Ecological studies on moorland ground beetles (coleopteran : carabidae)

Houston, W. W. K.

ECOLOGICAL STUDIES ON MOORLAND GROUND BEETLES

(COLEOPTERA : CARABIDAE)

by

W.W.K. Houston, B.Sc.

(St. Cuthbert's Society)

.... being a thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham, 1970.

ACKNOWLEDGMENTS

The writer wishes to express his sincere thanks to Dr. J.C. Coulson for his help and criticism throughout the study, and to Professor D. Barker for providing facilities in the Department of Zoology, Durham.

I would also like to thank :

Members of the Department of Zoology for helpful discussion and advice,

The staff of Moor House Research Station, and Tom Buffey, the Site Research Officer at Cow Green, for their generous assistance and hospitality,

Dr. M.L. Luff for the identification of some of the material, particularly the larvae,

Dr. J.W. Coles of the British Museum (Natural History) for identifying the Nematomorpha,

Mr. E. Henderson for photographic assistance,

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

and Aileen, for many reasons.

The work at Cow Green was supported by a grant from the I.C.I. Teesdale Trust Fund.

CONTENTS

I. INTRODUCTION

Pearsall (1950) remarked that "Upland Britain .... is equal in area to lowland Britain". Despite this large expanse, which is mainly mountain and moorland (Hart 1955), the Carabidae of these areas have received little attention. Sharp (1916) mentions some common beetles to be found in upland areas, and more recently Davidson (1961) published some notes on Cumberland and Westmorland Coleoptera, which included some Carabidae records from the north Pennines; Pearson & White (1964) listed some Carabidae from moorland in north Wales; Greenslade (1968) discussed some Carabidae found in Argyll, Scotland, and Goodier (1968) some Coleoptera found on Welsh mountains.

Cragg (1961) discussed some aspects of the ecology of moorland animals and stressed the need to evaluate the functions of organisms in the ecosystem. But many studies on the moorland fauna have been concerned mainly with distribution and numerical abundance of a few common species or groups and knowledge of their role in the ecosystem is often only superficial.

With the initiation of the International Biological Programme on tundra and sub-arctic terrestrial ecosystems (in 1967), the emphasis in the moorland ecosystem is now on biomass and energy turnover, but progress in this field is often being restricted by the lack of basic biological information on many of the organisms.

By studying a limited range of organisms on moorlands, several workers emphasise the patchy distribution of individual species and the habitat mosaic filled with different species (Block 1963; Cherrett 1961; Hadley 1966). They have also stated that predators and parasitism appear to have negligible effect on the numbers of dominant insects, and have demonstrated how single environmental factors dominate changes in density, and may be used to predict future densities.

As the determination of the densities of most Carabid species is often a highly erratic and disruptive process and of little value unless related to other factors, the emphasis in this study is on quality and not the quantity of the Carabid fauna. It attempts to evaluate the status of the Carabidae on moorland fairly typical of the north Pennines, with emphasis on habitat and life history phenomena, and to lay a broad foundation for any future detailed investigation.

II. THE STUDY AREA AND SAMPLING SITES

1. Location and physiography

Most of the work described in this thesis was conducted on the Moor House National Nature Reserve (N.R.80 : Nat.Grid.Ref. NY/758329) (Conway 1955). A subsidiary study was conducted on the Cow Green area of Widdybank Fell, Upper Teesdale (Nat.Grid. Ref. NY/812301) (Bellamy et al 1969).

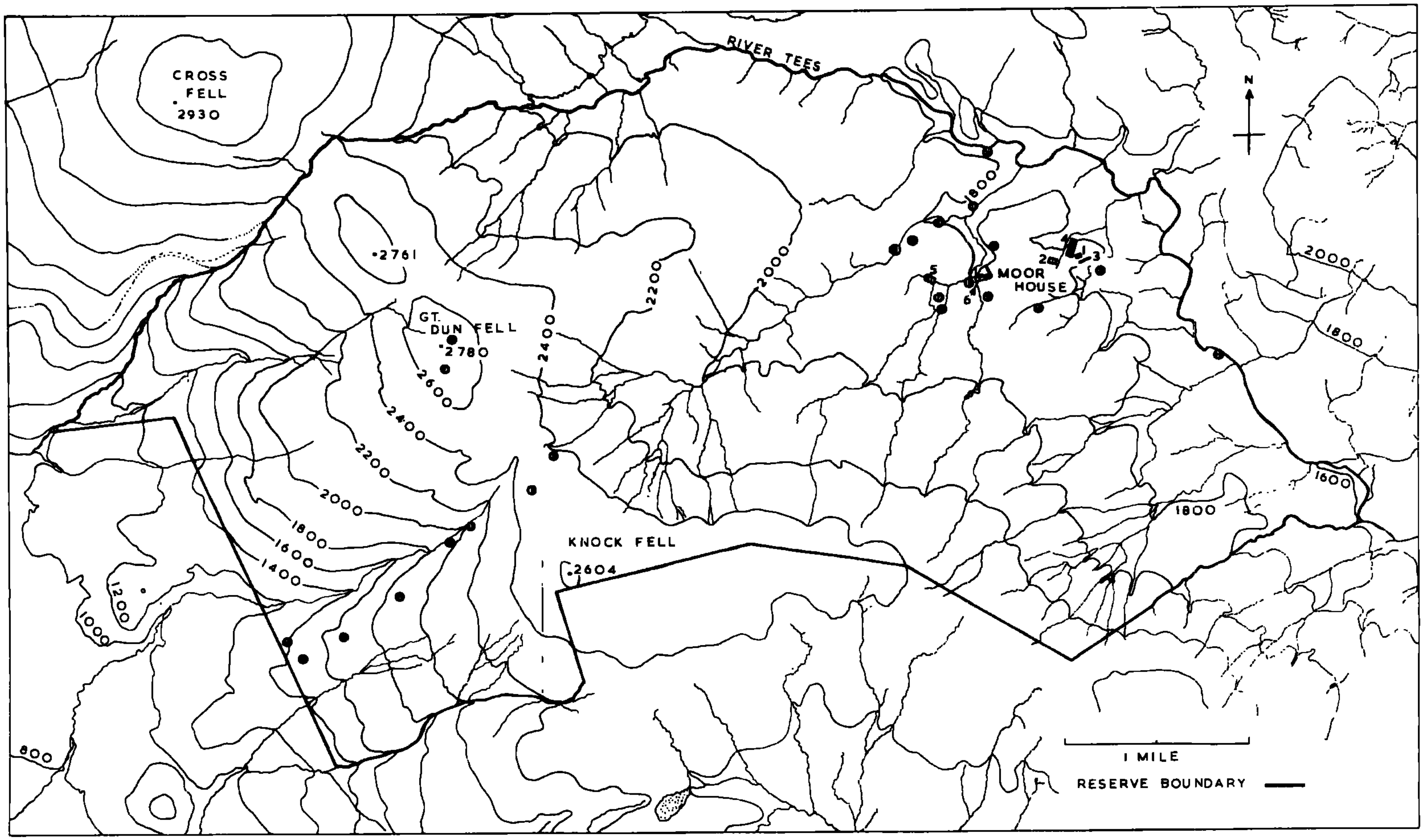
a) The Moor House Reserve

The Moor House Reserve (Fig.1) occupies 10,000 acres (4,000 hectares) of moorland typical of the northern Pennines. Situated in Westmorland, 12 miles to the east of Penrith and 11 miles to the south of Alston, it is separated from County Durham by the River Tees (which forms part of its northern and eastern boundary) and is less than 4 miles from the Yorkshire border. It features the characteristic dip and scarp slopes of the northern Pennines. The three principal fells, Knock Fell (2,604ft; 794m), Little Dun Fell (2,761ft; 842m), and Great Dun Fell (2,780ft; 845m), form the summit ridge which is continuous with Cross Fell (2,930ft; 893m), the highest peak of the Pennines, lying just outside and to the north of the reserve.

The entire area is dissected by numerous streams which flow into the River Eden on the west, and the River Tees on the east. Only the main streams are shown in Fig.1.

FIGURE 1

Map of the Moor House National Nature Reserve, showing the location of the major pitfall trap sites (black rectangles 1 - 6) and the main miscellaneous pitfall sites (black circles).


CROSS FELL
2930
RIVER TEES
N
2761
GT. DUN FELL
2780
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
KNOCK FELL
2604
MOOR HOUSE
1
2
3
4
5
6
I MILE
RESERVE BOUNDARY

The bed rock consists chiefly of the Carboniferous Yoredale series, a complex series of beds of limestone, sandstone, shale and coal, covered extensively by glacial drift overlaid by peat. To the east of the summit ridge Blanket Bog predominates, except on the high slopes and adjacent to streams where redistributed peat or minerals soils support rush and grass dominated areas. To the west of the summit ridge, rush and grass dominated areas predominate.

The geology has been comprehensively studied by Johnson & Dunham (1963) and Hornung (1969), whilst the vegetation has been described by Eddy et al (1968). General descriptions of the reserve have been given by Conway (1955) and Cragg (1961).

b) Cow Green

Cow Green, situated in County Durham, less than 2 miles ESE of the Moor House Reserve and about one mile north of the Yorkshire border, is only separated from Westmorland by the River Tees. The area studied is at an altitude of about 1,550ft (472m) and will soon be flooded to form a reservoir when the construction of a dam, to the south of the area, is complete.

2. Climate

a) Moor House

Meteorological records have been kept at Moor House since 1932 and Manley (1936, 1942, 1943) describes the climate as sub-arctic, having many features comparable to those at sea level in southern Iceland. It is typical of the montane regions of Britain (Pearsall 1950).

Figs. 2 & 3 show details of temperature and rainfall. The 1953-65 averages show a high number of rain days (248 per year); an average annual rainfall of 74.5 inches; an average daily sunshine of 3.7 hours; strong winds are common throughout the year; snow may lie until May and there is no month in which frost has not occurred. Throughout this thesis temperature is described in degrees centigrade.

The soil moisture content, of great importance to the immature stages of Carabidae, is very variable. The mean annual precipitation * is 74.8 inches and the mean potential evaporation rate is 17 inches. Thus the soil is gaining more than four times as much water from the atmosphere as it is losing by evaporation. Much of the precipitation is biologically relatively unimportant as it falls during the winter months. However, on a few occasions the precipitation to evaporation ratio drops below unity for several weeks. Monthly averages will not always reveal when the moor is drying out but the last two weeks of May and the first two of June is usually the driest period. Further dry spells generally occur in August and September. During the May/June dry spell the soil moisture content is at its lowest; the non-wet**

* based on a ten year record by Manley (1943)

** The degree of moisture in the soil is often referred to when describing the habitats of terrestrial insects. Murdoch (1967) described marshes, bogs, fens, flushes and the wet edges of streams and lakes etc. as "wet" habitats and the grasslands as "non-wet" habitats. Species living in wet habitats were termed "wet" species and those in non-wet habitats as "non-wet" species. This classification is used here.

FIGURE 2

Air temperatures ($\frac{\text{max.} + \text{min.}}{2}$) recorded at the Moor House Meteorological Station c.558 m O.D. Lat. 54° 41'N., Long. 02° 23'W. Nat.Grid. Reference No. NY 757328, and at Great Dun Fell c.655 m O.D. Lat. 54° 35'N. Long. 02° 28'W. Nat. Grid. Reference No. NY 710322.

Key

Figure 2a monthly averages:

●——● 1953-65 at Moor House

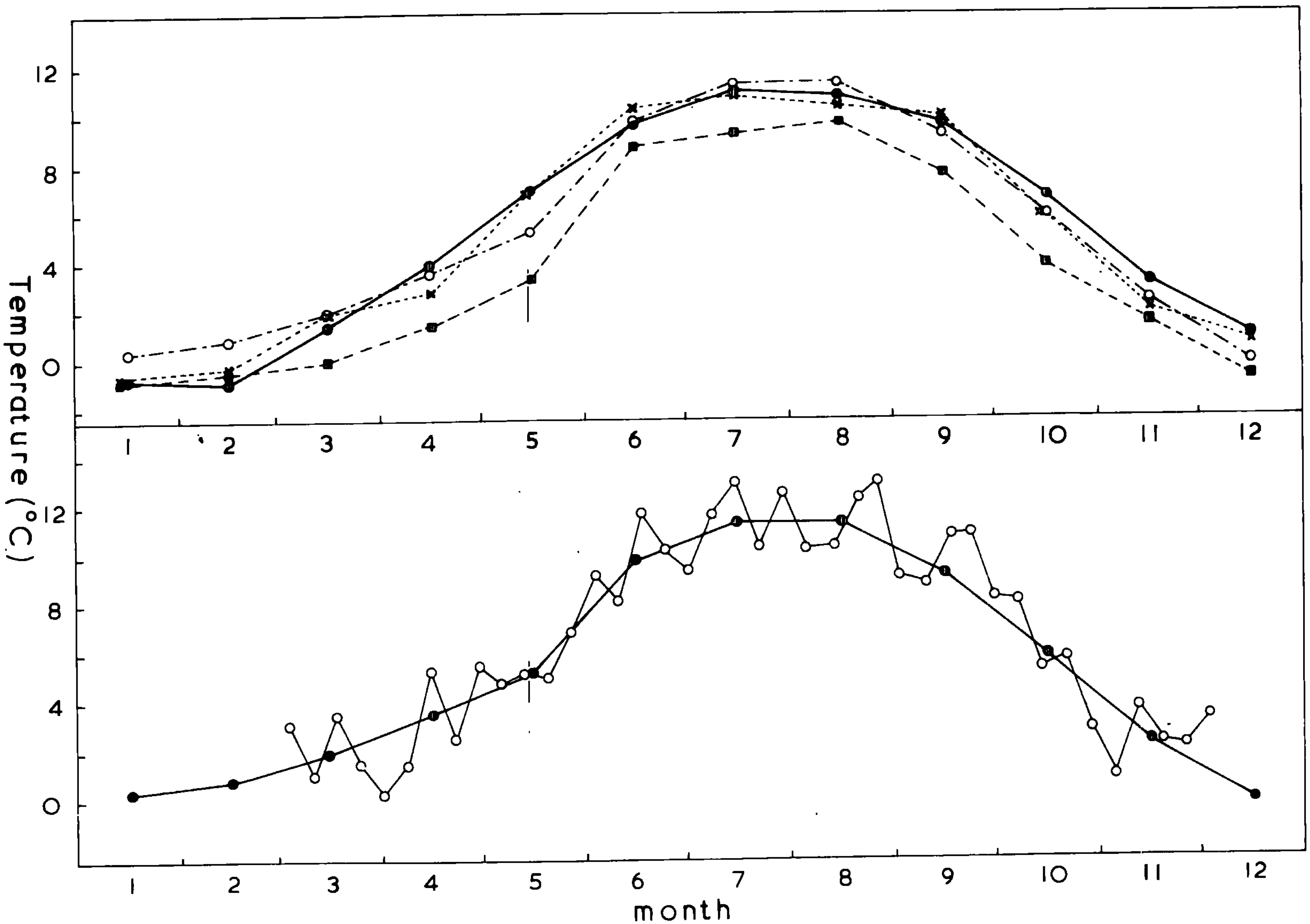
X-----X 1966 at Moor House

O-·-·-O 1967 at Moor House

■-—-■ 1967 at Great Dun Fell

Figure 2b ●——● 1967 monthly averages at Moor House

O——O 1967 averages per pitfall trapping period (mainly weekly intervals) at Moor House



Temperature (°C)
12
8
4
0
1
2
3
4
5
6
7
8
9
10
11
12
month

FIGURE 3a Daylength at 55°N. (Moor House field is 54° 41' N.)

Lower line - sunrise to sunset

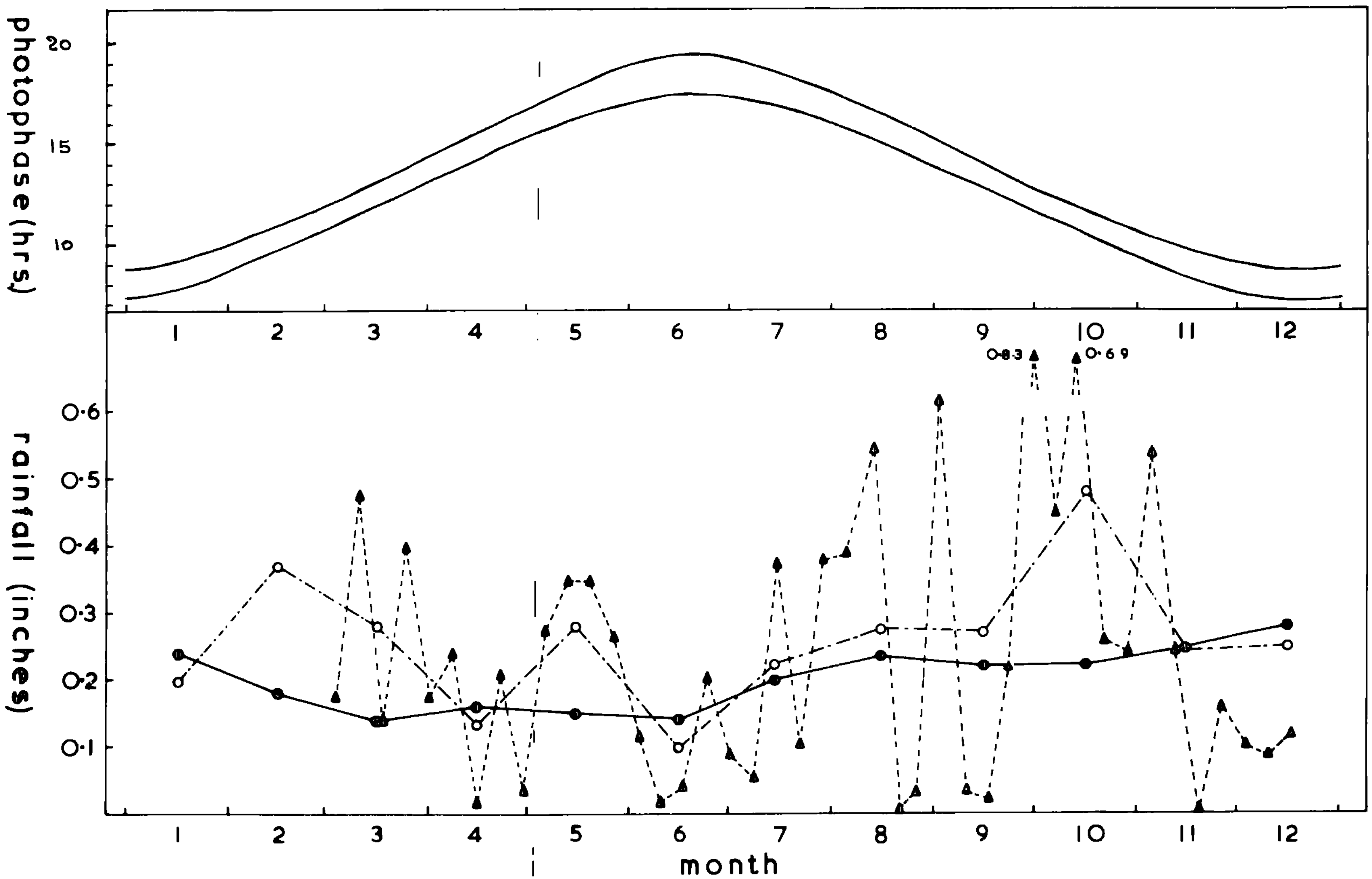
Upper line - sunrise to sunset including civil twilight

FIGURE 3b Rainfall (inches) recorded at the Moor House Meteorological Station

●———● 1953-65 Monthly averages

O-·-·-O 1967 Monthly averages

▲------▲ 1967 Weekly averages


photophase (hrs)
20
15
10
1
2
3
4
5
6
7
8
9
10
11
12
0·83
0·69
rainfall (inches)
0·6
0·5
0·4
0·3
0·2
0·1
month

habitats, e.g. Alluvial grasslands, became very dry and terrestrial arthropods are rarely seen, but the wet habitats, e.g. Blanket Bog, always remained moist. On the wet habitats, even during exceptionally dry spells at Moor House, when cracking of the peat occurs, the soil just below the surface, into which Coleoptera burrow, was still moist. The areas under Sphagnum hummocks and carpets of lichen and the stem bases of Eriophorum hummocks were always moist and served as refuges during the exceptionally dry spells.

During the autumn dry spells the conditions experienced on the non-wet habitats in the early summer rarely occurred and terrestrial arthropods were frequently taken.

b) Cow Green

Meteorological records have been kept at Cow Green since July 1967. A summary of the temperatures and rainfall for 1968 is given (Fig.4) and compared with those recorded at the Moor House meteorological station.

Although the temperature is slightly higher and the rainfall lower than Moor House, the climate still remains severe. Potential evaporation was not determined, but like Moor House the habitats are at their driest in the early summer and the late summer/early autumn. The non-wet habitats became very dry on the surface but the wet habitats always remained moist.

3. Sampling Sites

a) Moorhouse

Fig.1 shows the main study areas at Moor House. Detailed

FIGURE 4a Rainfall (inches) recorded at Moor House and at Cow Green in 1968

●———● Monthly averages at Cow Green

▲- - - -▲ Weekly averages at Cow Green

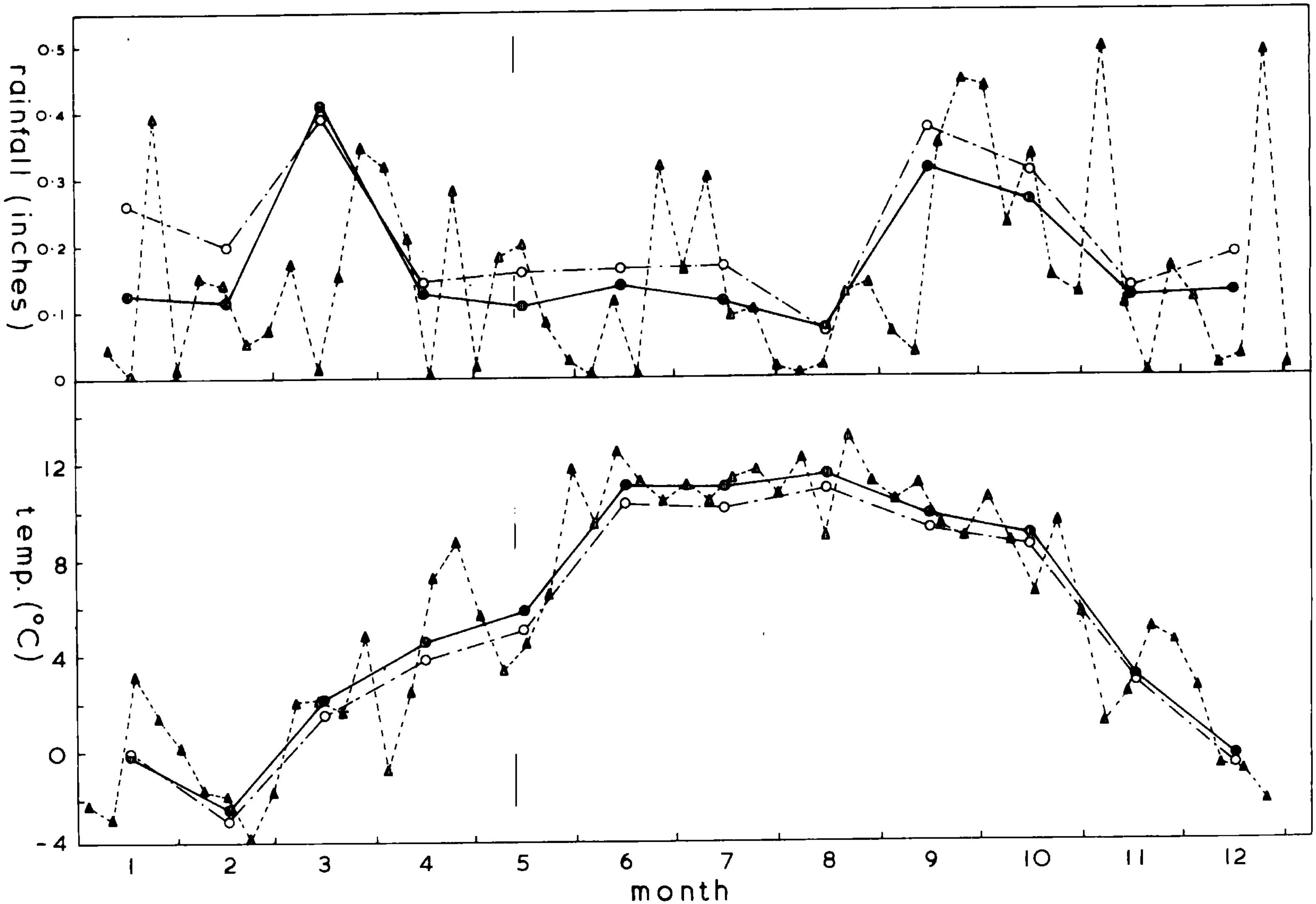
O-·-·-O Monthly averages at Moor House

FIGURE 4b Air temperatures ($\frac{\text{max + min.}}{2}$) recorded at Moor House and Cow Green in 1968

●———● Monthly averages at Cow Green

▲— — —▲ Weekly averages at Cow Green

O— · —O Monthly averages at Moor House



rainfall (inches)
0·5
0·4
0·3
0·2
0·1
0
temp. (°C)
12
8
4
0
-4
1
2
3
4
5
6
7
8
9
10
11
12
month

investigations were made on sites 1 to 6. Other sites, where less detailed studies were conducted, are marked with a black circle. Investigations, however, were not confined to these sites.

Site 1. Blanket Bog, Bog End (1800ft; 549m) Plate 1.

This is a Calluneto-Eriophoretum site typical of the Blanket Bog of the Pennines and part of an area chosen for I.B.P. studies on Blanket Bog.

The site supports a dwarf shrub vegetation dominated equally by bushes of Calluna vulgaris alternating with tussocks of Eriophorum vaginatum over a carpet of mosses, chiefly of Sphagnum rubellum. Lichens are well represented, especially the richly branched Cladonia sp. It is a wet habitat.

Site 2. Well drained Blanket Bog, Bog End (1,825ft; 557m)

This site is situated on a steep north facing slope. Calluna vulgaris is dominant and the bushes are taller than on site 1, giving more cover, with a corresponding reduction in Eriophorium vaginatum, over a carpet of mosses - chiefly Sphagnum recurvum. Lichens are scarce. It is perhaps closer to a Callunetum vulgaris than a Calluneto-Eriophoretum. It is a wet habitat.

Site 3. Juncetum squarrosus Bog End (1,800ft; 549m)

The vegetation on this site has developed from a slightly flushed Blanket Bog which was used as a track in mining days of the nineteenth century. It has only in the last century been colonised by Juncus squarrosus where it is the clear dominant, but Polytrichum commune has a high cover value. Between the Juncus rosettes there are tufts of grass, chiefly Deschampsia flexuosa and Festuca ovina making the swards fairly attractive to sheep. Herbs and lichens are scarce but there is a rich variety of bryophytes.

Species poor Juncetum squarrosus sub alpinum occurs at all levels of the reserve, being very widespread on the central ridge and the western escarpment, but infrequent on the eastern plateau. The site has been described in considerable detail by Welch (1967). It is a wet habitat and similar to site 5.

