Ventral spiracular lobes short. A darkened area below each spiracular disc. Dorsal surface of abdomen obviously patterned (Fig.19B)

DOLICHOPEZA ALBIPES

Larvae in moss and liverworts on banks or in streams.

2b. Dorsal and lateral spiracular lobes short. Abdomen not obviously patterned (_T._ _montium_ and T. *coerulescens* have a sightly patterned abdomen) 3.

3a. Dorsal spiracular lobe with conspicuous darkened area. 4.

3b. Dorsal spiracular lobe without conspicuously darkened areas (some faint markings may be present). 6.

4a. All six spiracular lobes extensively dark brown, the darkened areas of approximately similar size and shape. Anal gills composed of 8 elongate tubes (Fig. 19 E).

TIPULA SUBNODICORNIS

Larvae abundant on peat moors.

4b. Darkened areas on spiracular lobes differing markedly in size and shape. 5.

5a. Dark area on dorsal spiracular lobes differing markedly extending to apex, not nearly meeting below (Fig. 19F). Body with microscopic pile and will not wet in water.

TIPULA EXCISA

5b. Darkened area on dorsal spiracular lobes not extending to apex and meeting or nearly meeting below Fig. 19 I).

TIPULA VARIIPENNIS.

Larvae on alluvial grassland.

6a. Anal gills formed of six, long tubes, the longest pair equal to the diameter of the abdomen. Each spiracular lobe of similar size and shape and little darkening. An inconspicuous dark line down the centre of the ventral spiracular lobes. Dorsal surface of abdomen slightly patterned. Two lobes present between and slightly anterior of dorsal and lateral spiracular lobes (Fig. 19 A).

TIPULA MONTIUM or TIPULA COERULESCENS.

Larvae aquatic, living in vegetation in shallow streams.

6b. Anal gills not as extensive as above. No lobes present between dorsal and lateral spiracular lobes. 7.

7a. Anal gills consisting of 8 tubes (larvae live in moss) 8.

7b. Anal gills less dissected with only 2 or 4 cone-shaped tubes. 9.

8a. Dorsal spiracular lobes shorter than lateral lobes, with slightly darkened area between dorsal spiracular lobe and spiracular disc, this ajoining the latter. (Fig. 19 G).

TIPULA MARMORATA

8b. Dorsal spircaular lobes sub-equal to lateral lobes. No darkened area on upper, inner side of spiracular disc (Fig.19 D).

TIPULA ALPIUM.

9a. A dark area touching the spiracular discs on the dorsal-lateral sides. Dorsal and ventral spiracular lobes not darkened. Dorsal lobes noticeably shorter than lateral lobes. (Fig. 19 J).

TIPULA PAGANA.

9b. Faint dark marks on dorsal and lateral spiracular lobes but these not touching edge of spiracular disc. Dorsal and lateral spiracular lobes sub-equal. (Fig. 19 H).

TIPULA PALUDOSA
(Tipula oleracea)

Fig. 19. The posterior ends of some _Tipulinae_ larvae.

A. _Tipula montium_ and _Tipula coerulescens_

B. _Dolichopeza albipes_

C. _Prionocera turcica_

D. _Tipula alpium_

E. _Tipula subnodicornis_

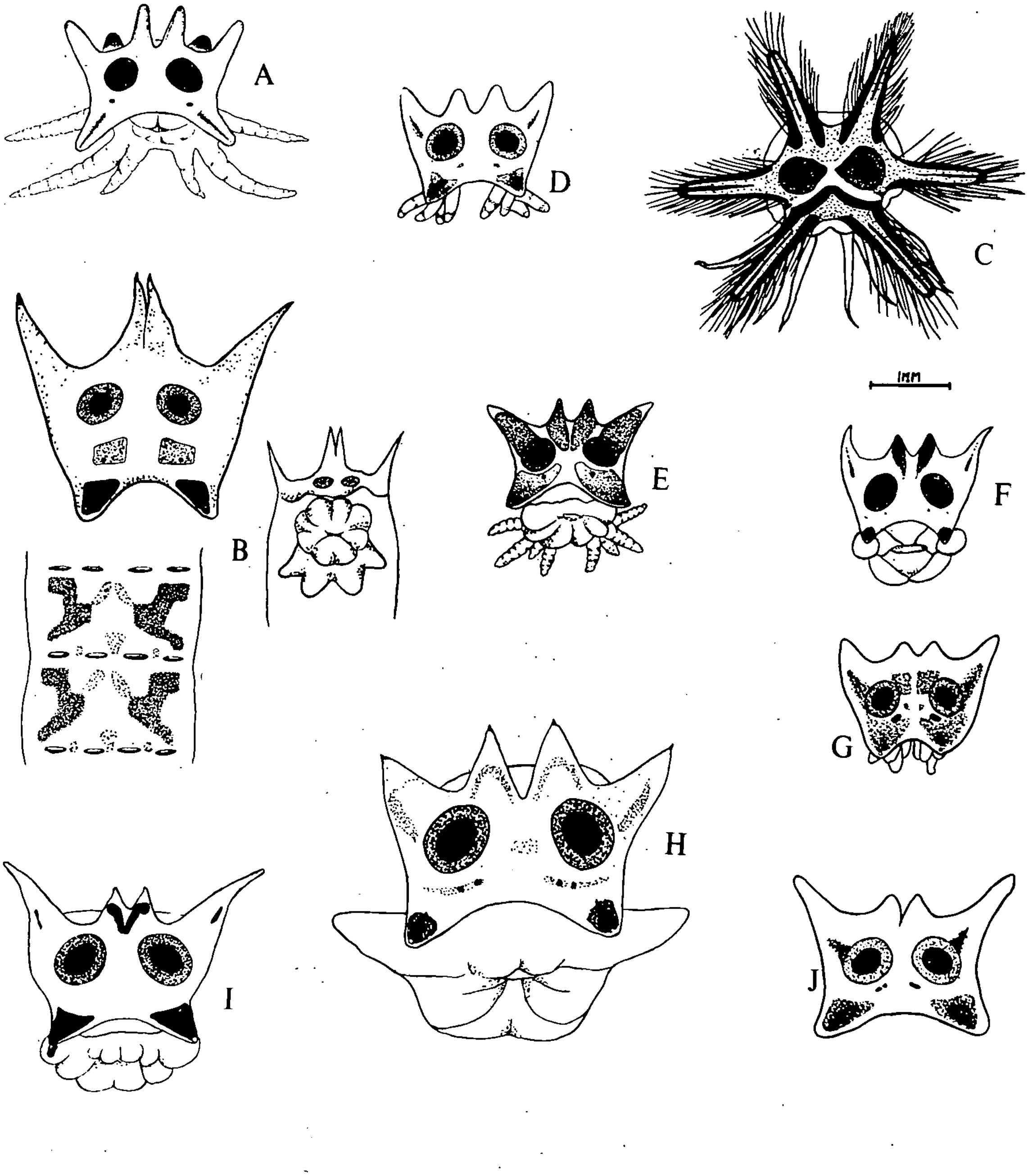
F. _Tipula excisa_

G. _Tipula marmorata_

H. _Tipula paludosa_ and _Tipula oleracea_

I. _Tipula variipennis_

J. _Tipula pagana_


A
D
C
1MM
B
E
F
G
H
I
J

V <u>An ecological and biological study of Tipula subnodicornis</u>.

1. <u>Adults</u>. <u>Tipula subnodicornis</u> has been studied in greater detail because it occurred in large numbers over most of the moor and material was readily obtained. There was only one generation per year, the adults emerging between the middle of May and the middle of June. On afternoons, when the emergence was at its peak, the whole moor was a shimmering mass of males flying in search of females.

The males usually flew against the wind provided that it was not too strong. Table IV shows the captures of males on a series of 20 sticky traps each divided into four directions.

Table IV

Direction of capture of male <u>T. subnodicornis</u>

Date	Wind direction	Number of males captures on quarters of the traps				
		NW-NE	NE-SE	SE-SW	SW-NW	Total
25.5.55	S.E.	75	17	12	27	131
26.5.55	S.E.	2	10	4	4	20
27.5.55	S.W.	13	10	7	13	43
1.6.55	S.E.	100	60	41	62	263

On 25 May and 1 June there was a marked indication that the males were moving against the wind and not down wind as would have been expected had the captures been caused by wind carried males. The data for the remaining two days, 26 and 27 May, suggested that activity was supressed and there were no well defined movements.

2. The females of T. subnodicornis are unable to fly because of their reduced wings, but they have shorter, stouter legs than the males, enabling them to walk more efficiently.

Movement of females.

On 2 June 1955, 35 marked females were released at the centre of a series of concentric rings, each 1 metre apart, placed on a Juncus squarrosus moor. The area was searched 14 hours later within a radius of 6 metres of the point of release and the time given to searchibg was proportional to the area between each ring so that the numbers recovered would be representative of the distance travelled. Only 7 females were recovered and their movements are shown in Table V. The average movement was less than 1 metre

Table V

The movement of seven females of T. subnodicornis after 14 hours.

Movement (metres)	0-.5	.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-4.0	4.0-6.0
Number	1	3	1	1	1	0	0	0

and the greatest movement was 2 metres 10 cm. The lack of a greater number of recoveries was no doubt due to the thick mat of vegetation which probably hid the remaining females. The average movement per female was about 7cm. per hour and these data suggest that the females do not generally move far from the place of emergence.

3. Emergence rhythm of the females.

The females were invariably attended by at least one male as soon as they came above the ground level. The females which were obviously newly emerged, as was evident by their elongated and almost transparent abdomen, usually climbed a near-by stem by which time the males had found and paired with them.

Copulation lasted several hours, the females in an upright vertical position, with the males in the reverse position, hanging downwards and both motionless. Thus, during copulation, the presence of newly emerged females was made obvious and during 1954 it was noticed that there appeared to be a rhythm in emergence. In 1955 quantitative data were collected and use was made of counts of the number of newly emerged females in copulation and also those which had apparently laid some eggs and were older. Fig. 20 shows the numbers of females in copulation and also male activity. It is evident that the number of newly emerged females in copulation reached a peak between 13.00 and 16.00 hours G.M.T.

This suggested that the females emerged about noon and that no emergence occurred at night. With the exception of 1 June, no rhythm was recorded in the numbers of older females in copulation except that it appeared to occur mainly during daylight hours. It is interesting to note that the male activity followed very closely the total number of females in copulation.

On long, sunny days the emergence, or rather

Fig. 20. The number of females of _Tipula subnodicornis_ mating; a measure of the emergence period. Note relationship between females mating and male activity.

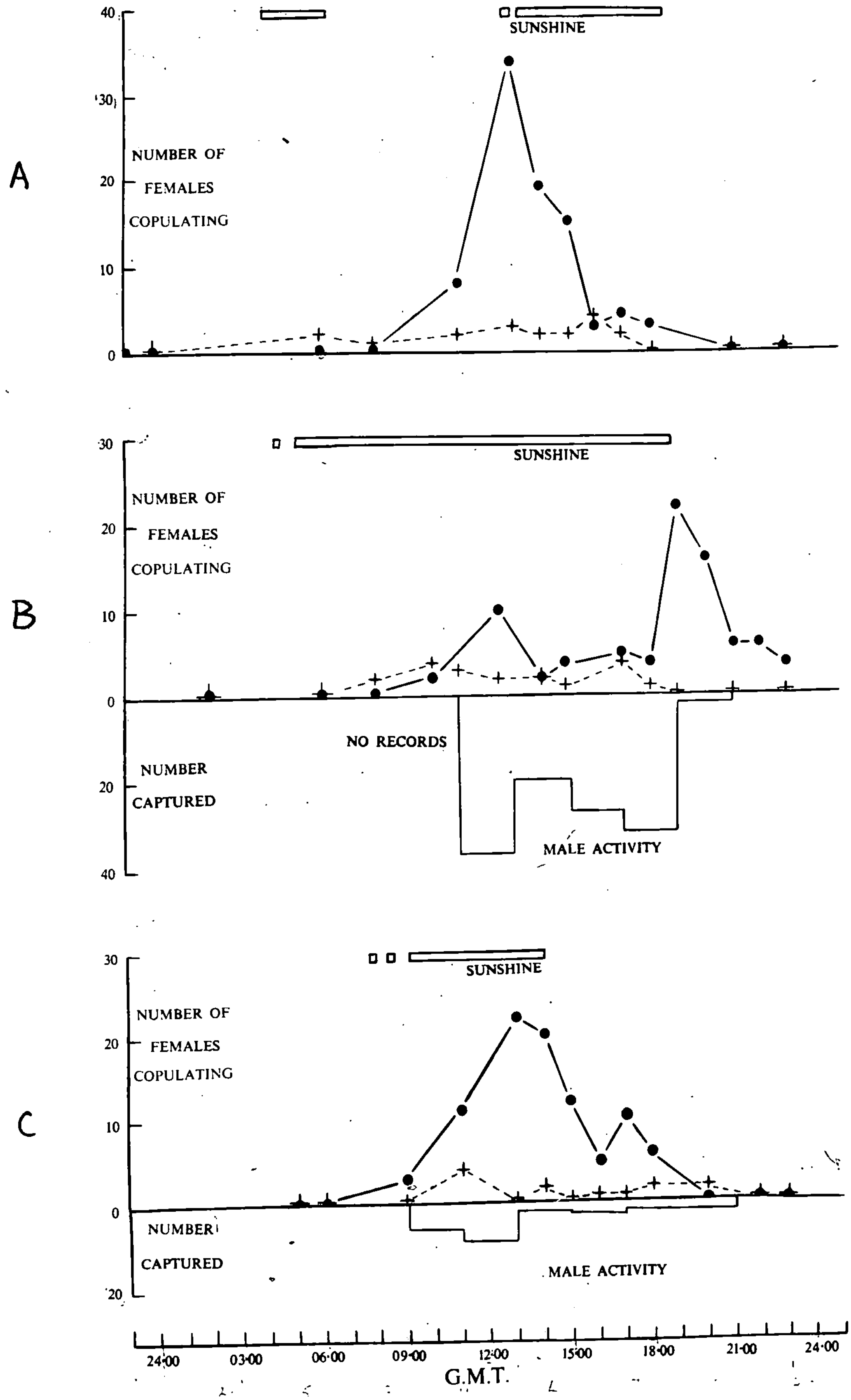
A. 24 May 1955 on 25 sq. yards.

B. 25 May 1955, as A.

C. 26 May 1955, as A.

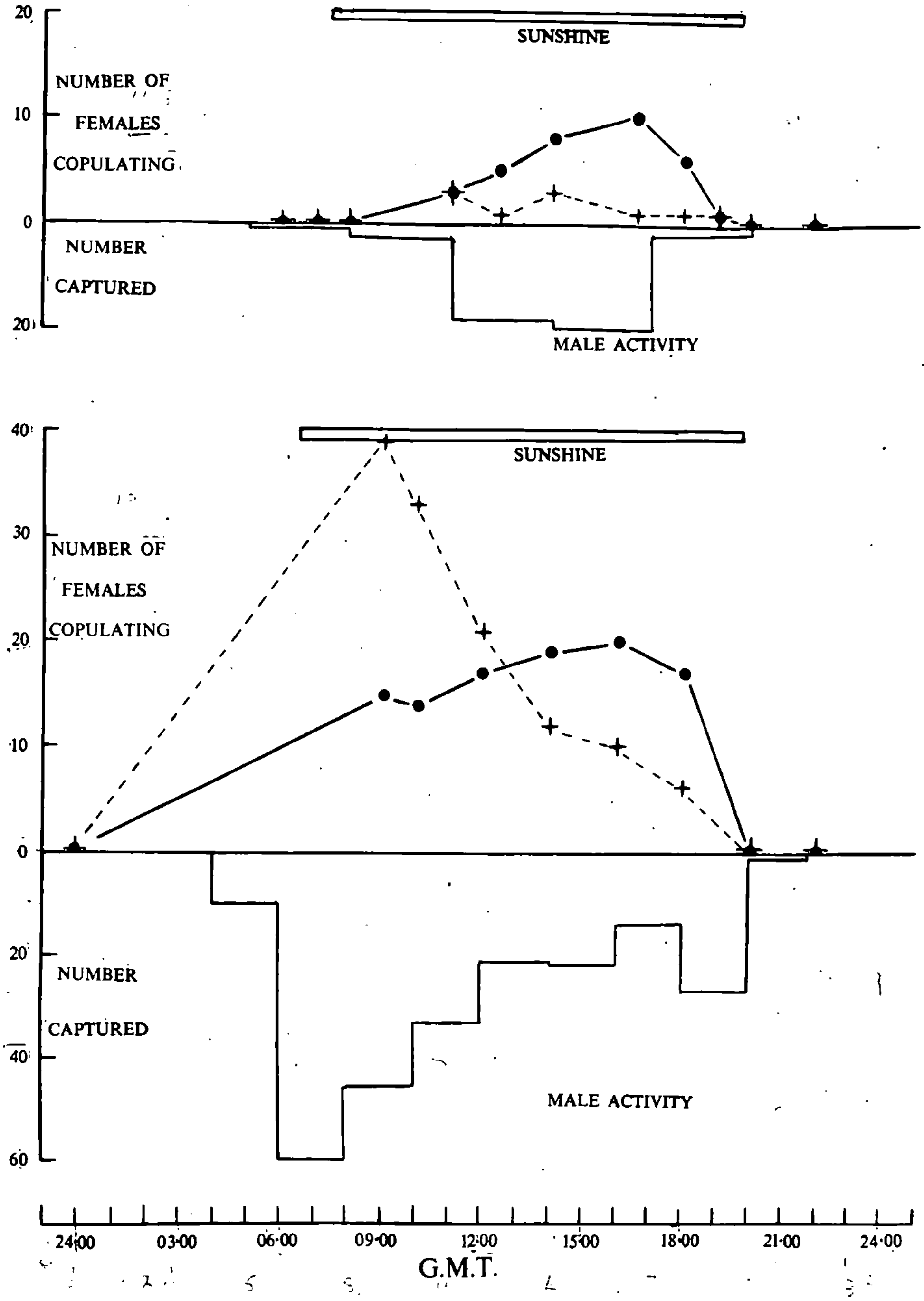
D. 27 May 1955, as A

E 1 June 1955, on 25 sq. yards but different locality from A-D.


A
B
C
SUNSHINE
NUMBER OF
FEMALES
COPULATING
40
30
20
10
0
SUNSHINE
NUMBER OF
FEMALES
COPULATING
30
20
10
0
NO RECORDS
NUMBER
CAPTURED
20
40
MALE ACTIVITY
SUNSHINE
NUMBER OF
FEMALES
COPULATING
30
20
10
0
NUMBER
CAPTURED
20
MALE ACTIVITY
24·00
03·00
06·00
09·00
12·00
15·00
18·00
21·00
24·00
G.M.T.

D

E



SUNSHINE
NUMBER OF FEMALES COPULATING
NUMBER CAPTURED
MALE ACTIVITY
20
10
0
20
SUNSHINE
NUMBER OF FEMALES COPULATING
NUMBER CAPTURED
MALE ACTIVITY
40
30
20
10
0
20
40
60
24·00
03·00
06·00
09·00
12·00
15·00
18·00
21·00
24·00
G.M.T.

the appearance of females above the vegetation was delayed. The females which came up later on sunny days were well advanced in their hardening of the cuticle suggesting that the emergence took place at the same time as on dull days, but that they stayed in the loose litter out of the sun until the temperature began to drop or that the higher temperature quickened the process of hardening the cuticle.

As already stated, it was exceedingly uncommon to find a newly emerged female unattended by males and when the appearance of females above the ground was delayed, then the male activity was delayed by a similar length of time. It is possible that both the males and the females were reacting to temperature or humidity or that the males were reacting to some stimulus produced by the females.

4. Egg laying

The eggs of *T. subnodicornis* were fully developed when the female emerged and laying occurred almost immediately after the completion of copulation. The sub-apterous female moved over the terrain, probing with the ovipositor until a suitable cavity was found into which the greater part of the abdomen was inserted. On Juncus squarrosus moor, the females frequently disappeared into the surface of loose leaf litter and oviposition presumably took place under these circumstances.

Laboratory studies indicated that unfertilised females would not lay eggs. Three females which were found with their abdomens still in the pupal case were placed under an inverted jar on suitable peat for oviposition. Seven other females were put under two similar jars along with the males with which they were in copulation. All the females were killed 24 hours later and preserved for dissection. As Table VI shows,

Table VI

The effect of fertilisation on the number of eggs laid by *T. subnodicornis*

	Eggs per female after 24hrs.		
	Fertilised		Unfertilised
	37	0	315
	28	0	234
	24	0	201
	0		
Mean	13		247

the unfertilised females still contained the majority of their eggs (247 each) while the fertilised females contained an average of 13 eggs each.

A second experiment demonstrated that fertilised females did not lay eggs until a suitable substrate was found. Six fertilised females were placed in a clean, dry jar and left for 24 hours. Seven eggs were found in the jar at the end of this period. Three of the females were then transferred into a similar jar containing dry cotton wool and the remaining three were placed into a jar in which the cotton wool was damp. The females in the latter jar commenced oviposition immediately but those in the former had laid no eggs after 24 hours. These results have been confirmed many times.

The use of a wet pad of cotton wool as a suitable oviposition site enabled egg laying to be studied in the laboratory. The cotton wool facilitated observation since the ovipositor had difficulty in penetrating any distance into the pad. Egg laying took place very rapidly and it was impossible to follow every action in detail.

The substrate was probed by the ovipositor with the cerci and sternal valves in the normal position. Then the sternal valves were lowered and an egg appeared in the cavity between these valves and the cerci. The cerci were then lowered slowly over the outer side of the sternal valves and suddenly the cerci and sternal valves returned into their normal positions and the egg had disappeared. The rapidity of this last movement was too fast for the human eye to follow.

The decapitation of a female already laying eggs allowed the process of egg laying to proceed without the necessary stimulus, but apparently in the same manner. This showed that the eggs were expelled from the ovipositor with considerable force. Table VII summarized the distance travelled by eggs of T. subnodicornis when ejected horizontally from a platform 6 cm. above a sheet of wet paper. The mean horizontal movement was 29 cms.

On the data it is possible to estimate the initial velocity with which the egg left the ovipositor, ignoring air resistance and assuming that the egg is a sphere.

Table VII

The distance travelled horizontally by eggs ejected by _T._ _subnodicornis_ from a tower 6 cm. high

Distance (cms.)								
	less than 10.0	10.0- 14.9	15.0- 19.9	20.0- 24.9	25.0- 29.9	30.0- 34.9	35.0- 39.9	40.0- 44.9
Number	0	1	1	3	4	8	3	0
Mean distance travelled 29.0cms.								

Using the relationship

$$s = ut + \tfrac{1}{2}at^2$$

Resolving vertically, then $u = 0$

therefore $s = \tfrac{1}{2}at^2$ 1.

Resloving horizontally, then $a = 0$ since a = gravity..

therefore $s = ut$ 2.

Using equations 1 and 2, it is possible to evaluate u, the initial velocity, from the relationship-

$$u = s'\sqrt{\frac{a}{2s''}}$$

where s' =horizontal movement
s'' =vertical movement.

therefore $u = 29.0\sqrt{\frac{981}{2\times 6}}$

$= 287$ cms. per second.

It is now possible to calculate the energy involved from the relationship

$$e = \tfrac{1}{2}mu^2$$

where m is the mass of an egg and e the energy involved.

Thus each egg uses

$$.5 \times .0010 \times 287^2 \text{ ergs}$$

that is 41 ergs per egg.

Now the average females has 240 eggs (see below), thus the energy involved in laying all the eggs is 9,650 ergs, say 10,000 ergs

Under natural conditions, *T. subnodicornis* did not usually lay its eggs outside of cavities and therefore the eggs did not travel anything like the average distance of 29 cms. The powerful propulsion of the egg would ensure that the eggs were sent well into the cavity and away from the end most likely to be exposed to dessication.

5. <u>Rate of egg laying</u>.

On 26 May 1955, 75 females which were obviously newly emerged were placed in perforated zinc canisters together with a similar number of males, and then left on the peat moor. At intervals of a few hours, samples were taken, killed rapidly in ethyl acetate , preserved in 4% formalin and dissected later. The actual number of eggs per female are given in Table VIII and Fig. 21 shows the mean number of eggs per female plotted against time.