Site 4. Blanket Bog, Bog End (1,800ft; 549m) Plate 1

This site, the main Calluneto Eriophoretum site studied, was adjacent to Site 1 but was on a gentle north facing slope. It was also slightly better drained and the Calluna growth more vigorous than Site 1. It is a wet habitat.

Site 5. Vegetation on re-distributed peat (1,825ft; 549m) Plate 2

The soil bordering most of the numerous streams is a mixture of redistributed peat and mineral soils, supporting a very variable and mosaic type of vegetation. Nardus stricta and J.squarrosus are the dominant plants but the proportions are very variable and patches where J.effusus or Sphagnum sp. are dominant frequently occur.

PLATE 1. Site 4, _Calluna - Eriophorum_ Moor at Bog End. The tops of the canes are approximately two feet above the litter layer.

December 1968

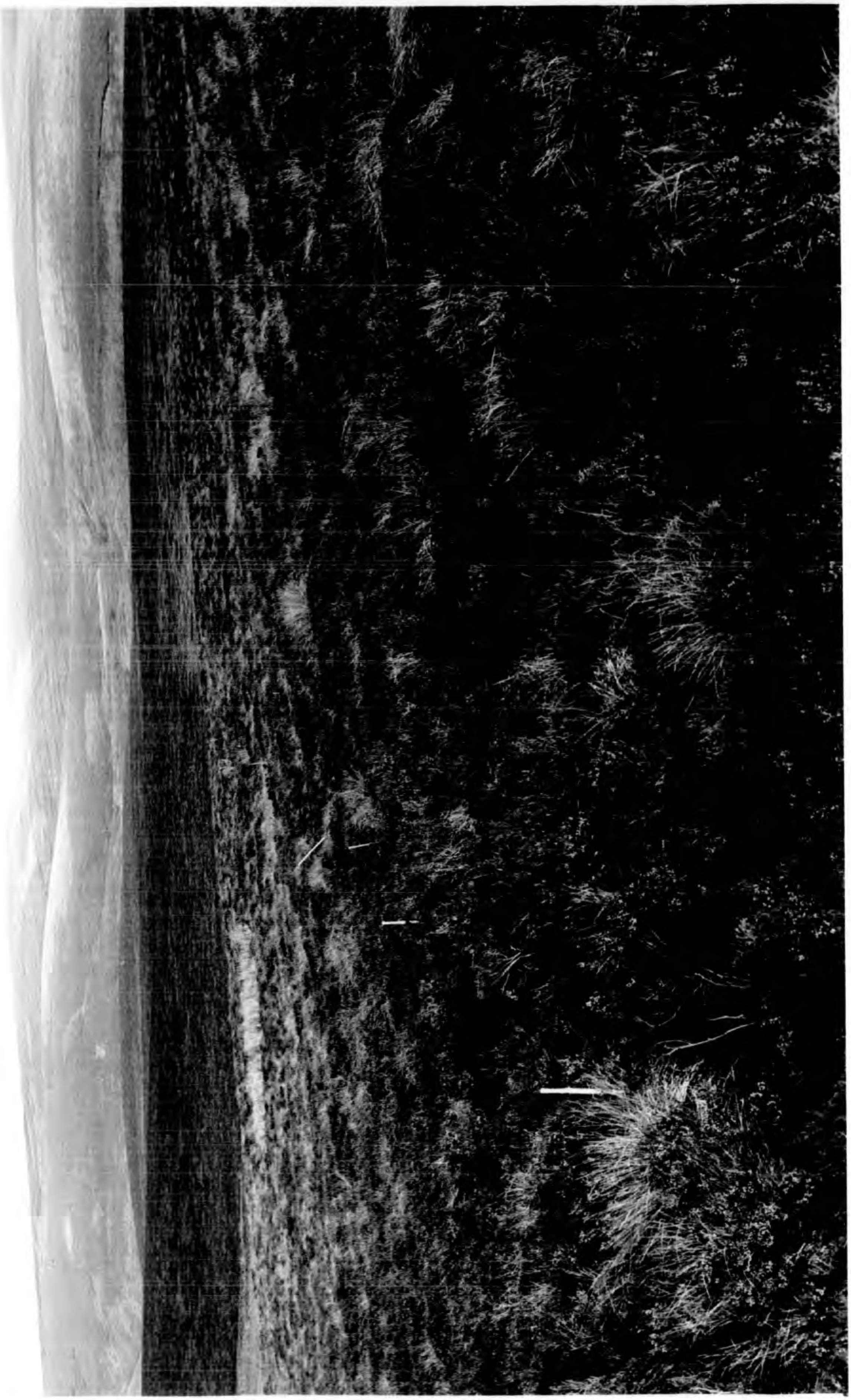


PLATE 2. Site 5, Vegetation on redistributed peat. The eroding edge of the Calluna - Eriophorum moor is seen in the top left hand corner. The area in the foreground (mainly alluvial grassland) and the banks of the streams at the Juncus effusus level are often flooded.

December 1968

Although this stream bank type of vegetation does not occupy a large percentage of the eastern reserve it is very widely dispersed and its importance should not be underestimated. As a habitat for carabids it is very similar to the type of vegetation found at site 3 and is widely distributed on the west side of the reserve.

The area chosen was dominated equally by N.stricta and J.squarrosus, but J.effusus was common. It is a wet habitat.

Site 6. Meadow (1,825ft; 549m). Plate 3.

This site, adjacent and to the north of the field station building, is located on an area of Tyne Bottom Limestone overlaid by mineral soil. It is derived from Agrosto-Festucetum and flush units present before enclosure about 100 years ago. Many of the plant species present may have been introduced and are rare or absent in the other grasslands of the reserve. Sheep were prevented from grazing this area and the hay was normally cut in August. It is an atypical moorland habitat. Although essentially a non-wet habitat the soil moisture content remained high mainly as a result of the vegetation cover.

An area of Limestone grassland adjacent to the Meadow which is kept close cropped by sheep is shown in Plate 3. This typical Festuca-Agrostis grassland has a vegetation mat about three centimetres thick and a well aerated soil.

PLATE 3. An area of Limestone grassland, showing the effect of sheep grazing. The area enclosed by the wall in the background is the Meadow (Site 6). December 1968

b) Cow Green

Three main sites, which had been permanently marked out and used by other investigators, were studied in detail, but collecting was not confined to them.

Site 7. Sugar Limestone Grassland (1,550ft; 473m) Plate 4.

This was a *Festuca ovina* grassland on Melmerby limestone. The limestone has been partly metamorphosed by the Whin Sill intrusion and a unique habitat has formed, colloquially known as Sugar Limestone grassland.

The site, well drained, but with a poor plant cover, is a mosaic of vegetation and bare soil and in the summer months the soil surface became very dry. The area has in the past been heavily grazed - mainly by sheep, but during this study sheep were prevented from grazing the site. It is a non-wet habitat.

Site 8. *Calluna* grassland (1,550ft; 473m) Plate 5.

This site, adjacent to site 7, is a *Calluna* grassland on glacial drift overlying Melmerby Limestone. It is also well drained but although it has a good plant cover and a good litter layer, the surface often became very dry in the summer months. Like site 7, it had also been heavily grazed. It is a non-wet habitat.

Site 9. Vegetation on Redistributed Peat (1,525ft; 465m) Plate 6.

This is a small area about 50 metres from Site 8. *Nardus stricta* and *Polytrichum commune* are the dominant plants on

PLATE 4. Site 7. Sugar Limestone Grassland at Cow Green. The small dark patches in the foreground are devoid of vegetation.

December 1968

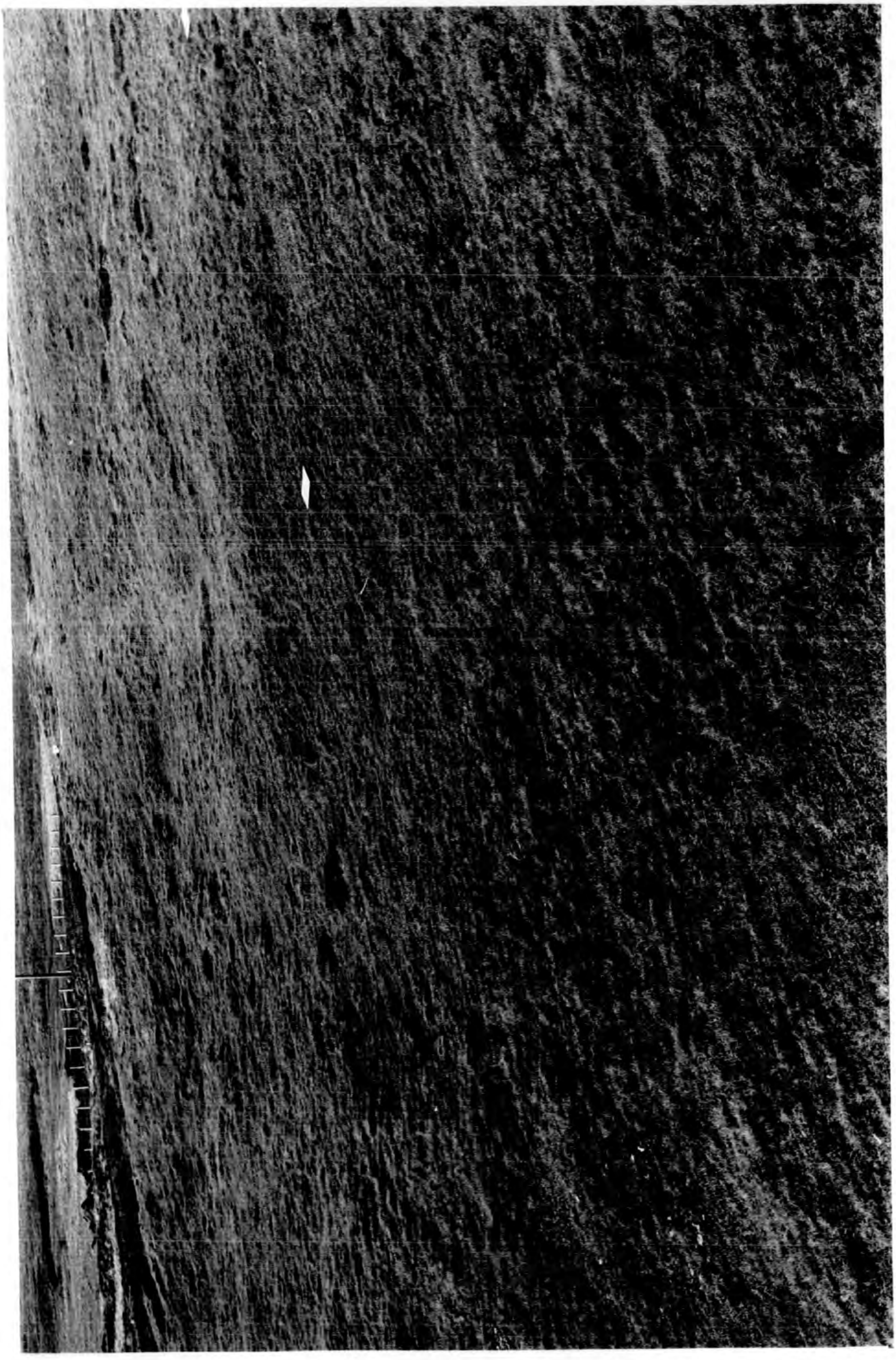


PLATE 5.

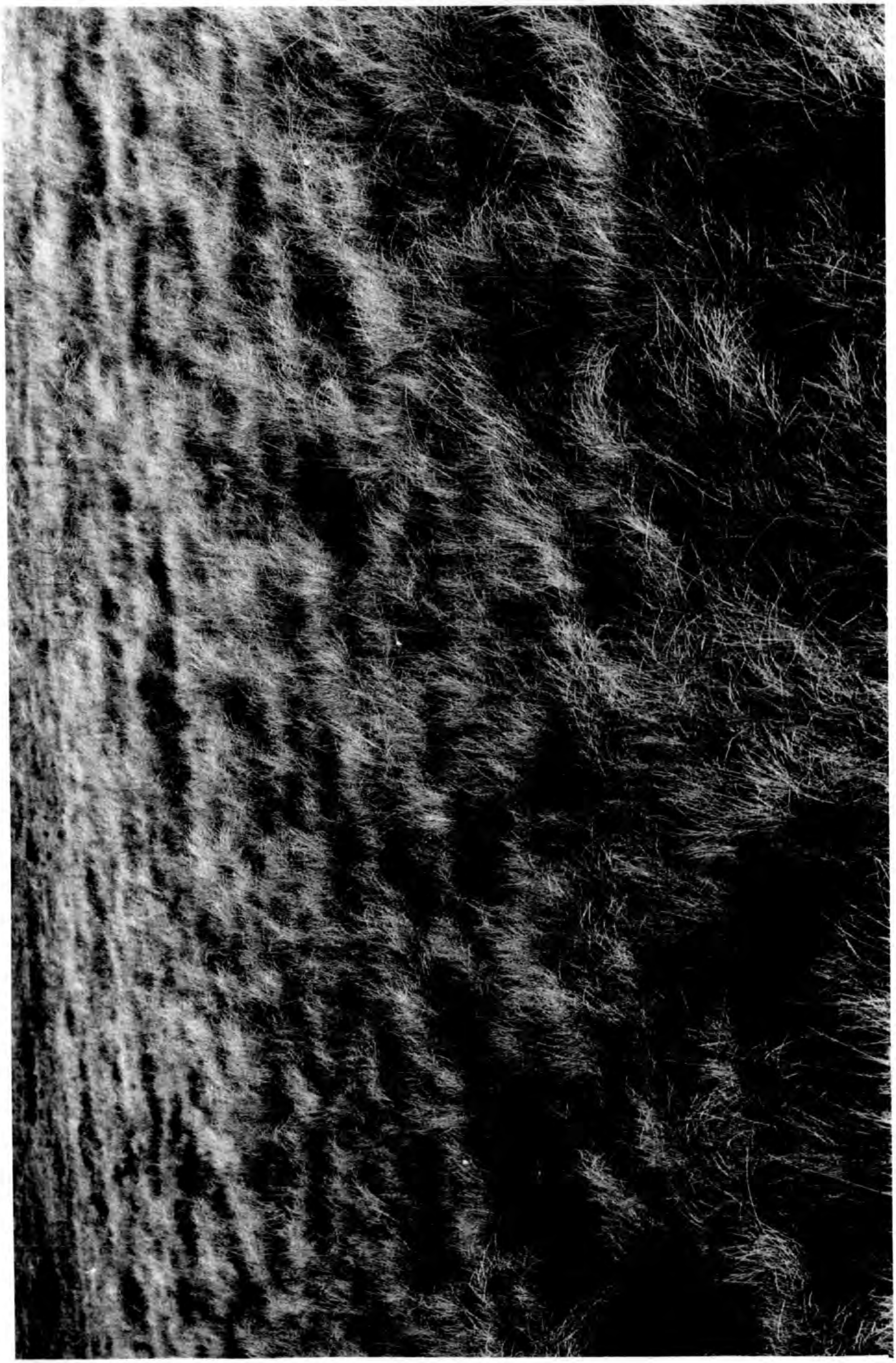
SITE 8. Calluna grassland at Cow Green.

December 1968

PLATE 6.

Site 9. Vegetation on redistributed peat at Cow Green. (The photograph was taken in the late autumn before the vegetation had been flattened by the snow).

December 1968



redistributed peat which is slightly flushed with the run off from the Sugar limestone grassland.

Except in the summer months, this site was constantly waterlogged and pools of standing water were often seen. The litter layer was always wet, even during the dry spells in the summer months. Grazing was slight. It is a wet habitat.

III. SAMPLING METHODS

Morris (1960), in a review of sampling methods, stressed the importance of clearly defining, in advance, the objectives for which sampling is required.

As the information concerning Carabidae on the north Pennines at the outset of this study was very limited, a general survey was made before work on detailed aspects of the ecology of moorland carabids was undertaken.

The sampling programme was planned primarily to discover which species were present, their distribution, abundance and phenology, and also to lay a foundation for any further work on Carabidae at Moor House, Cow Green, and the immediate areas. Various methods were employed.

1. Pitfall Trapping

a) Method

The pitfall trap has been widely used as a method for catching surface active arthropods.

Greenslade (1964) reviewed the method and assessed its value as a sampling method for carabids. He noted that for studies on life histories "the chance of variation in catches due to seasonal changes in vegetation must be noted and results from pitfalls are best combined with observations on larvae and gonad dissections".

As a sampling method pitfall traps have numerous drawbacks and the results must be treated with caution. Williams (1959) noted that "pitfall traps do not give a very representative sample of Notiophilus species for close observation ... . showed that beetles were able to avoid the traps and were not caught at random. Pitfall counts, therefore, do not give a true indication of the abundance of the beetles and interpretation of the results must be made with some reserve".

At Moor House it was noted that, as well as Notiophilus species, Leistus rufescens was also able to avoid the traps and adults were rarely caught even though their larvae were taken frequently.

Larvae of most species were seldom caught in pitfall traps except when they were searching for a pupation or hibernation site. Other collecting methods were employed to obtain the larvae, pupae and adults which might not have been caught in the pitfalls.

Greenslade (1964) found that the highest catch was obtained when the surface vegetation surrounding the traps was cleared and when the rim of the trap (jam jar) was level with the ground surface. However, on the north Pennine moors, especially on the wet habitats, this invariably resulted in a pool of water forming around the trap and flooding it due to the high rainfall and waterlogged conditions. It was therefore necessary to set the traps in a slight hump built up from the soil or to place the trap on a natural hummock.

To minimise predation, escape and deterioration of the specimens in the pitfall traps, preservatives have often been added, e.g. alcohol (Fitcher 1941), formalin (Heyderman 1956) and phenyl mercuric acetate (MacFadyen 1963).

Experiments at Moor House revealed that many carabids, except Carabus and other similarly large species, were able to crawl out of traps (e.g. one pound jam jars) which were left with only water in them and especially from traps which were set dry. In the traps which were left dry, condensation invariably formed on the glass and the beetles could then crawl out aided by a drop of water which collected between their ventral surface and the trap. The surface tension of the drop held the beetles to the side and provided this tension was not broken it was possible for them to crawl out. When the trap was set with some water in it, it was more difficult for the beetle to escape, especially if the side of the jar remained clean and dry. However, in practice the traps soon became dirty, litter fell in, and condensation formed on the sides. Small beetles, e.g. Trechus obtusus, were often unable to crawl up the side of the jar in the water filled traps as they were usually unable to break away from the surface tension of the main body of water.

Luff (1968b) noted that except for T. obtusus and Cholevidae (mainly Catops and Choleva species) there was a significantly higher catch of Coleoptera in formalin filled traps than in water filled traps and suggested that the formalin acted as an attractant rather than as a repellant.

No long term experiments with formalin were conducted at Moor House but whether or not formalin acted as an attractant, escape from water filled traps (death prevents escape from formalin filled traps) would result in a comparatively greater number of beetles being found in the formalin traps.

Various preservatives were tried, but a 10% - 20% solution of "Hospital Teepol L" was finally chosen. It rapidly killed specimens, prevented their escape and predation and was easy and not unpleasant to use. There was no evidence that this detergent acted as an attractant or repellant to the beetles.

Specimens after about two weeks in a 10% - 20% solution of Teepol L were found to be sufficiently well preserved to enable dissection to determine, *inter-alia*, their reproductive condition, gut contents and extent of their fat reserves.

A variety of types of pitfall were tested. They included 2 x 1 inch glass tubes, 2 x 2 inch plastic containers, plastic drinking cups, and jam jars of various sizes. One pound glass jam jars (mouth diameter approximately 5.6cm) were found to be the most useful under moorland conditions. They were easy to find, they could be placed in the ground without breaking and rarely floated out when the water level was high. They were also easy to remove, empty, clean and reset. They were, however, susceptible to frost damage and pitfall trapping was discontinued during the winter to prevent breakage due to freezing. Carabid activity had almost completely ceased by the time they were removed for the winter. Unfortunately they could not be replaced in the spring until it was certain that damage to traps due to freezing would only be slight. By this time the beetles were active and some information from pitfalls in the early spring was lost. This loss was unavoidable but was not considered important as specimens were obtained by other methods.

The contents of the traps from each site were emptied into a bucket and then poured into a labelled polythene bag. When heavy rainfall coincided with the trapping period the traps were often partly filled with water and on the wet habitats a few were flooded. The contents of the traps were then filtered through a fine strainer, in the field, before being placed in a polythene bag. First instar larvae of the small species could pass through the strainer and some may have been lost. It was not practical to use a finer mesh and other methods were employed to obtain first instar larvae.

b) Pitfall Trap Sites

I. Moor House

Pitfall traps were set in many areas. The more important sites are shown in fig.1, and sites 1 to 6 have already been described.

Site 1. Blanket Bog. 25 traps were set on a grid with each trap 4m apart. Trapping was continuous from 3 June 1966 to 21 November 1966.

Site 2. Blanket Bog (well drained). 20 traps were set in two lines running down the slope, 20m apart with the traps in each line 4m apart. Trapping was continuous from 3 June 1966 to 21 November 1966.

Site 3. Juncus squarrosus. As this was a comparatively small area only 10 traps were set. They were in two lines, 2m apart with the traps in each line 4m apart. Trapping was continuous from 28 May 1966 to 21 November 1966.

Site 4. Blanket Bog. On 16 August 1966 a further 30 traps were set up on the Blanket Bog. They were in two lines, 25m apart with each trap in each line about 4m apart. Trapping was continued until 21 November 1966. In April 1967 trapping on this site was increased to 150 traps. They were laid in three parallel lines, each line about 25m apart and with the traps in each line about 4m apart. Trapping was continued until 5 December 1967.

Site 5. This site was situated on redistributed peat on the banks at the junction of two streams (Moss Burn and Netherhearth Sike). 20 traps in two lines, each line about 5m apart and the traps in each line 4m apart, were set on the south bank of Moss Burn while 10 traps, in one line, each trap 4m apart, were set on the north bank. They were in use from 11 April 1967 to 5 December 1967.

Site 6. The Meadow. A line of 10 traps, each trap 4m apart, was used. Intermittent trapping occurred in 1966 but in 1967 trapping was continuous from 11 April to 5 December.

II. Cow Green

Trapping at Cow Green commenced on 20 July 1967 and was discontinued on 10 December 1968. The traps were not visited from 30 October 1967 to 22 May May 1968 owing to an outbreak of foot-and-mouth disease.

Sites 7 & 8. Sugar limestone grassland and Calluna grassland. Each site had a line of 8 traps, each trap 4m apart.

Site 9. Redistributed peat. The 8 traps were in 2 lines 20m apart with the traps in each line 10m apart. This was a very wet site and the traps were frequently flooded, reducing the effective number of trap days and the number of beetles caught.

III. Miscellaneous sites

Pitfall traps were set at numerous other sites. These traps were not in regular use as it was not always possible to visit, collect and sort the material from them. Use was also made of material collected by other workers using pitfall traps on the Moor House Reserve. These traps were not in continuous use and the results are only of limited value. Where these sites have been mentioned, an indication of the vegetation is also given.

Only the main miscellaneous sites, shown as black circles, are given in fig.1.

All pitfall traps on sites 1 to 9 contained a 10 - 20% solution of detergent which was changed each time the traps were visited. The traps on some of the miscellaneous sites contained either a 2% formalin solution, a 2 - 5%, or a 10 - 20% detergent solution, plain water, or were left empty. Heavy rainfall diluted the solutions but they still remained effective.

2. Hand Collecting

Hand collecting was extensively employed on all sites and specimens were commonly found under large flat stones. Stones were rarely found on the Blanket Bog and the redistributed peat and hand collecting on these areas was not very productive. Stones, of various shapes and sizes, were placed on the Blanket Bog and vegetation on the stream banks but few specimens were found underneath them.

3. Soil Samples

Soil samples were taken with a view to obtaining an estimate of density of certain species as well as obtaining larvae and adults to supplement information from other sampling methods.

Due to the tough nature of the plants and the softness of the peat on the Blanket Bog and redistributed peat sites, a soil corer with a serated cutting edge and tapered on the outside only, was constructed to minimise the chance of injuring specimens, due to compression during coring.

The sampler took cores with a surface area of 0.01 of a square metre. They were extracted in a Tullgren Funnel as described by MacFadyen (1955).

It was soon apparent that the density of the carabids was too low to obtain a worthwhile population estimate by this method as the effort involved would have been too great and habitats would have been destroyed.

Soil samples were therefore used primarily to obtain larvae and inactive adults for life history and distribution data.

Hand sorting and extracting, using flotation methods, were tried but they were not so convenient as the Tullgren Funnels.

4. Soil sieving

Carabid larvae will often pupate in loose mould such as mole heaps, and can be found by carefully sorting the heap. Using this technique, mounds of loose sandy mould or loose peat were placed on several sites. A tile or flat stone was placed on top of the mounds to prevent rain compressing them, washing them away and to reduce desiccation. These mounds were inspected for pupae, whose whitish forms showed up clearly. If care was taken, it was also possible to find their exjuviae.

5. Stomach analysis of predators

The gut contents of several predators were analysed and details are given in the appendix. Several species were found only in frog stomachs.

IV. EXAMINATION OF SPECIMENS

1. Adults

The following were determined on most of the specimens caught :

A. Species

B. Condition of the mandibles and claws

C. Wing length

D. Reproductive condition

E. Fat reserves

A. Species

The keys of Fower (1887), Reitter (1908), Joy (1932), Jeannel (1942) and Kevan (1949) were used to identify the species. The nomenclature used follows that of Moore (1957a). Most species were checked against specimens in the British Museum (Natural History). *Bembidion* species and a few other species were identified by Dr. M.L. Luff, who also checked the identification of all other species.

Positive identification of *Patrobus* species was not always possible using the above keys. The form of the genitalia of both sexes, which are characteristic of the species, was therefore used to separate them. A key to the adults and the larvae of the British species of the genus *Patrobus* has been prepared (see appendix).

B. Condition of the mandibles and claws

The mandibles and claws of newly emerged adults are sharply pointed and become blunt as the beetle ages. Using this character alone, it has been possible to distinguish between those beetles that had recently emerged and those that had not and were entering at least their second year as adults.

Some *Carabus* species have been reported to live for up to three years (Grum 1962), and the degree of wear of their mandibles was therefore examined in greater detail. The results are given in the section on mandibles.

C. Wing length

Atrophy of wings is a common feature of carabids, especially those in stable habitats. Darlington (1943) termed species with reduced wings as - winged, those with fully developed wings as + winged and polymorphic species as ± winged. His convention is followed here. The wings of certain species are of an uncertain status, but this is discussed in the section on wing lengths.

D. Reproductive condition

Gilbert (1955), Van der Drift (1959) and Vlijm *et al.* (1961) recorded that activity in carabids is greatest during the breeding season. This relationship has been used by several authors to determine the breeding season of carabids (Larsson 1939; Lindroth 1949). During 1966, this relationship was used and beetles from pitfall traps were dissected only to confirm their breeding season but in 1967 and 1968 all females and most males were dissected and, inter alia, their reproductive condition noted.

i. Females

The reproductive condition of the females was split into the following categories :

a) Teneral

Recently emerged adults with the cuticle not fully hardened and in certain cases not fully of the mature colour were classed as teneral.

They were immature (see below) and their fat reserves were clearly visible but their abdomens were never distended with fat reserves.

In the laboratory the mature colour of Patrobus assimilis, Nebria rufescens and Pterostichus nigrita was reached about 12 hours after emergence from the pupa. In the field, the cuticle of many species, e.g. Carabus glabratus and P. nigrita, remained soft for several weeks, but some, e.g. Loricera pilicornis and P.assimilis, were fully hardened after a few days. Some small species, e.g. Trechus obtusus, had a thin, soft, light coloured cuticle throughout their adult life and it was often difficult to determine whether or not they were teneral.

In the graphs the term teneral includes also recently emerged specimens with a fully hardened cuticle to distinguish them from immature specimens which were entering at least their second year as adults.

b) Immature but not teneral

A distinction was made between immature females which had bred and those which had not, but were not teneral. Immature females which had not bred had very small white and opaque ovaries which showed no signs of development, or of corpora lutea. The mandibles were normally sharp to slightly worn and large fat reserves often present.

The mandibles and claws of some beetles were very worn; the ovaries, although small, were not so compact as the above specimens; corpora lutea were normally visible and a loose network of trachea was often visible around the ovaries. This indicated that their ovaries had matured at least once - presumably during the species breeding season. Fat reserves were very variable.

c) Developing

This category could be split into those that had bred in a previous breeding season and those that had not.

In both, the ovaries were enlarged and developing oocytes were visible. However, in those that had bred, corpora lutea were visible at the base of the ovarioles and their mandibles showed a greater degree of wear than those without corpora lutea.

d) Mature

Females were termed mature when eggs were visible in the uterus or when eggs of an equivalent size were seen in the ovarioles. Mature eggs can also be recognised by the presence of a chorion (Wigglesworth 1953), but this could not be seen unless the egg was mounted for microscopic inspection. The abdomen was often distended due to mature and developing eggs. Corpora lutea, normally yellow, but sometimes white, were visible at the base of the ovarioles if eggs had been laid or if eggs were present in the uterus. Fat reserves were small.

Females that had no eggs in the uterus and no corpora lutea visible, but had developing or mature eggs in the ovarioles, would normally be developing eggs for the first time. Laboratory experiments showed that if at this stage mature or developing females were starved, or the temperatures or photoperiod changed adversely, e.g. simulating approaching winter, the eggs could be absorbed; dissection would reveal that the beetle appeared to have produced eggs but no corpora lutea would be visible.

e) Spent

The ovaries of spent females were small, generally rather transparent and the ovarioles, with corpora lutea loosely held together. A well developed network of trachea was often visible. The uterus occasionally had the appearance of a deflated balloon and in a few cases contained one or two hard and opaque eggs.

Although some beetles may appear spent at the end of a breeding season, this does not imply that if they survive they cannot breed in the following season.

The extent of the fat reserves was very variable. The abdomen in some cases was distended with fat reserves and dissection was necessary to distinguish them from gravid females.

At the end of the breeding season females of certain species were found which had corpora lutea and appeared to have developing ovaries. Investigations of fresh or well preserved specimens suggested that they were not developing but were absorbing their immature eggs. They were characterised by having immature eggs, corpora lutea, a large uterus with the appearance of a deflated balloon, and loosely packed ovarioles with an abundance of trachea.

In poorly preserved specimens it was sometimes impossible to distinguish between developing ovaries and ovaries, the contents of which were being absorbed. They were classed as developing if they were caught before the peak of the breeding season and spent if caught after.

ii. Reproductive state of the males

a) Teneral

External features as for females. The testes and vesiculae seminales were small and fat reserves normally filled the abdominal cavity.

b) Immature but not teneral

The specimens were not teneral but the testes and vesiculae seminales were similar to those in teneral specimens and the mandibles and claws were well worn. Fat reserves were usually large.

c) Developing

The testes and vesiculae seminales were larger than above but were not yet mature.

d) Mature

In all specimens seen copulating the testes and vesiculae seminales were large and specimens in this condition were classed as mature. Fat reserves were variable.

E. Fat Reserves

The extent of the fat reserves in the abdominal cavity were assessed visually and grouped into four categories :

f1. Fat reserves more or less exhausted. Often found in spent or starved beetles.

f2. Fat reserves plainly visible but not filling the abdominal cavity.

f3. Fat reserves filling the abdominal cavity but not causing distention of the abdomen.

f4. Fat reserves causing distention of the abdomen. Beetles in this condition resembled very gravid females.

In fresh specimens there was a difference in the colour and texture of the fat reserves of callow specimens and those of older individuals which were building up fat reserves at the onset of winter. In P.assimilis the fat in callow specimens was yellowish and slightly translucent, while fat reserves added during its life were generally whiter and more opaque.

2. Larvae

Where possible, larvae were identified to species and head widths noted. A Key to British species of the genus Patrobus is given. Details used to separate Nebria larvae are also given.

3. Pupae

Pupae could only be identified to species by the 3rd instar exjuvia and/or by breeding them through to adults.

V. THE SPECIES

1. Distribution and abundance

A total of 49 Carabid beetles from 23 genera were collected from Moor House and Cow Green and these are listed in Table 1. Of this total, 46 species were found at Moor House and 30 at Cow Green. One species, Harpalus rufipes Degeer, is not listed, as the only specimen taken was on the Moor House field station car park and it is unlikely to be indigenous.

In the county distribution lists of the British Carabidae, Moore (1957b) records 70 species from Westmorland and 165 from Durham. This study adds 14 species to the Westmorland list and 4 species to the Durham list (Houston, in press). Except for Notiophilus aestuans, this is perhaps due to the very limited amount of collecting on the uplands of Britain and the failure to publish records, as many are known from neighbouring counties (Moore 1957b; Frank 1964; Luff 1968a). One of these species, Nebria brevicollis, is common in County Durham and has clearly been overlooked.

Including the species new to the county lists, 55% (46/84) of those recorded from Westmorland were found on the Moor House Reserve, while only 18% (30/169) of those recorded from Durham were recorded from Cow Green. The species found at Moor House and Cow Green are considered to be representative of these areas but it is probable that the Westmorland County list is far from complete.

TABLE 1. SUMMARY OF THE CARABIDAE RECORDED AT MOOR HOUSE AND COW GREEN

Notes :

1. The nomenclature follows that of Moore (1957a)
2. D = species new to the Durham list and

   W = the Westmorland list of Moore (1957b)
3. Habitats :

   Moor House

   1. Alluvial grasslands
   2. Limestone grasslands
   3. Flushed or ungrazed grasslands, e.g. The Meadow
   4. Vegetation on redistributed peat
   5. Calluna - Eriophorum Moor (Blanket Bog)

   Cow Green

   6. Sugar Limestone Grassland
   7. Calluna grassland
   8. Vegetation on redistributed peat
4. Specimens from the 2780 feet altitude zone are from Fell Top Podzol only
5. Assessment of abundance

   S - Scarce

   C - Common

   A - Abundant

   Letters in parentheses indicate there is no evidence that the species breeds in these habitats

Table 1. Summary of the Carabidae recorded at Moor House and Cow Green

Carabid species	Species new to :		Altitude Zone (feet)				HABITAT								Daily Activity time		Wing condition		
							Moor House					Cow Green							
							Dry			Wet		Dry		Wet					
	Durham	Westmorland	1400 - 1550	1700 - 1900	2400 - 2500	2780	1	2	3	4	5	6	7	8	Nocturnal	Diurnal	+	±	-
Carabus glabratus Paykull	.	.	S	A	.	.	.	(S)	.	(S)	A	(S)	.	(S)	*	.	.	.	*
C.problematicus Herbst	.	.	C	A	C	.	A	A	S	A	A	C	S	.	*	.	.	.	*
C.violaceus L.	.	.	S	S	.	.	S	S	S	S	S	S	S	S	*	.	.	.	*
Cychrus caraboides (L.)	.	.	S	S	.	.	.	.	.	.	S	S	.	.	*	.	.	.	*
Leistus rufescens (F.)	.	W	S	C	.	.	.	.	S	C	C	.	S	S	*	.	.	.	*
Nebria brevicollis (F.)	D	W	S	S	.	.	(S)	S	S	.	.	S	.	.	*	.	*	.	.
N.salina Fairmaire & Laboulbène	D	W	C	C	.	.	C	C	S	.	.	C	.	.	*	.	*	.	.
N.rufescens (Ström)	.	.	S	S	A	A	(S)	C	(S)	A	A	.	.	S	*	.	*	.	.
Notiophilus aestuans Motschoulsky	D	.	S	.	.	.	.	.	.	.	.	S	.	.	.	*	*	.	.
N.aquaticus (L.)	.	W	S	S	S	(S)	(S)	(S)	S	(S)	.	.	(S)	.	.	*	.	.	*
N.germinyi Fauvel	D	W	S	S	C	A	(S)	C	S	.	.	S	S	.	.	*	.	.	*
N.biguttatus (F.)	.	.	C	C	C	.	C	C	C	C	C	.	.	.	.	*	.	*	.
Elaphrus cupreus Duftschmid	.	.	S	.	.	.	.	.	.	.	.	.	.	S	.	*	*	.	.
Loricera pilicornis (F.)	.	.	C	C	C	.	(C)	(C)	C	C	C	.	.	C	.	*	*	.	.
Clivina fossor (L.)	.	.	S	S	.	.	(S)	(S)	.	.	.	S	.	.	*	.	.	*	.
Dyschirius globosus (Herbst)	.	.	C	.	.	.	.	.	.	.	.	C	.	.	*	.	.	.	*
Miscodera arctica (Paykull)	.	W	.	.	S	.	.	.	.	S	.	.	.	.	.	*	*	.	.
Bembidion lampros (Herbst)	.	.	.	.	S	.	.	(S)	.	.	.	.	.	.	.	*	*	.	.
B.nitidulum (Marsham)	.	W	.	S	.	.	.	(S)	.	.	.	.	.	.	.	*	*	.	.
B.bruxellense Wesmael	.	.	.	.	S	.	.	(S)	.	.	.	.	.	.	.	*	*	.	.
B.atroviolaceum Dufour	.	W	.	S	.	.	.	.	.	(S)	.	.	.	.	.	*	*	.	.
Trechus secalis (Paykull)	.	W	S	S	.	.	.	.	.	(S)	.	.	.	(S)	*	.	.	.	*
T.quadristriatus (Schrank)	.	.	S	S	.	.	(S)	(S)	S	.	.	S	.	.	.	*	*	.	.
T.obtusus Erichson	.	.	A	C	A	C	C	C	.	C	C	A	C	S	*	.	.	.	*
T.rubens (F.)	.	W	.	S	.	.	.	.	.	(S)	.	.	.	.	.	*	*	.	.
Trechoblemus micros Herbst	.	W	.	S	S	.	.	(S)	(S)	.	.	.	.	.	*	.	.	.	*
Patrobus assimilis Chaudoir	.	.	C	A	A	A	(C)	C	.	A	A	.	.	C	*	.	.	.	*
P.atrorufus (Ström)	.	.	C	A	.	.	C	C	A	(S)	(S)	S	.	(S)	*	.	.	.	*
Bradycellus ruficollis (Stephens)	.	.	.	S	.	.	(S)	(S)	(S)	.	.	.	.	.	*	.	*	.	.
B.harpalinus (Serville)	.	W	.	S	.	.	(S)	(S)	.	.	.	(S)	.	.	*	.	*	.	.
Trichocellus cognatus (Gyllenhal)	.	W	S	S	.	.	(S)	(S)	.	(S)	(S)	.	.	.	.	*	*	.	.
Amara lunicollis Schiödte	.	.	.	S	S	.	.	(S)	.	.	.	.	.	.	.	*	*	.	.
A.aulica (Panzer)	.	.	.	S	.	.	.	.	S	.	.	.	.	.	*	.	.	.	*
Pterostichus adstrictus Eschscholtz	.	.	C	C	S	.	(S)	(S)	(S)	C	C	(S)	.	S	*	.	*	.	.
P.melanarius (Illiger)	.	.	S	S	S	.	.	S	S	.	.	.	.	.	*	.	.	.	*
P.nigrita (F.)	.	.	C	C	S	.	(S)	(S)	.	C	C	.	.	C	*	.	.	.	*
P.strenuus (Panzer)	.	.	S	C	.	.	(S)	(S)	C	.	.	.	.	(S)	*	.	.	.	*
P.diligens Sturm	.	.	C	C	.	.	.	.	.	C	C	.	.	S	*	.	.	.	*
P.aethiops (Panzer)	.	.	S	S	.	.	.	.	S	S	.	.	.	.	*	.	.	.	*
P.madidus (Fabricius)	.	.	C	C	.	.	.	C	.	C	.	C	C	.	*	.	.	.	*
Abax parallelepipedus (Piller & Mitterpacher)	.	.	S	S	.	.	.	S	.	.	.	.	.	.	*	.	.	.	*
Calathus fuscipes (Goeze)	.	.	S	.	.	.		(S)	.	.	.	.	.	.	*	.	.	.	*
C.melanocephalus (L.)	.	.	C	S	S	(S)	.	S	.	.	.	C	C	.	*	.	.	*	.
C.micropterus (Duftschmid)	.	.	S	C	S	.	(S)	(S)	.	S	S	(S)	(S)	.	*	.	.	.	*
Odontonyx rotundatus (Paykull)	.	.	S	S	S	.	S	(S)	.	.	.	.	.	.	.	*	.	*	.
Agonum ericeti (Panzer)	.	W	S	S	.	.	.	.	.	S	S	.	.	S	.	*	.	.	*
A.mulleri (Herbst)	.	.	C	.	.	.	.	(C)	.	.	.	.	.	.	.	*	*	.	.
A.fuliginosum (Panzer)	.	.	C	C	S	.	.	.	.	C	S	.	.	C	*	.	.	.	*
Totals 48 Species	4	14	37	40	20	6	22	33	19	24	18	18	9	16	30	18	19	4	25

Sixteen species found at Moor House were not recorded at Cow Green. Notiophilus biguttatus and Bembidion species, although expected, were not found. Whilst most of the other species were rare at Moor House, some were probably immigrants from the Vale of Eden and therefore not typical or permanent components of the upland fauna.

All have been recorded from Scandinavia (Lindroth 1949) and nine from the restricted fauna of Iceland (Larsson & Gigja 1959), showing strong affinities with the arctic and sub-arctic fauna.

Six of the eleven species classed as essentially montane by Fowler (1887) and Joy (1932), (Carabus glabratus, Nebria rufescens, Miscodera arctica, Patrobus assimilis, Pterostichus adstrictus and P.aethiops) were found at Moor House and four (C.glabratus, N.rufescens, P.assimilis and P.adstrictus) at Cow Green. Two species, (Agonum ericeti and Bembidion atroviolaceum) are confined to the northern counties of Britain, while a further two (Notiophilus aestuans and Calathus micropterous) are confined to the northern and the extreme southern counties (Moore 1957b).

All but three species found at Cow Green were also taken at Moor House. Two of these (Dychirius globosus and N.aestuans) were only found on the Sugar Limestone Grassland (site 7), a habitat not present at Moor House.

On the Moor House Reserve, Eddy et al (1969) found that 57% of the area was Calluna-Eriophorum Moor, while vegetation on redistributed peat was about 30% of the total area and the alluvial and limestone grasslands totalled about 1% and 4% respectively.

At Moor House, nearly twice as many species of Carabid (34 to 18) were taken on the limestone grasslands as on the *Calluna-Eriophorum* Moor, but there is no evidence that they all breed on these habitats.

Of the four vegetation types listed above, the Limestone grassland is considered the habitat with the greatest biological productivity, followed by the alluvial grassland, the vegetation on the redistributed peat and finally the *Calluna-Eriophorum* Moor (Cragg 1961). Although the limestone and alluvial grasslands areas are only 5% of the Reserve, 46% (21/46) of the species were found on these habitats and not on the *Calluna-Eriophorum* Moor, whilst only 11% (5/46) were recorded on the latter but not the former. Five species found on both the grasslands and the moor are probably migrants from the moor or the redistributed peat areas but only one species (*Patrobus atrorufus*) appears to be a migrant (but very rare) from the grasslands to the moor. The importance of studying the less dominant vegetation types is clearly indicated.

The numbers of species taken on the Sugar Limestone Grassland and the redistributed peat at Cow Green were similar (18 to 16), but only nine were found on the *Calluna* grassland. A total of 11 species were found on the Sugar Limestone grassland

and not the Calluna grassland, but only two species vice-versa although the sites were adjacent. This clearly shows that the carabid fauna is reacting to either the change in vegetation which is characteristic of these two sites or the environmental conditions to which the vegetation has also reacted.

Ungrazed grasslands such as the Meadow (site 6), although essentially limestone grassland, are atypical moorland habitats. Unlike the normal limestone grasslands, which are heavily grazed by sheep, they support hygrophilous as well as xerophilous and mesophilous species and partly indicate the effect of the sheep on the fauna of the Limestone grasslands.

2. Altitude and Fauna size

Reduction in the mean body size and increase in melanism of several carabid genera has been observed with increase in altitude (Mani 1962) and Thiele & Kirchner (1958) found that populations of Pterostichus were characterised by markedly smaller individuals on mountains than in the plains.

Many species of carabid from Moor House and Cow Green were also smaller and darker than lowland individuals and in a few species a difference was noted in size and colour within the altitude range of the Moor House Reserve.

The total number of species per genera and their mean body length also decreased with elevation (Tables 2 and 3).

TABLE 2. ALTITUDE AND FAUNA SIZE - ALL SPECIES

	Altitude (feet)			
	1400-1550	1700-1900	2400-2500	2780
Numbers species	37	40	20	6
Numbers genera	17	19	14	5
No.species/genera	2.2	2.1	1.4	1.2
Mean body length (mm)	9.75	9.23	7.18	6.16

TABLE 3. ALTITUDE AND FAUNA SIZE - EXCLUDING OCCASIONAL SPECIES

	Altitude (feet)			
	1400-1550	1700-1900	2400-2500	2780
Numbers species	34	31	13	4
Numbers genera	16	15	10	4
No.species/genera	2.1	2.1	1.3	1.0
Mean body length (mm)	10.0	10.5	7.6	6.1

The number of habitats also decreased with an increase in altitude until at 2,780 feet only Fell Top Podzol remained. Many species appear to be capable of surviving the lower temperatures and the shorter active seasons found at the higher altitudes and the absence of certain vegetation types is probably an important factor restricting their range.

A significant reduction in body size with elevation is seen in populations of Patrobus assimilis within the altitude range of the Moor House Reserve (Table 4).

TABLE 4. PATROBUS ASSIMILIS ADULTS. THE RELATIONSHIP BETWEEN BODY LENGTH (mm) AND ALTITUDE (feet) ON THE MOOR HOUSE RESERVE (EAST SIDE)

Altitude	Mean body length	n	S.D.	S.E.	d	P.
Males						
2780	6.65	43	0.29	0.04		
					3.412	< 0.001
2450	6.87	41	0.28	0.04		
					4.2	< 0.001
1800	7.05	52	0.20	0.03		
2780/1800					4.38	< 0.001
Females						
2780	7.12	45	0.27	0.04		
					3.38	< 0.001
2450	7.31	43	0.27	0.04		
					6.02	< 0.001
1800	7.66	38	0.25	0.04		
2780/1800					9.4	< 0.001

3. Colour Polymorphism

a) Nebria rufescens

In Britain Nebria rufescens is represented by four colour forms : gyllenhali (Schonherr) totally black, balbii (Bonelli) black with reddish yellow legs, rufescens (Strom) black with brown elytra and fourthly a nameless form which has both reddish yellow legs and brown elytra. It is unfortunate that *rufescens*, one of the rarer forms, is the one which was originally described and is therefore the type name.

The forms *rufescens* and *gyllenhali* were taken at Moor House but only *gyllenhali* at Cow Green. The distribution of these forms varied with habitat and altitude (Table 5).

TABLE 5. ALTITUDE AND COLOUR FORMS OF *NEBRIA RUFESCENS* AT COW GREEN (1550 feet) AND MOOR HOUSE (1800-2780 feet)

	Altitude (feet)							
	1550		1800		2450		2780	
	♂	♀	♂	♀	♂	♀	♂	♀
Total individuals	2	5	13	16	197	238	110	134
Nos. *rufescens*	0	0	0	3	69	69	11	25
% *rufescens*	0	0	0	19	35	29	10	19

Specimens at 1550 feet were found on site 9 - a wet habitat; at 1800 feet the three females with brown elytra came from the Meadow, the others from wet habitats; at 2450 feet from a *Juncus squarrosus* dominated habitat between Blanket Bog and Limestone grassland (both forms were found on all three habitats and their origin is not known); and those at 2780 feet from the Fell Top Podzol of Great Dun Fell. Only the form *gyllenhali* was found along the stream margins. Greenslade (1969) also noticed this and suggested that there may be ecological differences between the forms.

Isolated populations of this species were often encountered in lowland areas, including sea level on the east coast on the border of England and Scotland, but only the variety *gyllenhali* was taken.

There is no significant difference (using Chi-squared test with Yates' correction) in the distribution of the colour forms between the sexes (2450 feet $\chi^2_1 = 1.54$; 2780 feet $\chi^2_1 = 2.94$) but there is with altitude. The proportion of the brown form is greater at 2400 feet than at 2780 feet (♂ $\chi^2_1 = 6.06$ $p < 0.05 > 0.01$, ♀ $\chi^2_1 = 3.8$ but not significant) but less at the lower elevations (2450/1800 feet ♂ $\chi^2_1 = 5.29$ $p < 0.05 > 0.01$, ♀ $\chi^2_1 = 3.82$ but not significant) indicating that altitude may not be the only factor influencing the distribution of these two colour forms.

No significant difference was found in the size of these two forms at the same altitude but the elytra of mature *rufescens* individuals were softer than those of *gyllenhali*. Similarly, the reddish yellow area of cuticle on the femora of the variety *balbii* from Ben Macdhui, Banffshire, Scotland) was softer than on the black legged forms from the same habitat.

Pupae kept at identical laboratory conditions gave rise to both the Moor House forms. No larvae were bred through to adult *ex ovo* and the reason for the occurrence of these colour forms remains obscure.

b) Pterostichus madidus

Pterostichus madidus is found in two colour forms either with legs black (v.concinnus Sturn) or with at least trochanters and femora red. In Scotland, Greenslade (1969) noted that the percentage of the black legged form increased with altitude and at Silwood Park, Berkshire, the black legged form tended to be less frequent in the hottest part of the year and in open grassland (Greenslade 1961).

The black legged form was taken less frequently at Cow Green (Table 6) and Moor House (Table 7) except at 1400 feet where nine out of fifteen specimens were black legged.

Specimens were obtained from pitfall traps and by hand collecting and there is no evidence that they are a true reflection of the distribution of the colour forms.

TABLE 6. DISTRIBUTION OF THE TWO COLOUR FORMS OF PTEROSTICHUS MADIDUS AT COW GREEN ON SITES 7 & 8

	Site 7		Site 8	
	Limestone		Calluna grassland	
	♂	♀	♂	♀
Total individuals	25	34	26	40
Number black-legged	4	7	5	15
Percentage black legged	16	21	19	38

At Cow Green the black legged form was found more frequently on the Calluna grassland than on the Sugar Limestone Grassland, but the difference is not significant. However, these sites are adjacent and the degree of migration from one habitat to the other is not known.

The effect of altitude (Table 7) is more obscure as the numbers were small and the vegetation of the different sites also varied.

TABLE 7. PTEROSTICHUS MADIDUS. ALTITUDE AND COLOUR FORMS FROM THE WEST SIDE OF THE MOOR HOUSE RESERVE

	Altitude (feet)							
	1400		1600		1900		2050	
	♂	♀	♂	♀	♂	♀	♂	♀
Total individuals	5	10	20	7	22	12	3	3
Numbers black-legged	1	8	8	4	1	2	1	1
Percentage black legged	20	80	40	57	5	17	33	33

Specimens at 1400 feet were taken from flushed grassland; 1600 feet from limestone grassland; 1900 feet from a Juncus squarrosus dominated area and 2050 feet from another flushed grassland.

The cause of the two colour forms is not known. It may be the direct effect of temperature on the immature stages (Greenslade 1969), the time of the emergence of the adults, genetic, past breeding success (Luff, pers.comm.) or even the effect of the proportion of time spent underground (and therefore exposure to solar radiation) during the immature stages, e.g. the larvae on the non-wet habitats burrowing more than those on a wet habitat as a result of the drier and more exposed conditions.

c) Calathus melanocephalus

Calathus melanocephalus is also found in two colour forms. The usual form has a clear red pronotum while the melanic form nubigena Haliday, normally found in mountainous districts, has a dark red to black pronotum.

Only two specimens of the melanic form were found. One, an immature brachypterous female, was taken on the top of Great Dun Fell while the other, a mature brachypterous female, was found at Cow Green.

d) Agonum ericeti

Agonum ericeti was found in two colour forms; bright metallic coppery and dull, almost black with little or no metallic colour. The reduction of the metallic colour of the cuticle and the resulting increase in the black colour is probably an adaptation to absorb more radiant heat (Mani 1962), no doubt an advantage in areas of low temperatures and short potential developmental periods. Both colour forms were taken by frogs and it is unlikely that the black form is nocturnal.

4. Life History Patterns

a) Introduction

The phenology of most of the Danish Carabidae has been described by Larsson (1939) and the Fenno-Scandinavian Carabidae by Lindroth (1945, 1949). Larsson classified them into those which bred either in the spring or the autumn, but Lindroth divided them into those with larvae during the winter and those with only adults during the winter. The spring breeders generally have larvae in the summer months and overwinter as adults, while those which spend the summer as adults breed in the autumn and normally overwinter as larvae.

The life histories of most of the common Carabidae of lowland Britain have been described and Greenslade (1965) and Murdoch (1967) have summarised the results of numerous workers. Many of these species breed at approximately the same time in Britain as in Denmark (Larsson 1939), but some breed at different times of the year in other parts of the continent of Europe (Lindroth 1949; van de Drift 1959; Schøtz-Christensen 1961) and their results are not necessarily applicable to Britain.

Murdoch (1967) found that almost all the wet species appear to have larvae in the summer and only adults during the winter, while large numbers of non-wet species spent the winter as larvae. He concluded that in Britain the proportion of species which have larvae in the winter would probably be 60% or more in non-wet species and less than 10% in wet species.

Lindroth (1949) studied most of the 301 species in Fenno-Scandinavia and found that a significantly higher percentage of the non-wet species had larvae during the winter; of those whose life history was known, only 8.9% (11/124) of the wet species, but 41.5% (68/164) of the non-wet species had larvae during the winter.

Many authors have relied on noting "peak" numbers to indicate the breeding season. The results of dissections in this study confirm that the method provides a good indication of the breeding season of most species, but care must be taken - especially with biennial life histories and 'low-catch' species.

b) Life history patterns at Moor House and Cow Green

The life histories and habitats of most of the Carabidae taken at Moor House and Cow Green have been elucidated and are summarised in Table 8. The life histories and habitats of the 15 species marked with an asterisk require confirmation, but there is no evidence to indicate that they are different from those found by other authors. Details of each species are given in the appendix.