Table VIII

The number of eggs remaining in females after given times.

Time after emergence	Number examined	Number of eggs	Mean number of eggs
Few minutes	35	345 336 315 312 310 307 298 287 276 263 259 257 243 242 241 240 238 233 230 225 223 215 186 185 182 181 171 170 163 162 149 146 137 135 132 + 297 eggs laid after collecting	240

Table VIII cont.

Time after emergence	Number examined	Number of eggs			Mean number of eggs
4 hours	8	223	82	81	70
		66	60	37	
		39	0		
7 hours	16	190	126	97	35
		71	36	24	
		16	2	1	
		0	0	0	
		0	0	0	
			0		
14 hours	8	72	37	5	14
		0	0	0	
		0	0		
26 hours		69	18	2	11
		0	0	0	
		0	0		

The eggs were laid very rapidly after the completion of copulation and the rate of laying eggs was initially high but gradually decreased as fewer eggs were left in the females. After three hours, over 50% of the eggs had been laid and 90% had been laid after 10 hours.

The short period after emerging when egg

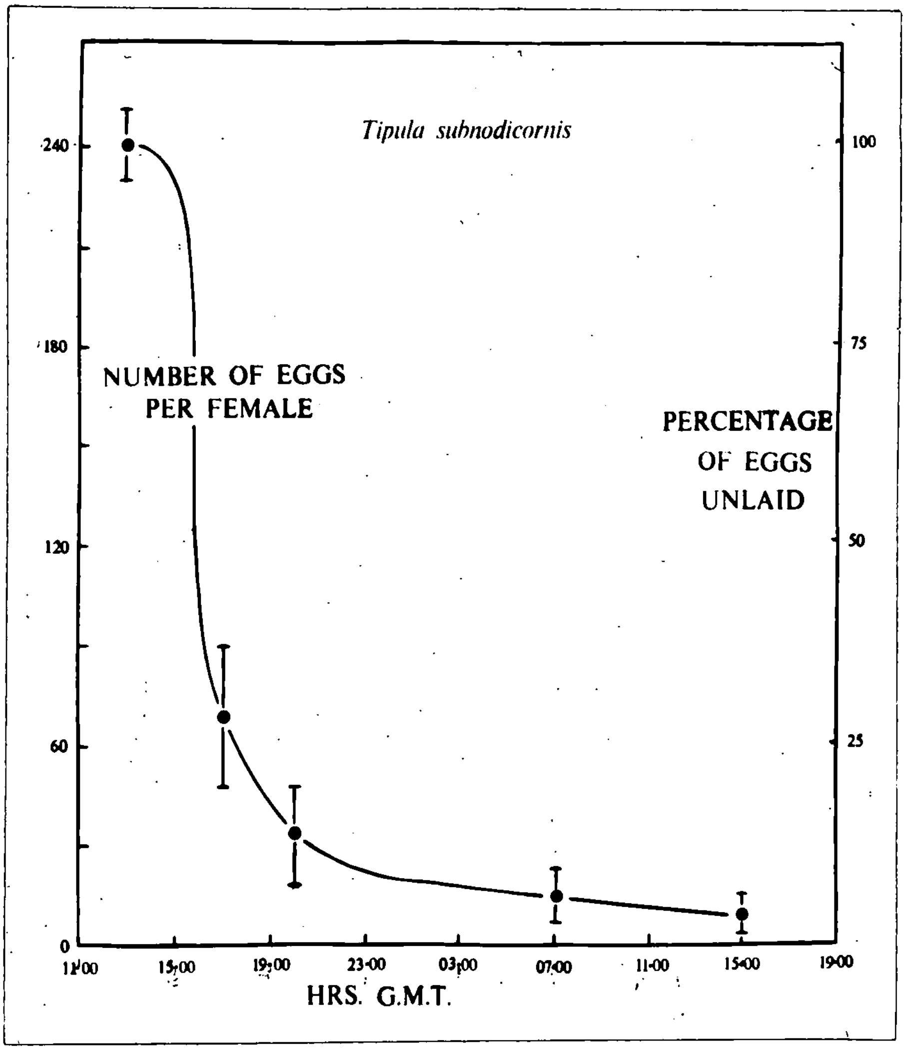


Fig. 21. The egg laying of T. subnodicornis.

laying commenced and the short distance that the marked females moved suggested that the majority of eggs were laid very close to the place of emergence.

2. Release and recapture marking experiments on adults

The method of triple recapture suggested by Bailey (1951) was employed, but modified to deal with the very high mortality found in the adults of this species. This high mortality meant that very few marked animals were recovered on the following day and this was overcome by marking at random throughout the population and recapturing later on the same day.

Marking was carried out between 13.00 and 15.30 hrs. G.M.T. by moving over the 15 metre square study area (Juncus squarrosus dominant) in parallel lines, marking all adults encountered. The area was covered three times in each marking period and always in the same north to south direction. The adults were marked without removing them from their locality, males being marked by placing a hand over them and the females were marked as they moved over the vegetation. Many adults were also marked while they were in copulation, at which time they remained immobile.

The males were marked with a spot of thick cellulose paint at the tip of the sub-costa, as this did not cause the wing to crumple as had been observed when the marks were placed in other positions on the wing. Since the males' flight was weak and occurred readily over a short period of the day, it was felt that marking would not reduce the activity to a marked extent.

The females were divided into two groups; those which were recently emerged and had extended abdomens and pale coloration and those which had been present for at least 4 hours and were fully coloured. The newly emerged females were marked with a spot of paint on the wing tip abd the older females were marked at the base of the wing. The short wings of the females were convenient for marking as they were not used for flight and so unlikely to affect activity.

Recaptures were recorded during the period of marking and also between 16.00 and 18.30 hrs. G.M.T. when the area was covered in parallel lines at right angles to those employed whilst marking.

Marking was carried out on 23 and 24 May and recapturing took place on these days and also on 26 May.

Table X

The numbers of female T. subnodicornis marked

and recaptured.

CAPTURES												
Date	colour	Number captured		Unmarked		Already marked					
						New			Old		
		New	Old	New	Old	B	G	R	B	G	R
23 May 1955	Blue	84	37	84	37	-	-	-	-	-	-
24 May	Green	112	67	112	56	6	-	-	5	-	-
25 May	Red	60	45	60	40	1	2	-	1	1	-
26 May	-	-	-	-	-	-	-	-	-	-	-

Date	RECAPTURES											
	Number of recaptures		Number unmarked		number already marked as							
					New				Old			
	New	Old	New	Old	B	G	R	G + B	B	G	R	G + B
23 May 1955	64	21	55	17	9	-	-	-	4	-	-	-
24 May	64	35	51	26	1	13	-	0	3	5	-	1
25 May	64	15	60	12	0	2	4	0	0	0	1	0
26 May	-	29	-	25	0	0	3	0	0	0	1	0

Table IX

The numbers of male T. subnodicornis marked and recaptured.

CAPTURES								RECAPTURES					
Date	Colour	Number captured	Number unmarked	Number already marked				Number captured	Number unmarked	Number already marked			
				B	G	R	B + G			B	G	R	B+G
23 May 1955	Blue	150	150	-	-	-	-	157	137	20	-	-	-
24 May	Green	152	140	12	-	-	-	211	180	10	20	-	1
25 May	Red	104	97	5	2	-	0	163	150	1	4	8	0
26 May	-	-	-	-	-	-	-	211	195	2	4	10	0

The numbers of marked and recaptured adults are given in Tables IX and X and the relationships used to determine the mortality, expectation of further life and population are given in Appendix I.

The population estimates of male and females of *T. subnodicornis* are given in Table XI

Table XI

The number of adults of *T. subnodicornis* on the study area of 225 sq. metres.

Date	Number of males	Number of females		Total females	Estimate total females
		Recently emerged	Older		
23 May	1,129±246	546±181	163±95	709	743±181
24 May	1,465±318	520±137	344±145	864	895±192
25 May	1,895± 614	780±465	360±231	1,140	1,400±723

Density per square metre			
Date	Males	Females	Total
23 May	5.0	3.3	8.1
24 May	6.5	4.0	10.3
25 May	8.4	6.2	14.6

There was little difference, except on 25 May, in the estimates of the female populations using the total number of females marked and those marked as old and newly emerged calculated separately, (Table XI). The error on 25 May was almost certainly caused by the low number of old females recaptured on that date and the grouped value probably gave the best estimate of the female population on that date.

During the period of marking, the population increased throughout the three days, and there was a preponderance of males in the ratio of 3:2 (Table XII).

Table XII

The sex ratio of Tipula subnodicornis during the period of marking

Date	Percentage males	Percentage females	Total
23 May	60.3	39.7	100
24 May	62.1	37.9	100
25 May	57.5	42.5	100

These results confirmed observations made in the field that the females were less numerous than the males, although it was possible that this impression was due to females being less conspicuous.

The mortality estimates for the males and females are given in Table XIII.

Table XIII

The mortality of adults of Tipula subnodicornis.

Date (May)	Males		Females	
	Percentage mortality per day	Expectation of further life (hours)	Percentage	Expectation of further life (hours)
23-24	39±18	48	58± 18	32
24-25	71±12	22	88± 9	15
23-25	65[1]	26		
23-25	56[2]	31		

[1] Estimated from mark and recapture data and is independent to results given above.

[2] Calculated from mortalities given above.

Over both periods of 24 hours, the male mortality was markedly less than that of the females, the difference being 19% and 17% on the 23-24 and the 24-25 May respectively. This difference in the mortality of males and females may well account for the predominance of males in the population as dissection of larvae suggested that the sex ratio was very close to equality (see p.90). The differential mortality between the sexes gave the males an expectation of further life of one and a half times that of the females.

The mortality of both males and females was markedly increased on the second day of study and this appeared to be entirely caused by the increased radiation from the sun and lower humidity on this second day (Table XIV).

Table XIV

Climatic conditions on 23-25 May 1955 at Moor House.

Date (May)	Max. temp.	R.H.	Rain	Duration sunlight
23-24	52°C	89%	Nil	7.6 hours
24-25	56°C	59%	Nil	13.4 hours

Humidity read at 09.00 hrs. G.M.T.

Table XV shows the emergence or immigration of adults into the population. The fact that the emergence factor was unity for both males and the older females in the 24 hour period on the 25-26 May (i.e. there was no immigration or emergence during this period) suggested that this factor measured emergence only, but it was possible to estimate

Table XV

The emergence of _T. subnodicornis_

Date (May)	Emergence factor		Emergence over 225 sq. m.		
	Males	Females	Males	Females	Total
23-24	1.93±.56	1.67±.19	1,050	498	1,548
24-25	3.13±1.0	5.61±2.3	2,120	4,126	6,246
25-26	.99±.30	-	0	-	-

Note. On 25-26 May the female emergence could not be calculated.

the number of females which entered into the old female grouping. During the 24 hours on the 23-24 May, the emergence factor was 3.37±1.51 being equivalent to an entry of 376 females into the old female grouping. On the 24-25 May the value was 5.81±1.51, being equivalent to an entry of 1,654 females, but on 25-26 May the value was 1 (from a small amount of data) which suggested that no females had entered this group. Thus the data suggested that no emergence took place in the 24 hours after marking on 25 May.

The results of the marking and recapture work showed that *T. subnodicornis* had a very high mortality under the conditions in which the study was carried out, namely dry, sunny days. Since the captures on sticky traps (Fig. 16) indicated that the numbers of adults present increased to one major peak and then declined rapidly, the rate of emergence must take a similar form to the distribution of the numbers captured on sticky traps. Thus the size of the population will almost completely be controlled by the emergence rate and not by the mortality rate.

Soil samples, which were taken in early May, indicated that there was a population density of 117 larvae per square metre on the area at Netherhearth where the marking experiment was carried out. On the 25 May, the day on which the population of adults was almost certainly at its maximum, there was a density of 14.6 adults per square metre, thus representing at least 13% of the total number of possible adults on the area.

3. The egg stage

The eggs of *Tipula subnodicornis* are black (like all members of the genus *Tipula*), lack a conspicuous micropyle and also lack an egg filament. The egg is elongate oval, slightly flattened on one face and the surface is finely etched. The average size, base on 100 eggs from 10 females, was .901 ± .045 mm. long by .334 ± .017 mm. broad.

The eggs took some three or four weeks to hatch in the field and Table XVI shows the time taken for eggs kept on moist filter paper to hatch under controlled temperature conditions in the laboratory.

Table XVI

The time for eggs of *T. subnodicornis* to hatch.

Number of eggs	Temperature °C	Spread of hatching (hours)	Mean time	Percentage hatching
112	14 with fluctuations	24-48	12.5±.5	58
47	"	12-24	11.5±.5	38
52	20	12-24	8.5 ±.5	44
68	10	12-24	21.5 ±.5	38

At 20°C the eggs hatched in 8.5 days but at 10°C, a temperature much more likely to be encountered in the field, the development period was 21.5 days. It is worth noting that the average percentage of eggs which hatched was 47%. The low value was probably produced by factors other than the technique used since Barnes (1937) recorded low hatching rates for eggs of Tipula paludosa. As will be seen below, 25% of the eggs failed to hatch under field conditions and it was possible that a high proportion of the eggs were infertile.

Egg mortality under field conditions.

After all eggs should have hatched, samples of peat were collected and dispersed in magnesium sulphate solution to float out the eggs.

Table XVII

Hatching success of Tipula subnodicornis

Year	Number of eggs examined	Hatched		Unhatched		Chorion broken, contents destroyed	
		No.	%	No.	%	No.	%
1954	1,011	792	78	178	18	41	4
1955	364	261	72	40	11	63	17

Eggs which had hatched successfully had a longitudinal split along the chorion, while those which had been split or holed elsewhere had probably been sucked by predatory arthropods. Table XVII gives the data for 1954 and 1955 and while these figures may give a reasonable estimate of the fate of the eggs, eggs which were completely destroyed could not be considered.

This data suggested that between 70 and 80% of the eggs hatched, while about 15% are infertile or die during development and at least 10% were destroyed by predators which pierced the chorion.

The differences between the percentage hatching in 1954 and 1955 was not significant but that for the predation was highly significant, ($P < .001$).

The vertical distribution of eggs

Table XVIII gives the number of eggs recovered from samples taken to estimate the egg density. Each sample was sub-divided into the three layers that are found on Juncus squarrosus moor, namely the new, upper layer, the old, middle layer and the bottom solid peat layer. The majority of the eggs were

Table XVIII

The vertical distribution of eggs of *T. subnodicornis* on *Juncus squarrosus* moor

	New litter	Old litter	Solid peat	Total
Average depth (cms)	0 - 1.0	1.0 - 3.0	below 3.0	
Number of eggs	61	185	119	365
Percentage of eggs	17	51	32	100

laid in the middle layer and a third of the total were laid in the solid peat.

4. The larval stage

White (1951) states that *Tipula lateralis* has four instars and Alexander (1920) quotes Bengtsson,(1897) as stating that *Phalacrocera replicata* has at least 8 and possibly 10 moults. Apart from these statements, nothing has been published indicating the number of instars in *Tipulidae*. Most authors (Alexander 1921 and Barnes 1937) merely refer to the first stage or final larval stage.

An attempt was made to determine the number of larval stages in *T. subnodicornis* by means of head capsule measurements, but these failed to give satisfactory results for two reasons. First, the capsule took some time to harden off and appeared to grow during this period, and secondly because the head capsule flanges tended to open and flatten out as the larva approached the next stage, thus giving variable results within one instar.

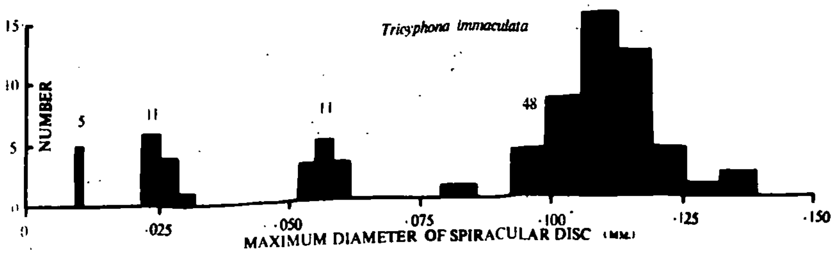
Measurements were repeated using the maximum diameter of the spiracular discs and these gave satisfactory results, not only for

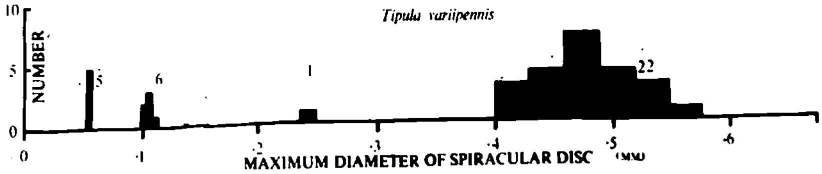
T. subnodicornis, but for other species studied. The maximum diameter of the spiracular disc was used as this disc changed from a circular form in the first instar larvae, to an oval in later larval stages and in the case of the latter, the greatest diameter was the most easily measured. Fig. 22 shows the distributions of the diameter of the spiracular discs for *T. subnodicornis* and it will be noted that they fall into four well defined groups. These groups were not the result of four different collections of larvae, as larvae were collected on at least 10 occasions and also larvae collected on the same day contributed two of the distributions but showed no intermediates.

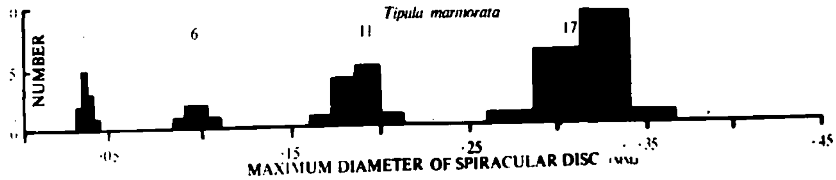
Data collected for *Tipula paludosa*, *T. variipennis*, *T. marmorata* and *Tricyphona immaculata* and presented in Fig. 22 all indicated that these species were like *T. subnodicornis* in having four larval instars. It should be added that for all of these species, larvae were hatched from eggs to ensure that the first instar had been recorded.

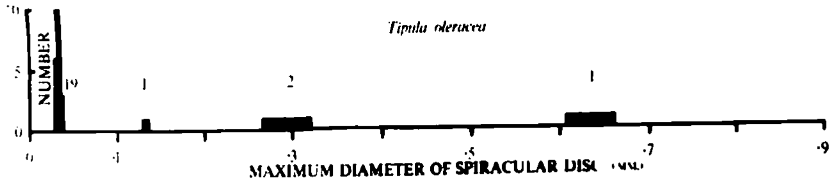
The spiracular region of the first instar

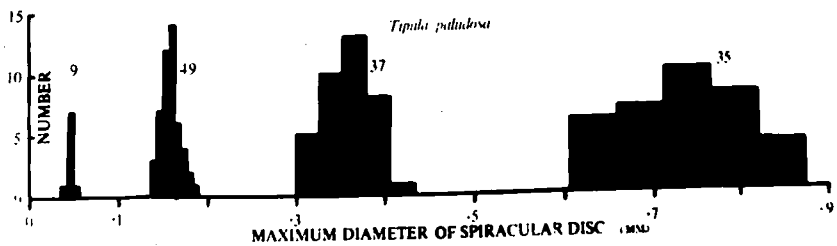
Fig. 22. The maximum diameter of the spiracular discs of samples belonging to six species of *Tipulidae*, indicating that each species had four instars.

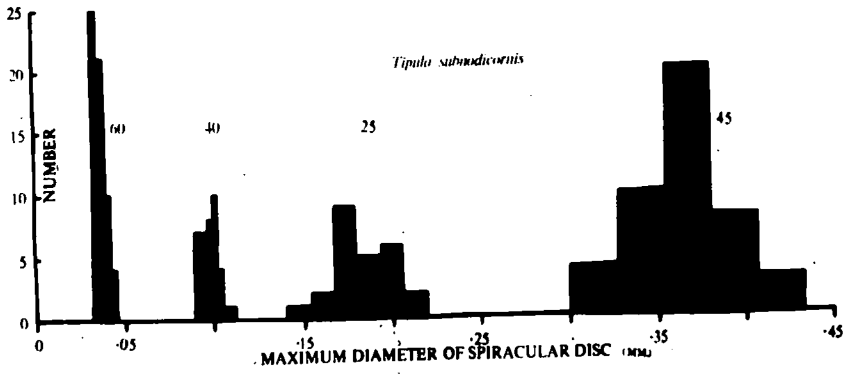

Tricyphona immaculata
NUMBER
MAXIMUM DIAMETER OF SPIRACULAR DISC (MM)
5
11
11
48
0
·025
·050
·075
·100
·125
·150


Tipula variipennis
NUMBER
MAXIMUM DIAMETER OF SPIRACULAR DISC (MM)
5
6
1
22
0
·1
·2
·3
·4
·5
·6


Tipula marmorata
NUMBER
MAXIMUM DIAMETER OF SPIRACULAR DISC (MM)
6
11
17
·15
·25
·35
·45


Tipula oleracea
NUMBER
MAXIMUM DIAMETER OF SPIRACULAR DISC (MM)
19
1
2
1
·3
·5
·7
·9


Tipula paludosa
NUMBER
MAXIMUM DIAMETER OF SPIRACULAR DISC (MM)
15
10
5
9
49
37
35
·1
·3
·5
·7
·9


Tipula subnodicornis
NUMBER
MAXIMUM DIAMETER OF SPIRACULAR DISC (MM)
25
20
15
10
5
0
60
40
25
45
·05
·15
·25
·35
·45

larva of Tipula subnodicornis, (Fig.18) differed markedly from that of the remaining three instars, illustrated in Fig. 19 E, in having only four spiracular lobes, in the shape of the spiracular disc and in having many long hairs which may serve to prevent the larvae from drowning as these hairs appear to function in a similar manner to those of mosquito larvae in keeping the spiracular disc above water level.

Population study.

A population study on T. subnodicornis larvae was carried out on a Juncus squarrosus dominant area at Netherhearth. This area held a large population in 1953, 1954 and 1955 but in 1956 the population disappeared.

The monthly population estimates are graphed in Fig. 23 and the actual sample data in Appendix II. This figure illustrated the very large mortality that a species with a fecundity as large as this tipulid must encounter, if the adult population is to remain relatively constant from year to year. In both 1954 and 1955, the major part of the mortality occurred during the

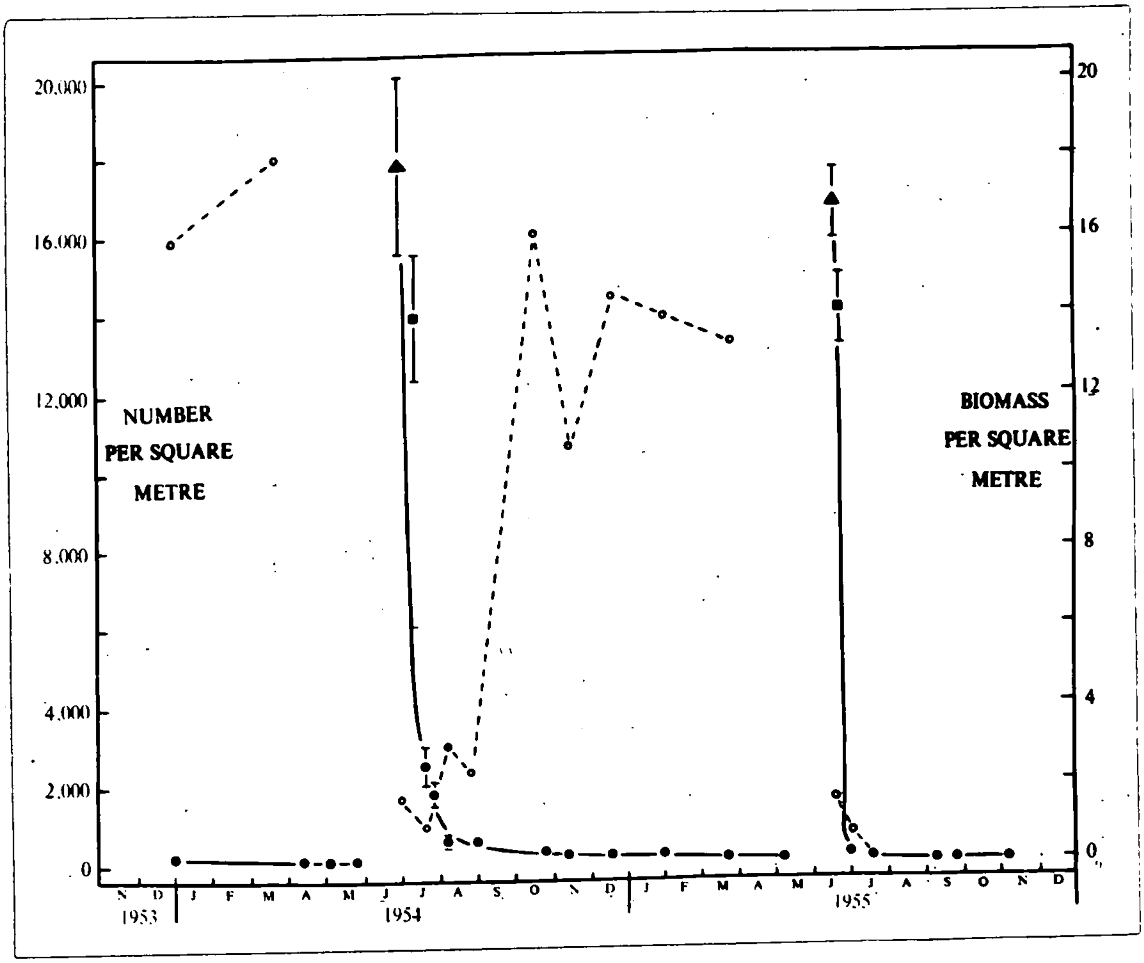


Fig. 23. The immature populations and bio-mass of T. subnodicornis, 1953 to 1955. Solid line represents population; interrupted line, bio-mass. Triangle = egg population; square = hatching population (estimate); circles = larval population

egg and the first instar stage, the mortality being approximately 95% of the total number of eggs laid in 1954 and 100% in 1955. There was little difference in the form of the curves in these seasons, yet in 1954-55 season the final population of larvae was 168 larvae per square metre, while in season 1955-56, the population was well below 7 larvae per square metre (no larvae were found in 90 samples and at P = .05, the maximum population present was less than 7 per sq. m.).

The overwinter mortality in 1953-54 season was calculated from samples that were taken on 2 December, 1953 and the 3 and 4 May, 1954. This gave an estimate of 50% mortality during the 4 months. In season 1954-55, the mortality was estimated from samples taken on 7 November and 22 December, and 4 and 10 May. The overwinter mortality was 37%, the population decreasing from a density of 185 to 117 larvae per square metre.

Duration of stages.

From the samples of larvae taken throughout the season, it is possible to determine the duration of the four instars, as well as that of the egg and pupa.

Egg	Late May to mid-June	3-4 weeks
1st. inst instar	Mid-June to mid-July	4 weeks
2nd. instar	Mid-July to mid-August	4 weeks
3rd. instar	Mid-August to mid-September	4 weeks
4th. instar	Mid-September to late April	32 weeks
Pupa	Late April to late May	4 weeks
Adult	Late May to early June	3-7 days

Growth of larvae under field conditions

The growth curve of T. subnodicornis under field conditions in the season 1954-55 is shown in Fig.24. It will be noticed that the rate of growth slowed down in October and November, this probably being caused by the fall in temperature at this time of

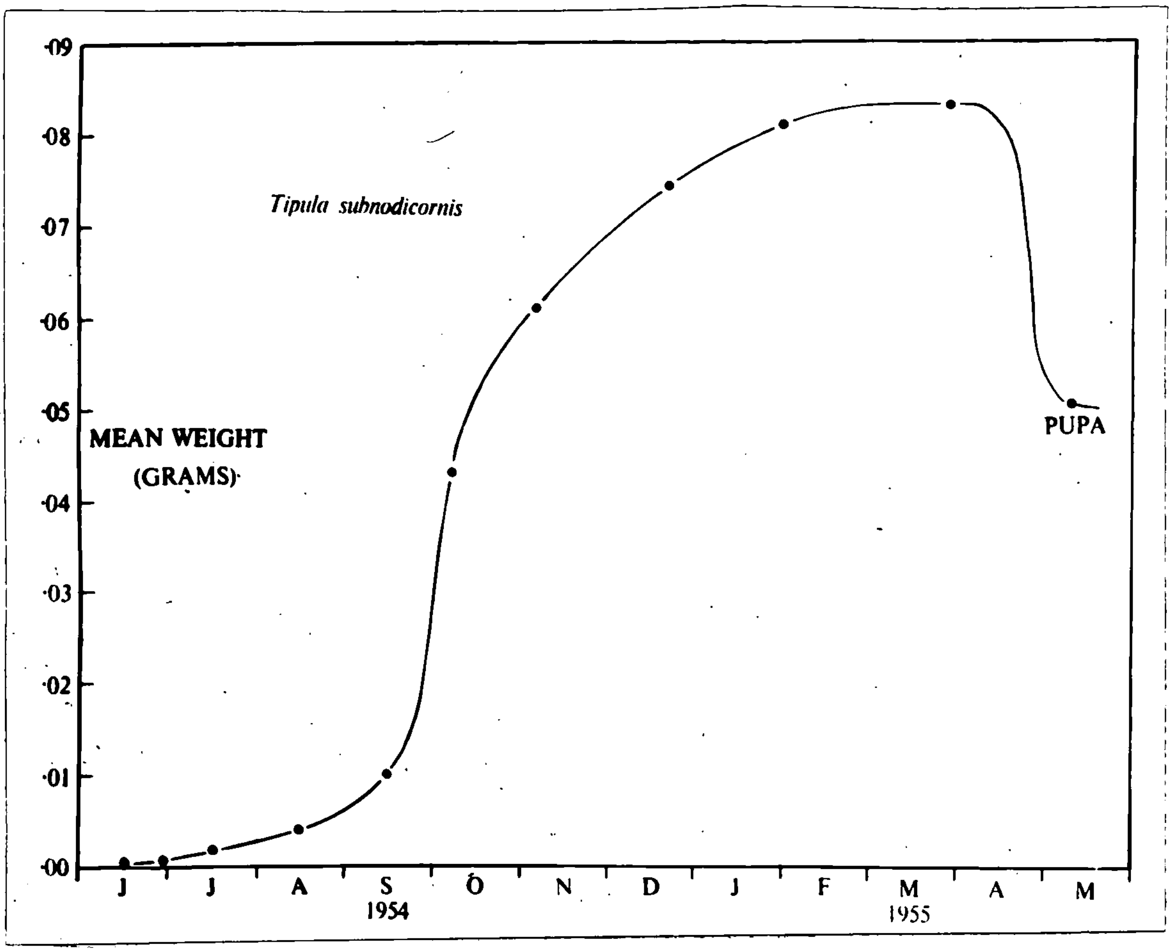


Fig. 24. Field growth curve of Tipula subnodicornis larvae.

year. The growth rate did not increase again in the Spring as the larvae had apparently become fully developed by this time.

Fig. 23 illustrates the change in population size and bio-mass. The peak of bio-mass occurs in late September, a time when larvae had just entered into the final instar, and it was estimated that there was 16.0 grams live weight per square metre. The bio-mass increased very rapidly during the summer and came to a peak in September, followed by a fairly steady value, where the growth was balanced by the over winter mortality.

The weight of the pupae was markedly lower than that of the last instar larvae and this was almost certainly caused by loss of water.

Sex ratio of larvae.

Difficulty was found in determining the sex ratio of this species since emergence traps did not function satisfactorily and two sexes differed markedly in their behaviour in the adult stage. It was found possible to sex final instar larvae by dissection, as the gonads were well developed by this time. The paired ovaries were cream coloured, lenon-shaped structures and were transparent enough to show the ova <u>in situ</u> under x7 magnification. The testes were flattened (almost disc shaped), opaque, white bodies with no obvious structure under low magnification. They appeared to be a much less compact body than the ovaries.

The dissection of 85 larvae taken in March, 1955 gave 43 females and 42 males, a result which suggested that the sex ratio was near equality.

Larval populations on different vegetation types. As already mentioned, *T. subnodicornis* larvae have been recorded from most localities on which peat occurred, irrespective of the type of plant vegetation that was present. However Table XIX shows that the population density varied considerably from one vegetation type to another. The data given in Table XIX was selected from samples taken in late December to early April, so as to give a reasonably representative and comparable value of the larval populations. The highest densities were obtained from samples taken on *Juncus squarrosus* dominant areas and on an area with thick growth of *Eriophorum vaginatum*. The lowest densities were obtained on a Sphagnum Bog and also on the well drained tops of peat hags with a complex of *Calluna* and *Cladonia*.

Table XX shows data from seven habitats chosen as representatives of different types of vegetation and also the significance of the differences between

Table XIX

Population densities of *T. subnodicornis* larvae

Locality	Vegetation	Number of samples	Larvae per sample	Density per sq. m.
Netherhearth 1953-54	Juncus squarrosus	60	1.37	168
Netherhearth 1954-55	Juncus squarrosus	30	1.13	140
Valley Bog 1953-54	Juncus squarrosus	29	0.90	111
Valley Bog 1954-55	Juncus squarrosus	19	0.84	104
Above Netherhearth	Eriophorum vaginatum	40	0.84	104
Trout Beck	Calluna-Sphagnum	60	0.55	68
Top of House Hill	Eriophorum-Sphagnum	42	0.51	63
Burnt Hill	Calluna-Eriophorum (errosion)	58	0.48	60
Bog Hill	Sphagnum-Calluna	15	0.33	41

Table XIX cont.

Locality	Vegetation	Number of samples	Larvae per sample	Density per sq. m.
Valley Bog 1954-55	Sphagnum	31	0.29	36
House Hill	Calluna-Cladonia (Hag tops)	20	0.15	19
Valley Bog 1953-54	Sphagnum	22	0.14	17
Moss Burn	Alluvial drift grassland	60	0.00	0

the larval densities.

Since the larval populations in the seasons 1953-54 and 1954-55 were very similar (e.g. Valley Bog and Netherhearth, Table XIX), it was possible to compare samples taken from different plant communities in the two years. Further, since these years appeared to be years of maximum abundance of the species, then the order of habitats in Table XX gives the order of maximum number of larvae that these areas are capable of supporting.

Table XX

Vegetation type	Date of sampling	Number of samples	Larvae per sample	Density per sq. m.
1. Juncus squarrosus	6.4.54 12.4.54	60	1.13	140
2. Eriophorum vaginatum	7.4.55	40	.84	104
3. Calluna-Sphagnum-Eriophorum	20.3.54	58	.48	60
4. Calluna-Sphagnum	7.4.54	15	.33	41
5. Sphagnum	22.12.54 1. 2.55	53	.23	28
6. Calluna-Cladonia	13.4.55	20	.15	19
7. Alluvial grassland	30.3.55	30	.00	0

Table of probabilities

	2.	3.	4.	5.	6.	7.
1.	n.s.	.001	.001	.001	.001	.001
2.		.04	.02	.001	.001	.001
3.			n.s.	.02	.01	.001
4.				n.s.	n.s.	.03
5.					n.s.	.001
6.						n.s.

n.s. = not significant

Note. The distribution of larvae in samples suggested that there was little tendency to aggregation and the mean has been used as the best estimate of the variance.

The suitability of habitats for *T. subnodicornis*.

Juncus squarrosus moor, which held the largest population of *T. subnodicornis* recorded, seemed to be so suitable to this species because of the thick layer of loose, damp, plant remains found on the surface of the peat. This layer was often over 3cms. deep and gave the habitat a third dimensinn , in contrast to the others.

Eriophorum vaginatum was the second most favoured habitat and here there was some evidence that the liverworts, which were found commonly between the *Eriophorum* stems, were important in the distribution of this tipulid. Table XXI

Table XXI

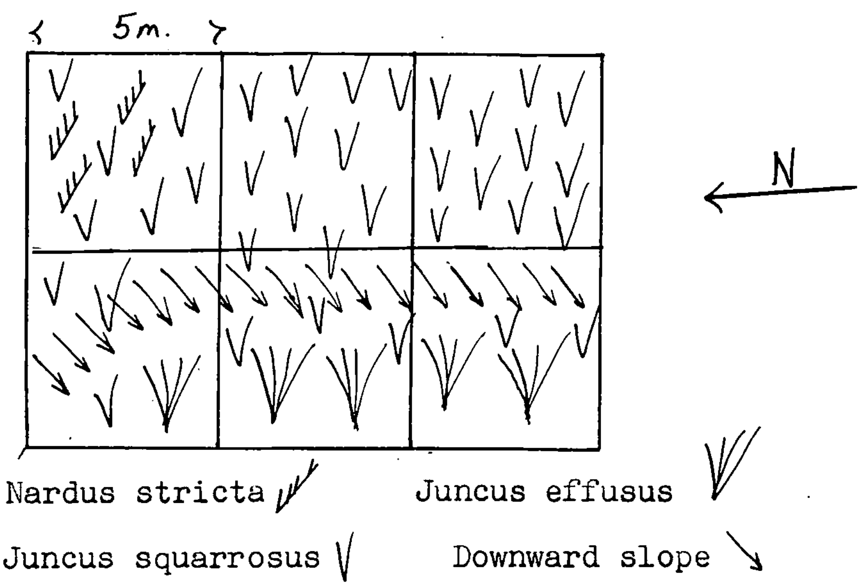
The distribution of *T. subnodicornis* on an *Eriophorum* moor according to the liverwort distribution.

	No liverworts	Liverworts present
No. of samples	22	18
No. of samples with T. subnodicornis	7	13
No. of tipulids found	10	24
No. tipulids per sample	.45	1.33

shows that there was a marked preference for areas covered by liverworts. A 2 by 2 contingency table was made of samples with or without liverworts and with or without larvae of T. subnodicornis. After Yates correction had been applied, a χ^2 test of5.0 with 1 d.f. was obtained (P$\leq$.05). A χ^2 test was also carried out on the total numbers of tipulid larvae found in samples with liverworts as against those without liverworts and a χ^2 = 7.0 with 1 d.f. (P<.01).

5. Distribution of T. subnodicornis on a Juncus squarrosus moor.

The study area at Netherhearth was divided into six areas, thus:-



The major part of the area was covered by <u>Juncus squarrosus</u> but at the north end of the area, <u>Nardus stricta</u> occurred commonly. On the west side of the area there was a dip with a few plants of <u>Juncus effusus</u> at the base.

Tables XXII, XXIII and XXIV show the distribution of larvae, adults and eggs in each of these six areas.

Table XXII

The distribution of larvae on the study area.

				Total
	16	24	30	70
	24	39	41	104
Total	40	63	71	174

Note. These totals consist of samples taken on 14.9 and 7.11.54 and 1.2, 22.3 and 4.5.55.

Expected in all six areas = 29 larvae.

χ^2 = 16.0 with 5 d.f. (P < .01)

Expected in east three areas and west three areas =87

$\chi^2 = 6.6$ with 1 d.f. $(P < .01)$

Expected in the north centre and south areas

= 58

$\chi^2 = 9.1$ with 2 d.f.   (P almost = .01)

There was a significant tendency for the larval population to be less towards the north and east of the area.

Table XXIII

Distribution of adults on the study area.

				Total
	6	12	27	45
	8	20	19	47
Total	14	32	46	92

Note. The numbers were the result of a direct count made on 24. 5. 55.

No statistical difference existed between the top three areas (east) and the bottom three areas (west).

The expected for the north, centre and south sections = 30.6

$\chi^2 = 16.7$ with 2 d.f. $(P < .01)$

There was a significant difference between the numbers of adults found on the north and south of the area; the population being greatest to the south.

Table XXIV

Distribution of eggs on the study area.

				Total
	39	56	79	174
	50	58	82	190
Total	89	114	161	364

There was no significant difference between the number of eggs laid on the top (east) and the bottom (west) of the area.

The expected number of eggs in the north, centre and south areas was 121.

χ^2 = 20 with 2 d.f. was obtained ($P < .001$)

A significant difference was found in the distribution of the numbers of eggs laid and more eggs were laid in the southern part of the area than in the north.

There were marked similarities between the distribution of larvae, the subsequent adults and also their eggs on the study area. They were all more numerous on the southern, deeper peat area than on the northern shallow peat area. In all the three stages, there was also a trend for more tipulids on the bottom part of the area.

6. Causes of mortality in *T. subnodicornis*.

Egg.

There appeared to be no egg parasites. The greater part of the egg mortality was caused by infertility, dessication and probably to a lesser extent, predation.

Larva.

Of many hundreds of larvae reared in the laboratory, only one larva was found to be parasitised. The parasite was *Crocuta* (= *Bucentes*) *geniculata*, a tachinid *Diptera*, adults of which were taken frequently in the field and moor by sweeping the vegetation. It was therefore thought that *T. subnodicornis* was not the major host of this species and it was possible that some other species of tipulid was parasitised more frequently.

Over wintering larvae were found parasitised by a fungus which appeared to invade the tracheal system and turned the trachea black. This fungus appeared to be fatal to the larvae and none which were infected, survived in the laboratory. It was thought possible that this might have been the cause of much of the over winter mortality, although never more than 8% of the population was ever found infected at any one time.

There was no evidence that any vertebrate used the larval stage of this tipulid as a major item of food; the moor being virtually deserted by birds during the final instar stage of the tipulid.

Pupa.

No mortality was recorded for pupae but a number of cases were recorded where the adult had died while only partly out of the pupal case.

Adult.

The majority of the adult mortality appeared to be caused by the exhaustion of the food reserves or dessication. Adults of this species were never observed feeding but were found drinking on sunny days. Spiders, an empid *Empis borealis*, the common Frog and the Meadow Pipit were recorded as preying on the adults. Dead adults have been seen to be devoured by *Arion ater*.

7. *The effects of drought and high rainfall on the numbers of T. subnodicornis*.

At Moor House, the seasons 1954 and 1955 were years of extremes as far as rainfall was concerned. 1954 was excessively wet while the following year was unusually dry during the summer months. In 1954, the annual rainfall was 102 inches and was distributed evenly throughout the year. This high rainfall, which represented about 133% of the average, had very little effect upon the final larval population in the following Spring, as the population was similar to that of the previous year.

1955 was exceedingly dry during the Summer months of June, July, August and September. Sampling on the Netherhearth *Juncus squarrosus* moor showed that similar numbers of eggs were laid and hatched during this period as in the previous year (Table XXV), but that few larvae survived the first instar stage and subsequent sampling produced no larvae. The data in Table XXV may

Table XXV

Egg and larval populations at Netherhearth <u>Juncus squarrosus</u> moor in 1954 and 1955.

Year	Density of eggs per sq. m.	Percentage of eggs hatching	Density of larvae per sq. m.	
			First instar	Second instar
1954	18,000	78	3,300	1,300
1955	17,000	72	180	0

be correlated with the condition of the moor in 1955. The peat began to dry out in late June (after heavy rain in May) and by July, the surface peat had dried out. Table XXVI shows the water content of the peat on 20 July and 7 November and by the latter date, there had been some rain but the peat was still noticeably dry.

The term "relative humidity" has been used in the sense used by Crump (1913) and Pearsall (1950) as a measure of the water content of peat

Table XXVI

"Relative humidity" water content of _Juncus squarrosus_ peat at Netherhearth on 20 July and 7 November, 1955.

Sample point	20 July		7 November	
	Top, loose peat	Bottom, solid peat	Top, loose peat	Bottom solid peat
A	2.6	3.2	4.9	3.8
B	2.4	2.8	5.0	5.3
C	3.3	4.8	6.3	4.5
D	5.6	4.1	8.3	6.6
E	2.1	3.9	5.9	4.7
Mean	3.20	3.76	6.08	4.98

soils:-

$$\text{"Relative humidity"} = \frac{\text{water}}{\text{dry weight}}$$

The samples were dried at 98°C.

As will be seen from Table XXVI, the peat was drier on the surface, loose peat, the habitat of _T. subnodicornis_ larvae and eggs. The area continued to dry out during August and early

September and the samples taken in November showed that the rain had increased the water content of the top peat to a greater extent. This was obvious from general observation, for, as late as December, peat cores could be broken into two distinct parts, the upper wet peat, which was easily separated from the still dry lower peat (3-10 cms.).

Rennie (1917) and personal observations have shown that first and second instar larvae of various species of the genus <u>Tipula</u> were very susceptible to dessication and the former quotes a country saying that "a wet autumn brings many leather jackets in the following Spring." This presumably applies to <u>T</u>. <u>paludosa</u>.

Rogers (1942), working in Michigan, U.S.A., gives information about the effects of a very dry year, followed by an excessively wet one , on populations of <u>Tipulinae</u>. The years were 1936 with only 57% of the normal rainfall during the Summer, and 1937 with abundant rainfall during the Summer. In 1936, species which required very wet larval habitats were plentiful but in 1937 they were rare.

This was attributed to the fact that the females ovipositing in 1936 placed their eggs in situations liable to be flooded in the following year, and this caused the wholesale drowning of larvae and pupae. However it seemed more likely that the drop in the adult population in 1937 was a result of the greater mortality of young larvae through dessication in 1936. Since no quantitative sampling was carried out, the cause of the mortality remains obscure. It is also worth noting that the adult populations had returned to about normal in 1938 which indicated that the excessive rain did not have an adverse effect upon the larvae. This was in agreement with the observations at Moor House in 1954 when there was excessive rain.

8. The effect of dry weather on the larval populations of *T. subnodicornis* in different habitats.

The sampling of *T. subnodicornis* populations between 1953 and 1956 showed that the densities of final instar larvae were similar in 1954 and 1955, but showed that considerable changes occurred in 1956, apparently because of the effect of the very dry summer in 1955. Table XXVII gives the larval population density in three habitats in these years. It is at once evident that in 1954 and 1955 the *Juncus squarrosus* area supported the largest population, being followed by the *Eriophorum*, while the *Sphagnum* Bog supported a very small population. In 1956, the *Juncus sqarrosus* and *Eriophorum* had exceedingly few larvae while the *Sphagnum* Bog population had not decreased significantly. Thus these wet, boggy areas may not be able to support a high population of this tipulid but can act as a reservoir for the species in years when the rainfall is low.

Table XXVII

Population density of final instar larvae of *T. subnodicornis* (per sq.m.)

Habitat	1954	1955	1956
Juncus sqaurrosus	168	140	0
Eriophorum	70	104	4
Sphagnum Bog	17	36	14

9. *The food of larvae of T. subnodicornis.*

Larvae, recently collected in the field, were placed in clean, damp tubes and under these conditions faeces could be collected and examined. It was found that many plant cells passed through the intestine without damage to the cell wall or chloroplasts and that species of plants used as food could be determined in most cases. No quantitative study was made but the following materials were recorded from the faeces of *T. subnodicornis*.

1. *Juncus squarrosus* moor

Rootlets and root-hairs of *J. squarrosus* and the dead "leaflets" of *Polytrichum commune*.

2. *Eriophorum* moor

The larval faeces produced little other than pieces of liverworts. These were found to be mainly *Diplophyllum albicans* and to a lesser extent, *Ptilidium ciliare*. The first named species was the commoner over both the locality and within the faeces.

3. *Sphagnum* Bog

Only the typical structure of Sphagnum was found in the faeces.

VI Study of *Tipula paludosa*.

1. Adults.

The duration of adults at Moor House (measured by sticky traps) and Rothamsted experimental station, Harpenden, Herts. (measured by light trap captures) are shown quantitatively in Fig. 25. There was a very marked difference in the time of emergence at these two stations, the modes being about eight weeks apart. Although the records were carried out in different years (1933-36 at Rothamsted; 1954-55 at Moor House), there was little evidence of annual fluctuations in the time of emergence at either station and the earlier emergence at Moor House is almost certainly real.

Since Moor House has lower temperatures and a more severe climate than Rothamsted, it was surprising to find that *T. paludosa* was emerging earlier at the former station.

Emergence rhythm.

General observations carried out in 1954 suggested that *T. paludosa* emerged during darkness.