TABLE 8. LIFE HISTORY TYPES OF THE MOOR HOUSE AND COW GREEN CARABIDAE. Note. Where there was insufficient evidence of a species' habitat or breeding season, data from other sources has been used and it is marked with an asterisk.

a. Wet species with "summer" larvae and only adults overwinter

Agonum ericeti	Elaphrus cupreus
A.fuliginosum	Loricera pilicornis
A.müllerі	Miscodera arctica
* Amara lunicollis	Notiophilus aquaticus
*Bembidion atroviolaceum	Pterostichus adstrictus
* B.bruxellense	P.diligens
* B.lampros	P.nigrita
*B.nitidulum	P.strenuus
* Bradycellus ruficollis	* Trechus rubens
Calathus micropterus	* Trechoblemus micros
* Clivina fossor	* Trichocellus cognatus

b. Non-wet species with larvae overwinter

* Abax parallelipipedus	N.salina
Amara aulica	Notiophilus aestuans
* Bradycellus harpalinus	* Odontonyx rotundatus
* Calathus fuscipes	Patrobus atrorufus
C.melanocephalus	Trechus quadristriatus
Nebria brevicollis	* T.secalis

c. Wet species with larvae in summer and winter

Carabus glabratus

d. Species with summer larvae found on non-wet habitats

Dyschirius globosus

e. Species with larvae in summer and winter, found on wet and non-wet habitats

Carabus problematicus	*Patrobus assimilis*
C.violaceus	*Pterostichus aethiops*
Cychrus caraboides	*P.madidus*
Nebria rufescens	*P.melanarius*
Notiophilus biguttatus	*Trechus obtusus*
N.germinyi	

f. Species with larvae in winter, found predominantly on wet habitats

Leistus rufescens

71% (34/48)of the species exhibit the typical life history patterns associated with the wet and the non-wet habitats; of these 46% (22/48) are wet species with summer larvae and only adults overwinter while 25% (12/48) are non-wet species with larvae overwinter. The remaining 14 species fall into various other categories but they still show a tendency towards the typical life history patterns. Many show interesting adaptations and are discussed in detail.

Baker (1938), on the evolution of the breeding season, states that "the causes of the breeding seasons will never be understood without a study of the natural environment in response to which they have evolved".

The most marked difference in the life history patterns is seen between wet and non-wet habitats and the soil moisture content is probably the prime selective force. It affects all stages, either directly, e.g. desiccation or inundation, or indirectly, e.g. desiccation reducing the food available.

Although resistance to desiccation is widespread amongst the arthropods, culture experiments indicated that eggs, the first and the early second instars and pupae of many species had little resistance to desiccation. Females in laboratory experiments would not lay eggs in dry conditions. The late second and the third instars, especially of the larger species, were more resistant, but most only for short periods. The adults survived at low humidities provided they had ample fat reserves or access to food.

The shortage of available food on the non-wet habitats in the "dry" season appears to be a result of the dry conditions and probably accounts for the lack of adaptation of these immature stages to withstand low humidities.

Unusual egg laying habits, which no doubt help protect the egg from desiccation, have been noted in some Carabidae. Dicker (1951) noticed that the eggs of <u>Agonum dorsale</u> Pontoppidan were laid in May, June, and July on the underside of young strawberry leaves and encased in soil. The larvae on hatching burrowed into the soil. A similar habit was found by Luff (pers.comm.) in Pterostichus madidus. This species may breed on non-wet habitats in the summer and protects its eggs individually in cocoons of soil. The larvae on hatching burrow into the soil. This species thus also avoids the probable dry surface conditions and is able to breed in a non-wet habitat in the "summer" months.

Most of the eggs laid by specimens in culture were embedded in the filter paper and the egg laying habits mentioned above may be common amongst the Carabidae, especially those breeding in non-wet habitats.

Eggs survived short periods of inumdation but the first and early second instars of the small short legged species, e.g. P.assimilis, readily drowned - mainly because they were unable to overcome the surface tension of the water; but P.assimilis third instars and adults of many species survived long periods completely submerged (Section V.10). Long legged larvae, e.g. Nebria and Leistus species and large larvae, e.g. Carabus species, were not trapped by the surface tension and rarely drowned.

i) Wet species with summer larvae

Typical wet species with summer larvae are shown in Table 8a. They breed in the spring and early summer; their larvae occur in the "summer months" and the new generation adults emerge in the late summer and the autumn. The first and early second instars occur when the water level is at its lowest and only adults are present when the ground is at its wettest. If the litter layer of the wet habitats becomes too dry, the larvae can easily burrow into a Sphagnum or Eriophorum hummock or even the peat, where there is always a high humidity. The immature stages, the most vulnerable, develop at a time when the temperatures are at their highest and therefore their development time shortest. The females also have a greater chance of realising their full reproductive potential in one breeding season and it is significant that very few old specimens are found in the autumn.

ii) Non-wet species with winter larvae

Typical non-wet species with winter larvae are shown in Table 8b. They breed mainly in the autumn and their larvae are present in the autumn, winter and spring. Most adults emerge in the spring and early summer but a few, mainly on damp grasslands such as the Meadow, emerge later, and biennial life cycles may be found. The larvae are not present during the very dry conditions that may occur on the non-wet habitats in the summer months, but the adults, which are comparatively resistant to desiccation, are. Old adults are often found in the spring and autumn probably because they were unable to realise their full reproductive potential in their first breeding season (Murdoch 1966). A few may resume breeding in the early spring, but it appears to be a continuation of the autumn breeding season. Others survive until the following autumn and have a second breeding season.

Abax parallelipipedus was only found breeding in the autumn at Moor House but Murdoch (1967) found mature adults from March to September, and van der Drift (1951) showed that in Holland it breeds in spring, summer and autumn. The species may have a biennial life cycle at Moor House but requires further study.

iii) Miscellaneous life history patterns

The remaining 12 species (Tables 8c-f) which show exceptions to the above trends are discussed below.

Carabus glabratus (Table 8c) appears to be a typical wet species breeding in the summer with the new generation adults emerging in the late summer and autumn. Larval development, however, is not complete by the autumn and the third instars overwinter giving rise to a biennial life cycle.

Carabus problematicus, C.violaceus and Cychrus caraboides (Table 8e) are autumn breeders, and have larvae overwinter. They are found predominantly on non-wet habitats, but have been found breeding on wet habitats.

C.problematicus and C.violaceus have biennial life cycles similar to C.glabratus except that their breeding season is later. Although probable, there is insufficient evidence to confirm that C.caraboides has a biennial life cycle. The early part of these three species life history is similar to normal autumn breeders on non-wet habitats. The third instars are thought to aestivate in summer (no pupae could be found) and pupate in the late summer/early autumn.

They have larvae which are resistant to desiccation and drowning, enabling the early instars to survive the wet conditions found on the wet habitats in the autumn, and the third instars the dry conditions found on the non-wet habitats in the summer.

Patrobus assimilis (Table 8e), a montane species, is perhaps the most interesting carabid on the Reserve. It shows a tendency towards typical summer larvae on wet habitats at and below 1800 feet, but at higher altitudes adults and larvae overwinter.

At Moor House it is common on all habitats above about 2,400 feet. Below about 2,000 feet on the non-wet habitats it is almost totally replaced by P. atrorufus, but it is common on the wet habitats.

At 2,780 feet it is a spring/summer breeder, but larval development is not complete by the autumn and it overwinters as a third instar larva (occasionally as a second) and has a biennial life cycle.

At 1,800 feet on the wet habitats it is a spring/summer breeder. It has a predominantly annual life cycle but overwinters mainly as a third instar, with the majority of the new generation adults emerging in the spring. Like the typical wet species (Table 8a) the early instars thus occur in the summer months and the waterlogged conditions found in the autumn, on the wet habitats, are avoided. At this altitude a few callow adults were found from the middle of July to the end of October. Those found in July and August were probably specimens which were larvae the previous year and thus would have a biennial life cycle as found at 2,780 feet.

A few mature females were found in the early spring, but these appear to be specimens which had emerged the previous year. The life history therefore shows a gradation from the typical annual pattern of a spring breeder on wet habitats to the biennial pattern found at 2,780 feet. The majority of the population at 1,800 feet had a life history pattern between the two, but the proportions no doubt vary from year to year.

Culture experiments (Section-VI) indicated that the third instar is sensitive to photoperiod and only pupated under long day conditions. It would be interesting to determine the critical photoperiods of adults and larvae at various altitudes. If populations, especially the third instars, at 1,800 feet have the same photoperiodic responses to those at 2,780 feet their potential development period at 1,800 feet might not be fully realised. This could account for the species overwintering predominantly as a third instar while other similar sized species, e.g. P.nigrita, complete their development and overwinter as adults.

Nebria rufescens (Table 8e), essentially a montane species, was found mainly on wet habitats at 1,800 feet, where N.brevicollis or N.salina (both non-wet species) were found on the non-wet habitats. At 2,400 feet and above it was found breeding on all habitats and its distribution is probably analogous to P.assimilis while N.salina and N.brevicollis may be analogous to P.atrorufus (Section ~~IV~~ V, 4c).

At 2,780 feet, on the Moor House Reserve, N.rufescens is a spring/summer breeder but has a biennial life cycle with larvae and adults overwinter.

At 1,800 feet on the wet habitats, the life history is similar except that the breeding season begins slightly earlier. The early instars occur in the "summer" months, but the third instars still overwinter. A few adults emerge in the early summer but there is no evidence that they breed in the same year. It seems that it is able to invade the wet habitats as it is essentially a summer breeder.

Trechus obtusus (Table 8e) is common on the non-wet habitats and at Cow Green has a typical non-wet species life history. But it also breeds on the well drained areas of the Calluna-Eriophorum Moor and a few areas of redistributed peat and at 2,780 feet it is a spring/summer breeder.

At Cow Green on non-wet habitats such as the Sugar Limestone and the Calluna grassland, mature females were found from the middle of July to the end of September and the species exhibited a typical non-wet species life history.

On the Moor House Reserve on wet habitats at 1800 feet mature females were found from the middle of June to the end of August with a peak in July. No larvae and very few adults occurred on areas liable to flooding and at Moor House no larvae were found on the redistributed peat. At Cow Green a few larvae were found on Site 9 - a very wet site, but only amongst the stems of *Nardus* and in *Polytrichum* hummocks well above the water level. It appears that it is able to invade these wet habitats because it avoids the water-logged areas and, also, the early instars occur when these habitats are relatively dry.

At 2500-2780 feet the life cycle was not studied in detail but mature females were only taken in May, June and July and it has a biennial life cycle. Whether the different breeding seasons found at 1500-1800 feet and 2500-2780 feet are a result of separate races, an extended cycle at 2500-2780 feet, the plasticity of its temperature and photoperiodic responses, or some other factor, requires further study.

Notiophilus germinyi (Table 8e) breeds at Cow Green in the autumn but at 2400-2780 feet at Moor House mature females were found in June and July and it has a biennial life cycle. Like *T.obtusus*, *N.germinyi* exhibits at Cow Green the life history pattern expected on non-wet habitats but the reason for its earlier breeding season at the higher altitudes requires further study.

Notiophilus biguttatus (Table 8e), a mesophilus species, has been widely described as a spring breeder with summer larvae (Larsson 1939; Lindroth 1945; Larsson & Gigja 1959; Davies 1959; Greenslade 1965). But at Moor House detailed examination revealed that the females first developed eggs in September and October and overwintering larvae were found. The adults resumed breeding in the spring and early summer, giving rise to the typical summer larvae.

The larva, a long legged form, is able to survive in very wet conditions and its food, Collembola, Acarina, and possibly other small arthropods, is abundant on the wet habitats throughout the year.

Tischler (1955) mentions that some small carabid species are bivoltine but there is no evidence that N.biguttatus has a bivoltine (or biennial) life cycle at Moor House. Greenslade (1965) suggested that N.substriatus Waterhouse might be bivoltine in Berkshire. If N.biguttatus was also bivoltine in the lowlands, an extended cycle at Moor House would be expected. An incomplete bivoltine cycle might therefore occur which could account for the species breeding in the late autumn and in the spring.

Dyschirius globusus (Table 8d) at Cow Green is a spring/summer breeder on the Sugar Limestone Grassland - a non-wet habitat. It is, however, a burrowing form and so can avoid the dry summer conditions. Its normal habitat is Sphagnum and marshy places where its life history is that of a typical wet species. If its microhabitat at Cow Green is taken into consideration it should be classed as a typical wet species.

Pterostichus madidus (Table 8e), like D.globusus at Cow Green, also breeds in the summer on non-wet habitats; but it has a biennial life cycle and the larvae as well as the adults overwinter. The eggs are wrapped in cocoons made from the soil and once the larvae emerge they go down into the soil (Luff, pers.comm.), thus overcoming the dry surface conditions found on the non-wet habitats in the summer. The new generation adults do not emerge until the autumn and the pupae are not present during the dry conditions.

On the west side of the Moor House Reserve P.madidus is also found breeding in the summer on a well drained Juncus squarrosus dominated habitat where the early stages follow a typical wet species life history pattern.

Pterostichus aethiops and P.melanarius (Table 8e) were only taken in small numbers, but the evidence suggests that their life history patterns are similar to that found for P.madidus.

Leistus rufescens (Table 8f) is found predominantly on wet habitats but has larvae overwinter. On the wet habitats mature females were found from the end of June to the end of August and Murdoch (1967) found them from June to October, unlike many species with winter larvae, which are autumn breeders. For example, L.ferrugineus and L.fulvibarbis (not found at Cow Green or Moor House) occur on non-wet habitats; they also have winter larvae but the mature females are not found until September (Murdoch 1967). Their breeding season may be delayed as a result of the dry conditions, but on the wet habitats this would be unlikely to affect L.rufescens. The early breeding season of L.rufescens on the wet habitats allows the early instars to develop while the water level is still low; but as the larva is a long legged form well adapted to survive wet conditions this may be relatively unimportant.

Their food source (Collembola) is abundant on the wet habitats throughout the year, whereas on the non-wet habitats it may be in short supply and certainly less accessible during the relatively dry "summer" conditions. The early breeding season of L.rufescens on the wet habitats is thus possible because the soil moisture content remains high and their food is always available.

It is interesting that L.rufescens was also found breeding - but not until September - on the Calluna grassland (a non-wet habitat) at Cow Green. It is a characteristic habitat for species with winter larvae and perhaps its original habitat.

c) Life History Patterns and Habitat Distribution of Patrobus assimilis and P.atrorufus

The habitat distribution of these two species at 1800 feet and below may be the result of their life history patterns limiting the breeding of P.assimilis to wet and P.atrorufus to non-wet habitats. As P.assimilis is a spring/summer breeder, with eggs and early instars not adapted to survive the dry "summer" conditions found on the non-wet habitats, it is restricted to wet habitats. P.atrorufus as an autumn breeder with early instars not adapted to survive the autumn conditions of the wet habitats is therefore restricted to non-wet habitats.

In the laboratory both species were catholic feeders and there is no evidence that food affects the habitat distribution.

At 1800 feet P.atrorufus exhibited annual, and in the Meadow, biennial life cycles. The biennial life cycle was probably only possible because the third instars and pupae were not subjected to the dry summer conditions normally found on the non-wet habitats. P.assimilis was entirely absent from the Meadow. Theoretically it is a habitat in which it could breed, and whether its absence is a result of competition with P.atrorufus, which is abundant, requires further study.

P.atrorufus was not found above 2000 feet, but if present above the heather line (approximately 2400 feet on Great Dun Fell) it would probably have a predominantly biennial life cycle.

Atypical habitats, such as the Meadow, are not present at these altitudes, but the non-wet habitats do not dry out to the extent found at 1800 feet, mainly as a result of the high cloud cover, high rainfall and heavy dew. Dry conditions are therefore unlikely to account for its absence.

Species breeding in the autumn were rarely found above 2400 feet and the only species found breeding on the Fell Top Podzol of Great Dun Fell (P.assimilis, Nebria rufescens, Trechus obtusus, Notiophilus germinyi and possibly N.aquaticus) bred in the spring/summer and had overwintering larvae and biennial life cycles.

5. Wing Condition

Among the Coleoptera the fore wings are much modified and form the elytra which protect the hind wings when the latter are in repose. In certain Carabidae the hind wings are atrophied and the function of flight is lost. It is the condition of the hind wings that is referred to in this section.

Darlington (1943) termed species with reduced wings as - winged, those with fully developed wings as + winged, and polymorphic species with both forms as $\pm$ winged. Greenslade (1968) noted that the length of wings of carabids observed in flight approached that of the body and defined - winged species as those with wings less than 75 per cent of the body length. These conventions are followed here.

The wing condition of the species, as found at Moor House and Cow-Green, is given in Table 1. The occurrence of + wings in an individual does not necessarily entail capacity for flight.

The only specimen observed in flight was a teneral *Loricera pilicornis*. Older individuals could not be induced to fly and dissection revealed that their wing musculature had atrophied. During the breeding season part of the ovaries often occupied the space that would have been taken by the wing musculature if it was well developed. Byers (1969) noted that a reduction of wings in a tipulid (Diptera; Nematocera) enabled a four per cent increase in the number of eggs. The ovaries of carabids are not fully developed when the adult emerges from the pupae, as in many tipulids, but if the wing muscles had atrophied there would be more space in which the ovaries could develop. At high altitudes/low temperatures, where the potential development period may be short, this could confer an advantage as more eggs could be produced at the same time. Also if wings and wing muscles do not have to be produced, development of the immature stages could be quicker. Wing muscle atrophy was observed in several + winged species and at no stage could they be induced to fly. Smith (1957) and Jackson (1928) also noticed wing muscle atrophy in otherwise + winged Coleoptera.

In many - winged species the wings are absent or vestigial, but in others atrophy has occurred to a limited extent and their status is uncertain.

Greenslade (1968) recorded that some species showed a continuous variation from + to - winged. Two of these species, Pterostichus adstrictus and P.nigrita, occur at Moor House and Cow Green, but only + winged specimens of the former and - winged of the latter were found. Lindroth (1949) described P.nigrita as constantly macropterous and capable of flight. At Moor House (1800ft) the percentage wing length to body length in 25 males was 59.2% S.D. 4.86 and in 40 females 59.68% S.D. 4.46. Their wing musculature was also poorly developed and flight is considered very unlikely.

A light trap, Rothamstead model (Williams 1948), but with a 12 volt fluorescent tube, was set up in the Meadow. Four of the Moor House vegetation types listed in Table 1 (1,3,4,5) were within 50 yards of the trap but the nearest alluvial grassland was about 150 yards away. The trap was run continuously from March to November 1967 but no Carabidae were caught. The low temperatures probably inhibited flight in nocturnal species but during the day it is unlikely that carabids in flight, if any, would be attracted to the light.

In this study 19 species are classed as + winged, 4 ± winged and 25 - winged (Table 1). Other authors have recorded three of the + winged and six - winged species as wing dimorphic; one ± winged and one -winged as macropterous, but ± winged species in the lowlands are frequently - winged at high altitudes (Mani 1962).

The proportion of + winged species decreased markedly with an increase in body length (Table 9) and all + and ± winged species were below 11mm.

TABLE 9. WING CONDITION IN RELATION TO SPECIES BODY LENGTH

	< 5	5-10	10-15	15-20	> 20	Total numbers
Nos.of species						
+ winged	8	8	3	0	0	19
± winged	0	4	0	0	0	4
- winged	4	11	4	2	4	25
% + or ± winged	67	52	43	0	0	48

The wing condition of species as found at certain altitudes is shown in Table 10. Except at 2780 feet, there is a slight increase in the percentage of + and ± winged species with elevation, but it is not significant. The only + winged species at 2780 feet (Nebria rufescens) had well developed wings but poorly developed wing musculature. The percentage wing length to body length was, in 39 males, 91.39% S.D. 8.75, and in 26 females, 90.19% S.D. 8.29. Three of the other five species found at 2780 feet (Notiophilus aquaticus, N.germinyi and Calathus melanocephalus) have been described as ± winged, but only - winged forms were found at this altitude.

TABLE 10. WING CONDITION OF ALL SPECIES AS FOUND AT CERTAIN ALTITUDES

	Altitude (feet)			
	1400-1550	1700-1900	2400-2500	2780
Numbers of species	37	40	20	6
Numbers + winged	10	13	7	1
Numbers ± winged	4	4	3	0
Numbers - winged	23	23	10	5
% + and ± winged	38	43	50	17

excluding 2780 feet { χ^2 = 0.457 2 d.f. P not significant

Of the 19 species taken occasionally (single or only a few specimens found), 13 are + winged, two ± winged, and four - winged. Their distribution with altitude is shown in Table 11. All the + winged and one of the ± winged species (Clivina fossor) have been described as capable of flight and they may be immigrants. Odontonyx rotundatus, the other wing dimorphic species, which is normally found on alluvial grasslands, was also taken at 2450 feet. The wing musculature was well developed and immigration by flight could not be ruled out. Of the - winged species, Calathus fuscipes was only found at 1400 feet on the reserve boundary; Trechus secalis and Trechoblemus micros were widely distributed but very scarce; and Amara aulica was + winged in the lowlands and may be the offspring of a recent immigrant population.

TABLE 11. OCCASIONAL SPECIES : WING CONDITION AS FOUND AT CERTAIN ALTITUDES

	Altitude (feet)			
	1400-1550	1700-1900	2400-2500	2780
No. of species				
+ winged	4	9	4	0
± winged	2	2	1	0
- winged	2	3	1	0
% + and ± winged	78	79	83	0

The + and ± winged occasional species formed a large proportion of the total numbers of + and ± winged species (Table 12), but the number of individuals was very small.

TABLE 12. THE + AND ± WINGED OCCASIONAL SPECIES AS A PERCENTAGE OF THE TOTAL + AND ± WINGED SPECIES WITH ALTITUDE

	Altitude (feet)			
	1400-1550	1700-1900	2400-2500	2780
Total no. of species + and ± winged	14	17	10	1
Nos. of + and ± winged occasional species	6	11	5	0
% + and ± winged occasional species	43	65	50	0

Although many of these occasional species breed at Moor House and Cow Green some may not be typical or permanent components of the upland fauna and the populations are probably derived and maintained by immigration.

6. Wing condition and habitat

In Carabidae, walking is the normal means of locomotion within the territory (Southwood & Johnson 1957; Southwood 1962), but flight, which normally takes the individual away from its population territory, is usually dispersive activity. A relation exists between the permanence of habitats and migratory activity; flight being more frequent in species with temporary habitats (Greenslade & Southwood 1962; Southwood 1962; Greenslade 1968).

The depth of peat on the *Calluna - Eriophorum* Moor indicates that this habitat is comparatively permanent and most sites have probably remained similar for several thousand years. The alluvial grasslands by comparison are less stable. They are often flooded as a result of heavy rainfall or rapid spring thaws and their physiography may be changed extensively by a flood.

Litter, when deposited by flood water, is often rich in insects, including Carabidae, which may have been carried downstream. No study has been made on the species composition and their wing condition, but it is possible that many have been washed off flooded grasslands and other streamside habitats. Flight, therefore, may play a significant role in taking the individuals back to these habitats.

The relation between wing condition and habitat is shown in Table 1. But as there is no evidence that species bred on all habitats on which they were found, the wing condition and the number of species breeding or expected to breed on the main habitats is also given (Table 13).

TABLE 13. THE RELATIONSHIP BETWEEN SPECIES WING CONDITION AND BREEDING HABITAT

(Species known to be wing dimorphic are included as ± winged even though only one form may have been found during this study)

A = Alluvial grasslands
F = "Flushed" grasslands
L = Limestone grassland
C = Calluna grassland
R = Redistributed peat
M = Calluna - Eriophorum Moor

	Habitat					
	A	F	L	C	R	M
Nos. of species + winged	4	7	6	0	8	4
Nos. ± winged	3	3	3	1	1	1
Nos. - winged	4	8	12	6	13	12
% + and ± winged	64	56	43	14	41	29

excluding Calluna grassland $\Sigma x^2 = 2.32$ 4 d.f. P = > 0.05

Calluna grassland excepted, the percentage + and ± winged species shows a decrease from the least stable and the minority habitats to the more permanent and major moorland habitat, but the difference is not significant. The area of Calluna grassland studied was small and the species found may not be representative of this habitat.

Two of the four +winged species of the Calluna - Eriophorum Moor were occasional species, but the other two (Loricera pilicornis and P.adstrictus) were taken more frequently on the redistributed peat and L.pilicornis was also common on the flushed grasslands. The $\pm$ winged species, N.biguttatus, was common on the Calluna - Eriophorum Moor but the + winged form was scarce.

The four - winged species of the Alluvial grasslands were all taken more frequently on other habitats and the populations could be maintained by immigration from adjacent areas.

If the above 9 species are excluded, then there would be only 7 + and $\pm$ winged species on the Alluvial grassland and only 12 - winged species on the Calluna - Eriophorum Moor.

Although + and $\pm$ winged species occur more frequently on temporary and open habitats, many of the occasional species are found on the more permanent-habitats and the reasons for flight, and the origins of these occasional species, requires further study.

7. Diurnal Activity

a) Introduction

The occurrence of diurnal rhythms throughout the animal and plant kingdom is a well known and a well described phenomenon (Harker 1961). Greenslade (1963b) described three types of daily activity cycle in Carabidae; nocturnal, diurnal and plastic. The last include species whose patterns of activity vary from day to day according to weather, habitat, and also some which show geographical variation apparently in response to climate (Greenslade 1965).

Nocturnal species are often black, whilst diurnal and plastic species often possess a metallic coloured integument (Tischler 1955), but dark morphs of otherwise metallic species are found at high altitudes (Greenslade 1968) and may indicate a change in activity times or an adaptation to absorb more radiant heat (Mani 1962).

Lewis & Taylor (1965) concluded from a wide range of flying insects that flight by day, temporary habitats, and long distance migration, are correlated. Greenslade (1968) demonstrated a relationship between diurnalism and open habitats and between + wings and temporary habitats. And, as temporary habitats were also open, between diurnalism and + wings.

The daily activity times of many of the species at Moor House and Cow Green is inferred from their colour and require confirmation. The activity of others was determined by direct observation, pitfall trapping (mechanical and manual), and frog stomach analysis.

b) By direct observation

Diurnal activity was observed in Loricera pilicornis, Trechus quadristriatus, Bembidion nitidulum and Notiophilus species. Teneral specimens only, of the three Carabus species were also active during the day and were often found crawling over the surface of the vegetation. C.problematicus and C.violaceus are a metallic bluish violet, C.glabratus a very dark green, and, on the basis of colour, diurnal activity would be expected. The older individuals of all three species avoided the light. It is not known if the tenerals were also active at night, but their behaviour is very different to the non-tenerals. Several specimens which were followed tended to crawl in a reasonably straight line. They are flightless and this behaviour may be associated with dispersive activity taking them away from their parent population, and be analogous to flight in certain winged species (Johnson 1969).

c) By pitfall trapping

i. Manual

The daily activity of several species was determined by pitfall traps which were inspected at set times each day. Two habitats were trapped but the results must be used with caution as the method has limitations. Diurnal species inhabiting the litter layer may avoid the exposed area produced by the trap and may only be caught at dusk and dawn, giving a false impression of activity times; certain species (Leistus and Notiophilus) are known to be able to avoid the traps; and also, the effect of disturbance, while the traps are inspected, may produce atypical activity.

Calluna - Eriophorum Moor

Fifty traps were in use from 0930 hours 8 July 1966 to 1000 hours 14 July 1966 on the Calluna - Eriophorum Moor. They were inspected at dawn (0400 - 0430 hours) and at dusk (2130 - 2200 hours). A summary of the results is given in Table 14.

Table 14. DAILY ACTIVITY. SUMMARY OF CARABIDAE CAPTURED ON THE CALLUNA - ERIOPHORUM MOOR

Species	Numbers : day	Numbers : night
Patrobus assimilis	4	12
Loricera pilicornis	1	0
L.pilicornis larvae	5	0
Carabus problematicus	0	1
C.violaceus teneral	1	0
Pterostichus diligens	0	1
P.nigrita	0	2
Trechus obtusus	0	4
Calathus micropterous	1	4
Agonum fuliginosum	0	1
Patrobus assimilis		
numbers per hour	0.23	1.85

The Meadow

Sixty traps (one pound jam jars) were in use in the Meadow from 0900 hours 20 July to 0700 hours 26 July 1966. They were inspected at 0400 hours, 0700 hours, 2000 hours and 2300 hours, splitting the periods into dawn (3 hours), day (13 hours), dusk (3 hours) and night (5 hours). The traps took 15 - 30 minutes to inspect. A summary of the results is given in Table 15.

TABLE 15. DIURNAL ACTIVITY. SUMMARY OF THE CARABIDAE CAPTURED IN THE MEADOW (SIX DAYS)

	0700 - 2000 hrs		2000 - 2300 hrs		2300 - 0400 hrs		0400 - 0700 hrs	
	Day		Dusk		Night		Dawn	
	♂	♀	♂	♀	♂	♀	♂	♀
Patrobus atrorufus	5	2	14	8	76	79	12	7
Loricera pilicornis	2	6	1	1	2	0	1	0
L.pilicornis (larvae)	15		0		1		3	
Notiophilus bigutattus	1	2	0	0	0	0	0	0
N.bigutattus (larvae)	2		1		0		0	
N.germinyi (larvae)	1		0		0		0	
Nebria brevicollis	0	0	0	0	0	1	0	0
Pterostichus strenuus	0	0	0	0	1	0	1	0
Carabus violaceus	1	0	0	0	1	0	0	0
Patrobus atrorufus nos. per hour	0.4	0.2	4.7	2.7	15.2	15.8	4.0	2.3

ii. Mechanical Pitfall Trap

Determination of daily activity cycles employing the previous methods has distinct limitations and involves immense effort. Williams (1958) described a piece of apparatus for the mechanical time sorting of pitfall captures and the literature concerning trapping methods was reviewed by Southwood (1966).

An apparatus, which is a modification of Williams' (1958) method, was designed to separate the pitfall captures of Carabidae into predetermined periods of each day and which, if required, could be left to run unattended for eight days. A detailed description of the apparatus is given in the appendix. The apparatus was used in conjunction with a length of gutter, as employed by Schjøtz-Christensen (1965), to increase the number of individuals captured.

After preliminary trials the trap was set up on the top of Great Dun Fell in the second half of June. Slates were placed over the gutter in an attempt to simulate the light intensity found in the litter layer. The trap was run for two consecutive periods of seven days, but the results of the second period are probably invalid as exceptionally heavy rain (1.7 inches in 24 hours) flooded and damaged the trap.

Daylength (sunrise to sunset) was about 17 hours, but 21 hours if civil twilight is included.

The results of the first 7 day period, 19 - 26 July 1968, is given in Table 15.

TABLE 16. DAILY ACTIVITY, 2780 FEET. SUMMARY OF CARABIDAE CAPTURED USING A MECHANICAL TIME SORTING TRAP DURING A SEVEN DAY PERIOD

		Species					
		Patrobus assimilis		Nebria rufescens		Notiophilus germinyi	
Hour		♂	♀	♂	♀	♂	♀
01		0	1	0	0	0	0
02		0	0	0	0	0	0
03	Sunrise	1	0	0	1	0	0
04		0	1	0	0	0	0
05		0	0	0	1	0	0
06		1	1	0	0	0	0
07		0	2	0	0	0	0
08		0	0	0	0	1	0
09		2	1	0	0	0	1
10		0	0	0	1	0	0
11		0	0	0	0	0	1
12		0	0	0	1	1	1
13		0	0	0	0	0	0
14		0	0	0	0	0	0
15		0	0	0	0	0	0
16		0	1	0	0	0	1
17		0	0	0	1	0	0
18		0	0	0	0	0	0
19		0	1	0	0	0	0
20		3	2	0	0	0	0
21	Sunset	1	3	0	0	0	0
22		0	2	1	1	0	0
23		0	1	0	0	0	0
24		1	0	0	0	0	0
	Total	9	16	1	6	2	4
Numbers "Day"		7	12	0	4	2	4
Numbers "Night"		2	4	1	2	0	0

The diurnal activity experiments on the Calluna - Eriophorum Moor and the Meadow show that Patrobus assimilis and P.atrorufus are essentially nocturnal. In the Meadow similar numbers of P.atrorufus males and females were taken at night, but the males were more active than the females at other times ($\chi^2 = 4.08$ 1 D.F. $P = < 0.05 > 0.01$).

At 2780 feet P.assimilis was taken mainly at dawn and dusk. Few specimens were taken at night, but this may be due to low temperatures reducing activity as they are essentially nocturnal at 1800 feet on the Calluna - Eriophorum Moor. Mani (1962) considers that insect activity on high mountains is dependent on high day time temperatures and is consequently mainly diurnal. A similar effect probably occurs at 2780 feet but no specimens were caught in the mid-day period.

Further evidence is required to confirm the daily activity of Nebria rufescens at 2780 feet but like P.assimilis it avoids the light. Notiophilus germinyi is often seen during the day and the six specimens caught in the traps at 2780 feet also indicate a diurnal activity.

d) —Frog Stomach Analysis

The common frog, Rana temporaria, a common moorland predator, is essentially a daylight feeder on the reserve, and prey most active during the day were predominant in its gut. A summary of the Carabidae from the stomachs of 434 frogs is given in Section V. 11. i. on predators.

8. Daily Activity times at Moor House and Cow Green

Of the 48 species in this study, 30 can be classed as essentially nocturnal, and 18 as diurnal. There is a significant association between nocturnalism and - wings, and diurnalism and + wings. ($\chi^2 = 12.3$ $P. < 0.001$) (Table 17).

TABLE 17. THE RELATIONSHIP BETWEEN WING CONDITION AND DAILY ACTIVITY TIME. ALL SPECIES

Numbers species	Daily activity time Nocturnal	 Diurnal	 Total Nos.
+ winged	6	13	19
$\pm$ winged	2	2	4
- winged	22	3	25
% + and $\pm$ winged	27	83	48

$$\chi^2 = 12.3 \quad 1 \text{ d.f.} \qquad P = < 0.001$$

Two of the - winged diurnal species, Notiophilus aquaticus and N.germinyi, have been described as $\pm$ winged. Agonum ericeti, the other - winged diurnal species, has reduced wings.

The low temperatures found on the moors, especially at night, severely restricts flight and may, in part, account for the relationship between - wings and nocturnal activity.

All the diurnal and four of the nocturnal occasional species (Table 18) are probably capable of flight in the lowlands. Of the four nocturnal - winged species, Calathus fuscipes was only found at 1400 feet on the Reserve boundary; Amara aulica was + winged in the lowlands and may be the offspring of a recent immigration population; Trechus secalis and Trechoblemus micros were widely distributed but very scarce and their status requires further study.

TABLE 18. OCCASIONAL SPECIES; THE RELATIONSHIP BETWEEN DAILY ACTIVITY AND WING CONDITION

	Daily activity time		
	Nocturnal	Diurnal	Total nos.
Nos. + winged	3	10	13
Nos. ± winged	1	1	2
Nos. - winged	4	0	4
% + and ± winged	50	100	79

That 84% (16/19) of the occasional species may fly, at least in the lowlands, and of these 69% (11/16) appear to be diurnal, may further indicate that many are immigrants or the offspring of recent immigrants. Alternatively, flight may result in a wide distribution and subsequent low numbers of an indigenous population.

The relationship between daily activity times and habitat is obscure as many species were found on habitats other than their breeding habitats. The numbers of nocturnal and diurnal species found breeding on certain habitats are therefore listed (Table 19), but the differences are not significant.

TABLE 19. THE RELATIONSHIP BETWEEN DAILY ACTIVITY AND BREEDING HABITAT

A = Alluvial grasslands — C = *Calluna* grassland

F = "Flushed" grasslands — R = Redistributed peat

L = Limestone grassland — M = *Calluna - Eriophorum* Moor

	Habitat					
	A	F	L	C	R	M
Nos. of species diurnal	3	5	2	1	5	4
Nos. nocturnal	8	10	13	6	13	13
% diurnal	27	33	13	14	28	24

excluding the *Calluna* grassland

$$\sum \chi^2 = 0.654 \quad 4 \text{ d.f.} \quad P => 0.1$$

The Alluvial grassland, compared with the *Calluna - Eriophorum* Moor, is a very temporary open habitat. The relationship between daily activity times and wing condition of species on these habitats is given in Tables 20, 21 and 22, but the numbers are too small to show any significant difference.

TABLE 20. ALLUVIAL GRASSLAND; DAILY ACTIVITY TIMES AND WING CONDITION. ALL SPECIES

	Wing condition			
	+ & ±	-	Total	% + & ±
Nos. nocturnal	7	8	15	47
Nos. diurnal	5	2	7	71
Total nos.	12	10	22	55
% diurnal	42	20	32	

Eleven of the species in the above table are unlikely to breed on the alluvial grassland and the numbers found breeding are therefore listed (Table 21).

TABLE 21. ALLUVIAL GRASSLAND; DAILY ACTIVITY TIMES AND WING CONDITION. BREEDING SPECIES ONLY

	Wing condition			
	+ & ±	-	Total	% + & ±
Nos. nocturnal	4	4	8	50
Nos. diurnal	3	0	3	100
Total nos.	7	4	11	64
% diurnal	43	0	27	

TABLE 22. <u>CALLUNA - ERIOPHORUM</u> MOOR. DAILY ACTIVITY TIMES AND WING CONDITION. BREEDING SPECIES ONLY

	Wing condition			
	+ & ±	-	Total	% + & ±
Nos. nocturnal	2	11	13	15
Nos. diurnal	3	1	4	75
Total nos.	5	12	17	29
% diurnal	60	8	24	

Unlike the alluvial grassland, all but one of the species taken on the Calluna - Eriophorum Moor (Patrobus atrorufus - a nocturnal - winged species) were found breeding on this habitat.

9. Mandible condition

a) Introduction

A species which has a well synchronised life cycle and one emergence period each year would, if it survived until the time the next generation emerged, have mandibles distinctly different from the newly emerged adults. If it survived for another year, making it a two year old adult, a further year's wear might distinguish it from a one year old beetle. Three separate generations (and perhaps more) might therefore be distinguished. Variations due to time of emergence, temperature, feeding rates, food, injury and structure of the mandibles may give a false impression of age but a general trend would be expected if the habitat was uniform.

The degree of wear on the mandibles and claws has therefore been used as a guide to the age of a beetle. Teneral Pterostichus nigrita adults, for example, can be distinguished from those entering their second year of adult life by their comparatively sharper mandibles and claws.

The degree of wear of the mandibles and the reproductive condition of Carabus sp. taken at Moor House was investigated, as they have been known to live for more than one year and have large mandibles.

FIGURE 5. Left mandibles, ventral view, of *Carabus glabratus* showing the four classes representing the degree of wear.

(after page 78)

In the spring the degree of wear of the mandibles of Carabus glabratus and C.problematicus formed three main groups. A fourth group, where the mandibles were very sharp, appeared in the summer and autumn and were the newly emerged adults. Figure 5 shows the four classes, henceforth referred to as M1 (the newly emerged adults with sharp mandibles), M2, M3, and M4. The last had very worn mandibles and comparatively few were caught. Attempts were made to measure the exact degree of wear but due to variation in size and shape this was impractical. The degree of wear was therefore assessed and placed in one of the above categories. If the degree of wear of a specimen was doubtful it was placed in the older class, e.g., a specimen with mandibles halfway between M2 and M3 was classed as M3.

The condition of the mandibles of C.glabratus and C.problematicus and their reproductive condition, taken on the Blanket Bog (Site 4) and the redistributed peat (Site 5) at Moor House during 1967 is shown in Figures 6 - 9.

Similar results were found with numerous specimens from many other sites.

b) Carabus glabratus

All teneral C.glabratus adults displayed the M1 condition (Figure 6). All other specimens with M1 were immature and had sharp claws indicating that they had recently emerged.

In the spring and early summer of 1967 all immature and developing M2 C.glabratus females were without corpora lutea,

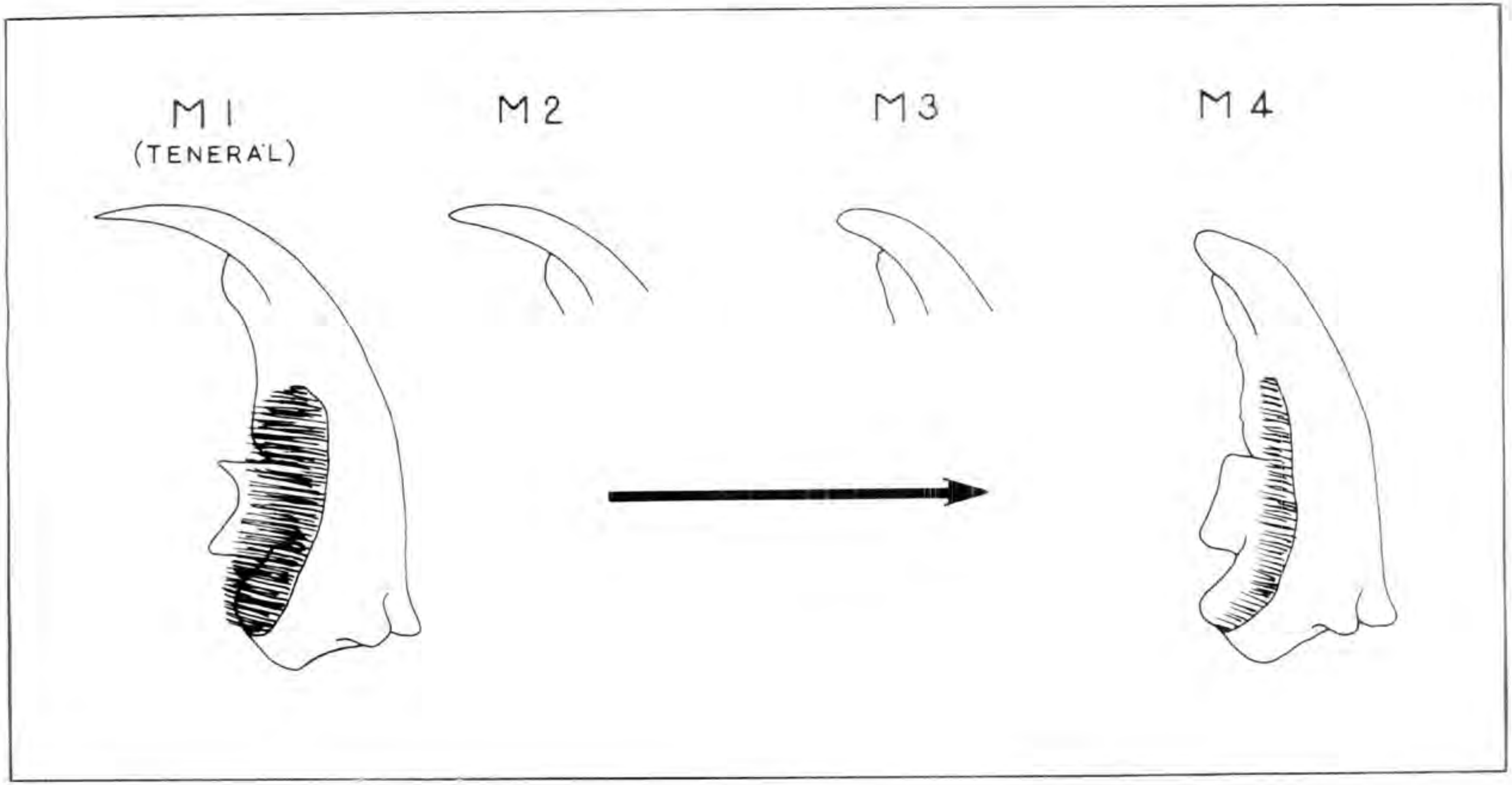
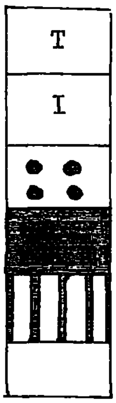

M1
(TENERAL)
M2
M3
M4

FIGURE 6. Carabus glabratus females. Pitfall trap catches on Sites 4 and 5 in 1967 showing their reproductive condition, grouped according to the degree of wear of the mandibles.

Key to Figure 6 (and other similar figures) showing the reproductive condition of the adults. For further details see Section IV. 4.



- newly emerged adults (tenerals and non-tenerals)
- not recently emerged, but gonads 'immature'
- gonads developing
- gonads mature, females with mature eggs
- spent or gonads being absorbed
- specimens not dissected

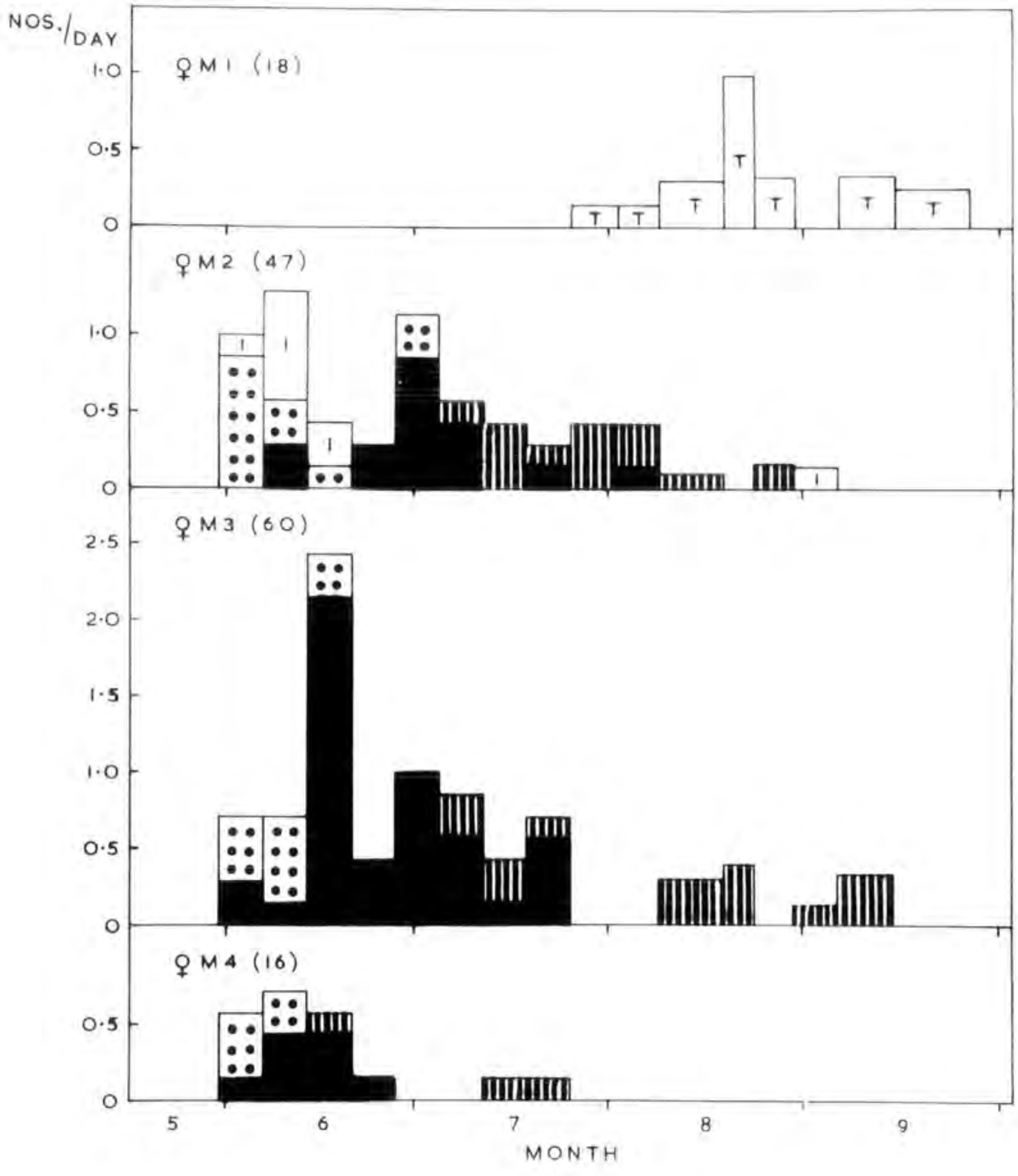
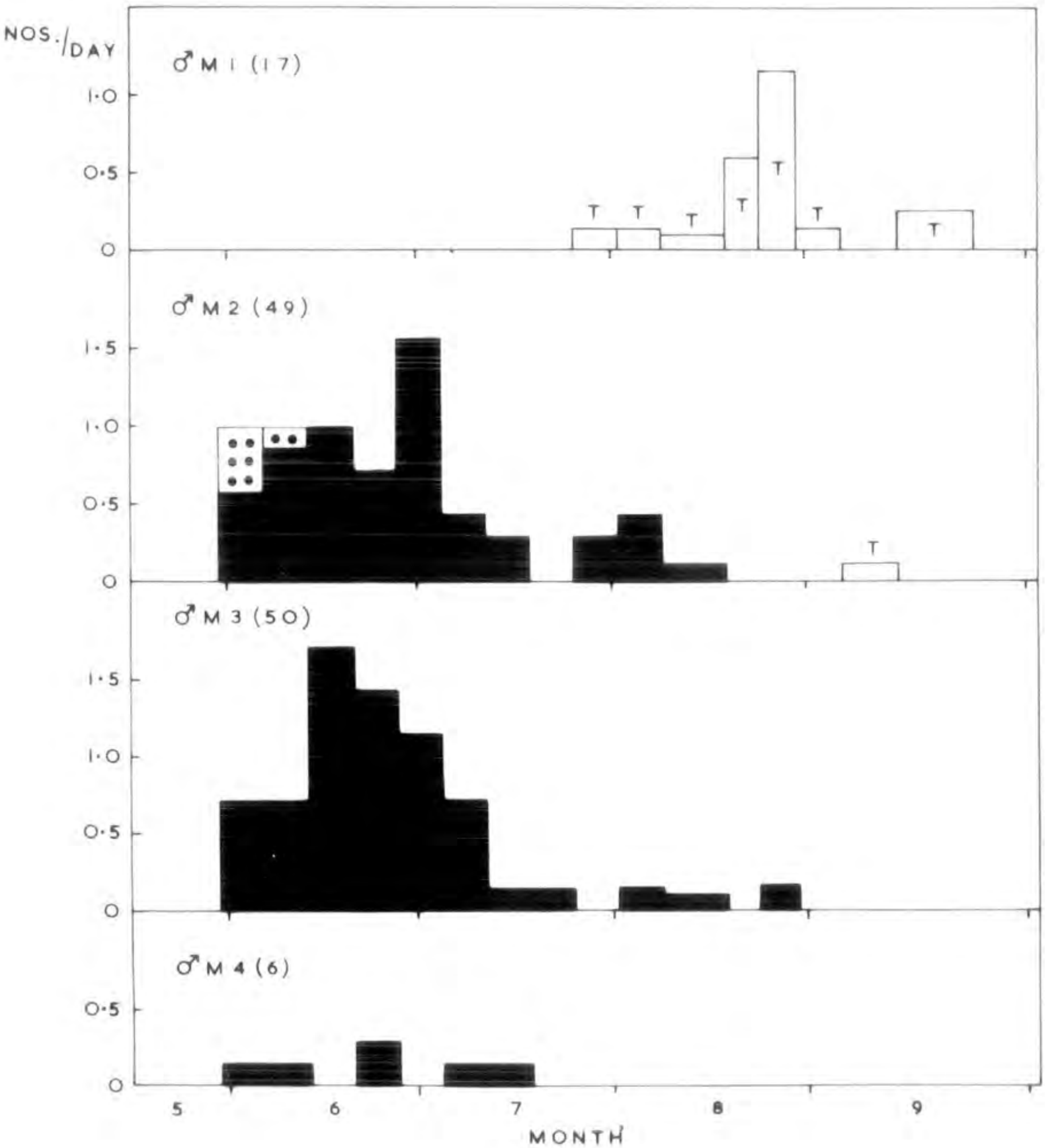

NOS./DAY
♀M1 (18)
♀M2 (47)
♀M3 (60)
♀M4 (16)
1·0
0·5
0
2·5
2·0
1·5
T
I
5
6
7
8
9
MONTH

FIGURE 7. *Carabus glabratus* males. Pitfall trap catches on Sites 4 and 5 in 1967 showing their reproductive condition, grouped according to the degree of wear of the mandibles.

Key as in Fig.6.



NOS./DAY
♂ M 1 (17)
1·0
0·5
0
T
♂ M 2 (49)
1·5
1·0
0·5
0
T
♂ M 3 (50)
1·5
1·0
0·5
0
♂ M 4 (6)
0·5
0
5
6
7
8
9
MONTH

indicating that they were entering their first breeding season and had emerged in the late summer/autumn of 1966. In the autumn of 1967 a few immature M2 specimens were found. The females had no corpora lutea and were probably adults which had emerged in 1967.

In Figure 6 all the developing M3 females had corpora lutea, indicating that they had passed through at least one breeding season and were therefore entering at least their second.

As no developing M2 females with corpora lutea were found at the start of the breeding season, all 1966 M2 females must have therefore become M3 before they were caught in the spring of 1967. If 1967 was similar to past years, M2 females which were in, or had had, their first breeding season, would change from M2 to M3 before the next spring. If they were mature or spent they would be more or less indistinguishable from females which were in, or had had, at least their second breeding season. There is no evidence that the M3 stage lasts for more than one year and therefore M3 adults, except for the recruitment of past M2 individuals, are probably second year adults.

Most M4 specimens taken in the spring and early summer of 1967 were probably in their third year of adult life, i.e. teneral 1964, and those found in the late summer and autumn, old 1967 M3 specimens.

Alternatively, they may have been M1 (teneral) in 1965, M2 and M3 in 1966, and their mandibles wore quicker than other specimens.