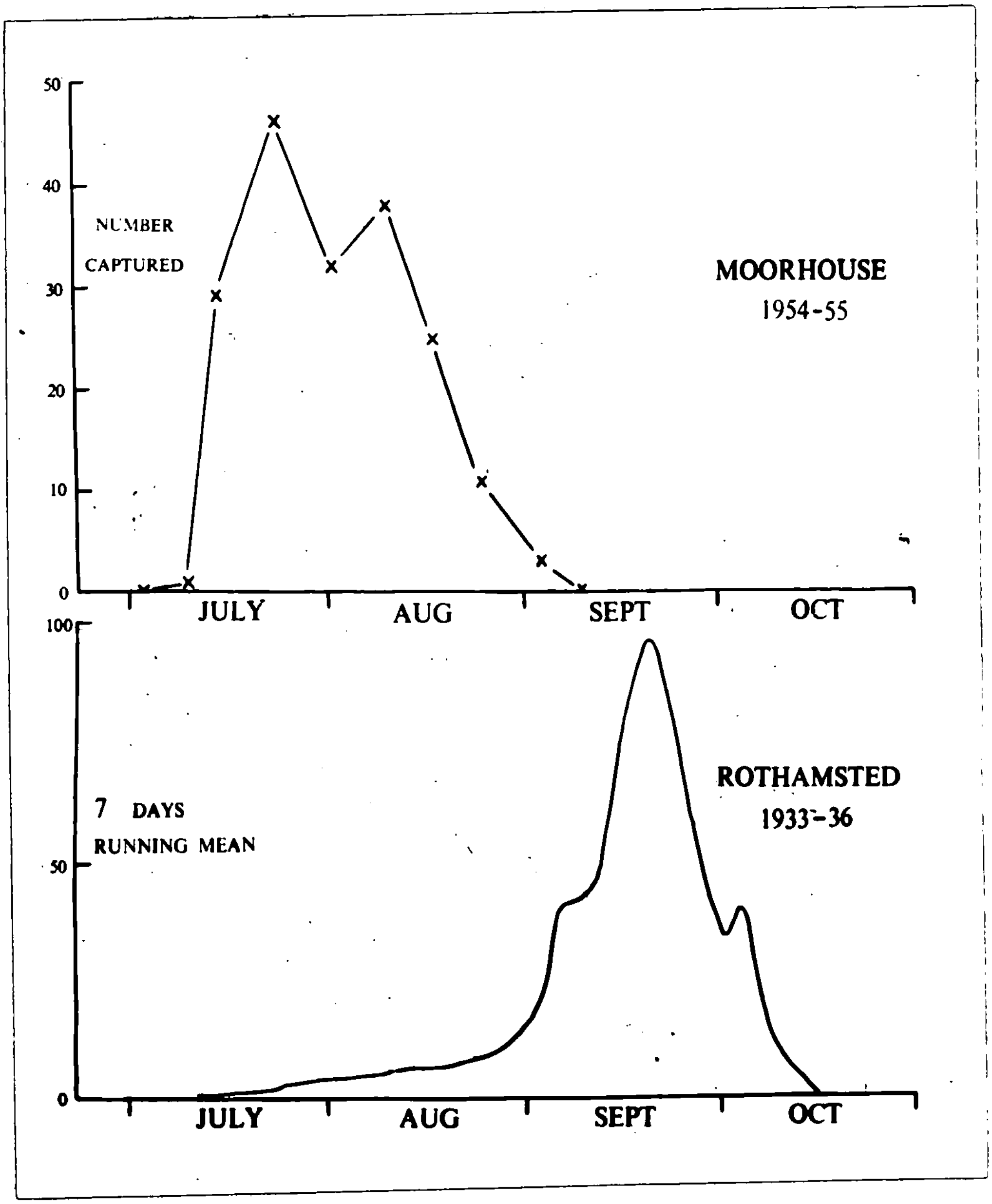
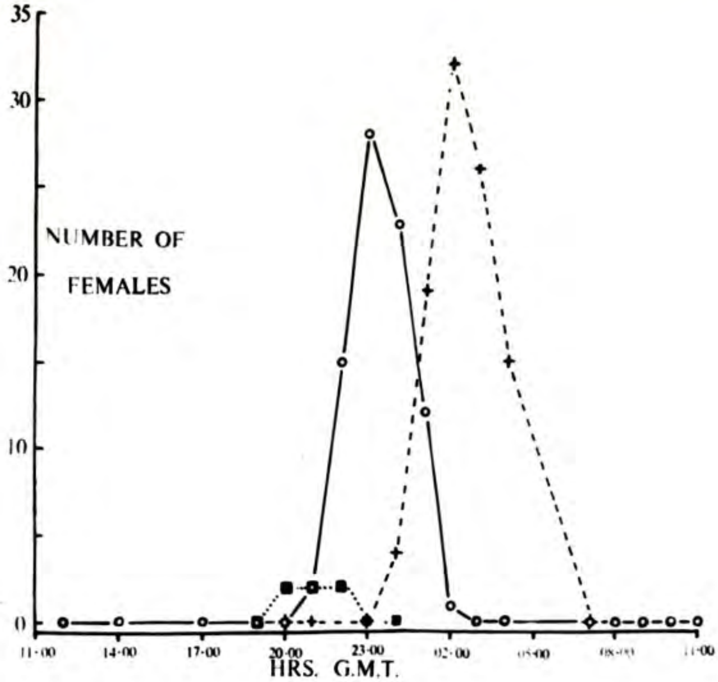


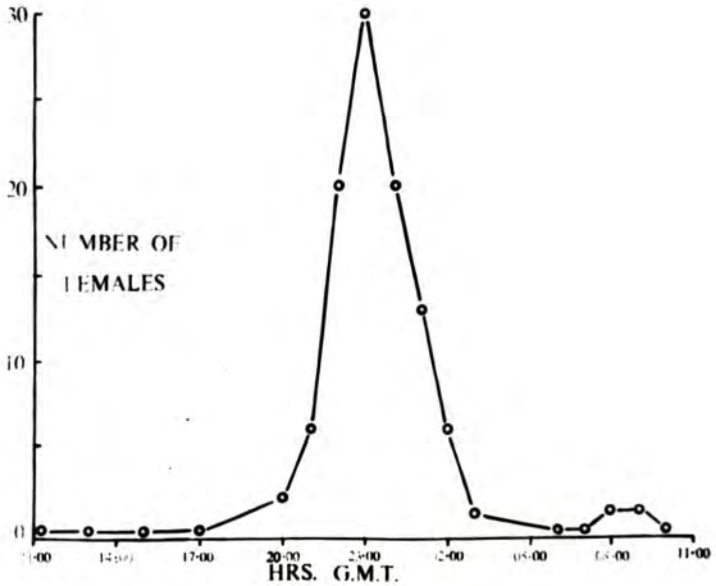
Fig. 25. The duration of adults of *Tipula paludosa* at Moor House and Rothamsted.

Fig. 26. The number of newly emerged females mating on 64 sq. meters.

Bottom. 11 July, 1955.
Middle. 12 July, 1955.
Top. 18 July, 1955.

Circles, females mating.
Crosses, females egg laying.
Squares, females emerging.


35
30
NUMBER OF
FEMALES
20
10
0
11·00
14·00
17·00
20·00
23·00
02·00
HRS. G.M.T.
11·00


30
20
10
0
11·00
17·00
20·00
23·00
HRS. G.M.T.
11·00

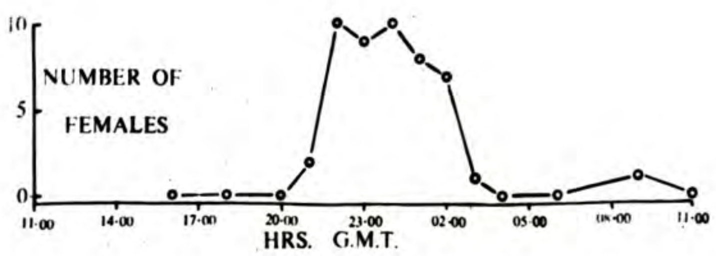

10
NUMBER OF
5
FEMALES
0
11·00
14·00
17·00
20·00
23·00
02·00
05·00
HRS. G.M.T.
11·00

Fig. 26 gives quantitative data of the number of newly emerged females found in copulation and, on one date, the number of females that were laying eggs. Since copulation followed immediately after emergence, the graphs give an indication of the time of emergence. The emergence began with the onset of dusk and reached its peak before 23.00 hrs. The conclusion of copulation, which usually occurred about an hour before dawn, was followed by egg laying and this continued extensively for the first hour or two after dawn.

When these observations were made, the weather consisted of long periods of cloudless skies and the grass minimum fell to within a degree or so of freezing point in the early hours of the morning. As the evening progressed, male activity lessened so that by dawn the males were virtually inactive and had been flightless since 23.00 hrs. The newly emerged females made no attempt to fly and depended entirely upon their legs for movement. On emergence from the soil, the adult females made for a tall tuft of grass, _Juncus squarrosus_ or _J. effusus_ stems, climbed it and entered into copulation with a male.

Activity.

When a particular area was examined before dawn and at about 09.00 hrs. G.M.T., it was clear that the population was more apparent on the former occasion. Some mornings, the entire population disappeared from view, giving the impression that the population was very low or non-existant. Investigation of this apparent absence showed that the adults took cover in tufts of Juncus effusus, working their way into the debris and long grass found at the base of these tufts. Shaking the vegetation did not usually cause the flies to leave the vegetation, and a great deal of provocation was required before the adults could be induced to fly. As may have been expected, these areas shielded the adults from the direct radiation of the sun and gave less fluctuations of temperature throughout the day, (Table XXVIII). The differences in the temperatures inside and outside of the Juncus tufts were greater during sunshine than when the sun was behind clouds and, as was to be expected, after sun-set, the temperatures inside the Juncus tufts were higher than

Table XXVIII

Temperatures inside and outside of Juncus effusus tufts, July 18, 1955.

All readings taken 3 cm. above ground level.

Time G.M.T.	Direct sunlight	Temperature °C	
		Inside tufts	Outside tufts
14.00	No	17.5	19.5
14.30	Yes	19.5	23.5
15.25	Yes	19.0	23.0
16.00	Yes	21.0	26.5
16.10	Yes	20.5	27.0
21.00	No	13.0	11.0
22.00	No	11.5	8.5

those outside. The Juncus tufts appeared to have higher humidities than outside, but these were not measured, although it was noted that dew disappeared much later from the centre of the tufts .

The data in Table XXIX shows that adult males of T. paludosa lived longer in a high humidity. The adults were kept in similar jars and in similar

Table XXIX

The average number of days adult males of *Tipula paludosa* lived under controlled humidities.

60% R.H.		c. 90% R.H.	
Number used	Mean length of life (days)	Number used	Mean length of life (days)
18	2.67 st.dev.±1.3	39	5.80 st.dev.±2.1

The difference between the means = 3.13± .45 days ($P<.0001$)

positions. Both jars had a sheet of filter paper which in the case of one group was dry and in the other was dampened each day. The jars were sealed and tests with cobalt thiocyanide papers indicated that the relative humidity was 60% and 90% under these conditions.

This experiment indicated that there was a possible protective mechanism in the adults of *T. paludosa* seeking shelter in tufts of vegetation and thus avoiding direct radiation and low humidities.

A possible explanation of the differences in the time of appearance of adults of *Tipula paludosa* at Moor House and Rothamsted, may be found in the nocturnal activity of this species. Emergence, copulation and the major part of the egg laying take place at a time when the daily temperature is at a minimum. The minimum temperatures at Moor House during July, may reach as low as 1° or 2°C above freezing point and are reproduced in southern England during September (data from Greenwich, alt. 149 ft.), the time of emergence of *T. paludosa*. The Moor House minimum temperatures in September show many nights with marked ground frosts and obviously these temperatures would not be condusive to nocturnal activity by this tipulid. It is interesting to note that Robertson (1939) has shown that the degree of nocturnal activity of *T. paludosa*, as recorded by light trap captures, was governed by the daily minimum temperature.

If this suggestion is true, then *T. paludosa* has adapted its life cycle to the conditions found in these particular areas. Further data from other localities is required.

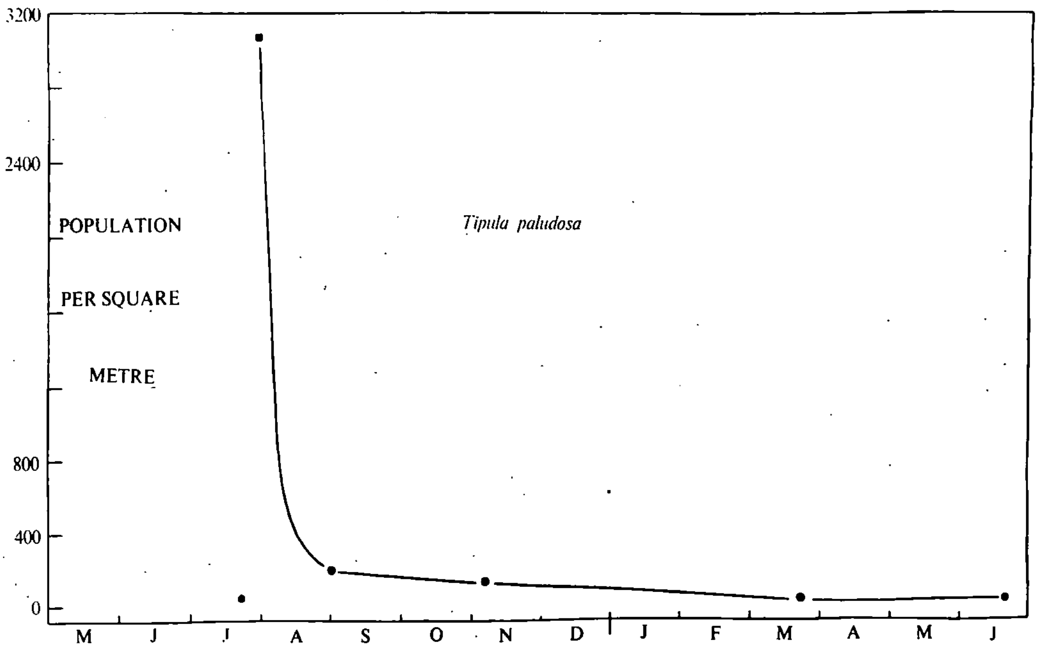


Fig. 28. Change in density of immature stages of Tipula paludosa, Moor House, 1955-56.

Rate of egg laying.

As in the case of T. subnodicornis, a large number of recently emerged females were placed in a canister and samples of females were taken at intervals of a few hours. These were preserved and dissected later to find out how many eggs they contained. Fig. 27 and Table XXX shows the results of this experiment.

Table XXX

The number of eggs present per female after given times

Time after emergence (hours)	No. of females examined	Number of eggs	Mean number of eggs per female
2 (females taken in copulation)	36	616 524 476 465 426 423 403 403 402 382 378 378 377 363 361 359 356 329 327 278 278 259 224 217	360
7	8	602 403 321 306 304 265 224 125	319

Table XXX cont.

Time after emergence (hours)	No. of females examined	Number of eggs				Mean number of eggs per female
9	15	344	293	285	267	174
		258	210	196	185	
		178	176	122	63	
		24	0	0		
12	16	266	251	229	172	103
		170	140	127	112	
		86	53	44	3	
		1	0	0	0	
17	24	194	177	130	112	36
		95	67	35	26	
		17	3	2	1	
		0	0	0	0	
		0	0	0	0	
		0	0	0	0	
33	5	39	0	0	0	8
		0				

These data suggest that although the females disappeared during the main part of the day light hours, egg laying probably continued during this period. Some confirmation of this was obtained when eggs were recovered from soil samples taken from the centre of tufts of Juncus effusus . While the general form

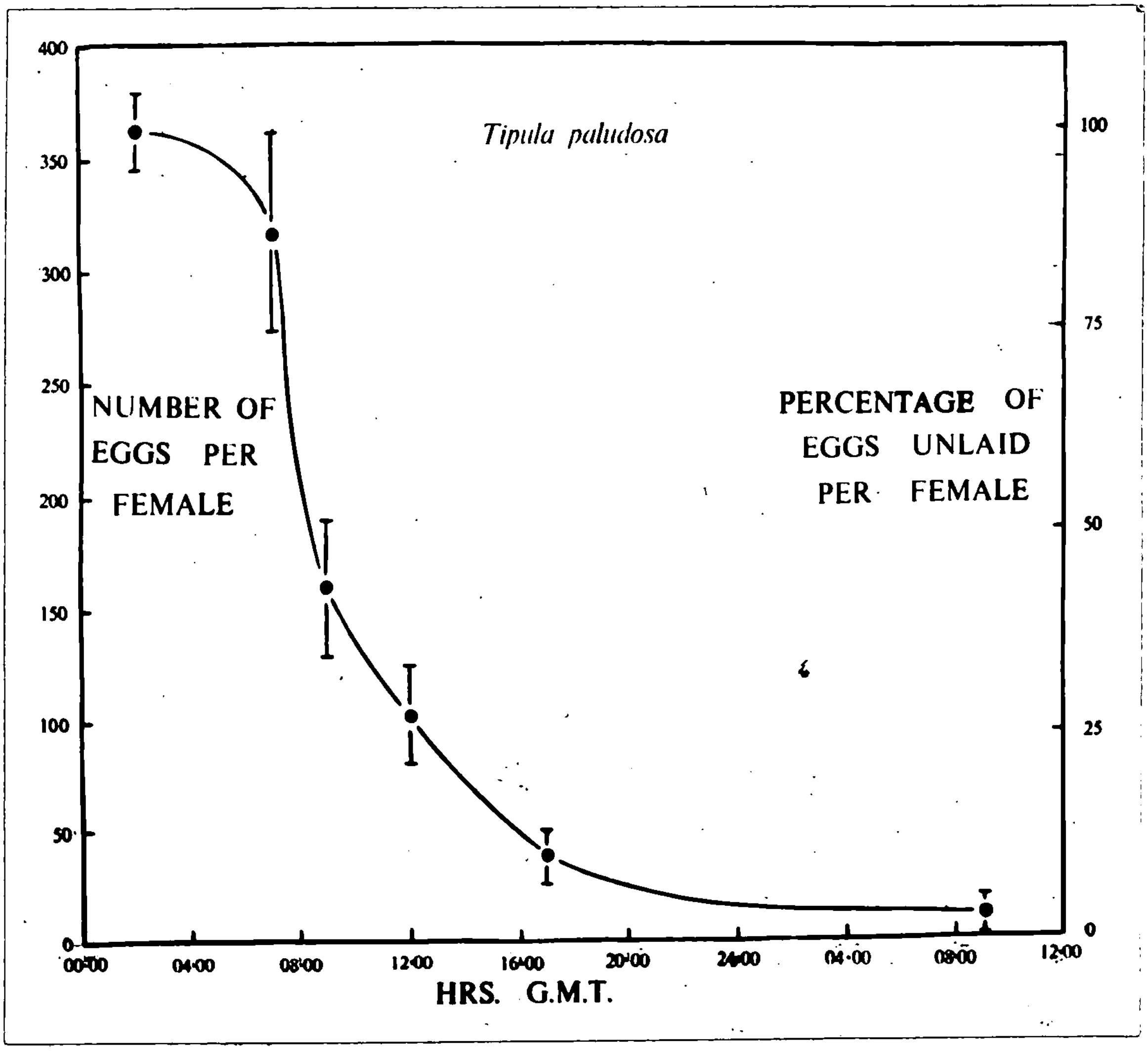


Fig. 27. The rate of egg laying by Tipula paludosa

of the curve of egg laying was similar to that of T. subnodicornis, the time spent in laying eggs was somewhat longer, but the rate of egg laying was somewhat greater since T. paludosa had half as many eggs again as T. subnodicornis. The first half of the eggs (about 180) were laid within 7 hours of the completion of copulation or about 9 hours after emergence, while 90% of the eggs had been laid 17 hours after the completion of emergence.

Development of new eggs in T. paludosa.

In addition to the ripe eggs found in the newly emerged females, it was noticed that most of the females contained very small ovaries with immature oocytes. In field captures females of unknown age, oocytes about half the size of the fully developed egg were found and it seemed possible that a new batch of eggs could be developed provided that females lived long enough.

The numbers of these unripened eggs were markedly fewer than those found in newly emerged females, there being less than 100 eggs in the females examined.

Oviposition.

Hemmingsen (1952) records that eggs were laid without deep boring in T. paludosa. In the present investigation it was noted that, unlike T. subnodicornis, the abdomen was not worked very far into the ground, usually no further than the base of the ovipositor. Soil samples confirmed that the eggs were near the surface. Each sample was divided into four units, 0-1 cm., 1-2 cm., 2-3 cm. and below 3 cm. from the surface. and the number of eggs recovered by flotation in magnesium sulphate solution is shown in Table XXI. Some two-thirds of the eggs present were found in the top centimetre layer.

Table XXXI

The vertical distribution of eggs laid by *Tipula paludosa*

		Depth at which eggs were found (cm.)			
	Total	0 - 1	1 - 2	2 - 3	below 3
Number	83	56	10	11	6
Percentage	100	68	12	13	7

Note. Data were obtained from 30 random samples.

Hemmingsen (1952) suggested that eggs were laid in large batches but as Table XXXII shows, there was little aggregation of eggs in the soil. This

Table XXXII

The numbers of eggs found in 30, 3.3 sq. cm. samples.

	Number of eggs per sample									
	0	1	2	3	4	5	6	7	over 7	Total
Number	6	2	8	5	2	3	1	3	0	30

implies that the eggs were probably laid singly or in twos and threes and not in larger batches as was suggested.

2. <u>Egg.</u>

The egg of <u>T. paludosa</u>, although very similar in shape to that of <u>T. subnodicornis</u>, is markedly larger and measured 1.10±.17 mm. long by .44±.11 mm. at the broadest part. The egg lacks an egg filament.

3. <u>Larvae</u>.

Fig. 22 shows that <u>T. paludosa</u> has four larval instars. The larval habitat at Moor House was almost entirely complementary to that of <u>T. subnodicornis</u> and larvae were found on most of the mineral soils.

The duration of the larval instars at

Moor House was as follows:-

Egg	late July to mid August	3 weeks
1st. instar	mid August to mid September	4 weeks
2nd. instar	mid September to late October	5 weeks
3rd. instar	late October to mid April	25 weeks
4th. instar	mid April to early July	12 weeks
Pupa	early July to late July	2 weeks
Adults	late July	1 week

Population study.

During 1955 and 1956, a population study was carried out on *T. paludosa*, on an area of 64 sq. metres. This area had numerous tufts of *Juncus effusus* and also small areas of typical limestone grassland. The soil on this area varied from a very black peaty soil under the *Juncus* to a rich clay-like soil. The area is illustrated in Fig. 2.

During the emergence of adults, pupal cases -

were collected at frequent intervals from this area. In all, 909 pupal cases were collected, giving a total pupal population of 14.2 per sq. metre (equivalent to a biomass 10.4 grams per sq. m. of fully grown larvae). These pupal cases consisted of 334 females and 575 males, which gave a sex ratio of 37 females per 100 animals. There were 5.3 females on each square metre and since these would lay on the average 360 eggs each, then a maximum of 2,000 eggs per square metre could be expected. In fact, the recovery of eggs gave an estimate of 2,770 eggs per sq. m. (standard error = 220). It is possible that a few eggs of _T. variipennis_ were mistaken for those of _T. paludosa_ as the eggs are of similar size. It is possible that some of the females managed to ripen a second batch of eggs and this could also account for the higher estimate. Fig. 28. shows the estimated population on this area presented in a graphed form. There appeared to be a very high mortality in the egg stage and the early larval stages. This may have been connected with the very dry weather at the time, but is more likely to be a normal mortality, similar to that recorded for *T. subnodicornis*.

Effects of the dry summer of 1955 on the population of *T. paludosa*.

As will be seen from Fig. 28, the population was able to maintain itself under the dry conditions of 1955. Table XXXIII gives some data of the water content of the soil at the time of dryness and also on 7 November, after some rainfall in the previous week, and illustrates that the soil contained only about one third of the water in July that it did in November.

Table XXXIII

Water content of alluvial soils at Moor House in 1955

Site	Percentage of water in total weight			
	27 July		7 November	
	0 - 1 cm.	1 - 3 cm.	0 - 1 cm.	1 - 3 cm.
A	33.5	21.6	53.4	46.2
B	17.9	21.6	66.7	57.2
C	9.7	28.5	60.0	57.0
D	49.7	56.0	60.6	50.2
E	32.2	60.7	56.0	47.6
Mean	28.4	37.7	59.3	51.6

VII Study of *Tipula oleracea*.