Mark-release experiments were conducted at Moor House but no long term recaptures of Carabus sp. were made. Schjøtz-Christensen (1959) noted that it was not exceptional for adult beetles to live more than one year and reproduce more than once. His marking experiments indicated that Harpalus smaragdinus Dft. adults survived for several years and one 4 - 5 year old individual was found.

c) Carabus problematicus

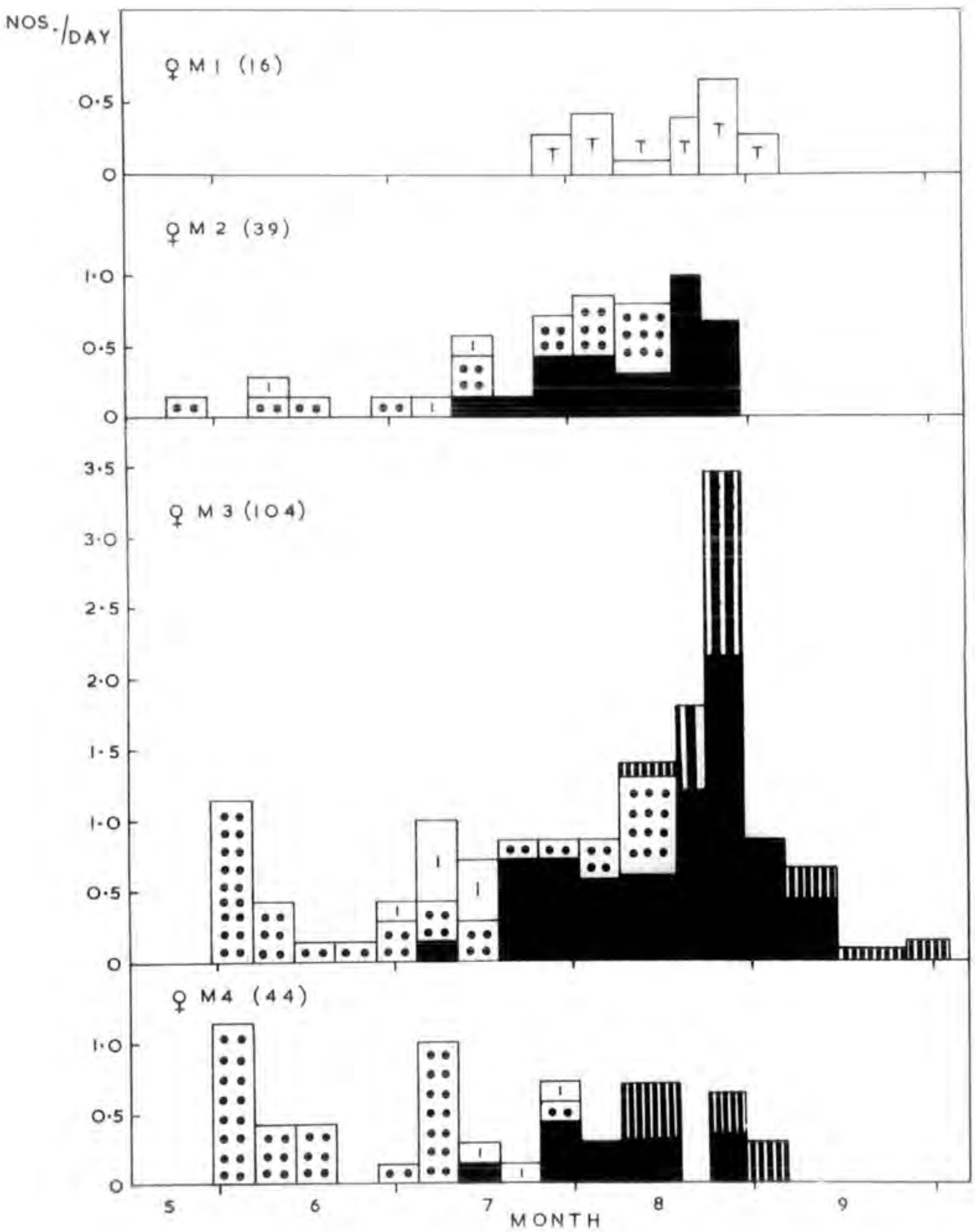
This species shows the same trend as C.glabratus but as it is an autumn breeder, the age groups overlap further and are not so clearly defined (Figures 8 and 9).

Tenerals (M1) occur in the autumn. All immature and developing M2 females were without corpora lutea, indicating that they were entering their first breeding season. Immature and developing M3 females taken in May, June and July had corpora lutea, but a few developing females taken in August did not. The latter appear to have been recruited from the 1967 M2 individuals. A few mature M3 females were perhaps also 1967 M2 individuals. The M4 females taken early in the year are thought to have been M3 in 1966. Some of the M4 females taken in the autumn were no doubt 1967 M3 females.

As with C.glabratus, long term marking experiments would be required to determine the exact status of most M3 females and all the M4 females.

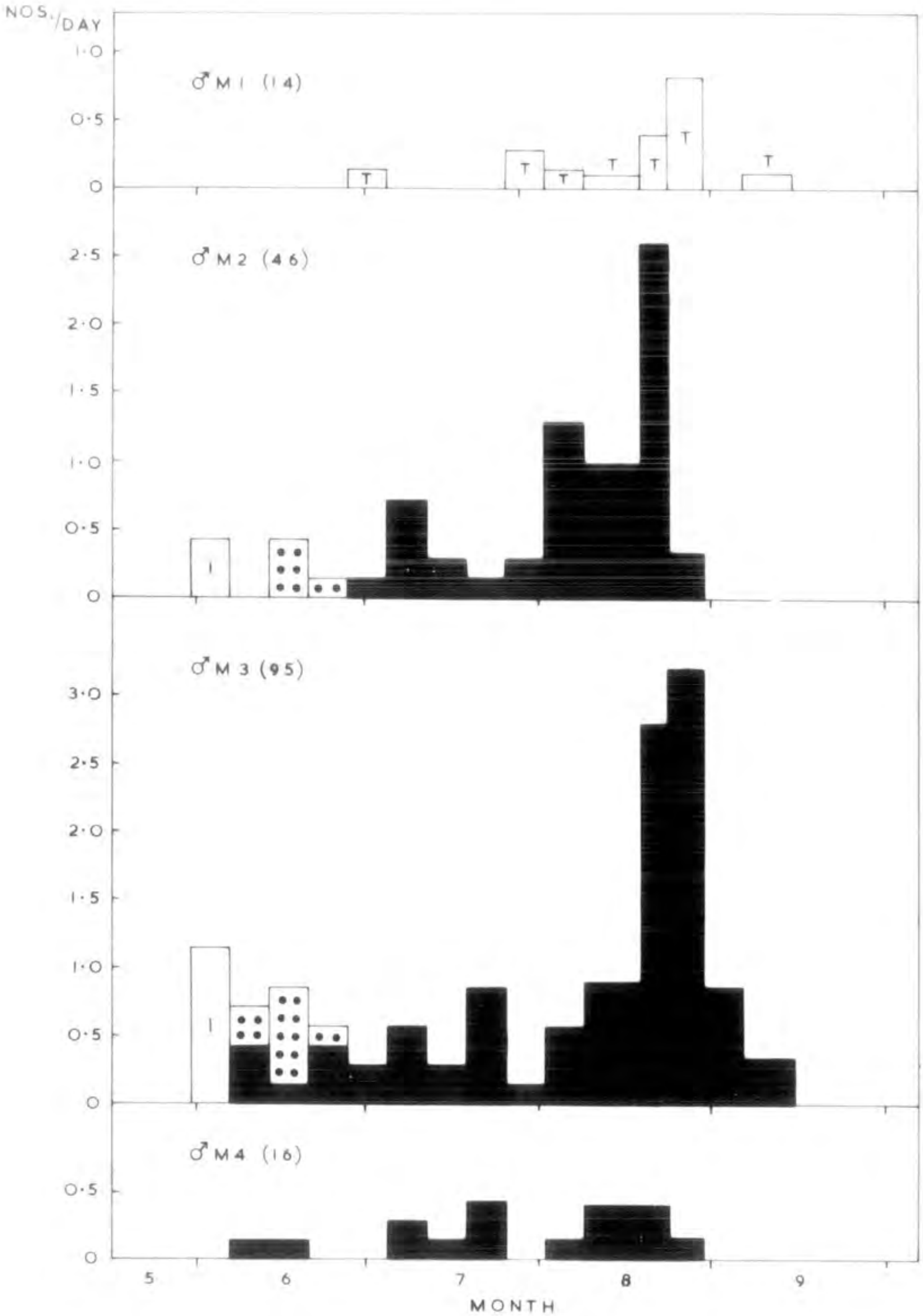
FIGURE 8. *Carabus problematicus* females. Pitfall trap catches on Sites 4 and 5 in 1967, showing their reproductive condition, grouped according to the degree of wear of the mandibles.

Key as in Fig.6.



NOS./DAY
♀ M1 (16)
♀ M2 (39)
♀ M3 (104)
♀ M4 (44)
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
T
I
5
6
7
8
9
MONTH

FIGURE 9. *Carabus problematicus* males. Pitfall trap catches on Sites 4 and 5 in 1967 showing their reproductive condition grouped according to the degree of wear of the mandibles.


NOS./DAY
♂M1 (14)
♂M2 (46)
♂M3 (95)
♂M4 (16)
MONTH

The males of both species show a similar pattern (Figures 7 and 9) to the females but marking experiments would be required to confirm their status.

d) Mark Release Experiments

Mark release experiments were conducted on the Calluna - Eriophorum Moor at Bog End, and on the Fell Top Podzol at 2780 feet. The main aims of the experiments were to determine the longevity and confirm the degree of wear on the mandibles in relation to age and habitat of the common species.

Although many species were marked and released, there were no recaptures on the Moor. At 2780 feet four Patrobus assimilis individuals were recaptured once and one Nebria gyllenhali three times, but all were recaptured within eight days of being marked.

The aims of the experiment were not achieved but a reliable and permanent method for marking Carabidae was developed. The method which could also be applied to certain other arthropods is described in the appendix.

10. Resistance to Desiccation and Drowning

a) Introduction

High temperatures and high humidities are favourable to Carabidae (Tipton 1960; Kless 1961) but the temperature and humidity of the environment commonly vary inversely.

A cover of vegetation lowers mean temperatures at ground level and reduces and retards the daily and seasonal fluctuation in comparison with more open habitats (Geiger 1959). At Moor House the open habitats are invariably grasslands on mineral soils while those with a thick vegetation cover are normally organic. Open habitats (e.g. Limestone grassland) therefore are normally well drained with a poor plant cover, impoverished by sheep grazing. The litter layer and top three centimetres of the soil shows large daily and seasonal fluctuations in temperature and humidity (Springett 1957) but the litter layer of the habitats on organic soils (e.g. Calluna - Eriophorum Moor) invariably has a high humidity with a comparatively small daily temperature fluctuation and is often waterlogged.

Species breeding on the non-wet habitats, such as the Limestone grassland, may therefore be subjected to desiccation and those on wet habitats inundation. Investigation of their life histories have shown that on the non-wet habitats, with few exceptions, only adults are present during the 'dry' season, but on the wet habitats all stages may be present during the 'dry' season.

b) Resistance to drowning

Resistance of adults and larvae to desiccation and drowning was investigated in the field and the laboratory. Culture experiments indicated that the early instars of small short-legged larvae are more susceptible to drowning than those of long-legged species.

In the field, adults and larvae may be affected by flood water in several ways; they could be completely submerged with no access to air, except that which might be trapped under their elytra; submerged with access to a pocket of air trapped in the vegetation; or they may be floating on the surface.

Third instar larvae of *Patrobus assimilis* (a small short-legged form - a reflection of its subterranean habit (Sharova 1959)), *Notiophilus germinyi* (a small long-legged form) and *Carabus problematicus* (a large short-legged form) and adults of numerous species were placed on submerged vegetation on the moor. All crawled up the plants and out of the water within minutes, but *P. assimilis* took the longest. Experiments to see what would happen when *P. assimilis* adults and larvae were physically trapped in the water were conducted.

Method

Patrobus assimilis adults and larvae, collected from the top of Great Dun Fell at the end of August were kept in a 10° constant temperature cabinet, with a photoperiod of 12L : 12D, for three days before the start of the experiment to acclimatise the specimens and ensure no mortality due to the collecting.

Three 20cm crystallizing dishes were filled with tap water and twenty 2 x 1 inch tubes were submerged in each of them. A fourth dish contained moist filter paper. Lids were placed on all dishes and they were left in the 10° cabinet for 24 hours.

All the air bubbles which had formed on the glass were shaken free.

Adult beetles were placed, without food, in the dishes as follows :

Dish 1. Twenty adults running free on moist filter paper acted as a control.

Dish 2. The tubes were half emptied of water and one beetle was left floating in each tube. (The lid of the dish held down the floating tubes and prevented any beetles escaping).

Dish 3. All tubes were inverted and one beetle was added to each tube. Air pockets, varying in size from about 1cc down to the size of the head of a *P.assimilis* adult, were added to the tubes and left in contact with the specimens.

Dish 4. All tubes were inverted and one beetle placed inside each tube, ensuring that no air bubbles entered.

The specimens were inspected at intervals, when some specimens in Dish 4 were removed and their apparent complete recovery time noted. Specimens from the other dishes were only removed if they showed no sign of activity.

Results

Dish 1. After seven days all specimens were alive.

Dish 2. On day 5, four specimens had mould growing on them; one of which had sunk and was dead. All others were alive.

On day 7, the three specimens with mould had sunk and were dead. All the others were alive and when removed appeared to be fully recovered within 30 minutes.

Dish 3. On day 6, the four specimens with pockets of air the size of their heads appeared to be dead. They were removed but had fully recovered within three hours. All the others were removed and when inspected 30 minutes later appeared to be fully recovered.

Dish 4. Specimens were removed at intervals ranging from five minutes to 19 hours 30 minutes. Those removed after five and ten minutes recovered in 30 - 80 seconds; those after 30 and 35 minutes in 3 - 6 minutes, and those after 80 minutes to 19 hours 30 minutes appeared to be fully recovered within 120 minutes.

Larvae

Six third instar larvae were submerged in water in tubes as in Dish 4 above. They were removed after 26 hours and all appeared to be fully recovered within 30 minutes.

Thus, wet conditions probably have little physical effect on the adults and third instars. Why early instars of the small short-legged forms, e.g. *P.assimilis*, cannot tolerate the wet conditions when many small Staphylinidae larvae, e.g. *Lesteva* and *Olophrum* do, is not known.

c) Resistance to desiccation

Culture experiments also indicated that larvae were more susceptible to desiccation than adults and, of the three types of larvae mentioned above, the small short-legged forms were the most susceptible. Adults of many species and larvae of Carabus species survived long periods of low humidity provided they had ample fat reserves or access to food. In the field food may be scarce on the non-wet habitats during the 'dry' season, but water lost by a beetle during the day can normally be replenished at night from the heavy dew. Notiophilus germinyi larvae also survived low humidities if food was available, but all instars of P.assimilis, P.atrorufus and Pterostichus nigrita soon became desiccated and died even with unlimited food.

The eggs of all the above species were not resistant to desiccation and required high humidities throughout their incubation period. Unless they are protected from desiccation, as in Pterostichus madidus, they are therefore only likely to survive on the non-wet habitats outside the 'dry' season. If the larvae also cannot survive in low humidities, there is thus strong selection pressure preventing spring/summer breeding on the non-wet habitats.

11. Predators and Parasites

a) Introduction

Several workers have stated that predators and parasites appear to have negligible effect on the numbers of dominant insects, and have demonstrated how single environmental factors dominate changes in density (Coulson 1956; Reay 1959; Cherrett 1961; Cragg 1961).

In this study many of the possible predators and parasites of Carabidae were observed, but except perhaps for shrews and spiders, their effect on carabid populations appears to be slight.

b) Invertebrate predators

In the laboratory adults and larvae of many carabid species were fierce predators and cannibalism was common. Grum (1967) observed cases of cannibalism under natural conditions and noted that the victims were always young individuals. The areas of occurrence of imagines and larvae of the same species do not completely coincide (Grum 1962) and probably serves to reduce intraspecific predation of the adults on the larvae.

Spiders are common predators on the moor (Cherrett 1961), with the Lycosidae (Wolf Spiders) one of the dominant families at Moor House. Their effects on the Carabidae has not been determined.

On made ground, e.g. old mine heaps, centipedes and ants were common and, probably as a result, Carabidae were very scarce on these areas.

c) Vertebrate predators

i. Frogs

The Common Frog, Rana temporaria, a common moorland predator, was found feeding throughout the daylight hours but not at night. No specimens were captured at dawn to determine the extent of digestion of the prey, but the stomachs of specimens taken throughout the daylight hours contained freshly caught material.

A total of 434 frog stomachs were examined. Only 25 stomachs were empty but they were mainly from frogs which were found dead in ponds after a cold spell in the spring where they may have been trapped by ice.

Carabidae were regularly found in the stomachs, but Diptera, Arachnida, Staphylinidae and Hemiptera were much more frequent. The proportion of food animals found in the stomachs is unlikely to be a true reflection of the rate at which they were taken, as large prey with tough cuticles (e.g. Carabidae) probably took longer to be digested and removed from the stomach than delicate prey such as Collembola. This is reflected by the number of instances where only carabid elytra were found.

A detailed analysis of the stomach contents is in preparation and only a summary of the Carabidae is included here (Table 23).

TABLE 23. FROG STOMACH ANALYSIS. A SUMMARY OF THE CARABIDAE FOUND IN THE STOMACHS OF 409 COMMON FROGS

a = adults : l = larvae

Carabid species		No. of frog stomachs	No. of carabids
Carabus glabratus	l	1	1
C.problematicus	a	1	1
Leistus rufescens	a	3	3
	l	1	1
Nebria salina	a	1	1
N.rufescens	a	12	16
	l	7	9
Notiophilus sp.	a	7	8
	l	1	1
Loricera pilicornis	a	8	11
	l	4	5
Bembidion atroviolaceum	a	3	3
Trechus secalis	a	1	1
T.obtusus	a	11	12
T. rubens	a	2	2
Patrobus assimilis	a	61	81
P.atrorufus	a	9	21
Amara aulica	a	1	1
Pterostichus nigrita	a	5	6
	l	1	1
P.strenuus	a	6	6
P.diligens	a	6	6
Calathus micropterus	a	1	1
Agonum ericeti	a	5	6
Total with adult Carabidae		143	186
Total with larval Carabidae		15	18

The total number of food items in the 409 stomachs ran into thousands, and if the length of time the evidence of Carabidae, such as elytra, remains in the stomach is taken into consideration, they probably form a relatively small part of their diet. Although the density and feeding rate of the frog on the moor requires further study, it probably has only a limited effect on the Carabidae.

ii. Shrews

The common shrew, Sorex araneus, and the pigmy shrew, S.minutus, were found frequently in pitfall traps on the Calluna - Eriophorum Moor. Rudge (1968) stated that Coleoptera adults are dominant prey of S.araneus in terms of both their constancy throughout the year and their size. He also confirmed that it is an opportunist feeder whose diet is governed more by changing availability of prey than by taste or preference.

Ideally a gut analysis should allow actual numbers of prey to be counted or their relative bulks to be measured (McAtee 1912). This is possible in frogs which bolt prey whole, but quantitative analysis of shrew gut contents is virtually impossible as the numerous, easily fragmented, small prey, is chewed up very finely.

Eighty Common Shrews and 73 Pigmy Shrews were collected from pitfall traps at Moor House in 1967. Only 5 and 7 stomachs respectively were empty. A preliminary investigation of the stomach contents of both species from the Calluna - Eriophorum Moor at Bog End indicates that Aranae, Opiliones and Coleoptera were frequently taken. Carabidae were present but identification further than genus was often impossible. Specimens of Patrobus (? assimilis), Pterostichus (? nigrita), Trechus (? obtusus) and *Carabus* sp. third instar larvae were found.

The density of these shrews requires investigation, especially as close inspection of the *Calluna - Eriophorum* Moor shows that the vegetation and detritus is riddled with their tunnels. Each day the shrew requires a mass of food in the form of invertebrates equal to its own body weight (Crowcroft 1957; Hawkins & Jewell 1962) and their significance as predators on the moor should perhaps not be underestimated.

iii. Birds

The Meadow Pipit (*Anthus pratensis*) is the commonest bird on the Reserve (Coulson 1956) but Carabidae were not noticed in its diet.

Red Grouse (*Lagopus scoticus*) chicks feed on invertebrates, including Carabidae, but as they are not usually common on the moors they are probably relatively unimportant predators.

iv. Sheep

Although sheep cannot be regarded as intentional predators of Carabidae, their trampling effect on population numbers may be considerable if they graze an area frequently and in high densities, as on the Alluvial and Limestone grasslands.

d) Parasites

i. Hymenoptera

Although Hymenoptera have frequently been recorded as endoparasites of carabid larvae (Davies 1959), no parasitised carabid larvae were found, but Phaenoserphus species (Proctotrupidae) were seen in Staphylinid larvae.

ii. Nematomorpha

About sixty carabid adults were found to be parasitised by Gordiids. Most of the infected specimens were taken on the west side of the reserve on redistributed peat sites. Only one, a Patrobus assimilis female, was found on the Blanket Bog.

Two species of Gordiid were identified; Parachordodes violaceous (Baird 1853), the most common, was recorded from P.assimilis (5 males, 4 females), P.atrorufus (one female), Carabus problematicus (one male, 2 females), Pterostichus nigrita (one female), P.diligens (one female), P.madidus, red legged form only, (6 males, 6 females), Calathus micropterous (2 females) and Parachordodes wolterstorffii Camerano 1888 from Patrobus assimilis (3 males, 2 females only).

The ovaries of most of the infected females were not visible but in those that were,no corpora lutea were present indicating that the parasite prevented the maturation of the gonads. Infected males were also immature.

Although in this study only the red legged form of P.madidus was parasitised (Table 24), it is not significant, and Gordiids have been recorded from the black legged form (Luff pers.comm.)

TABLE 24. NUMBER OF PTEROSTICHUS MADIDUS INFECTED WITH PARACHORDODES VIOLACEOUS

	Colour form			
	Black legged		Red legged	
	♂	♀	♂	♀
Total numbers caught	18	33	69	59
Numbers parasitised	0	0	6	6
	0%		9.4%	

χ^2 on number of infected beetles of the two colour forms = 3.33 1 d.f. $P > .05$

VI. LABORATORY CULTURES

The influence of certain environmental factors on the development of several species of carabid was studied in the laboratory. Specimens were taken either from the field or bred from eggs.

1. Method

a) Containers

Adults were kept either in 3 x 1 inch glass tubes or 4 x 3 inch glass jars to which, respectively, a 4 x 3/4 inch strip or two circles of moistened filter paper had been added. Eggs were normally found embedded in the filter paper but occasionally they were laid on the surface.

Eggs, larvae and pupae were kept singly in 2 x 3/4 inch and 2 x 1 inch glass tubes or 2 x 2 inch plastic containers. Two circles of moist filter paper, cut with a cork borer, were placed in the bottom of each tube and strips of filter paper in the containers. The specimens were inspected daily, when the larvae were placed in clean tubes with fresh food and filter paper.

b) Humidity

To prevent desiccation of the immature stages it was essential that the filter paper was kept moist, but not super-saturated, and that the tops of the tubes formed an airtight fit. The comparatively small, short legged larvae, e.g. Patrobus species, especially the first and early second instars, were very susceptible to drowning, but the long legged forms, e.g. Nebria, Leistus and Notiophilus species and the larger larvae, e.g. Carabus species, rarely drowned. The adults were more resistant to desiccation but the females only laid eggs in very moist substrates.

In the following experiments the percentage humidity was not controlled precisely, but in each case the size of the airtight containers, the filter paper substrate, and the volume of water added remained constant and the relative humidity must have been about 100%.

c) Food

In the laboratory, Enchytraeidae and various small arthropods were readily taken as food, but it was not possible to obtain a large and constant supply and other foods were substituted.

Rabbit liver was readily available and all specimens in many experiments were fed on the same liver. Unused liver was kept in a deep freeze at -25° to -30°C. A few species would not at first take liver, but if a piece was carefully placed against their mouthparts and then gently moved, it was usually snatched away and readily eaten. Thereafter liver was usually taken if left on the filter paper. The adults and larvae of Notiophilus sp. would not take liver and they were given live Collembola.

Larvae, especially newly hatched first instars, frequently became caught on the liver, often resulting in their death. In an effort to reduce this mortality other methods of presenting the food were tried.

In some preliminary feeding experiments the larvae of a few species readily ate "Brands Chicken Essence" and were rarely trapped by the food. A liver homogenate was therefore made up into a jelly using agar and was readily consumed by several larvae and adult carabids. As carabids have been recorded as pests of strawberries (Briggs 1961; Luff, pers.comm.) a liver homogenate was made using a commercial brand of strawberry jelly, but one made up from plain agar, liver homogenate, and sugar was found to be equally successful.

Not all species of carabid studied could be induced to consume the agar mixtures and for convenience liver was used.

When using an agar mixture the mortality due to the larvae adhering to the food was negligible and there was also visible evidence if any of the food was eaten. This method could prove a useful and standard way of feeding certain carabids in culture and may repay further study.

d) Temperature

Most cultures were kept in constant temperature cabinets or constant temperature rooms. The temperatures used in the cabinets were 5^{o}, 10^{o}, 15^{o}, and 20^{o}C and were accurate to $\pm 1^{o}$. The constant temperature rooms were at $15^{o} \pm 1^{o}$ and $26^{o} \pm 1.5^{o}$.

The cultures in the cabinets were removed for a few minutes each day when they were inspected.

e) Acclimatisation

Specimens were acclimatised for 24 hours for each 5^{o} change from field temperatures to which they were subjected. For example, adults taken from field temperatures of 5^{o} for experiments at 20^{o} were kept for 24 hours at 10^{o} and 24 hours at 15^{o}.

f) Photoperiod

Each constant temperature cabinet was lit by an 8 watt fluorescent tube controlled by a time switch. The 15^{o} and 26^{o} rooms were lit by 40 watt fluorescent tubes. The photoperiod in the 15^{o} room was controlled by a time switch but in the 26^{o} room the light was constantly on and scotophase was induced by placing the cultures in a light tight container for the required period.

The cultures were placed where the intensity of the light, as shown by incident light meter readings, was similar. The light intensity reaching the specimens in the tubes was not identical but Lees (1955) found that in general the photoperiod reaction in arthropods is independent of intensity above a critical level.

The photoperiods were kept to a 24 hour rhythm and sets of cultures subjected to different photoperiods. Specimens were also kept under natural photoperiods but it was not possible to simulate moorland field temperatures.

The photoperiods given in this section are described as the number of hours in the light (L) and in the dark (D); e.g. with a daily rhythm of 24 hours, a photophase of 10 hours and a scotophase of 14 hours is abbreviated to 10L : 14D. Specimens under artificial lighting were either in the light or in darkness as there was no twilight period. Photoperiods with a photophase greater than 12 hours are described as a long day.

Where possible the cultures were examined during the photophase and at the same time each day. Specimens with a photoperiod of 0L : 24D actually had a few minutes light each day when the cultures were examined.

2. Experiments

Experiment a) The effect of different temperatures and photoperiods on immature *Patrobus assimilis* adults

Patrobus assimilis adults were collected from the top of Great Dun Fell in the first two weeks of May 1968. Dissection of 5 males and 5 females revealed that four males were immature and one had developing gonads while all the females were immature but three had corpora lutea and were entering at least their second breeding season.

The remaining specimens were kept in groups in 4 x 3 inch jars at different temperatures and photoperiods (Table 25).

TABLE 25. EXPERIMENT a. THE NUMBERS OF PATROBUS ASSIMILIS ADULTS (MALES/FEMALES) AND THE TEMPERATURES AND PHOTOPERIODS AT WHICH THEY WERE KEPT

	Temperature (^{o}C)				
Photoperiod	5^{o}	10^{o}	15^{o}	20^{o}	26^{o}
0L : 24D	5/5	10/10	10/10	5/5	5/5
10L : 14D	5/5	10/10	10/10	0	0
12L : 12D	5/5	10/10	0	0	0
21L : 3D	5/5	10/10	10/10	0	0
24L : 0D	5/5	10/10	10/10	5/5	5/5

The cultures were inspected and given fresh food (rabbit liver) daily. Any dead specimens were removed and dissected. After 30 days in culture the remaining specimens were killed and dissected.

Results

5^{o} There was no mortality. Specimens at all photoperiods were immature and had large fat reserves.

10^{o} All specimens with a photoperiod of 0, 10 and 12 hours photophase were immature but their abdomens were very distended with fat reserves. Three specimens were found dead; one on day 22 and one on day 29 at 12L : 12D, and one on day 25 at 10L : 14D. The dorsal surface of their abdomens were split and part of their very large fat reserves were extruded. There was no evidence that they had been attacked by other beetles and the split appeared to have been caused by the pressure of the contents of the abdomen. Further experiments were conducted on this problem with similar results (Experiment d).

After 30 days all but one of the specimens under a photophase of 21L : 3D and 24L : OD were mature; the females having both mature and developing eggs and the males large testes. The fat reserves of the females were small but most of the males had considerable reserves of fat. The one exception was a female under 21L : 3D which was found dead on day 14. The mandibles and claws were very worn indicating an old beetle. The ovaries were small but corpora lutea were visible and the fat reserves were almost exhausted.

<u>15°</u> Specimens at all photoperiods were immature and had large fat reserves. Before the end of the experiment nine specimens were found dead but they were all immature with large fat reserves.

<u>20°</u> At the end of 30 days only four specimens were alive. They were immature with small fat reserves.

<u>26°</u> After 12 days all specimens were dead. All were immature with small fat reserves.

Experiment b) The effect of temperature and photoperiod on mature <u>Patrobus assimilis</u> adults

<u>P.assimilis</u> adults taken from the top of Great Dun Fell in the middle of June were kept for 21 days at 10° and a photoperiod of 21L : 3D to ensure that the females had mature eggs.

After 21 days the abdomens of all the females were at least slightly distended and five females which were dissected had mature eggs. It was assumed that the other females were also mature and had all mated.

The females were then placed singly in 4 x 1 inch tubes (as described above) and kept at the temperatures and photoperiods shown in Table 26.

The cultures were inspected daily and eggs removed and placed in separate tubes. Dead specimens were dissected when found and the remaining specimens were killed and dissected as shown in Table 26.

TABLE 26. RESULTS OF EXPERIMENT b.

These results are summarised in Figure 10.

D = specimen found dead; K = killed; f1, f2, f3, f4 = condition of fat reserves (see Section IV. 1, E)

	Days in culture	K/D	Nos.Eggs laid	Days when eggs laid	Reproductive condition
5^{o} long day					
(21L : 3D)	30	K	0	-	) All had small
	30	K	0	-	) ovaries with
	30	K	4	2	) developing and
	30	K	2	4	) mature eggs; f2

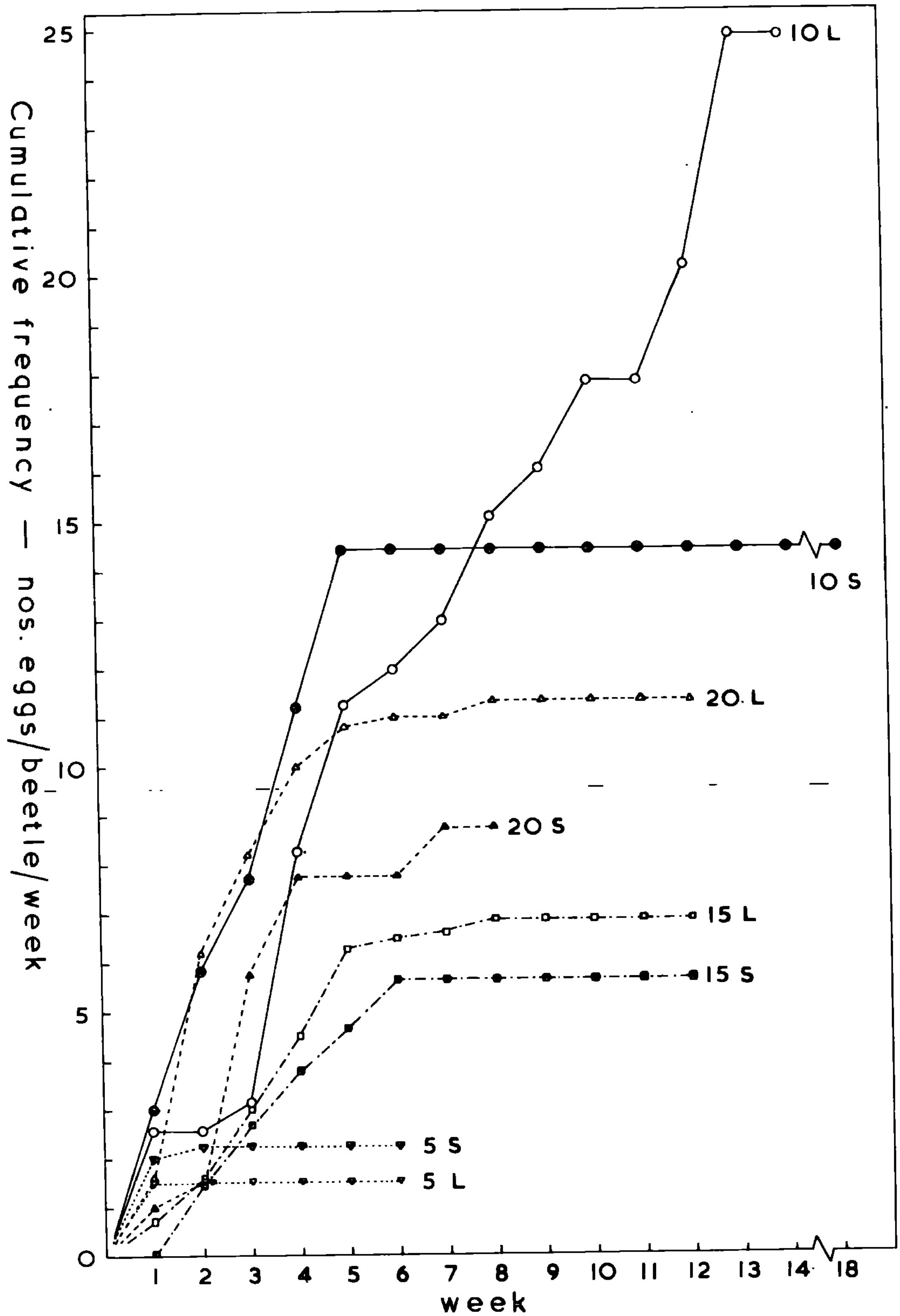
	Days in culture	K/D	Nos. Eggs laid	Days when eggs laid	Reproductive condition
<u>5° short day</u>					
(10L : 14D)	30	K	0	-	All had smaller
	30	K	0	-	ovaries than those
	30	K	1	9	at 5° LD; but
	30	K	8	2	developing and
					mature eggs were
					present; f2
<u>10° long day</u>					
(21L : 3D)	23	D	3	2, 3 & 20	All with abdomens
	23	D	2	2	distended, with
	77	K	14	7 - 67	developing and
	77	K	6	55 - 69	mature eggs;
	77	K	31	22 - 69	f1 or f2
	96	K	33	4 - 90	
<u>10° short day</u>					
(10L : 14D)	20	K	2	7 & 19	Developing eggs present but no mature eggs; f3
	25	D	1	11	Ovaries small, no mature eggs; f4
	32	D	25	5 - 23	Two mature eggs in the uterus, ovaries very small; f3
	41	D	4	6 - 25	Ovaries very small; f4
	49	D	0	-	Ovaries very small; abdomen burst; f4 ++
	71	K	34	7 - 37	Ovaries very small; f4
	101	K	25	2 - 30	Ovaries very small; f4

	Days in culture	K/D	Nos.Eggs laid	Days when eggs laid	Reproductive condition
15^{o} long day					
(21L : 3D)	30	D	6	6 - 20	One mature egg in uterus, ovaries small; f2
	45	D	8	32	Ovaries very small; f2
	56	D	6	9,11 & 56	Five old mature eggs in the uterus; ovaries very small; f3
	58	K	0	-	Two old mature eggs in the uterus; ovaries very small; f4
	61	K	19	6 - 36	Two old eggs in uterus, ovaries small, f2
	67	D	11	22, 23 & 44	Ovaries small, f3
	70	D	2	22 & 52	Ovaries immature, f3
	85	K	2	3 & 6	Ovaries immature, f3
	85	K	1	8	Ovaries immature, f4
	85	K	11	10 - 37	Ovaries immature, f4
15^{o} short day					
(10L : 14D)	15	D	1	12	Many developing, but no mature eggs; f2
	15	D	14	11 - 13	Signs of developing eggs; f2
	19	D	4	9,10 & 17	Many developing, but no mature eggs; f1
	30	D	0	-	Ovaries small; f3

	Days in culture	K/D	Nos. Eggs laid	Days when eggs laid	Reproductive condition
15° short day (10L : 14D)	(Contd.)				
	33	D	1	20)	Ovaries small; f2
	34	D	0	-)	Ovaries small; f3
	35	D	1	11)	Immature; f3
	43	D	0	-)	Ovaries small; f4
	56	D	1	11)	Ovaries small; f4
	58	D	1	16)	Ovaries small; f4
	62	D	13	20 - 30)	Ovaries small; f3
	70	D	2	33 & 41)	Immature; f2
	85	K	0	-)	Immature, f4
	85	K	23	15 - 42)	Ovaries small; f4
20° long day (21L : 3D)	40	D	5	19 - 21)	Ovarioles just differentiated, f1
	43	D	1	10)	Ovaries small, f3
	72	D	24	10 - 50)	Ovaries small, f2
	85	K	5	20 - 38)	Immature, f3
	85	K	21	4 - 29)	Ovaries small, f3
20° short day (10L : 14D)	12	D	1	8)	Mature and developing eggs present; f1
	15	D	1	10)	Mature and develop- eggs present; f1
	27	D	1	21)	Mature eggs in uterus, developing eggs very small; f1
	35	D	13	4 - 27)	Immature; f1
	37	D	9	20 & 27)	One old mature egg in the uterus; ovaries small; f2
	54	D	10	18-20 & 45)	Immature, abdomen very distended with fat reserves

FIGURE 10. Experiment b. *Patrobus assimilis*

Cumulative frequency of the number of eggs laid per beetle per week at 5°, 10°, 15°, and 20° long (L) and short (S) day.



Cumulative frequency — nos. eggs/beetle/week
25
20
15
10
5
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
18
week
10 L
10 S
20 L
20 S
15 L
15 S
5 S
5 L

The results of experiment b are summarised in Figure 10. Although initially eggs were laid at all temperatures and photoperiods, only specimens at 10° long day continued to develop and lay them. At 5° short day the contents of the ovaries were being absorbed but at 5° long day gonad development was probably only arrested. The significance of these results is discussed later.

Three females cultured at 10° short day (10L : 14D), under identical conditions to those in the above experiment, were placed under long day conditions (21L : 3D) after 57 days at the short day. They laid no eggs after the third week in the short day conditions. Results from other experiments indicated that they would be building up fat reserves and not developing eggs.

In the fourth week after the change from short day to long day, two females resumed egg laying. When dissected in the fifth week they had large ovaries with many mature and developing eggs.

Seven days after the change the third female laid one egg, which later hatched. No more eggs were seen and it was dissected after 109 days in culture (52 days after the change). The ovaries were large and many mature and developing eggs were present.

Similarly four females at 10° long day were placed under short day conditions after 57 days in culture. They had all laid eggs within five days of the change.

After the change of photoperiod, fertile eggs were laid by all four specimens but only in the first two weeks. They were dissected after 109 days in culture (52 days after the change). All had very small ovaries and very large fat reserves but one specimen had an old mature egg in the uterus.

Experiment 1c The effect of different temperatures and photoperiods on overwintering *Patrobus assimilis* females

P. assimilis females were taken on 22 October 1968 from the top of Great Dun Fell. Five females were dissected. They all had very small ovaries - four with corpora lutea. The fat reserves were very large, slightly distending the abdomen.

The other females were placed singly in 4×1 inch tubes and placed at the temperatures and photoperiods shown in Table 27. They were killed and dissected after 23 days.

TABLE 27. EXPERIMENT c) NUMBERS OF OVERWINTERING *PATROBUS ASSIMILIS* FEMALES AND THE TEMPERATURES AND PHOTOPERIODS AT WHICH THEY WERE CULTURED

	Temperature (°C)		
Photoperiod	5°	10°	15°
long day (21L : 3D)	2	5	2
short day (10L : 14D)	1	5	2

Results

5° long and short day

The ovaries of the females at both photoperiods showed no sign of development; corpora lutea were present and fat reserves large. It is not known if those under long day conditions would have matured if the experiment had continued longer.

10° long day

The ovaries of all five specimens showed signs of development and small oocytes were visible; corpora lutea were present in only one specimen but all had moderate reserves of fat.

10° short day

The ovaries of all five specimens showed no sign of development; two had corpora lutea and all had abdomens distended with fat reserves.

15° long and short day

The ovaries showed no sign of development; all had corpora lutea and their abdomens were distended with fat reserves.

Results of Experiments a, b, and c indicate that, in the laboratory, long day induces gonad development and short day inhibits it. At 15° and above, regardless of the photoperiod, gonad development is also inhibited and in the females developing eggs are absorbed. Egg production can be "turned on or off" by changing the photoperiod and/or temperature. Short day thus favoured fat accumulation and low temperatures inactivity.

Application of this data to field-conditions must be made with caution, especially as the effect of fluctuating temperatures and photoperiods, and the length of time required at certain temperatures to inhibit gonad development under long day was not determined.

Assuming that a photophase of greater than twelve hours and a temperature above 5° is required for gonad development in the field, then a method of synchronising the breeding season can be demonstrated.

The photophase would only be suitable for gonad development between the middle of March and the middle of September (plus about two weeks either side if civil twilight is included). The temperature limits the breeding season further. The 5^{o} average (1953 - 1965) at 1800 feet is not reached till the end of April (middle of May in 1967) and at 2780 feet till about the end of May. This coincides with when the first mature Patrobus assimilis females were found. The gonads no doubt began to develop during the "warm" periods in April and May, but during the colder periods development was probably arrested.

It is not known if and how the adults in the field were affected by the high temperatures which inhibited gonad development in the laboratory, but by the end of July, when temperatures were at their highest, most females had laid eggs and were dead.

Provided the temperature is favourable, gonad development is theoretically possible until September when the photophase is again equivalent to short day. It is of interest therefore that at 1800 feet the ovaries of a few recently emerged females taken in September were developing. But mature eggs were never found. If eggs were laid in September it is unlikely that they would hatch before the onset of winter; if they could, the first instar larvae would be unlikely to survive the winter conditions and only the original spring/summer breeding season would remain.

At 2780 feet many adults survive for more than one year but no mature females were found after the second week in July. The mean monthly temperature in 1967 remained below 10°, but the temperature in the litter layer on sunny days in June, July and August often reached 10° - 15° and occasionally 15° - 20°. Whether it was exposure to these temperatures which inhibited gonad development in the females, or some other factor, such as past photoperiod history, requires further study.

Experiment d) The effect of short day on fat production in Patrobus assimilis at 10°C

In previous experiments specimens at 10° and a photophase of 12 hours or less built up enormous fat reserves and a few were found dead with split abdomens. The possibility of injury, or bursting after death due to water uptake, could not be ruled out, and a further five males and five females were kept at 10° and a photoperiod of 10L : 14D. They were taken from the top of Great Dun Fell in the middle of June and placed singly in 4 x 1 inch tubes with very slightly moistened filter paper which was changed daily. Liver, Enchytraeidae and crushed arthropods were used as food and given daily in excessive amounts.

In the third week of culture two males and one female and, in the fourth week, one of each sex was found dead with its abdomen split. They were all immature and had extremely large fat reserves. Another female was found dead in the fourth week but its abdomen had not split. Like the remaining specimens dissected after four weeks in culture, it was immature and had enormous fat reserves resulting in the abdomen being greatly distended.

The death of these specimens appears to have been caused by the excess fat reserves and it seems that a feed-back mechanism to prevent the adult from producing excess fat is absent or had broken down.

In the spring, at the top of Great Dun Fell, when the photophase (sunrise to sunset) is 12 hours, the mean temperature is near freezing point, and in the autumn when the photophase is again 12 hours, the average temperature is $< 6^{o}$. When the average temperature nears 10^{o} the photophase is at its peak and the adults are producing eggs and not fat reserves. The combination of temperature and photoperiod used to induce the production of fat reserves in the laboratory would not therefore be experienced in the field, at least for long periods, and a feed-back mechanism would not be needed.

The critical temperatures and photoperiods and their duration affecting egg/fat production are not known, but even in an exceptionally warm spring or autumn the overproduction of fat is unlikely.

e) Patrobus assimilis; egg development

The eggs laid by P.assimilis in the culture experiments were either embedded in the filter paper or else they were left on the surface. No eggs were laid in dry conditions. Eggs laid on the surface were kept separate from those that were buried and the numbers completing development were recorded. Only two eggs which showed signs of development failed to hatch.

Eggs were removed daily and placed in 2 x 3/4 inch tubes with two circles of moist filter paper. They were kept at various temperatures and photoperiods.

There was no evidence that any buried eggs were eaten by the adults but eggs laid on the surface were occasionally eaten. The number of eggs produced may therefore be underestimated.

The eggs were inspected daily and the larvae removed and kept singly in 2 x 1 inch tubes to prevent cannibalism.

Eggs laid in experiment b) and by other females under identical conditions were incubated at the temperatures at which they were laid but under a photoperiod of 21L : 3D. The egg mortality (Table 28) was high. Development times are given on page 115.

TABLE 28. PATROBUS ASSIMILIS - EGG MORTALITY (EGGS IN TUBES WHICH BECAME DESSICATED OR "MOULDY" WITHIN THE EXPECTED HATCHING PERIOD ARE NOT INCLUDED)

	Embedded		Surface	
	% egg mortality	Numbers	% egg mortality	Numbers
10^{o} short day	62	(46/74)	82	(14/17)
10^{o} long day	33	(14/43)	93	(14/15)
15^{o} short day	46	(16/35)	88	(23/26)
15^{o} long day	48	(15/31)	92	(23/25)
20^{o} short day	85	(22/26)	78	(7/9)
20^{o} long day	46	(24/52)	100	(8/8)

Eggs laid at 5^{o} and 10^{o} long and short day, but kept at 5^{o}, showed no sign of development after three months. At the end of this period many tubes contained mould. A few mould free tubes were returned to 10^{o} but the eggs failed to develop.

There was a significant lower mortality of those laid embedded in the filter paper as opposed to those left on the surface (10^{o} long day ($P < 0.001$), 15^{o} long and short day ($P < 0.01$), and 20^{o} long day ($P < 0.02$). Although there was a 20 percent difference between the mortality of "embedded" and "surface" eggs at 10^{o} short day, it was not significant.

As desiccated, mouldy, or injured eggs were not included, these differences suggest a change in the adult behaviour, e.g. the fertilisation of the egg.

A significant difference was also found in the mortality between those eggs laid embedded in short day as opposed to long day conditions at 10° and 20° ($P < 0.01 > 0.001$), but no significant difference was found at 15°. The cause of this different mortality is not known but there is no evidence of an egg diapause.

Eggs are thus capable of surviving at high (Moor House) temperatures, e.g. 20°, and hatch successfully providing the humidity is high and no mould forms. In the field, however, before the temperature of the litter layer regularly reaches 20°, the humidity is normally low and egg laying has probably ceased as a result of the high temperatures.

f) *Patrobus assimilis* larval development

Patrobus assimilis larvae were kept under various laboratory conditions and a few were bred *ex ovo* to adults. Unsuccessful moulting and adhering to the food resulted in a high mortality and the results are of limited value. They do however show that *P. assimilis* larvae are sensitive to photoperiod.

The mortality of larvae, cultured at the temperatures at which the eggs were laid and incubated, but under a photoperiod of either 21L : 3D (long day) or 10L : 14D (short day), is shown in Table 29.

TABLE 29. PATROBUS ASSIMILIS; LARVAL MORTALITY IN LABORATORY CULTURES

Temperature (°C)	Short day % mortality	Short day Nos.	Long day % mortality	Long day Nos.
First instars				
10	100	15/15	37	19/52
15	100	15/15	83	15/18
20	100	14/14	100	6/6
Second instars				
10	-		43	12/29
15	-		67	2/3
Third instars				
10	-		83	10/12
15	-		100	1/1

Although the mortality was high, only those under long day conditions developed further than first instars. Their development times are given below (Table 30).

TABLE 30. PATROBUS ASSIMILIS MINIMUM, MEAN AND MAXIMUM DEVELOPMENT TIMES (DAYS) AT 10°, 15° AND 20°C LONG DAY

	Temperature (°C)											
	10°				15°				20°			
	min	mean	max	nos.	min	mean	max	nos.	min	mean	max	nos.
Eggs	23	24.4	26	(34)	17	20	22	(42)	10	11.8	13	(8)
L1	24	27	32	(33)	-	13	-	(2)	-	-	-	
L2	29	31.9	36	(15)	-	-	-	-	-	-	-	
L3	-	36	-	(1)	-	-	-	-	-	-	-	
Pupae	-	14	-	(2)	-	-	-	-	-	-	-	
Total	(126)	133.3	(144)									

The larvae at 20° died within a few days of hatching. At the other temperatures mortality was partly due to the larvae adhering to the food or "drowning"; under long day, failure to moult successfully and under short day, total failure to moult, were also contributory causes. Unsuccessful moulting normally resulted in head deformities, as the larvae failed to shed the old cuticle entirely before the new one had begun to harden.

First instars at 10° and 15° short day, built up such large fat reserves that they resembled second instars. They failed to moult and eventually died. Six first instars, also cultured at 10° short day, were transferred to 10° long day 42 days after hatching (15 days later than the expected L1 - L2 moult). They all had large fat reserves and resembled second instars. Under long day all moulted within a week but were deformed and soon died.

Similarly, six second instars cultured at 10° long day were transferred to 10° short day shortly after the L1 - L2 moult. Two developed into third instars but the other four were found dead before the expected moulting date. The latter had large fat reserves and the cause of death is not known.

Third instars (including those taken from the field in the spring and autumn as second or third instars) only pupated under long day conditions.

A rise in temperature from the field conditions, found on the top of Great Dun Fell (2780 feet) at the end of October (approx. mean 3°) and the end of January (approx. mean -1°), to 10° short day did not induce pupation. Five third instars, taken from the top of Great Dun Fell in October and three in January, were kept at 10° short day. They built up further fat reserves then ceased to feed and became inactive. Three of the larvae taken in October were transferred to 10° long day on 4 December and two, taken in January, on 15 February. They pupated within a week.

Low, but above freezing temperatures, did not inhibit larval development provided the photophase was equivalent to long day. One third instar even pupated at 1° long day.

The role of fluctuating temperatures and photoperiods and past photoperiod history has not been determined; but if the above results are applicable to field populations then photoperiod plays a significant part in their development.

Many other species were kept in culture but owing to the effort involved in obtaining large numbers of live specimens and keeping them in culture, the experiments were limited. A few of the more conclusive experiments are given below.

Experiment g) The effect of long and short photoperiods on Pterostichus nigrita females

Twelve first year females, taken in the middle of April 1967, were kept singly, each with a male, in 4 x 1 inch tubes at laboratory temperatures (15^{o} - 20^{o}). Four were dissected the day they were caught, four were kept in a light tight container, except for a few minutes each day, while the other four were kept under shaded, natural daylight conditions (photophase 14 hours). They were inspected every day and fed on rabbit liver. Further experiments were conducted in 1968.

Results

The four dissected at the start of the experiment had well developed eggs and large fat reserves.

Short day

After 35 days the specimens kept in the dark were killed and dissected. All had very large fat reserves and their abdomens were distended, resembling those of very gravid females. Their ovaries were immature and no corpora lutea were visible.

Long day

One female was killed at the end of April. Its abdomen was distended with both mature and developing eggs but there was no evidence that it had laid eggs.

Two females were killed after 35 days in culture. One had laid one egg and the other nine. Their abdomens were distended with mature and developing eggs.

The other female, seen mating on 18 and 19 April, first laid eggs on 26 April (the male was then removed) and by 26 May it had laid 63 eggs. It was found dead on 8 July. The ovaries were spent and fat reserves were almost exhausted.

Experiment h) The effect of different temperatures and photoperiods on developing and mature *Pterostichus nigrita* adults

P. nigrita females taken at Moor House in May 1968, during their breeding season, were kept singly in 4 x 1 inch tubes at various temperatures and photoperiods (Table 31).

On capture all the females had slightly distended abdomens and as all but one female taken in pitfall traps in May were mature, it is likely that the above specimens were also mature, or at least had well developed eggs.

TABLE 31. EXPERIMENT h). RESULTS

	Days in culture	K/D	Nos. Eggs laid	Days when eggs laid	Reproductive condition
5° short day (10L : 14D)					
	49	K	0	-	Ovaries small, f3
	49	K	0	-	Ovaries small, f3
5° long day (21L : 3D)					
	49	K	0	-	Ovaries small, 3 mature eggs in the uterus but no eggs laid, f3.
	49	K	0	-	Ovaries small, 4 mature eggs in the uterus, f3
	49	K	0	-	Ovaries small, no mature eggs, f3
10° short day (10L : 14D)					
	49	K	15	4 - 17	Ovaries small, f4
	91	D	0	-	Ovaries very small, f4
	176	K	1	55	Ovaries very small, f4
10° long day (21L : 3D)					
	49	K	0	-)	Abdomen slightly distended with mature and developing eggs, f1
15° short day (10L : 14D)					
	42	K	0	-	Ovaries small, f4
15° long day					
	42	D	1	19	Developing but no mature eggs
	62	K	0	-	Ovaries small, f4

Experiment i) The effect of different temperatures and photoperiods on hibernating *Pterostichus nigrita* adults

New generation *Pterostichus nigrita* adults, taken from hibernating sites at Cow Green (*Polytricum commune* hummocks) at the end of September 1968, were kept singly in 4 x 1 inch tubes at various temperatures and photoperiods (Table 32).

TABLE 32. EXPERIMENT i). RESULTS

Temperature & photoperiod	No. of specimens	Days in culture	Reproductive condition
5° short day (OL : 24D)	2♀	58	Immature, f4
5° long day (OL : 24D)	2♀	58	Immature, f4
10° short day (10L : 14D)	2♂	46	Immature, f4
	2♀	46	Immature, f4
10° long day (21L : 3D)	3♂	58	Mature, f2
	3♀	58	Ovaries developing, f3 to f4
15° short day (OL : 24D)	2♀	42	Immature, f3
15° long day (21L : 3D)	1♂	42	Mature, f3
	2♀	42	Immature, f3
	1♀	42	Ovaries small but ovarioles differentiated, f3

A further three males and three females were dissected on the day of capture. They were immature with large fat reserves. No corpora lutea were found in any of the females used in this experiment.

The above three experiments (g, h, i) indicate that P.nigrita adults are similar to Patrobus assimilis. Within a certain temperature range, long day induces gonad development while short day inhibits it and results in an increase in the fat reserves. There is no evidence of an obligatory diapause between adult emergence and gonad maturation. Temperatures outside a certain range - regardless of photoperiod, also inhibit gonad development and induce either aestivation or "hibernation", but "winter" diapause is induced by low temperatures and short day length. Further experiments are required to determine the critical temperatures and photoperiods and the effects of temperature fluctuations and gradual increase or decrease in the photoperiod. However, the photoperiodic reaction in insects is thought to be based on the action of absolute day-length and definite critical values of it; if the direction of the changes in daylight plays any role it is only secondary, in the nature of an additional adaptation (Danilevskii 1965).