1. Adults.

Tipula oleracea is very closely related to *T. paludosa* and the two species were confused in the literature for many years. The adults differ from *T. paludosa* in the distance between the lower part of the eyes, the length of the wings in the females and in the form of the male genetalia.

T. oleracea was not found at Moor House until 1955 when two females were captured in early July and two males in October. Thus this species would appear to be rare at Moor House and it was possible since the adults are strong fliers, that the 1955 captures may have come from the Eden Valley.

In 1955, a comparative study of the eggs and habitats of *T. oleracea* and *T. paludosa* was made with the hope of elucidating the reasons for the latter being common at Moor House while the former was rare.

Distribution of adults.

The distribution of the adults of *T. oleracea* in the Durham City area was markedly restricted as compared with T. paludosa. Adults were confined to the banks of streams, edges of woods and in sparcely wooded copses and rarely occurred in pastures. T. paludosa, on the other hand, was wide spread and particularly common in pastures. The typical habitat of T. oleracea was not found at Moor House while those prefered by T. paludosa were extensive.

Eggs.

The eggs of T. oleracea were noticeably smaller than those of T. paludosa, the mean measurements of 100 eggs taken from 10 females were .831±.090 mm. long by .314±.077 mm. broad. The smaller egg size appeared to be related to a greater number of eggs per female. Table XXXIV gives the number of eggs found in 4 newly emerged females and the mean of 582 eggs is close to a value of 600 eggs referred to in Alexander (1920).

Table XXXIV

Number of eggs per newly emerged female of T. oleracea

Number of eggs				Mean
761	603	535	430	582

The most striking difference between the eggs of _T. oleracea_ and _T. paludosa_ was the presence of an egg filament in the former species (Hemmingsen, 1952). This filament takes the form of a coiled pad at one of the apices and this uncoils into a long thread many times the length of the egg.

Larva.

The larvae of _T. oleracea_ and _T. paludosa_ have not been separated and are undoubtedly very similar. Measurements of the maximum diameter of the spiracular disc suggested that first instar larvae of _T. oleracea_ were distinctly smaller than those of _T. paludosa_ with no overlap in size (Table XXXV).

Table XXXV

The maximum diameter of the spiracular discs of first instar larvae of _T. paludosa_ and _T. oleracea_

	Maximum diameter of spiracular disc (mm.)					
	.0340-.0374	.0374-.0408	.0408-.0442	.0442-.0476	.0476-.0510	.0510-.0544
Tipula oleracea	6	10	3	0	0	0
Tipula paludosa	0	0	0	1	7	1

The last three instars showed an overlap with those of _T. paludosa_ and therefore the two species could only be separated in the first instar.

VIII Study of the Meadow Pipit by means of nest record cards and ringing recoveries.

This study consists of an analysis of nest record cards and ringing recoveries of the Meadow Pipit accumulated by the British Trust for Ornithology. Use has been made of 380 B.T.O. nest record cards collected up to and including 1953, along with data from 111 and 27 nests from the diaries of A. Whitaker and F.C.R. Jourdain respectively. All of the B.T.O. ringing recoveries of birds ringed prior to 1950 and 25 recoveries of birds ringed on the Continent have been used.

The Meadow Pipit has an extensive breeding range within Great Britain and particular attention has been paid to the relationships between breeding biology and altitude.

1. Breeding.

Determination of start of egg laying.

The date on which the first egg of a clutch was laid was determined by one of the following methods.

1. If the nest was found while eggs were still being laid, then the date of laying of the

first egg could be calculated, since one egg was laid each day.

2. If the hatching date was known, then the date of the egg was determined by subtracting the average incubation period (13 days) and one less than the number of eggs in the completed clutch.

3. If the date of fledging was known, then the mean fledging period was subtracted and then treated as in 2.

4. If none of these stages was recorded, then use was made of estimates of the age of the young and, failing this, it was assumed that the nest contents were half way through the stage in which they were found.

Determination of the altitude of nests.

Six percent of the cards gave National grid references from which the altitude could be determined . The remaining cards had the nest sites recorded by their proximity to particular topographical features. Using one inch Ordnance Survey maps, it was possible to place 76% of the nest-sites into one of the following groups: 0-50 feet; 50-250 feet; 250-750 feet; 750-1,000 feet and over 1,000 feet. These groups were chosen to give approximately equal samples of nests.

The remaining 24% of the cards could not be used, either because insufficient data were given as to the location of the nest, or because the nest was located in an area with extensive variations in altitude.

Time of breeding.

The cards were grouped by altitude and also by location north or south of a line joining the Wash to the estuary of the River Dee, Cheshire. Each group was sub-divided into weekly periods according to the date that the first egg was laid and the data are presented in Fig. 29. It should be noted that it was impossible to separate late first broods from early second broods, and also that there were apparently fewer records of second broods. The latter probably arose, in part, from the increased difficulty of finding nests and to the decline in the number of observers as the breeding season progressed. A similar lack of second brood nests of the Greenfinch (Chloris

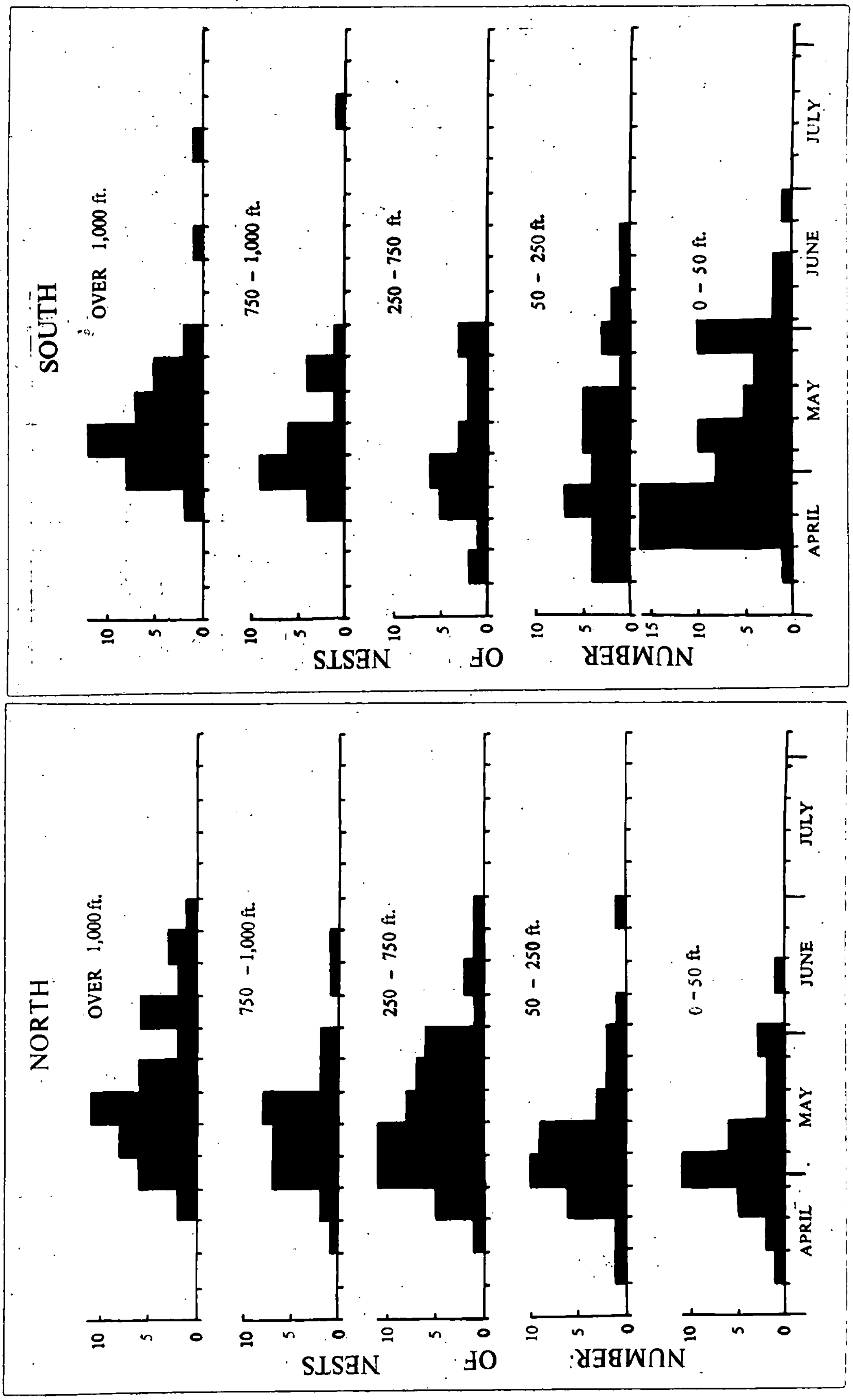


Fig. 29. The time of laying of the first egg by the Meadow Pipit according to region and altitude.

chloris) was found by Monk (1954). It was also possible that only a proportion of Meadow Pipits laid a second clutch. Whilst this may be so, personal observations at Moor House Nature Conservancy Reserve, Westmorland (altitude of observations, 1,700 to 2,300 feet) suggested that at least half of the pairs raised two broods each year.

With the marked decrease of records of second broods, the study of the time of breeding of the Meadow Pipit had to be carried out using all records, there being no reason to suspect a higher proportion of second broods in any of the groups. Table XXXVI shows the unweighted mean dates of laying at different altitudes and latitudes, (the unweighted mean being used to remove the effect of either altitude or altitude when consideration was being given to the other factor). The mean date of breeding was 3.8 days earlier in the south than in the north, this difference being statistically significant at the 2% level. It was also found that the mean date of breeding was later as the altitude increased (significant at

Table XXXVI

THE EFFECT OF ALTITUDE AND LATITUDE ON THE TIME OF BREEDING OF THE MEADOW PIPIT

A. Southern Records.						
Altitude group (ft.)	*0—50*	*50—250*	*250—750*	*750—1,000*	*Over 1,000*	*Unweighted mean of all groups*
No. in group	76	37	24	26	33	
Mean date of first egg (May)	7.2	6.9	5.5	10.5	12.2	8.46
B. Northern Records.						
No. in group	32	36	54	31	49	
Mean date of first egg (May)	5.9	8.0	14.6	12.4	20.8	12.34
C. Unweighted Mean of Northern and Southern Records.						
Unweighted mean date of first egg	6.55	7.45	10.05	11.45	16.50	—

Table of variance

	Sum-square	Degrees of freedom	Variance
Due to latitude	28.92	1	28.92
Due to altitude	85.10	4	21.25
Total for both	1917.00	388	4.94

1% level), the mean date being about one day later for every 130 feet rise in altitude.

2. <u>Clutch Size</u>.

Use was made of all completed clutches. Completion was assumed when the number of eggs had not increased at a second visit more than 24 hours after the first.

Witherby et al. (1938) stated that the clutch size of the Meadow Pipit is "usually 3 or 4 to 5, seldom 6 in the British Isles". The data from nest record cards showed, however, that clutch sizes of 4 and 5 eggs were the most frequent, with a few clutches of 3 and 6 eggs. The mean clutch size was 4.30 but, since the clutch size varied with altitude, this has little meaning (see below).

Effect of latitude on the clutch size.

The British records for the altitude groups 0-250 feet were examined for the presence of a difference in the clutch size between northern and southern regions. These particular altitude groups were used as they gave the most extensive and comparable sample. The data are presented in Table XXXVII and it will be noted that there was

Table XXXVII

THE CLUTCH SIZE OF THE MEADOW PIPIT IN THE SOUTH AND NORTH OF GREAT BRITAIN IN THE ALTITUDE RANGE 0—250 FEET

	No. of nests with clutches of					
	3	4	5	6 eggs	Total	Mean clutch size
South	0	25	20	1	46	4.48
North	2	22	17	3	44	4.48

no difference between the means, which suggested that the clutch size was independent of latitude within Great Britain.

Data for 77 nests in Iceland and 56 nests in Norway are presented in Table XXXVIII.

Table XXXVIII

CLUTCH SIZE OF THE MEADOW PIPIT IN NORWAY AND ICELAND

Locality	*Authority*	4	5	6	7 *eggs*	*Total*	*Mean*
Finmark, N. Norway	F. C. R. Jourdain .. (diary in B.T.O.)	2	4	7	0		
Finmark, N. Norway	R. H. Read .. (diary in B.T.O.)	0	1	6	0		
Finmark, N. Norway	H. M. S. Blair .. (pers. comm.)	0	0	6	2		
	Total	2	5	19	2	28	5.75
Hardanger Vidda, South Norway ..	H. M. S. Blair .. (pers. comm.)	3	11	14	0	28	5.39
S.W. Iceland ..	F. C. R. Jourdain .. (diary in B.T.O.)	0	1	6	0		
Iceland	F. Gudmundsson .. (pers. comm.)	5	35	29	1		
	Total	5	36	35	1	77	5.42

The mean clutch size of 5.75 in north Norway (Finmark), 5.39 in south Norway (Hardanger Vidda) and 5.42 in Iceland were all markedly larger than that of 4.52 (see Table XXXIX) in the 0-50 feet altitude group within Great Britain.

The Meadow Pipits in Iceland and Norway rarely have second broods (F. Gudmundsson pers comm., H.M.S. Blair pers. comm.) but in Great

Britain two broods are usual, so that in fact birds in Great Britain produce more eggs per pair in a breeding season than those in more northern regions.

Relationship of clutch size to altitude.

The clutch size was examined in relationship to the altitude of the nest site and Table XXXIX shows that there was a tendency for the clutch size to decrease as altitude increased, changing from a mean value of 4.52 near sea-level to 4.07 at over 1,000 feet. These differences were significant at

Table XXXIX

THE CLUTCH SIZE OF THE MEADOW PIPIT IN RELATION TO ALTITUDE

Altitude (ft.)	*No. of nests*	*No. of nests with clutch size of* 3	4	5	6 *eggs*	*Mean clutch size*
0—50	61	1	27	33	0	4.52
50—250	53	4	30	15	4	4.36
250—750	44	4	24	15	1	4.30
750—1,000	45	4	31	10	0	4.13
over 1,000	43	7	26	10	0	4.07
Total	**246**	**20**	**138**	**83**	**5**	**4.30**

A χ^2 test on clutches of 3 and 4 eggs compared with those of 5 and 6 eggs in each altitude group gave a $\chi^2=15.5$ with 4 d.f. which was significant at the 1% level.

the 1% level. The decrease in clutch size at high altitudes was not caused by the delayed onset of breeding, since differences were recorded between clutches at low and high altitudes during the same weekly periods.

Size of first and second clutch.

It was not possible to show the change of clutch size as the season progressed, because it increased with altitude and there were insufficient data to analyse each altitude group separately. Table XXXX shows the size of the first and second clutches at different altitudes. Nests were ignored where there was doubt as to which brood they belonged. In addition to showing that the clutch size was lower at high altitudes in both clutches, Table XXXX also demonstrates that, at the same altitude, the first clutch was smaller than the second (significant at 1% level).

Table XXXX

THE FIRST AND SECOND CLUTCHES OF THE MEADOW PIPIT IN RELATION TO ALTITUDE

Altitude (ft.)	First clutch		Second clutch	
	No. of nests	Mean clutch size	No. of nests	Mean clutch size
0—50	29	4.44	24	4.66
50—250	28	4.25	15	4.54
250—750	22	4.08	11	4.56
750—1,000	13	4.00	12	4.37
over 1,000	26	3.98	21	4.45

A t—test on the differences between the means of first and second clutches gave a value of t=8.2 with 4d.f. which was significant at the 1% level.

3. Incubation period.

The incubation period was determined from the laying to the hatching of the last egg and only observations made daily over the laying and hatching period were used, thus giving a maximum error of ± 1 day for each individual observation. There were 3 records of eleven days, 3 of twelve, 6 of thirteen, 5 of fourteen and 2 of fifteen; of the total 19 records, the mean is 13.0 days.

4. Fledging period.

The fledging period has been defined as the time spent in the nest (Ryves 1943) since the young tend to leave the nest before being able to fly. As for the incubation period, only those records were used which had been carried out daily over the critical periods. The mean fledging period was 12.5 days, determined from 36 records (2 of ten days, 7 of eleven days, 8 of twelve days, 10 of thirteen days and 9 of fourteen days).

5. Mortality.

When nest mortality is determined from nest record cards, consideration must be given to the possiblity that the observers were biassed in finding nests which were more liable to mortality. The possible causes seem to be:

1. The observers found nests most likely to be destroyed because they were either more conspicuous, or were situated near to habitation.
2. Nests once visited by observers were exposed to greater mortality because the visits helped predators to find the nest.

In the case of the Meadow Pipit, the first possibility does not seem likely to cause an error. Most nests of the Meadow Pipit were situated under cover at ground level and were found by chance flushing, or by watching the adult birds visit the nest. Furthermore, the nests were rarely situated close to habitation, so that a bias due to the first possibility might be considered unlikely. There is no information to indicate the effect of observers' visits on the nest mortality.

Total mortality of nests containing eggs.

Only 21 nests were found before the clutch was completed, so the methods employed in previous analyses, where many nests were found before the completion of the clutch, could not be used. It has been possible, however, to make an estimate of the nest mortality by making the assumption that the total nest mortality was constant throughout the incubation period.

Since Meadow Pipits nest on the ground and the nests are concealed, it might be expected that nests were found at random throughout the incubation period, that is, a constant number of nests, say x, were found on each day of the incubation period. On the first day of incubation, x nests would be under observation, on the second day 2x and so on, until the final day when 13x nests would be under observation. Thus, on the average, a nest would be under observation for half the incubation period, that is, 6.5 days. The actual value for nests in which eggs successfully hatched was 6.9 days, indicating that the nests were probably found at random throughout the incubation period. Extremely few nests were found after they had been destroyed or deserted, so that since the nests were under observation for half of the incubation period, then the recorded cases of mortality would have occurred during the period that the nests were under observation, which was half of the incubation period. Thus the actual number of nests in which eggs failed to hatch would be twice the number recorded by the observers. The following relationship was used to estimate the mortality, assuming a constant mortality rate:

$$\text{Percentage total nest mortality} = \frac{(\text{Number of nests recorded as destroyed} \times 2) \times 100}{\text{Number of successful nests} + (\text{No. of nests recorded as destroyed} \times 2)}$$

Number of successful nests = 105

Number of nests with total mortality = 37

Thus from the above relationship 41% of the nests which contained eggs, suffered total mortality.

The mortality of young in the nest was calculated by the above method and compared with the value obtained from observations of individual nests from hatching until the young were 9 days old. As will be seen below, the two methods gave similar results.

Total mortality of nests containing young.

Method 1. Observation of individual nests until the young were 9 days old; 12 out of 68 nests were destroyed, which gave a mortality of 18%.

Method 2. This method was the same as that used for estimating the mortality of nests containing eggs, but was calculated to cover the first 9 days of the chicks' lives.

Number of successful nests which were found between hatching and 9 day old chicks = 105

Number of nests with recorded mortality = 10

Hence the total brood mortality was 16% of the nests. This second method did not employ any of the data used in the first one and gave an independent estimate of the mortality.

The causes of nest mortality are given in Table XXXXI. Nests pulled out from the site probably indicated bird predators such as the Carrion Crow (Corvus corone) and Gulls (Larus sp.) (data on nest record cards from Skokholm, Pembrokeshire), while nests which had the contents removed without damage to the nest itself, were probably the result of predation by small mammals

Table XXXXI

CAUSES OF TOTAL NEST MORTALITY IN NESTS OF THE MEADOW PIPIT

Cause	Number	Percentage
Cause unknown, eggs or young disappeared but nest not disturbed	21	34
Nest pulled out from situation	14	23
Cuckoo (*Cuculus canorus*) (Only records used in which the nest was found before the young Cuckoo hatched; this made the mortality comparable with other causes)	13	21
Nest deserted	5	8
Nest trodden on by sheep or cattle	5	8
Nest flooded	3	5
Human predation (ignored in mortality study)	3	—
Total	64	99%

(although some may have been robbed by humans).

Relationship of altitude to total nest mortality.

Actual records of the proportion of successful and unsuccessful nests are given in Table XLII.

There were only a small number of records of mortality over 750 feet and the 750-1,000 feet and the over 1,000 feet groups have been combined. These data indicate that mortality decreased as altitude increased (significant at 1% level).

Table XLII.

OBSERVED TOTAL NEST MORTALITY IN RELATION TO ALTITUDE

Altitude (ft.)	*0—50*	*50—250*	*250—750*	*over 750*
Number of nests visited on two or more occasions	71	63	36	32
Number of cases where entire nest contents were found to have been destroyed on a subsequent visit	25	17	5	1
Percentage of nests with total mortality	*35*	*27*	*14*	*3*

The data were subjected to a 2 by 4 contingency test and gave $\chi^2 = 15.0$ with 3 d.f. which was significant at 1% level.

It was thought that these differences might have arisen by nests at low altitudes being under observation for longer periods than those at high altitudes. The mean number of days that successful nests (i.e. nests in which no mortality was recorded between the first and last visit to the nest) were under observation are presented in Table XLIII which shows that nests were observed on the average for slightly shorter periods at

Table XLIII

CORRECTED TOTAL NEST MORTALITY IN RELATION TO ALTITUDE
(CORRECTED TO 15 DAYS)

Altitude (ft.)	*0–50*	*50–250*	*250–750*	*over 750*
Mean number of days successful nests were under observation	15.2	17.2	13.9	13.4
Mortality corrected to an arbitrary number of days (15)	34.5	23.5	15.0	3.4

higher altitudes. When each altitude group was corrected to represent the mortality occurring in the same mean number of days (15 days), the data still showed the marked differences in the mortality as altitude increased.

Eggs which failed to hatch.

All records where hatching was recorded were examined and of 686 eggs which reached hatching, 35 or 5.1% failed to hatch.

Loss of eggs from nest.

167 nests were observed which contained 720 eggs. Later, 9 of these nests showed a loss of one or more eggs. These nests lost a total of 16 eggs which represented a loss of 2.2% of the eggs during half of the incubation period. Therefore the total loss during the 13 days of incubation was 4%.

Loss of young from the nest.

105 nests were observed of which 9 showed a loss of 13 young during the first 9 days in the nest. This represented a loss of 3% of the young which hatched.

Determination of mortality from ringing recoveries.*

Use was made of ringing recoveries of birds ringed before 1950. It has been assumed that the ringing

* Mr. R. Spencer, Secretary of the B.T.O. Ringing Committee, informed me that there was a possibility that some Meadow Pipits lost their rings through wear. In this case, the mortality estimates are probably slightly exaggerated.

recoveries of Meadow Pipits gave an accurate cross section of the age distribution of the species. Since ringing recoveries of Meadow Pipits ringed in Belgium, Holland and Denmark did not differ statistically from those ringed in Great Britain, they have been included to give a larger sample.

Mortality in first year of life.

Lack (1943), when determining the first year mortality of the Robin (Erithacus rubecula), used recoveries only after 1 August in the year of ringing because there was a heavy bias due to observers finding their own ringed birds prior to this date. This was not so in the case of the Meadow Pipit as the majority of dead recoveries were from outside this country, and in the present paper, the average mortality has been calculated from recoveries three weeks or more after the time the young were ringed in the nest. This meant that the mortality was measured from the time the young became independent of their parents.

The average mortality in the first year of life was determined from recoveries of birds ringed as nestlings. The data in Table XLIV show that

Table XLIV

MORTALITY OF THE MEADOW PIPIT IN THE FIRST YEAR OF LIFE

Number dying in	*1st year*	*2nd year*	*3rd year*	*over 3rd year*	*Total*
Ringed in Great Britain ..	29	8	2	0	39
Ringed on Continent ..	5	1	0	0	6
Total ..	34	9	2	0	45

Percentage mortality in first year of life = 76%.
Expectation of further life after becoming independent of parents = 10 months.

76% of all young which survived the first two weeks out of the nest, died in their first year of life.

Average annual adult mortality.

Two independent methods were used to determine the average annual adult mortality from recoveries of birds ringed as adults.

Method 1. Birds recovered dead.

This method gave an average annual mortality of 57% and an expectation of further life of 1.3 years (Table XLV).

Method 2. Birds recaptured alive by the ringer.

No recaptures have been used unless the bird had completed at least one migration after being ringed, the recoveries being grouped into the number of winters the birds were known to have survived from the time of ringing (Table XLVI).

Table XLV

AVERAGE ANNUAL ADULT MORTALITY DERIVED FROM RINGING RECOVERIES OF MEADOW PIPITS RINGED AS ADULTS

No. dying in years after ringing	*1st.*	*2nd.*	*3rd*	*4th*	*5th*	*6th*	*7th . . . 14th*		*Total*
Ringed in Great Britain	16	3	1	0	1	0	1	0	22
Ringed on Continent	18	4	2	0	0	0	0	1	25
Total	34	7	3	0	1	0	1	1	47

Average annual adult mortality=57%.
Expectation of further life=1.3 years

This method was used as the birds had all been ringed in the spring and summer. An average annual adult mortality of 58% was obtained by this

Table XLVI

AVERAGE ANNUAL ADULT MORTALITY OF THE MEADOW PIPIT DERIVED FROM RECAPTURES OF BIRDS RINGED AS ADULTS

	Number of birds recaptured in years after ringing	*Number dying during year*
1st year	70	34
2nd year	36	30
3rd year	6	2
4th year	4	1
5th year	3	2
6th year	1	1
over 6th year	0	0

Average annual adult mortality=58%
Expectation of further life=1.3 years

method.

It was possible that the former method may have been biassed through a disproportionate number of inexperienced, younger birds being recovered by bird-catchers in France, Portugal and Spain; but the similarity of this result with that of the second method, suggested that no such error was present.

It has been impossible to calculate the first year or adult mortality by altitude groups, because there were few recoveries of birds ringed at over 500 feet.

From the data given above, the hatching success has been calculated as 54% and the fledging success as 80%, giving a breeding success of 43% when all altitude groups were combined. On the average, each pair of adults produced 0.44 young per nest which lived to breed the following year.

Since the adults suffer an average of 57% mortality each year, then 57% of the birds in the spring population must be birds breeding for the first time.

6. <u>Discussion of nest record card data.</u>

This analysis of nest record cards has demonstrated that with increasing altitude, Meadow Pipits bred later and their clutch size and total nest mortality decreased.

The mean clutch size could be influenced by three factors; the age of the female birds, genetic factors and the effects of the environment. Young birds frequently lay smaller clutches than birds which have bred previously. It was unlikely that the proportion of young Meadow Pipits in a population (average proportion of first year birds was 57%) varied sufficiently in the different altitude groups to produce the observed differences in clutch size.

Many European passerines produce larger clutches in the north and east of their range (Lack 1947) and a similar difference has been shown for the Meadow Pipit nesting in Great Britain, Norway and Iceland, These variations in clutch size have probably resulted from the selection of the most successful clutch size for each area as has been suggested for the Starling (<u>Sternus</u>

vulgaris), Common Swift (Apus apus)and Alpine Swift (Apus melba) (Lack 1948; Lack & Lack 1951; Lack & Arn 1947).

In addition to these genetical differences, it is known that the clutch size can be modified by the effect of the environment. For instance, in most species studied, it has been shown that the clutch size does not remain constant throughout the breeding season but changes in a regular manner. Snow (1955) has shown that clutch size in the Song Thrush (Turdus ericetorum) and the Blackbird (T. merula) increased and then decreased as the breeding season progressed. He concluded that this variation was correlated with the length of daylight, increase in temperature and the availability of food. Further, the clutch size of the Song Thrush and the Blackbird varied in a similar but irregular manner in some years and it was suggested that these variations were in response to fluctuations in temperature.

In the case of the Meadow Pipit, there were two factors likely to produce the observed decrease in clutch size as altitude increased, namely, available food supply and environmental conditions. Whilst there was no evidence that the amount of food available for the Meadow Pipit was less at high altitudes than in lower habitats, the climate was more severe. There was less sunlight, higher rainfall, stronger winds and lower temperatures at higher altitudes. Further, the Meadow Pipit nests and feeds in open country and therefore it (and its food materials) come into contact with climatic conditions much more than birds living in sheltered lowland habitats such as woods, where the climate is moderated by the tree cover.

Climate could affect the female Meadow Pipit directly or indirectly through the feeding rate, causing those living under the more severe conditions to lay smaller clutches. Alternatively, the clutch size could be determined genetically through natural selection. The success of clutches of five eggs may decrease with increasing altitude, because the climate tends to prevent the parents collecting food as readily at high as at low altitudes. Cold weather prevented the emergence of insects which —

form the major food of this species, whilst wind and rain cause the insects to seek cover and become inactive. Thus at sea-level, clutches of 4 and 5 eggs might be equally successful, whereas above 1,000 feet, clutches of 4 eggs were probably the most successful.

Since the clutch size of the Meadow Pipit decreased as altitude increased, one or both of the following are possible:

1. There must be an immigration into higher altitudes by birds hatched at lower altitudes.
2. Mortality must be less at higher altitudes.

The former seems unlikely but, while it was not possible to support it by the few ringing recoveries of Meadow Pipits within this country, it cannot be ignored.

Meadow Pipits which breed in Great Britain, winter in the Iberian Peninsula (Verheyen & Le Grelle 1950) so there is no reason to expect that birds reared from any particular altitude group would suffer greater mortality away from the breeding grounds. Thus the differential mortality, if present, might be expected to exist only on the breeding grounds and it has been shown that the total nest mortality decreased as altitude increased (there were insufficient data to investigate post-fledging mortality by altitude groups).

At least 78% of the recorded cases of mortality could be attributed to predation, so that the reduction in mortality as altitude increased was almost certainly caused by a reduction in the number, or efficiency, of the predators. The Cuckoo appeared to be a less successful parasite as altitude increased, there being no nest record cards which recorded Cuckoos in Meadow Pipit nests over 1,000 feet and it appeared to be commonest below 250 feet. Personal observations suggested that small mammal predators were also fewer as altitude increased.

The smaller clutch size and lower nest mortality at higher altitudes may mean that each pair of Meadow Pipits rears approximately equal numbers of young, irrespective of altitude. The fact that the percentage difference between the clutch sizes was greater than that between the total nest mortality need not invalidate this suggestion, since many of the nests which were recorded as destroyed, were replaced within 10 days (Chance 1940).

IX Study of the Meadow Pipit at Moor House.

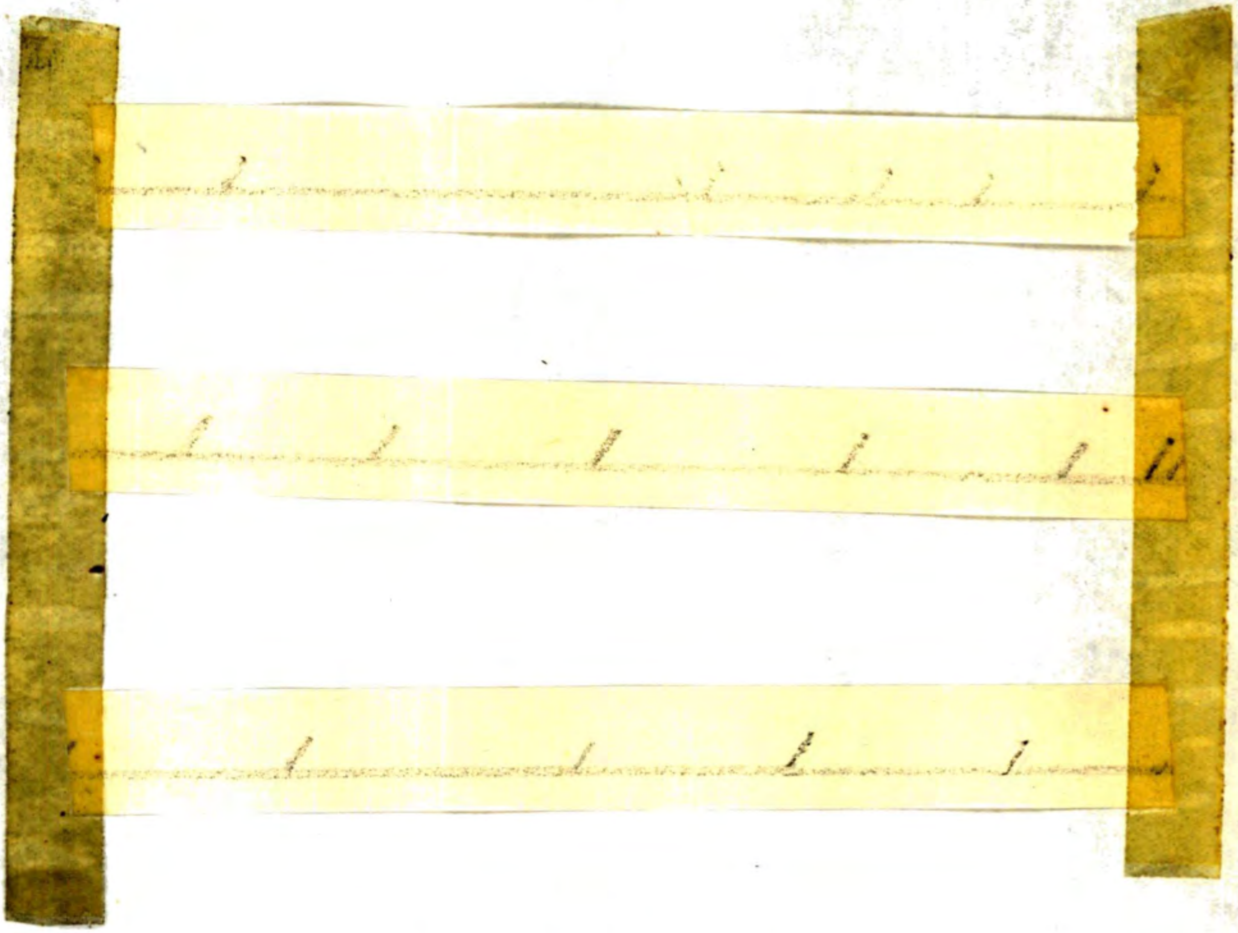
1. Methods.

Nest recorders.

Two types of recorders were used at Meadow Pipit nests in an attempt to find which was the more reliable and accurate.

Type 1. This was a modification of the type used by Gibb (1955). The main alterations were as follows:

1. The pointer which pierced the tape was replaced by a very soft photographic pencil. This kept a continuous trace on the tape and a visit was indicated by a line at right angles to the length of the tape (see example of tape below).
2. The spool which was attached to the clockwork movement was increased to 14 cms. in diameter, while the central core was enlarged to 12 cms. diameter. Thus there was an almost constant amount of tape wound on per hour and this enabled a much easier analysis of the frequency of visits to the nest.



Specimen of tape from nest visit recorder.

Type 2.

This recorder was similar to the above, apart from the following modifications:

1. Visits were recorded by an ink mark produced by an "Uno" pen, filled with recording ink.
2. The clock mechanism was used only to control the time intervals of a relay system, which completed an electrical circuit every 15 seconds. When the circuit was completed,

a solenoid was activated and this pulled a pivoted bar (A) towards it. On breaking the circuit, the bar returned to its normal position and in doing so, moved the spool (B) on by means of the cog wheel, (see Fig. 30).

Recorders of this type required a high current consumption which was entirely unsatisfactory when relying on batteries and the method was discarded in favour of the first type.

The flap-type of contact maker used at nest box entrances by Gibb could not be applied to the nest sites of the Meadow Pipit. A perch was placed across the entrance instead, and this completed an

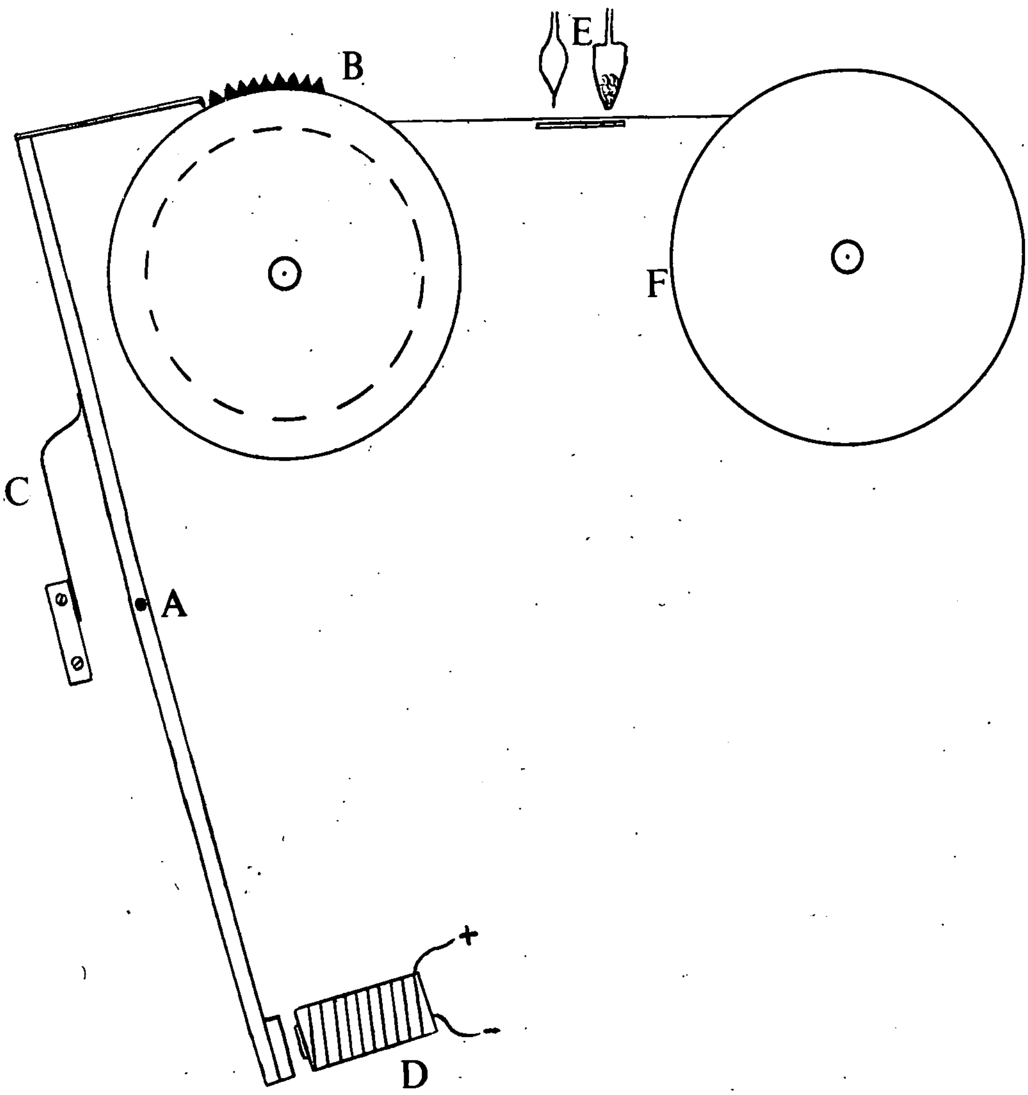


Fig. 30. Nest visit recorder.

A. pivot; B. spool and cogged wheel; C. spring;
D. solenoid; E. time and visit markers;
F. spool with reserve of tape

electrical circuit when it was depressed by the weight of the bird. The best results were obtained with the perch so placed that the adult birds stood on it while feeding the young. This avoided the difficulties of having to interprete whether the bird had stood on the perch both going to and from the nest for on some occasions, adults flew directly away from the nest without making a contact with the perch on leaving.

Finding nests.

Nests were located by the usual techniques employed in nest surveys, namely chance flushing, systematic covering of the area by walking or dragging a rope and, most frequently, careful observation of the movements of the adults.

Determination of the number of food items brought to the young.

This was determined in two ways. First, direct observations were made from a hide set up close to the nest and the type and quantity of food estimated as the bird walked to the nest. Later it was found that the adult bird usually fed in the same place for some hours and the number of food items picked up before the bird flew to the nest could be counted by use of binoculars or x35 telescope.

2. <u>Rate of feeding visits by adult Meadow Pipits to young in the nest.</u>

The visits of Meadow Pipits to their nests were recorded by the nest visit recorders and the data analysed into the number of visits per half hour. This enabled 33 values of the feeding rate to be obtained each day. This method was employed because two birds were involved in feeding the young and the period between each visit would not have given a satisfactory statistical distribution.

There was considerable variation between the rate of feeding of different pairs. For example, although the young were of the same age in both cases, one pair with four young fed them much more frequently than another pair with five young, (Table XLVII). The observations were made on the same days and there did not appear to be any difference in the quantity or quality of the food taken to the nests per visit. In both cases, *T. subnodicornis* was almost the only food material. The four young nest, received 3.2 visits per young per hour, while the five young nest only received 1.6 visits per young per hour. It was therefore surprising to find that the mean weight of the young from these nests differed by less than 1% of the average weight, the young in the nest with a brood of four being slightly heavier. This suggested that, during the period

Table XLVII

Feeding visit rates at two nests containing young of the same age.

Date	Average visit feeding rate (per hour)	
	Nest A Four young	Nest B Five young
1 June 1955	13.6	7.7
2 June 1955	11.6	7.9
3 June 1955	13.6	8.5
Mean per nest	12.9	8.0
Mean per young	3.2	1.6

of abundant food, the young received more food than they required and that a certain amount was passed through the digestive system without being completely utilised.

Diurnal rhythm of the feeding visits.

There was a marked diurnal rhythm in the number of visits to the nest. Table XLVIII shows the summed number of visits to the nest with food recorded in four 4-hour periods throughout the

Table XLVIII

Total number of visits with food recorded in pairs of four hour periods. Time G.M.T.

Time			
04.00-08.00	08.00-12.00	12.00-16.00	16.00-20.00
850	648		
	683	503	
		746	639

Numbers corrected to those in the first four hour period.

850	648	477	409
36%	27%	20%	17%

day. Since there were a number of days in which the recorders were working for only part of the day, the number of visits have been compared for the first and the second 4-hour periods of the day, using all the available data from first brood nest in 1955 for these eight hours. The second and the third 4-hour periods were then compared, followed by the third and fourth. These comparisons of paired, 4-hour periods were then corrected to make all four periods comparable and were then represented as a percentage of the total, (Table XLVIII).

After an initially high rate of feeding just after dawn, the rate declined gradually until sunset. The visit rate after dawn was double that in the last 4-hour period of the day.

Table XLIX gives the nest recorder data grouped by age of the young and also the number of young that were present in the nest. The data shows that broods of four young actually received more visits than broods of five young. This is probably the result of the data for broods of five young being collected from only two nests.

As will be seen from Table L, the nest with only one young received the greatest number of

Table XLIX

Number of visits to the nest per hour in four consecutive 4-hour periods.

One young.

6 and 7 days old			
Four hour period			
1	2	3	4
3.0	3.7	2.3	2.0
3.0	3.7	2.3	2.0

8 and 9 days old				
Four hour period				
1	2	3	4	
3.5	4.0	4.7	3.5	
3.0	1.3	2.5	5.0	
3.2	2.6	3.6	4.2	Mean

Four young.

6 and 7 days old			
Four hour period			
1	2	3	4
12.0	11.5	-	11.3
15.8	17.5	-	-
14.5	9.5	5.3	9.8
12.8	10.8	6.5	9.5
-	-	8.3	11.2
13.8	12.3	6.7	10.4

8 and 9 days old				
Four hour period				
1	2	3	4	
10.5	17.5	9.8	10.8	
19.3	-	-	8.5	
8.8	7.0	4.5	6.0	
9.5	7.5	7.3	7.8	
9.8	8.8	7.3	6.0	
11.6	10.2	7.3	7.9	Mean

Table XLIX cont.

Five young.

6 and 7 days old			
Four hour period			
1	2	3	4
13.3	9.8	8.0	8.0
-	11.8	8.6	8.3
13.3	10.3	8.3	8.2

8 and 9 days old				
Four hour period				
1	2	3	4	
9.5	7.5	7.3	7.8	
9.8	8.8	7.3	6.0	
9.7	8.1	7.3	6.9	Mean

Table L

Mean number of visits per nest per hour.

Nest containing	Age of young	
	6 and 7 days	8 and 9 days
One young	2.7	3.4
Four young	10.8	9.2
Five young	10.0	8.0

Table L cont.

Mean number of visits per young per hour.

Nest containing	Age of young	
	6 and 7 days	8 and 9 days
One young	2.7	3.4
Four young	2.7	2.3
Five young	2.0	1.6

visits per chick, but it was not far ahead of nests containing four young. Nests containing five young showed a marked decrease in the visit rate, the suggestion being that the adults with four or five young were collecting food at the maximum rate and each young in a brood of five received less food than its equivalent in a brood of four.

Further data were obtained by transferring one young from a "five young" nest and placing it in a nest with four young. The young one was exchanged for a period of 17 hours, which included one night, and data on the feeding rates were obtained for

11 hours,(Table LI). The result of this experiment was inconclusive. At nest B there was an

Table LI

Number of visits per hour at nests where one young had been removed from a brood of five young and placed in a brood of four young.

Nest A			Nest B		
No. of young	Visits per hour		No. of young	Visits per hour	
	per nest	per young		per nest	per young
5	8.3	1.66	4	10.7	2.67
4	8.5	2.12	6	16.0	3.20
5	7.4	1.48	4	11.1	2.77

indication of an increase in the feeding rate when the number of young was increased to five but this increase coincided with an increase in the nest which had been reduced from five to four young. Nest A did not show an increase in the visit rate when the brood was returned to five.

These data show that the difference between the feeding rates was not dependent on the number of young present in the nest, and it was possible that the parent birds were collecting food at the maximum of their ability.

Early in the 1955 breeding season, there was a spell of 5 days with frequent snow showers, during which time a recorder was running at a nest containing 4 young about 6 days old at the onset of the cold spell. The mean visit rate was 6.8 visits per hour (Table LII).

Table LII

Visit rate under cold and warm weather conditions.

	Visits per hour				
	Four hour periods				
	1	2	3	4	Mean
Four young cold, snowy.	6.3	7.8	8.8	5.5	6.8
Four young warm, sunny.	11.8	9.6	7.8	8.5	9.4

It will be seen that this rate was lower than that obtained from other nests studied later in the season which contained young of a similar age. The main differences in the feeding rate throughout the day were during the first and last four hours of daylight, when the feeding rate was about one third of that expected. This was probably caused by the ground being frozen and covered with snow in the morning and evening.

The young in the nest which was exposed to the cold, snowy weather, were weighed at 09.30 and 22.00 hrs. on May 18th., a day of many showers of snow and hail. Table LIII shows their weights at these two times and that the young actually lost an average of .5 gram each.

Table LIII

The weight of four young Meadow Pipits under cold snowy conditions. 18 May 1955.

Young	Weight (grams)	
	09.30 hrs.	22.00 hrs.
A	14.2	13.6
B	16.0	15.3
C	14.2	14.2
D	15.7	14.8
Mean	15.0	14.5

During this cold spell, two other nests were under observation. One had four young about three days old at the onset of the adverse weather, while in the other, three out of the five eggs hatched on the final day. All seven young died and observations suggested that the parents had spent too much time away from the nest searching for food, and did not brood the young long enough. This is supported by the fact that the remaining two eggs hatched the following day and these young were reared successfully. The nest with young over 6 days old at the onset of the cold weather survived, probably because the young were covered by feathers.

3. Second broods.

There was some evidence that all pairs did not rear two broods. It was known that two colour ringed birds failed to rear a second brood, but it was not known whether the eggs were laid and then destroyed, or whether no attempt was made to lay a second clutch. The records of second broods were fewer than the records of first broods but this was partly caused by the greater difficulty of finding second broods. Thus, while fewer nests were found (25 first brood; 13 second brood) belonging to the second brood, many additional adults were seen carrying food. Furthermore, three colour ringed birds were known for certain to have reared two broods in one breeding season.

Thus it can be stated that probably the majority of Meadow Pipits attempted a second brood at Moor House.

4. <u>Time of breeding at Moor House</u>.

The distribution of Meadow Pipit nests containing young is shown in Fig. 33. The mean date of breeding (mean data of first egg) was 16 May at Moor House, which was only slightly earlier than the data for the northern region above 1,000 feet collected from nest record cards. The difference was not statistically significant.

5. <u>The clutch size of the Meadow Pipit at Moor House.</u>

Table LIV gives the clutch size data for Moor House in the years 1953 to 1955 inclusive. It will be seen that the clutch size in 1955 was distinctly larger than that in 1953 or 1954.

Table LIV

Clutch size of the Meadow Pipit at Moor House

Year	Clutch size			Mean
	3 eggs	4eggs	5 eggs	
1953	0	3	1	4.25
1954	1	8	3	4.17
1955	1	9	7	4.35
Total	2	20	11	4.27

While the difference between the mean clutch size in 1954 and 1955 was not statistically significant, the 1955 data might be explained by the exceptionally fine weather in late April, just before laying commenced.

6. <u>Total nest mortality at Moor House</u>.

Out of 27 nests observed, only three cases of total nest mortality were recorded at Moor House. This represented a mortality of 16% over an observed period of 15 days (15 days was used in the nest record card study). Two of the three cases occurred during the extremely cold spell in the middle of May, 1955, and these should be considered as exceptions. If these are disregarded, then the mortality over an average period of 15 days becomes 6%, a value similar to that obtained in the nest record card study.

It is worth noting that at Moor House no case of nest mortality could be attributed to predation. This is of interest, since some 78% of the total nest mortality recorded on nest record cards was attributed to predation. Observations showed that suitable predators the Carrion Crow, the Cuckoo and small predator mammals were few in number on the area (the Cuckoo was absent from the high moors).

7. Feeding of the Meadow Pipit and related species.

Four species of the family Moticillidae have bred at Moor House, namely the Meadow Pipit, Pied Wagtail (*Motacilla alba*), the Grey Wagtail (*M. cinerea*)and the Yellow Wagtail (*M. flava*) and observations were carried out on the food and feeding methods of these species.

The Grey Wagtail differed from the other three species in that it's feeding was restricted almost entirely to stream sides and the food brought to the young was entirely riparian in origin.

The Meadow Pipit collected food by walking at a steady rate, picking up large insects which it encountered. It tended to collect food in areas with thick vegetation as well as on the short, sheep cropped grassland and stream sides.

On the other hand, the Pied Wagtail and Yellow Wagtail collected food by means of quick sprints, which suggested that insects were sighted at some distance.

These differences in feeding habits were reflected in the type of food collected. The Meadow Pipit collected slow moving insects such as Tipulidae and Ephemeroptera while the two Wagtails (Pied and Yellow) collected many strong-flying insects in addition to slower flying ones. Scopeuma sp. and Calypterate Diptera figured conspicuously in the food brought to the young.

8. Food brought to Meadow Pipit young.

Table LV shows the proportions of various foods carried to Meadow Pipit first broods during 1954 and 1955. The records were obtained by spending one hour twice per day at each nest under observation. Longer spells were not carried out in favour of shorter, more frequent sets of observation because the Meadow Pipit often collected food from the same locality for some hours and longer spells would have unduly biassed the food samples. There was little difference in

Table LV

Food brought to first brood Meadow Pipits

Species	1954 No. of records	1954 %	1955 No. of records	1955 %
Tipula subnodicornis	78	76	101	89
Tipula varripennis	3	3	1	1
Other adult Diptera	5	5	2	2
Dipterous larvae	1	1	0	0
Ephemeroptera	14	14	10	9
Plecoptera	1	1	0	0
Total	102	100	114	101

the type of food utilised in the two years, Tipula subnodicornis was the most abundant, followed by Ephemeroptera. These two food materials formed over 90% of the food.

As Table LVI shows, the food carried to second-broods was much more varied than that for

Table LVI

Food brought to second brood Meadow Pipit nests.

Species	1954		1955	
	No. of records	%	No. of records	%
Tipula paludosa	20	35	30	46
Other Diptera	10	17	4	6
Dipterous larvae	2	4	4	6
Ephemeroptera	12	21	25	38
Plecoptera	4	7	0	0
Adult Lepidoptera	7	13	2	3
Larval Lepidoptera	2	4	0	0
Total	57	101	65	99

the first brood; _Tipula paludosa_ was the most important single species, followed by _Ephemeroptera_ and _Lepidoptera_.

It is clear that the most important food collected by Meadow Pipits when feeding their young (and the food used by the adults) was _Tipula subnodicornis_, _T. paludosa_ and _Ephemeroptera_. The first mentioned species lived on peat moor, _T. paludosa_ occurred only on alluvial areas and the _Ephemeroptera_ were found on or close by the streams. This suggested that the most suitable breeding area for the Meadow Pipit would be areas with mixed feeding areas, thus supplying the food for both broods.

9. The association of Meadow Pipits with streams was illustrated by transects made between Moor House and Knock Fell (see map). The journey was repeated, in an opposite direction, on the following day and the number of Meadow Pipits flushed were recorded (Table LVII). Both transects showed that the Meadow Pipit was more numerous on the stream sides despite the fact that the observer was more

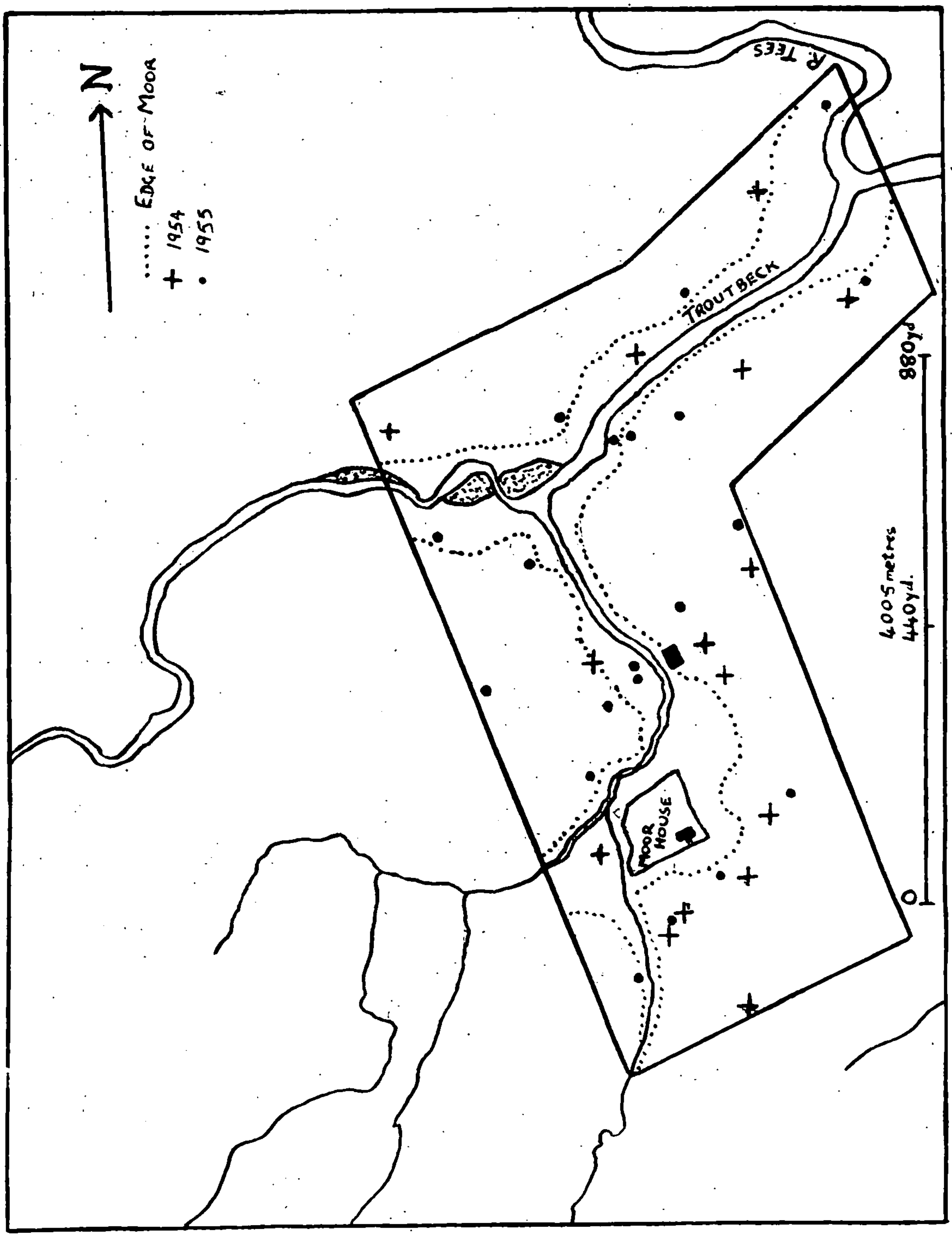


Fig. 31. Distribution of nests in the study area.

Table LVII

Transect from Moor House to Knock Fell and back

	Number of Meadow Pipits flushed		
	24 May 1955	25 May 1955	Total
By stream	12	10	22
Over moor	3	5	8
Total	15	15	30

conspicuous while walking over the open moor and flushed birds from a greater distance.

Distribution of nests.

Fig. 31 shows the distribution of all first and some second brood nests on the study area. This area was covered almost equally by peat moor (Calluna dominant) and alluvial terraces with streams. It is at once evident that few nests were built on the alluvial areas while the majority were situated on the edge of the Calluna moor. As the study of the food has suggested, the nests situated on the edge of the moor were most favourably situated for collecting food from any of the three types of habitat most frequently used, namely moorland, alluvial terraces and stream sides.

10. Density of Meadow Pipit at Moor House.

The density of Meadow Pipits on the Moor House Reserve has been estimated at 800 pairs or the equivalent of 8 pairs per 100 acres in 1954 (Campbell 1955).

Counts made in the present investigation suggested that this value was an over estimate and that the average population was in the region of 500 pairs (or 5 pairs per 100 acres). The density in the study area (which appeared to be the highest on the Reserve) was estimated at just under 10 pairs per 100 acres in 1954 and just over this value in 1955. An area of *Sphagnum* and *Calluna* of approximately 100 acres near Long and Green Hills produced only 2 pairs per 100 acres. This latter area had only one small stream and virtually no alluvial grassland and this may have accounted for the low density.

Lack (1935) gave data on the densities

of breeding Meadow Pipits from heathland and moorland in Great Britain. The majority of areas had between 20 and 30 adult Meadow Pipits per 100 acres and the data collected from Moor House in the present study suggested that the area carried a relatively low population density (10 birds per 100 acrea). This low population density was unlikely to be the result of fluctuations in the numbers of Meadow Pipit from year to year as the population seemed similar in three years. The most likely explanation of the low density of Meadow Pipits may be found in the fact that the moor was very wet and carried large areas of *Sphagnum* which appeared to be an unsuitable habitat for the species. Further, it is possible that the Meadow Pipit was on the edge of its altitude range over 2,000 ft. and this also, could account for the low density.

X Predation of the Meadow Pipit on the adults of *Tipula subnodicornis*

From the work carried out on the Meadow Pipit study area, it has been possible to estimate the proportion of the adult *Tipula subnodicornis* which were taken as food by the Meadow Pipit. The study area had an adult population of one pair per 10 acres in both 1954 and 1955, while samples taken on the area indicated that that there was a larval population of *T. subnodicornis* of at least 80 larvae per square metre in these years. Thus assuming a negligible pupal mortality, there would be 3,600,000 adult *T. subnodicornis* available on 10 acres, the territory of one pair of Meadow Pipits.

The nest recorders indicated that the average rate at which food was brought to their young was 10 visits per hour over 17 hours of daylight, that is 170 visits per day. This value applies to the time when the young were over 6 days old and assuming that the younger chicks were fed at a similar rate (this is an over estimation), then the young in the nest will receive 170x12.5 visits during the 12.5 days the young spend in the nest.

The young are fed by the parents for about another 12.5 days after they leave the nest so that the number of visits to the brood will be 170x25

= 4250 visits with food.

Table LVIII shows the number of tipulids collected by adult Meadow Pipits for each visit to the nest. These data were obtained by direct observation from a hide and from counting the number of food items picked up by adult Meadow Pipits which were feeding young.

Table LVIII

Number of adult tipulids collected for each visit to the nest by adult Meadow Pipits.

Number of tipulids	0	1	2	3	4	5	6	7	over 7
Frequency	0	1	7	8	15	31	22	8	2

Mean number of tipulids per visit

= 4.87

The number of tipulids fed to the young will be the product of the number of tipulids per visit and the total number of visits, 4.87x4,250

= 20,697 tipulids

say 21,000 tipulids

This represents .58 of 1% of the total available population of Tipula subnodicornis.

Even if an allowance is made for the fact that the two parents require a certain amount of food, it is quite obvious that no more than 1% of the T. subnodicornis population is taken as food for the Meadow Pipit. Further, when it is remembered that the mating and egg laying of this tipulid takes place in only a few hours and that many of the females taken will be already spent, the predation which is effective with regards to the following years population, is very small.

XI <u>The relationship of the Meadow Pipits and Tipulidae</u>

As the previous section indicates, the numbers of *Tipula subnodicornis* would not be affected to a significant extent by the predation of the Meadow Pipit although this tipulid formed some 75 to 90% of the food which was brought to the nest.

Fig. 32 shows that there was a remarkably close relationship between the emergence of *T. subnodicornis* and the presence of Meadow Pipit nestlings. The relationship appeared to be important to the Meadow Pipit for this tipulid was a most suitable food material, being large and also easily collected.

Fig. 33 shows the captures of adult insects on six sticky traps in 1955 and, in particular, the sudden emergence of insects in the second half of May, a phenomonon that appeared to be annual at Moor House. This emergence was mainly composed of *T. subnodicornis* and the yellow dung fly, *Scopeuma stercorarium* and it is interesting to note that while the former was used extensively the latter was rarely used as food for the young.

It was unlikely that the time of emergence of this tipulid and the time of breeding of the

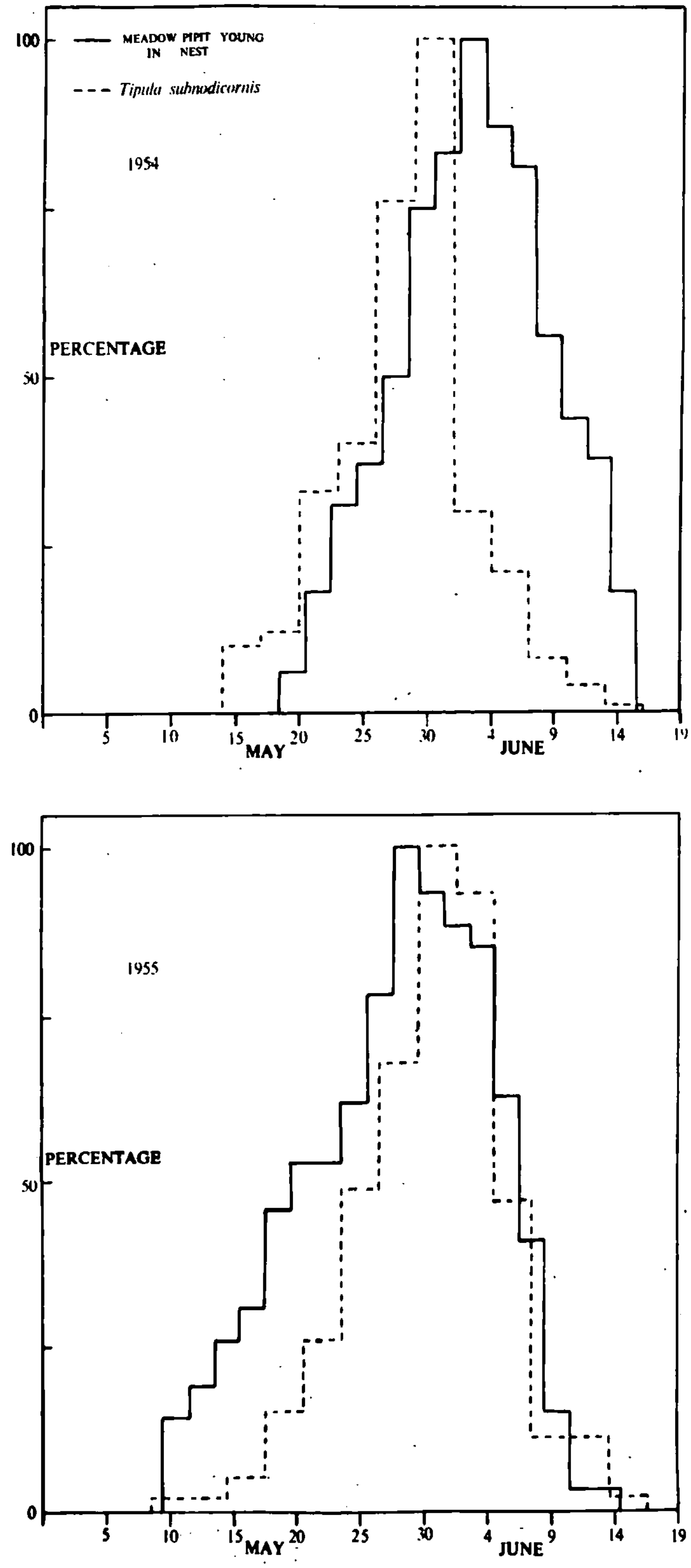
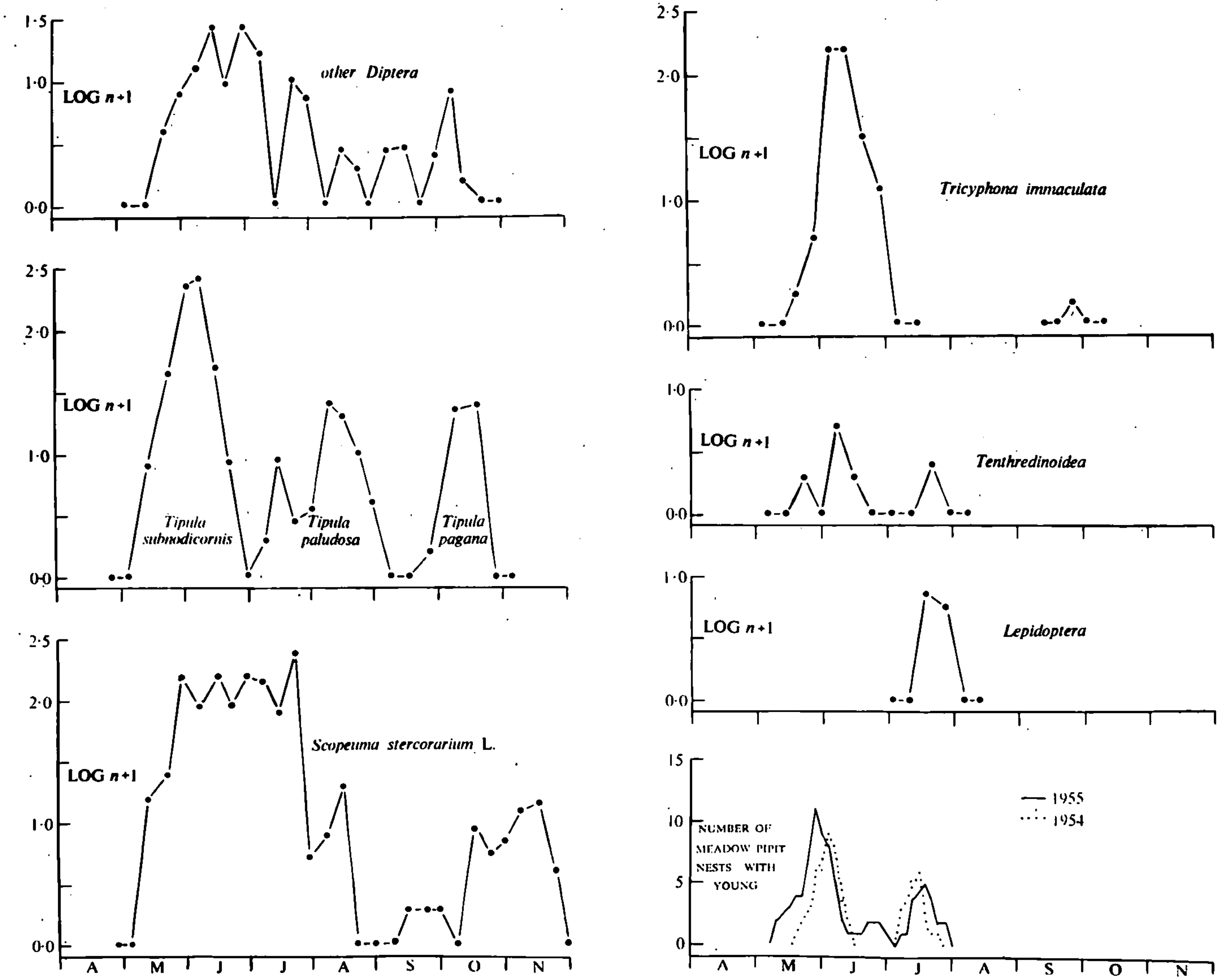


Fig. 32. The emergence of <u>Tipula subnodicornis</u> in relation to the breeding of the Meadow Pipit.

Fig. 33.
The captures of insects on 6 sticky traps, 1955.



other Diptera
LOG n+1
1·5
1·0
0·0
Tipula subnodicornis
Tipula paludosa
Tipula pagana
2·5
2·0
1·0
0·0
Scopeuma stercorarium L.
2·5
2·0
1·0
0·0
A
M
J
J
A
S
O
N
Tricyphona immaculata
Tenthredinoidea
Lepidoptera
NUMBER OF MEADOW PIPIT NESTS WITH YOUNG
— 1955
···· 1954
15
10
5
0

Meadow Pipit were directly related. It was more likely that the two animals were influenced by the changes in the environment which occur at this time of year, for example, the increase in temperature.

It would appear that the emergence of *T. subnodicornis*, one of the first insects to emerge on the Moor House Reserve was important for successful breeding of the Meadow Pipit. Its numbers, ease with which it can be caught by the Meadow Pipit and its size makes this tipulid an excellent food material for nestling Pipits, and these reasons probably account for the high percentage of *T. subnodicornis* in the food of the Meadow Pipit.

XII Discussion.

Much has been written concerning the processes which regulate the abundance of animals, but there still remains considerable divergence of opinion as to the effective agencies. This, in part, appears to be caused by the difficulty in analysing and isolating all the possible causes of control acting on populations. Further, many studies have been confined to only one or two factors and this has been particularly true of laboratory studies in which only one factor has been varied at a time.

Solomon (1949) has reviewed much of the literature on the control of animal populations. He divided the theories of population control into five classes, namely i. the early biotic factors ii. competition iii. physical theories iv. periodic fluctuations v. comprehensive theories.

Lotka (1925, 1932) and Volterra (1926, 1931) used the logistic curve as a basis of their mathematical models of population control. The limitations of the logistic equations have been pointed out by Andrewartha & Birch (1954) and the chief of these appears to be that the population must have a stable age distribution and that the depressive influences of density on the rate of increase must operate immediately. There must be considerable doubt that these two requirements actually occur in most populations and therefore the assumptions must be regarded as unrealistic.

Nicholson & Bailey (1935) have given consideration to predator-prey relationships and competition using theoretical models. Thompson (1939), Ullyett (1953) and Andrewartha & Birch (1954) have criticised the views of Nicholson & Bailey on the grounds that the assumptions of random searching is unwarranted, at least for certain parasites.

The physical theories of Bodenheimer (1930, 1931) have suggested that about 85% of the mortality of insects was in their early stages and this was the effect of the climate. He suggested that the remaining mortality, which was caused by predators or parasites was of only minor importance. There is undoubtedly a certain amount of truth in the first part of the suggestion, particularly amongst species which lay large numbers of eggs . Undoubtedly, large numbers of tipulid eggs and first instar larvae die because of dessication. However the remaining mortality should not be ignored for, assuming an 85% mortality due to climate and an equal sex ratio, then the population would still be able to increase 7.5 times on the numbers in the previous generation.

The various theories of periodic fluctuations do not need to be considered here, for, in most cases, there is considerable disagreement as to the cause and also these phenomona are only well authenticated from the arctic or sub-arctic or under severely controlled laboratory conditions.

A recent climatic theory of population control has been postulated by Andrewartha & Birch (1954). This is essentially an elaboration of Bodenheimer's ideas and it suggests that both population density and geographical distribution are limited by climatic conditions. There is a certain probability that the climate in a particular locality will be sufficiently severe so as to cause an excessive mortality in the population. This probability and its standard deviation, together with the fecundity of the species could account for the density of the population, the fluctuation in numbers and the occasionally very large numbers of animals. It was suggested that the probability of encountering less favourable climatic conditions for the species increases as the edge of distribution is approached and a certain probability determines the geographical boundary of the species. This theory does not imply a deliberate control (or governing Nicholson 1954) of the population as does the parasite-prey density dependent relationships of Nicholson & Bailey (1935), but merely an accumulation of chance climatic factors.

There are two main criticisms which must be raised against these theories. First, as Lack (1954) has pointed out, the theoretical work on animal control has far outstripped the available field observations. Secondly, much of the work gives the impression that the theories were based on observations of only a few types of animal groups. It must not be expected that the factors which control a population of Protozoa might be the same as those which limit the numbers of insects or a population of birds. Further, while one factor may limit one generation, another may be of importance in the following one and even a third factor may affect the size of the third generation.

Thus the type of control theory that must be envisaged is one that is comprehensive in style. This type of control theory is favoured by Thompson (1939) and Schwerdtfeger (1941) where a number of factors are thought to control animal population.

Many population studies have shown that the numbers of an animal vary markedly from year to year. Solomon (1949) gives many examples of these, some varying from a ratio of 10,000 to 1 for the maximum-minimum ratio for populations of the moth Panolis piniperda in Germany (Schwerdtfeger 1941) to as low as 3.8 : 1 for a scale insect in Palestine (Bodenheimer 1938). When population density varies extensively, as in the case of many insects, is it possible that they may not be "controlled" at all? Could they not just be randomly fluctuating between the upper limit (the limit of food supply) and the lower limit (virtually no population present)? Certainly, an animal which can vary between virtually zero and in such numbers that it can markedly reduce its food supply (e.g. defoliating caterpillars on pine and oak) then there seems to be little justification in describing the population as controlled. Consideration should be given to the possibility of chance fluctuations causing many observed fluctuations.

On the other hand, personal observations on particular colonies of the Kittiwake (Rissa tridactyla) suggest that the numbers of birds at the colonies were consistently similar from year to year. This consistemcy is almost certainly due to the very low annual mortality (10%) and the subsequent longevity of this species. The importance of longevity and the survival from one reproductive season to another must not be ignored in consideration of the fluctuations in animals. Thus the longer the expectation of life in relation to the length of the life cycle, the more buffering there will be on factors which cause fluctuation in numbers such as mortality rates and fecundity.

The present study on *Tipulidae* has suggested that these are animals which fluctuate markedly in numbers. *Nephrotoma submaculosa* and *Tipula subnodicornis* have been reduced from numbers which must be described as abundant to zero in a number of habitats and within one generation. Many other species of *Tipulidae* were found to fluctuate markedly in numbers from one generation to another.

The *Tipulidae* generally, would appear to be animals adapted to, and living in wet environments and are liable to dessication, particularly in the eggs and early instar stages. This liability to dessication was probably the cause of the reduction in the numbers of *T. subnodicornis* in in 1955, for there was no indication that the predation by Meadow Pipits or other vertebrates affected the numbers. Further, the two parasites found in this species, a tachinid Diptera and a fungus, were both effective only in the final instar and not in the first instar, the stage in which the mortality occurred.

It is reasonable to suggest that climate may be able to reduce the population of Tipulidae to a considerable extent. If the periods of dryness, which cause the mortality, occur sufficiently frequently during the time that the eggs are hatching, then it is possible that climate may prevent the populations reaching very high densities on many occasions. Thus competition and predator-prey relationships may be of rare occurence in the control of populations exposed to extensive climatic variations.

Lack (1954) has suggested that food is the most important factor in the limitation of bird populations. Evidence was found at Moor House that the Meadow Pipit was distributed in the vicinity of suitable feeding areas. This was further supported by the smaller clutch size at higher altitudes, the inference being that the clutch size was selected in relation to the most successful brood size (Lack 1954). There was not much evidence that the amount of food available for the Meadow Pipit was less at higher altitudes, and as has been previously suggested it is thought that climate, acting on the food materials, causes periods when food is difficult to obtain (such as in rain). Thus there is evidence food may limit the distribution of the Meadow Pipit but the effective means may be through the effect of climate.

Elton (1949) suggested that factors which were the most important in controlling animal numbers were density dependent factors, the chief of which are intra- and inter-specific competition, predators and parasites. While this may be so in many cases, more attention should be given to the chance effects of climate as has been suggested by Andrewartha & Birch (1954).

XIII Summary.

1. A study was carried out on the *Tipulidae* and the Meadow Pipit on the Moor House Reserve, Westmorland, an upland moor of 4,000 hectares.

2. Sixty-six species of *Tipulidae* were recorded from the Reserve, 18 of these belonging to the genus *Tipula*. Notes on the 66 species are given.

3. Of the 67 species of *Tipulidae* recorded from the northern Pennines, 43 have been recorded from northern Norway or Sweden, but only 15 from the Pyrenees and 4 from the French Alps. This indicates an affinity with the fauna of Scandinavia.

4. Two species were recorded for the second time and three species for the third time in Great Britain. Three species were recorded from England for the first time.

5. The majority of the larval habitats were "wet" situations.

6. It was found that the spread of emergence per species of *Tipulidae* was greater during the summer than in the autumn or spring.

7. The seasonal distribution of species was studied by means of sticky traps. *Tipula subnodicornis* was by far

the commonest species, occurring on most peat covered areas. On alluvial areas, T. paludosa, T. variipennis and T. pagana were common. Trichyphona immaculata appeared to be very common on the moors.

8. The Tipulinae were examined for the presence of egg filaments on the eggs. The majority of species possessed the filament. T. subnodicornis appeared to be the only major exception to the hypothesis that the filament was an adaptation to a wet environment.

9. The females of the majority of species of Tipulinae emerge with ripe eggs. Those which do not, (T. alpium and T. rufina) survive by finding shelter on the vertical surfaces of hags and rock outcrops.

10. Evidence is given for T. paludosa ripening a second batch of eggs.

11. A key is given for some of the larvae of the Tipulinae found at Moor House.

12. The biology of Tipula subnodicornis.
The flightless females appeared to move only a short distance. Average movement 1 meter in 14 hours.

13. There was a marked diurnal rhythm of emergence of females between 11.00 and 14.00 hrs. G.M.T.
This coincided with the peak of male activity. The emergence of the species occurred in less than 33 days.

14. The eggs were laid very rapidly after the emergence

of the female. Each female had an average of 240 eggs and 90% of these were laid within 10 hours of emerging.

15. Each egg required about 40 ergs to be laid; the eggs being projected with considerable force.

16. The results of a marking experiment indicated that the female mortality (73% per day) was larger than the mortality of the males (56% per day); that the mortality was higher on a dry, sunny day than on a damp, dull da y; that there was a large emergence each day and that at the peak of emergence the adult population was about 15 per square meter, that is, 13% of the larval population.

17. The eggs were elongate-oval, measuring .901 by .334 mm. at the maximum diameters. They took 21.5 days to hatch at 10°C. The majority of the eggs were laid within 3 cm. of the surface of the peat.

18. There are 4 larval instars in T. subnodicornis as there are in T. paludosa, T. variipennis, T. marmorata and Trichyphona immaculata.

19. A population study suggested that there was normally a large mortality in the egg and first instar stages of T. subnodicornis and a similar result was obtained for T. paludosa.

20. There was no renewal of growth in the spring by larvae of *T. subnodicornis* and the species over-wintered in the 4th. instar.

21. The sex-ratio of the forth (final) instar larvae was 1:1.

22. Larvae of *T. subnodicornis* were most numerous on *Juncus squarrosus* and *Eriophorum* moor. They were least abundant on *Sphagnum* bogs and the edges of peat hags.

23. There was a relationship between the number of eggs, la rvae and adults found on 6 neighbouring areas, suggesting that there was little movement of the immature stages.

24. In 1955, the population was markedly reduced by a drought during the hatching of the eggs. The entire population was killed on *Juncus sqarrosus* moor.

25. The drought appeared to have a selective effect on the populations in different plant communities. Little change in the population density took place on *Sphagnum* bog.

26. The food of larvae of *T. subnodicornis* was entirely of plant material, consisting of root-hairs of *J. sqarrosus*, *Polytrichum* and, in some areas, much liverwort.

27. Study of *Tipula paludosa*.

There was a marked difference between the time of emergence of adults at Rothamsted and Moor House. The emergence was about 8 weeks earlier at Moor House and it is suggested that this may be related to the nocturnal emergence of this species and the daily minimum temperature at these stations.

28. The females show a well defined daily emergence rhythm, emergence taking place shortly after sun-set.

29. Under sunny conditions, the adults were rarely seen during day-light since they sheltered at the base of tufts of *Juncus effusus*. This behaviour appeared to have a survival value.

30. On emerging, each female had an average of 360 eggs.

31. The eggs were laid very rapidly, 90% of the eggs being laid within 17 hours of emergence.

32. The eggs were laid within the top 1 cm. of soil and these measured 1.10 by .44 mm.

33. The larvae overwintered in the 3rd. instar.

34. The population in 1956 was similar to that in 1955 and the drought in 1955 had little effect.

35. The study of *Tipula oleracea*.

This species was closely related to *T. paludosa*.

T. oleracea was rare at Moor House.

36. T. oleracea differred from T. paludosa in the following respects. It had more eggs per female (582) and the eggs were smaller (.831 by .314 mm.). It was possible to separate the 1st. instar larvae of these two species.

The study of the Meadow Pipit

37. The breeding biology has been investigated by means of nest record cards and ringing recoveries, particular attention being paid to the effect of altitude.

38. Breeding was earlier in the south than in the north of Great Britain and was later as altitude increased (approximately one day later for every 130 feet rise in altitude).

39. The clutch size decreased from 4.52 near sea-level to 4.07 over 1,000 feet. These differences existed in both first and second clutches.

40. The Meadow Pipit laid larger clutches in Iceland and Norway than in Great Britain but no differences were found between the north and south of Great Britain.

41. The mean incubation period was 13.0 days from the laying of the final egg. The fledging period was 12.5 days.

42. The hatching success was 54% and the fledging

success was 80%, giving a breeding success of 43%. This was not uniform, however, for, as altitude increased, the total nest mortality decreased.

43. The mortality in the first year of life was estimated as 76% while the average adult mortality was calculated as 57% and 58% by two independent methods.

44. It is suggested that the decrease in clutch size as altitude increased was related to the more severe climatic conditions at higher altitudes and the decrease in mortality was due to a decrease in the nest predation at higher altitudes.

45. The feeding of young in the nest was studied by means of nest recorders.

46. The feeding rate was highest just after dawn and decreased until in the evening, it was reduced to half that in the early morning.

47. One young bird in the nest received the most visits per young (3.0 visits per hour) and the largest brood size (5) received least (1.8 visits per young per hour).

48. There was no difference between the rate of visits paid to nests containing 4 or 5 young. The inference being that the adults were collecting food at the

maximum rate.

49. Under cold, snowy conditions, the feeding visit rate dropped markedly.

50. Under very cold conditions, the older chicks lost weight (.5 gm. in 12 hours) and newly hatched young became moribund and died.

51. Some, but not all pairs raised second broods at Moor House.

52. The clutch size of the Meadow Pipit at Moor House was 4.27.

53. Tipulidae were the most frequent food material brought to the young. T. subnodicornis forming 76-89% of the food for the first broods and T. paludosa forming 35-46% of the food given to second broods.

54. It is estimated that the Meadow Pipits took .58 of 1% of the available T. subnodicornis in 1954 and 1955 although the time of breeding coincided with the emergence of this tipulid.

55. The density of the Meadow Pipit at Moor House was low, there being between 5 and 10 pairs per 100 acres in 1954 and 1955.

56. The Meadow Pipit appeared to be associated with the presence of streams and alluvial flats for feeding.

XIV REFERENCES.

Alexander, C.P. 1920. The crane-flies of New York. Part II: Biology and phylogeny. Cornell Univ. Agric. Exp. Sta. Mem. 38: 691-1,133.

Andrewartha, H.G. & Birch, L.C. 1954. The distribution and abundance of animals. Chicago.

Audcent, H. 1932. British Tipulinae (Diptera, Tipulidae). Trans. ent. Soc. S. Engl. 8; 1-34.

Bailey, N.T.J. 1951 On the estimating the size of moblile populations from recapture data. Biometrika 38: 293-306.

Barnes, H.F. 1925. The ecological distribution of adult craneflies in Carnarvonshire. J. Ecol. 13: 138-148.

Barnes, H.F. 1937. Methods of investigating the biometrics of the common crane-fly, *Tipula paludosa* Meigen, together with some results. Ann. appl. Biol. 24: 356-368.

Beling, T. 1879. Zweiter Beitrag zur Naturgeschichte (Metamorphose) verschiedener Arten aus der Familie der Tipuliden. Abh. K.-K. Zool.-Bot. Ges. Wien. Verh. 28 (1878): 21-56.

Beling. T. 1886. Dritter Beitrag zur Naturgeschichte (Metamorphose) verschiedener Arten aus der Familie Tipuliden. Abh. K.-K. Zool.-Bot. Ges. Wien. Verh. 36: 171-214.

Bengtsson, S. 1897. Studier öfver insektlarver I. Till kännedomen on larven af *Phalacrocera replicata* (Lin.)). K. Fysiogr. Sällsk Lund. Handl. 8 1-117. (In Alexander, 1920).

Bodenheimer, F. 1923. Beit zur Kenntriss der Kohlschnake (*Tipula oleracea*). Zeits. wiss. Zool. 121.

Bodenheimer, F. 1924. Beit zur Kenntriss von _Tipula_ _oleracea_. Zur Kenntriss der Larve. Zool. Jb. 48.

Bodenheimer, F. 1931 Der Massenwechsel in der Tierwelt. Gründross einer allgemeinen tierschen Bevölkerungslehre. Arch. Zool.(Ital.) Napoli. 16: 98-111.

Bodenheimer, F. 1938. Problems of Animal Ecology. London.

Broadbent, L. 1948. Aphis migration and the efficiency of the trapping method. Ann. appl. Biol. 35: 379-394.

Brown, E.S. 1947. _Tipula_ _gimmerthali_ Lackschewitz, new to Britain. Proc. R. ent. Soc. Lond. (B). 16: 120-123.

Brown, E.S. & Duncan, A.B. 1949. A list of the _Tipulinae_ (Diptera, Nematocera) of the Solway area, with some notes on the habitats of the adults. Scot. Nat. 61: 156-168.

Campbell, B. 1955. Ornithological surveys of Nature Reserves, 1954. Bird Study 2; 84-86.

Chance, E.P. 1940. The truth about the Cuckoo. London.

Coe, R.L. 1950. Handbook for the identification of British Insects. 9 (2). Diptera, Family Tipulidae.

Crisp, G. & Lloyd, Ll. 1954. The community of insects in a patch of woodland mud. Trans. R. ent. Soc. Lond. 104: part 13 269-314.

Crump, W.B. 1913. The coefficient of humidity. New Phytol. 12; 125.

Cuthbertson, A. 1926. The study of Clyde crane-flies; the larval habitats of some local species. Ent. Mon. Mag. 84-88.

Dunham, K.C. 1948. Geology of the northern Pennine orefields. D.S.I.R. Geological Survey.

Edwards, F.W. 1938. British short palped crane-flies. Trans. Soc. Brit. Ent. 5; 1-168.

Edwards, F.W. 1939. Additions to the list of British crane-flies. Ent. Mon. Mag. 75; 241-249.

Elton, C. 1949. Population interspersion: an essay on animal community patterns. J. Ecol. 37: 1-23.

Gibb, J. 1955. Feeding rates of Great Tits. Brit. Birds 48: 49-58.

Hemmingsen, A.M. 1952. The oviposition of some crane-fly species (*Tipulidae*) from different types of localities. Vidensk. Medd. dansk. naturh. Foren. Kbh. 114: 365-430.

Johnson, C.G. 1950. The comparison of suction trap, sticky trap, and tow-net for the quantitative sampling of small airborne insects. Ann. appl. Biol. 37: 268-285.

Lack, D. 1935. The breeding bird population of British heaths and moorland. J. Anim. Ecol. 4 : 43-51.

Lack, D. 1943. The life of the Robin. London.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302-352.

Lack, D. 1948. Natural selection and family size in the Starling. Evolution 2: 95-110.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford.

Lack, D. & Arn, H. 1947. Die Bedeutung der Gelegegrösse beim Alpensegler. Ornith. Beob. 44: 188-210.

Lack, D. & Lack E. 1951. The breeding biology of the Swift Apus apus. Ibis 93: 501-546.

Lackschewitz, P. 1935. Zur Kenntnis der polyneuren Nematoceren (Dipt) des Nordlichen Norwegens. Tromsø Mus. Aarsh. 53: No. 4 1-27.

Lotka, A.J. 1925. Elements of physical biology. Baltimore.

Lotka, A.J. 1932. The growth of mixed populations; two species competing for a common food supply. J. Washington Acad. Sc. 22: 461-469.

Mannheims, in Lindner, D 1940-53. Die Fliegen der paläarktischen Region. Studtgart. Parts 15 & 16, Tipulidae.

Manley, G. 1936. The climate of the Northern Pennines: the coldest part of England. Quart. J. R. met. Soc. 62; 103-115.

Manley, G. 1943. Further climatological averages for the northern Pennines, with a note on topographical effects. Quart. J. R. met. Soc. 69;

Miall, L.C. & Shelford, R. 1897. The structure and life history of *Phalocrocera replicata*. Trans. R. Ent. Soc. Lond. 343-361.

Monk, J.F. 1954. The breeding biology of the Greenfinch. Bird Study 1; 2-14.

Nice, M.M. 1937. Studies in the life history of the song sparrow. I A population study of the song sparrow. Trans. Linn. Soc. N.Y. 4; 1-247.

Nicholson, A.J. 1933. The balance of animal populations. J. Amim. Ecol. 2; 132-178.

Nicholson, A.J. 1954. An outline of the dynamics of animal populations. Australian J. of Zoology, 2; 9-65.

Nicholson, A.J. & Bailey, V.A. 1935. The balance of animal populations. Proc. Zool. Soc. Lond. 551-598.

Nielsen, Ringdahl & Tuxen, 1954. The Zoology of Iceland. Vol. 3, part 48. Diptera 1. Copenhagen & Reykjavik.

Oldham, J.N. 1928. On the final larval instar of Tipula paludosa Meigen and Tipula lateralis meigen. Proc. R. phys. Soc. 21; 217-252.

Pearsall, W.H. 1950. Mountains and Moorland. London.

Pierre, C. 1924. Faune de France, part 8, Dipteres: Tipulidae.

Pinchin, R.D. & Anderson, J. 1936. On the nocturnal activity of Tipulinae (Dipt.) as measured by a light trap.

(1) The time of flight and the proportion of sexes. Proc.R. ent. Soc. Lond. (A) 11; 69-78.

Rennie, J. 1916 On the biological and economic significance of *Tipula paludosa*. Part. 1. Mating and oviposition. Ann. appl. Biol. 2; 235-240.

Rennie, J. 1917. On the biological and economic significance of *Tipula paludosa*. Part 2. Hatching, growth and habits of the larvae. Ann. appl. Biol. 3; 116-137.

Robertson, A. G. 1939. The nocturnal activity of Crane-flies (*Tipulinae*) as indicated by captures in a light trap at Rothamsted. J. Anim. Ecol. 8; 300-322.

Rogers, J.S. 1933. The ecological distribution of craneflies of northern Florida. Ecol. Monogr. 3; 1-74.

Rogers, J.S. 1942. The crane-flies of the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Mich. No. 53.

Ryves, B.H. 1944 The fledging period of birds. Brit. Birds 37; 151-155.

Schwerdtfeger, F. 1941. Uber die Ursachen des Massenwechsels der Insekten. Z. Angew. Ent. 28; 254-303.

Snow, D. 1955. The breeding of the Blackbird, Song Thrush and Mistle Thrush in Great Britain. Part II. Clutch size. Bird Study. 2; 72-84.

Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. 18; 1-35.

Thompson, W.R. 1939. Biological control and theories of the interaction of populations. Parasitology 31; 299-388.

White, J.H. 1951. A study of the life history of *Tipula lateralis* in cress-beds. Ann. appl. Biol. 38; 847-858.

Witherby, H.F. *et al*. 1938-41. The Handbook of British Birds. London.

Ullyett, G.C. 1950. Competition for food and allied phenomona in sheep-blowfly populations. Phil. Trans. R. Soc. Lond. (B) 234; 77-174.

Verheyen, R. & le Grelle, G. 1950. Interpretation des resultants du baguage relatifs au pipit des pres *Anthus pratensis* (L.). Gerfaut 40; 124-131.

Volterra, V. 1928. Variations and fluctuations of individuals in animal species living together. J. Cons. int. Explor, Mer 3 (1) 3-51.

Volterra, V. 1931. Leçons sur la théorie mathématique de la lutte pour la vie. Paris.

XV Appendix

Appendix I.

Relationships used in mark and release study.

Total population x

$$x = \frac{a\ (n+1)}{(r + 1)}$$

where a animals were captured, marked and released,

n animals were recatured and of which

r were found to have been marked.

The best estimate of the variance was obtained by the following relationship

$$\text{var } x = \frac{a^2 n\ (n-r)}{r^3}$$

Death rate λ

$$= \frac{n_{11} \times n_2}{n_1 \times n_{21}}$$

where n_{21} animals which were marked on day 1 and were recaptured on day 2.

n_{11} animals which were marked on day 1 and recaptured later on day 1.

n_1 and n_2 were the total recaptures on days 1 and 2 respectively.

The estimate of the variance was obtained from the following relationship

$$\operatorname{var} \lambda = \lambda^2 \left(\frac{1}{n_{11}} + \frac{1}{n_{21}} + \frac{1}{n_1} - \frac{1}{n_2} \right)$$

The birth or emergence factor.

$$\mu = \frac{s_2 \,.\, n_{21}}{s_1 \,.\, n_{22}}$$

where s_1 and s_2 are the number of animals marked on days 1 and 2 respectively.

The estimate of the variance was obtained from the following relationship

$$\operatorname{var} \mu = \mu^2 \left(\frac{1}{n_{22}} + \frac{1}{n_{21}} \right)$$

Appendix II.

Samples of larvae of Tipula subnodicornis at Netherhearth, 1953-55.

Date	Diameter of core	No. of samples	Larvae per sample 0	1	2	3	4	5	6
2.12.53	4"	33							
18.3.54) 26.3.54)	4"	32	7	10	8	1	3	2	1
6.4.54) 12.4.54)	4"	30	11	10	5	2	2	0	0
3.5.54) 4.5.54)	4"	44	19	14	2	6	0	2	1
28.6.54	3.4cm.	11	0	3	2	1	2	1	1
8.7.54) 21.7.54)	3.4cm.	30	10	10	4	4	2	0	0
18.8.54	3.4cm	30	18	8	2	2	0	0	0
4.9.54	3.4cm.	30	19	7	1	1	2	0	0
18.10.54	3.4cm.	30	21	8	1	0	0	0	0
7.11.54	4"	30	8	12	5	1	2	2	0
22.12.54	4"	30	5	12	6	5	2	0	0
1.2.55	4"	30	11	7	4	6	1	1	0
22.3.55	4"	30	12	6	7	2	1	2	0
4.5.55) 10.5.55)	4"	40	18	16	3	1	0	1	0
30.6.55	1.0cm.	60	56	4	0	0	0	0	0
26.7.55	2.5"	30	30	0	0	0	0	0	0
13.9.55	4"	30	30	0	0	0	0	0	0
21.9.55	4"	30	30	0	0	0	0	0	0
18.11.55	4"	30	30	0	0	0	0	0	0

Samples of eggs.

28.6.54	3.4cm.	30
30.6.55	1.0cm.	60

Appendix III

Samples taken for larvae of Tipula paludosa on alluvial area below House. 1955-56.

Date	Diameter of core	No. of samples	No. of larvae	Larvae/ sample	Larvae per sq. meter.
1.9.55	3.4cm.	60	10	.167	167
4.11.55	2.5"	60	21	.350	116
21.3.56	4"	30	14	.463	57
18.6.56	4"	30	12	.400	49

Samples takensfor eggs.

23.7.55	3.4cm.	30	87 eggs, 2.77/sample 2,770 per sq. meter.