Experiment j) The effect of temperature and photoperiod on *Carabus problematicus* females

Carabus problematicus females taken at Moor House on 5 and 10 September 1968 were kept in 4 x 3 inch glass jars in constant temperature cabinets at 10^{o} and 15^{o} either under long day (21L : 3D) or short day conditions. Those under short day were kept in a light tight box, except for a few minutes each day when they were inspected and given an excess of fresh liver.

Examination of their mandibles revealed that they were at least second year adults and when dissected on 12 November 1968 all had corpora lutea.

Other females caught in September had undeveloped ovaries but a few had mature eggs in the uterus. Most of these eggs were not soft and the usual white and slightly translucent colour, but were hard and an opaque yellowish brown, indicating that they were old eggs that had not been laid during the breeding season. All but one of the mature eggs found in the culture specimens (Table 33) were soft, white and translucent.

TABLE 33. EXPERIMENT j). <u>CARABUS PROBLEMATICUS</u> CULTURE RESULTS

	Days in culture	Reproductive condition
10^{o} short day (24D)	68	Ovaries very small, one old and mature egg in uterus, f3
	68	Ovaries very small, f3
10^{o} long day (21L : 3D)	68	Many developing and 6 mature eggs, f3
	68	Many developing and 8 mature eggs, f2
	68	Many developing and 9 mature eggs, f2
15^{o} short day (24D)	63	Ovaries very small, f3
	63	Ovaries very small, f3
15^{o} long day (21L : 3D)	63	Ovaries small, f3
	63	Ovaries small, f4
	63	Many developing and 6 mature eggs
	63	Many developing and 6 mature eggs, f3

Although the numbers of specimens were small there is an indication that the females are sensitive to photoperiod - only those in long day conditions producing eggs. At 15^{o} long day only two of the four specimens produced eggs, suggesting that like <u>P.assimilis</u> there may be a critical temperature above which egg production ceases.

Experiment k) Pterostichus adstrictus

New generation, but not teneral, Pterostichus adstrictus adults, taken at Moor House on 27 August 1968, were kept in 4 x 3 inch glass jars at 10^{o}. Three females and two males were kept at a photoperiod of 21L : 3D, while two females and one male were kept in complete darkness except for a few minutes each day. After 28 days they were dissected.

Other similar females caught in August, September and October had undifferentiated ovaries and the males had small testes. Both had large fat reserves.

Specimens under the short day had very large fat reserves and showed no sign of development, but under long day the males had large testes and appeared to be mature, while the females had differentiated ovaries and developing oocytes were clearly visible.

Thus this species is also sensitive to photoperiod, gonad development being stimulated by "long" day and preparation for "winter" by "short" day. This experiment also indicates that there is no obligatory diapause before the maturation of the gonads occurs.

Experiment 1) Pterostichus strenuus

Five new generation Pterostichus strenuus females taken at Moor House on 1 October 1968 were kept at 10^{o} for 16 days, three at a photoperiod of 21L : 3D and two in total darkness except for a few minutes each day.

Other new generation females taken in September and October were immature.

The ovaries of the females kept under short day conditions remained undifferentiated but those under long day were developing and oocytes were clearly visible.

It is thus similar to *P. adstrictus*.

Experiment m) *Loricera pilicornis*

Six new generation *Loricera pilicornis* females also taken on 1 October 1968 were kept at 10^{o} for 16 days. Two were in total darkness except for a few minutes each day while the other four were kept at a photoperiod of 21L : 3D.

Like *P. strenuus* other new generation females taken in September and October and those kept under short day were immature while those under long day were developing.

SUMMARY OF THE MAIN RESULTS OF LABORATORY CULTURE EXPERIMENTS

1. At 10° gonad development was induced by long day and inhibited by short day in :

Patrobus assimilis	Pterostichus adstrictus
Carabus problematicus	P.nigrita
Loricera pilicornis	P.strenuus

2. At temperatures above 15°, regardless of photoperiod, gonad development was inhibited in :

   P.assimilis, C.problematicus, P.nigrita

3. No obligatory diapause was found in newly emerged adults before the gonads developed in :

   P.assimilis, L.pilicornis, P.adstrictus, P.nigrita, P.strenuus

4. Overproduction of fat, normally resulting in death, occurred in P.assimilis at 10° short day.

5. P.assimilis eggs were only laid in conditions of high humidity and were either embedded in the substrate or left on the surface. The latter had a significantly higher mortality than the former. A significantly higher mortality also occurred in those eggs laid embedded in short day, as opposed to long day conditions.

6. P.assimilis larvae. Short day inhibited development in the first, third, and probably second instars.

VII. GENERAL DISCUSSION

Investigation of ecological hypotheses, such as those concerned with ecological distribution, the regulation of animal numbers, and the energy turnover in "simple" habitats, is often desired.

Moor House, when chosen as Nature Reserve, was thought to be a region with a fairly simple and natural plant cover, relatively free from interference by man, with a rigorous climate and a limited fauna. However, as Cragg (1961) pointed out, it was soon shown to be a highly complex system, and the result of long-term natural changes, combined with the effects brought by man in managing the area - mainly for grouse and sheep.

The high rainfall and low temperatures experienced on these moorlands results in the accumulation of organic matter as seen on the extensive Blanket Bog, while the effects of the drainage of these areas forms the basis of many of the other habitats, e.g. stream bank vegetation and alluvial grasslands, which are maintained by grazing and erosion.

Towards the summit of Great Dun Fell there is an abrupt change from organic to mineral soil with good drainage, limited vegetation cover and wide fluctuations in ground surface temperatures on clear days. It can be regarded as a montane zone. Greenslade (1968) considered that this habitat resembled temporary open wet habitats, which are favourable to Carabidae, such as the mud, shingle or boulders at the margin of water bodies as described by Murdoch (1963). It is interesting therefore that the species found breeding at this altitude are present in abundance. The absence of many predators and parasites at these altitudes may also be a contributary factor.

The Carabidae of the Moorland zone consists of two main groups; the established and indigenous species, and the temporary immigrant species. The former are essentially lowland, montane or ubiquitous species. Many of the species derived from the lowland and the montane faunas are approaching the limits of their range.

Certain species are rare and those with winged forms are probably immigrants from lowland areas. They may form isolated breeding populations on the moor, but their status is obscure.

The investigations of the life histories of the Carabidae reveal characteristic patterns according to their breeding habitats.. With caution these patterns may be used to indicate the phenology of other species. Spring breeders with "summer" larvae are normally found on wet habitats and autumn breeders with "winter" larvae on non-wet habitats. The latter usually have only adults present during the summer.

Exceptions to the above patterns are the results of either biennial life cycles, change in breeding season with altitude (perhaps as a result of a biennial life cycle) or special adaptations.

Most species show two peaks of activity each year. One is the breeding season; on wet habitats normally in the spring/early summer and on the non-wet habitats in the autumn. The other is the emergence of the new generation adults; in the autumn on wet habitats and in the spring on the non-wet habitats.

However, with an increase in altitude and subsequent decrease in mean temperatures, the life cycles are extended temporally. Certain species exhibit only one annual (and often extended) peak, consisting of newly emerged adults and breeding adults. Some of the individuals exhibit a biennial life cycle, others an annual cycle and may breed in a second year, but the proportions no doubt vary from year to year according to the environmental conditions.

The large carabid species, e.g. Carabus species, and, also at high altitudes, some of the smaller species, e.g. Notiophilus species, exhibit two periods of activity in each year, resembling the typical spring and autumn breeders with annual life cycles. But the two peaks have crossed over due to distinct biennial life cycles and recourse to the immature stages must be made to confirm a biennial (or in extreme cases, multiennial) life cycle.

In certain species no peak of the activity of the new generation adults is found as they may pass the winter or summer within the pupal cell and only emerge at the onset of the breeding season (Larsson 1939). This may be the case in Patrobus assimilis at and below about 1800 feet, as few teneral adults were caught. But some third instar larvae were found during the winter and in the spring, and the overwintering stage may vary. Culture experiments indicate that it is probably controlled by photoperiod acting on the largae in the Autumn (Lees 1955).

Seven of the species with exceptional life histories are large carabids (12 - 28mm) and have biennial life cycles. Detailed studies of their mandibles indicate that they may live for several years. At the higher altitudes the smaller adults may also live for several years. The longer adult life span is probably an effect of the lower temperature and shorter breeding seasons reducing the amount of reproduction done during each breeding season (Murdoch 1966).

The selective forces producing and maintaining these life histories patterns appears to be primarily the soil moisture content. The immature stages of most species cannot survive low humidities and therefore on the non-wet habitats their life histories are such that only the adults are present during the dry conditions. Two of the exceptional species, Dyschirius globusus and Pterostichus madidus, have immature stages on non-wet habitats during the summer. However, they were subterranean forms and thus avoided the low humidities. Adaptation in other species is probably absent due to lack of available food during the dry season but this requires confirmation.

The fluctuations in the timing of the autumn breeders on non-wet habitats seen from year to year and between localities may therefore be partly dependent on the extent of the "dry" season.

A similar phenomena may occur in Tipulidae. At Moor House catches of Tipula paludosa adults from the Alluvial and Limestone grassland reached their maximum abundance in July - August (Coulson 1959) whereas at Rothamstead (Robertson 1939) their peak was in September. It is unlikely that seasonal separation at the two centres is a result of different collecting techniques and it is probably the occurrence at them of similar temperature and soil moisture conditions; the summer being longer at Rothamstead.

A similar effect is seen in the life history of Trechus obtusus at Cow Green and at 1800 feet on the Reserve. At these altitudes it is essentially an autumn breeder with winter larvae. On the wet habitats, where it also breeds, the mature females were found up to a month earlier than on the non-wet habitats. Distinct races on these adjacent habitats is unlikely and the potential start of the breeding season therefore appears to be delayed by the environmental conditions on the non-wet habitats. Murdoch (1967) records that in the south of England it does not breed until September but continues until March.

There is no evidence that adverse low humidity has a direct effect on gonad development in T.obtusus but indirectly it may by limiting the food supply. It does prevent oviposition in mature females in the laboratory.

The species possibly has a facultative summer diapause, perhaps induced by high temperatures, as seen in Patrobus assimilis and Pterostichus nigrita culture experiments. The effects of high temperature on P.assimilis and P.nigrita females were found to override the influence of day length; high temperatures (15°C) resulted in cessation of ovarial differentiation and development. Under long day it could be induced directly by high temperatures and ended by the reduction of these high temperatures to 10°C.

Although the diapause probably has the same adaptive significance as that of Nebria brevicollis, the factors controlling the diapause are different from those found by Penney (1969). She considers that in N.brevicollis the onset of diapause (which can be prevented by starving the animals) appears to be regulated by the fat content of the body and is not controlled by adverse low humidity, high temperatures or photoperiod.

However, Thiele (1969) concluded that arrest of N.brevicollis gonad development (on the continent) in summer is caused by high temperatures, e.g. 20°C and long day, while decline of temperature (to 15°C) is necessary but not sufficient condition for the termination of aestivation diapause of the adults.

The populations studied by Thiele and Penny may be different geographical races but in both cases short day is necessary for ovarian maturation.

The adaptive significance of diapause in N.brevicollis is probably to avoid the summer shortage of micro-arthropods (Evans 1955; Poole 1962; Penney 1969) which form a large part of the diet (Penny 1965, 1966).

Lees (1955) suggested that diapause should be regarded primarily as a timing mechanism to regulate the life cycle, either to synchronise adult emergence or, as Andrewartha (1952) has emphasised, to ensure that active stages are present when food supplies or physical conditions are suitable.

At 2780 feet Trechus obtusus breeds in May, June and July. This change in breeding season may be a result of the biennial life cycle and past photoperiod history.

In a review of photoperiodism in insects and mites De Wilde (1962) concluded that there was an accumulative effect of larval and adult photoperiodic treatment and that the effect was reflected by the state of development of the female reproductive system. For example, in the Colorado beetle _Leptinotarsa decemlineata_ Say., the photoperiod experienced by the larvae influenced the induction of diapause in the adults (De Wilde et al 1959).

The suppression of the photoperiodic reaction by lowered temperature is an important adaptation to survival of the lepidopteran _Spilosoma methastri_ in northern latitudes (Danilevski 1965) and a similar effect may occur in _Trechus obtusus_ at high altitudes.

The individuals in the three different zones may have different photoperiodic responses, but response to photoperiod (of specimens from 2780 feet) was not found in culture experiments, and it is postulated that gonad development could be controlled by a temperature induced summer diapause and not photoperiod. In the lowlands on non-wet habitats there will be strong selection against "summer" larvae and a summer diapause, induced by high temperatures (as seen in _P.assimilis_ culture experiments), could prevent the adults breeding until the autumn. At higher altitudes, e.g. 1800 feet at Moor House, the diapause could be shorter due to the lower temperatures and shorter dry season, resulting in the earlier breeding season. There would be a selection against "summer" larvae on the non-wet habitats but not on the wet habitats. As the life cycle is extended and the new generation adults do not emerge until summer, spring breeding is therefore not seen.

At even higher altitudes, e.g. 2780 feet, which is essentially a wet habitat, there is no selection against "summer" larvae (all species at this altitude were spring/summer breeders) and the threshold inducing summer diapause may not be reached. New generation adults emerge in the 2780 feet autumn and are thus present to breed in the spring.

The factors controlling the life history of this ubiquitous species clearly requires detailed experimental investigation.

On the wet habitats the autumn peak of the annual spring breeders consists almost entirely of new generation adults which have a period of transient activity before overwintering. Few individuals are found after the mean air temperature has dropped below 6°C, a point when most vascular plants have ceased to grow and day length is less than twelve hours.

The resumption of activity in the new year is not clearly recorded in pitfall traps. The mean air temperature does not reach 6°C until about the end of April, when day length exceeds 15 hours, but warm days inducing occasional activity in Carabidae may occur earlier.

The timing of the spring activity and the reproductive condition of the individuals vary according to the duration of the winter and the accumulation of temperatures suitable for their development. Thus, after a severe, long (late start to spring) winter, the peak of the breeding season will be later than after a mild long winter.

If winter is defined as the period when the mean temperature drops below about 6°C and vascular plants cease to grow, then the average winter at 1800 feet at Moor House is about six months.

Adults of most spring/summer breeding species are dead before the adult emergence of their offspring, probably because they have realised their full productive potential (Murdoch 1966). Autumn breeding in these species was not found, but a few new generation females taken in the autumn showed signs of ovarian differentiation and old and new generation adults taken in the autumn and kept in the laboratory under long day conditions at 10°C showed no signs of obligatory diapause before their gonads developed.

In contrast, autumn breeders on non-wet habitats may continue to breed in the spring, but, except for small species such as Notiophilus, it is unlikely that the offspring survive. Autumn breeding adults frequently survive to breed in a second autumn.

Photoperiodic reaction is one of the most general ecological adaptations of the most diverse groups of arthropods. The precision of the response to changes in day length is the result of rigorous selection, which in natural conditions is necessary in the process of photoperiodic regulation of the seasonal cycle and preparation for hibernation.

Perfect adaptations of the photoperiodic reaction of separate geographical populations to local conditions of climate and light lessens their ecological adaptability and ability to spread, actively or passively, even within the range of the species.

The studies on Patrobus assimilis indicate the selective forces producing and maintaining its characteristic life history pattern and demonstrate a method of synchronising the breeding season without the need for separate altitudinal races at Moor House.

Egg production in the five spring breeders studied was induced by long daylength and inhibited by short daylength. Several authors have recorded that short daylength is required by autumn breeders; Patrobus atrorufus (Thiele 1969), Nebria brevicollis (Ganagarajah 1964, 1965; Thiele 1969; Penney 1969), Galeruca tanaceti (Siew 1966). Culture experiments showed that development in P. assimilis larvae was dependent on long day. Photoperiod has no effect on the development of

Pterostichus vulgaris larvae but high temperatures (above 15°C) induce diapause (Thiele et al 1969).

The difference in the response to daylength between certain spring and autumn breeders suggests opposing control mechanisms. Alternatively, they may be sensitive to different thresholds of a range of photoperiods, the upper limit not being reached in long day species and the lower threshold not being reached in short day species; as in the dragonfly *Anax imperator* where long or short day induces diapause in the nymph, but a photoperiod between the two promotes growth (Corbet 1955).

Thiele (1967) noted that with four univoltine carabids, with a quite similar annual cycle of activity, different factors can control the synchronisation of breeding time with a favourable season, with differences existing between the sexes of one species as well as among species.

Ovarial differentiation and development in laboratory cultures occurred in *Carabus problematicus* (Moor House specimens) only under long daylength, but it is an autumn breeder and may breed for several years. Although the number of experimental animals was small, there is an indication that like *P.assimilis* ovarial development ceases at high Moor House temperatures (15°C).

On the Blanket Bog where *C.problematicus* and *C.glabratus* are abundant, the breeding seasons do not coincide and the timing of the period of adult activity may be critical in avoiding competition between the adults. Developing, but not mature, C.problematicus females are found in the spring and early summer. High temperatures may induce a summer inactivity, but, if egg development occurs in long day, the factors preventing spring breeding, especially on the wet habitats, remains obscure. It is unlikely to be the time taken for gonad maturation, as in C.glabratus a similar size species, this may occur in several weeks. C.problematicus males mature earlier than the females which suggests different controlling factors or the lack of an inhibitory mechanism. The peak of locomotor activity of males and females in the breeding season is similar, and it would be interesting to determine the factors controlling the timing of this peak.

SUMMARY

1. A study was made on the ground beetles (Coleoptera, Carabidae) on the Moor House National Nature Reserve, Westmorland, an area of moorland typical of the northern Pennines, from 1967 - 1968.

2. A subsidiary study was made on the Carabidae of the Cow Green area of Widdy Bank Fell, Upper Teesdale, Durham, from 1967 - 1968.

3. No previous detailed records of the Carabidae on these areas have been made, and in the present study 49 species from 23 genera were collected. 47 species were found at Moor House and 30 at Cow Green.

4. 19 species were only taken occasionally. Although a few were found breeding on the moors, many are probably recent immigrants from lowland areas.

5. This study adds 14 species of Carabidae new to the Westmorland county list and 4 species new to the Durham list.

6. The Carabidae of six principal macrohabitats, comprising the majority of the vegetation of the two areas, were studied in detail. The six macrohabitats were : Calluna - Eriophorum Moor, vegetation on redistributed peat, damp/flushed grasslands, limestone grasslands, alluvial grasslands, and Fell-Top Podzol. The species

distribution, especially in relation to their breeding habitats, was investigated mainly by pitfall trapping and hand collecting.

7. Movement of individuals from the *Calluna - Eriophorum* Moor and the vegetation on the redistributed peat (both wet habitats) onto the Limestone and alluvial grasslands (both non-wet habitats) was common, but not vice versa.
8. At Moor House, the *Calluna - Eriophorum* Moor is the dominant vegetation type (57% by area) and the Alluvial and Limestone grasslands only 5% by area. 46% of the species found on the Alluvial and Limestone grasslands were not found on the *Calluna - Eriophorum* Moor, but only 11% vice versa. The importance of also studying the less dominant vegetation types is clearly indicated.
9. The total number of species decreased with elevation and is probably due to the absence of certain vegetation types and resulting loss of microhabitats.
10. Most species were smaller and darker than lowland individuals and in a few species a significant difference was noted in the size and colour within the altitude range of the Moor House Reserve.
11. The distribution of the colour forms of *Nebria rufescens* and *Pterostichus madidus* was investigated, but factors other than the effects of altitude appear to influence their distribution.

12. Details of the life histories of most species is described. The reproductive condition and breeding season were determined by dissection. A total of 46% are "wet" habitat species with "summer" larvae, while 25% are "non-wet" species with "winter" larvae. The remaining 14 species fall into various other categories.
13. The wet species with summar larvae develop at a time when the temperatures are at their highest and therefore their development time shortest; the females have a greater chance of realising their full reproductive potential and the early instars are present when the water level is at its lowest.
14. The non-wet species with winter larvae do not breed until the autumn. The eggs and early instars are not therefore present during the very dry conditions that may occur on the non-wet habitats in the summer. There may also be a shortage of available food as a result of the dry conditions, which may account for the lack of adaptation to resist desiccation that is seen in these species.
15. It is suggested that it is the dry summer conditions on the non-wet habitats and the wet autumn conditions on the wet habitats that are the major critical factors restricting the breeding seasons.

16. Species at 2780 feet were spring/summer breeders even though they may be autumn breeders at lower altitudes. This may be an effect of the biennial life cycles but it ensures that eggs and early instars are not normally present during the winter months.

17. The distribution of Patrobus assimilis and P.atrorufus appears to be related to their life history patterns. P.assimilis is essentially a montane and wet species and a spring/summer breeder, while P.atrorufus is essentially a lowland and non-wet species and an autumn breeder.

18. A total of 19 species were classed as macropterous, 4 wing dimorphic and 25 as brachypterous or apterous. Many of the + winged forms are probably immigrants whilst the increase in the number of - winged forms is partly due to the absence of the + winged form of the wing dimorphic species, the reduction in wing length of + winged forms, or the elimination of + winged species. The proportion of macropterous forms decreased markedly with an increase in wing length.

19. The + winged occasional species formed a large proportion of the total + winged species, but the number of individuals was very small. 16 of the 19 species may fly, at least in the lowlands, and the populations are probably maintained by immigration.

20. The proportion of species with macropterous individuals showed a decrease from the least stable and minority habitats to the more permanent and major habitat.

21. 30 species are classed as essentially nocturnal and 18 as diurnal. There is a significant association between nocturnalism and - wings and diurnalism and + wings. This is probably related to the inability of flight at night due to the low temperatures.

22. A mechanical time sorting pitfall trap is described. It separates captures into predetermined periods of the day and can be left to run unattended for over a week. At 2780 feet, P.assimilis was caught mainly at dawn and dusk. At 1800 feet it is primarily a nocturnal species and the low nocturnal captures at 2780 feet may be due to low temperatures reducing activity.

23. The approximate age of a beetle could be determined by the degree of wear of the mandibles. Combined with data on the female reproductive condition and life histories it is shown that C.glabratus and C.problematicus may live for two years and have two breeding seasons. A few individuals probably survive and breed in at least a third year.

24. A reliable and permanent method for marking Carabidae, and certain other arthropods, using an abrasive technique, was developed and is described.

25. Notes on the taxonomy of the British species of the genus *Patrobus* and a key to their larvae is given.
26. Taxonomic characters used to separate the larvae of the *Nebria* species found during the study is given.
27. Taxonomic characters of the larvae of *Notiophilus germinyi* found during this study were different from those described by other authors. The differences are described.
28. The resistance to desiccation and drowning of certain species is described. Early instars of small short-legged larvae are least resistant to drowning and eggs and larvae of most small species were very susceptible to desiccation. The later instars of the larger species, and the adults of many species, were resistant to desiccation and drowning.
29. Parasites of the Carabidae were investigated. No hymenopterous parasites were found but two species of Gordiid were identified. The parasite prevented maturation of the gonads, but the infection rate was very low and it probably has little effect on the population numbers.
30. The stomach contents of 434 frogs taken in 1966 and 1967 were examined. Carabidae were regularly found but they form a relatively small part of their diet.

31. The stomach content of 80 common shrews and 73 pigmy shrews, taken in 1967, were examined. Carabidae were frequently found and the significance of the shrews as predators on the moor should perhaps not be underestimated.

32. The influence of certain environmental factors, especially temperature and photoperiod, on the development of certain species, was studied in the laboratory.

33. It is shown that gonad development in Patrobus assimilis can be induced or inhibited by changing the photoperiod and/or temperature. Long day induces gonad development and short day inhibits it. At 15°C and above, regardless of the photoperiod, gonad development is also inhibited. A method of synchronising the life cycle is demonstrated.

34. A feed-back mechanism in Patrobus assimilis adults to prevent the overproduction of fat reserves which eventually results in death appeared to be absent.

35. There was a significant lower mortality of the eggs of P.assimilis laid embedded in filter paper in culture experiments as opposed to those laid&left on the surface, and also in those laid embedded under long day conditions as opposed to short day conditions. There is no evidence of an egg diapause.

36. P.assimilis larvae were sensitive to photoperiod; short day inhibited development and induced the production of fat reserves.

37. Gonad development in five other species was induced by long day and inhibited by short day. There was no evidence of an obligatory diapause before maturation of the gonads occurs, but females breeding for the second time reach maturity before those breeding for the first time.

REFERENCES

ANDREWARTHA, H.G. 1952. Diapause in relation to the ecology of insects. Biol.Rev.27 : 50-107.

BAKER, J.R. 1938. The evolution of the breeding seasons. In : Evolution (Ed. by G.R. de Beer), pp.161-177, Oxford.

BELLAMY, D.J., BRIDGEWATER, P. MARSHALL, C. & TICKLE, W.M. 1969. Status of the Teesdale Rarities. Nature. 222 : 238-243.

BLAIR, K.G. 1950. 1. Some northern British Coleoptera, including Nebria nivalis Payk., a carabid species not hitherto known from Britain. Ent.Mon.Mag. 86 : 219-220.

2. Nebria nivalis Paykull (Col., Carabidae) in Scotland. Ent.mon.Mag. 86 : 220-222.

BLOCK, W.C. 1963. Studies on the Acarina of moorland areas. Ph.D. Thesis, University of Durham.

BODENSTEIN, D. 1953. In Insect Physiology, Ed. K.D. Roedeer. New York.

BOLDORI, L. 1951. Larve di Trechini VIII. Rass.Speleol.Ital., 11 : 141-151.

BOVING, A.G. & CRAIGHEAD, F.C. 1930. An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomol.Amer. 11 : 1-351.

BRIGGS, J.B. 1957. Some experiments on control of ground beetle damage to strawberry. Rep.E.Malling Res.Stn. 1956, 142-145.

BRIGGS, J.B. 1965. Biology of some ground beetles (Col., Carabidae) injurious to strawberries. Bull.Ent.Res.56 : 79-93.

BYERS, G.W. 1969. Evolution of wing reduction in crane flies. Evolution 23 : 346-354.

CHERRETT, J.M. 1961. Ecological research on Spiders associated with Moorlands. Thesis : Durham University Library.

CONWAY, V.M. 1955. The Moor House National Nature Reserve, Westmorland. Handb.Soc.Prom.Nat.Res. 1 - 7.

CORBET, P.S. 1955. The immature stages of the Emperor Dragonfly, Anax imperator Leach (Odonata, Aeshnidae). Ent.Gaz. 6 : 189-204.

COULSON, J.C. 1956. Biological studies on the Meadow Pipit (Anthus pratensis) and moorland Tipulidae; members of a food chain. Thesis : Durham University Library.

COULSON, J.C. 1959. Observations on the Tipulidae (Diptera) of the Moor House Nature Reserve, Westmorland. Trans.R.ent.Soc.Lond. 3 : 157-174.

CRAGG, J.B. 1961. Some aspects of the Ecology of Moorland Animals. J.Anim.Ecol. 30 : 205-234.

CROWCROFT, W.P. 1954. An ecological study of British Shrews. Unpubl. D.Phil.Thesis. Oxford University.

CROWCROFT, P. 1957. The life of the Shrew. London.

DANILEVSKII, A.S. 1965. Photoperiodism and seasonal development of Insects. Edin. and London.

DARLINGTON, P.J. 1943. Carabidae of mountains and islands : data on the evolution of isolated faunas and on atrophy of wings. Ecol.Monographs 13 : 37-61.

DAVIDSON, W.F. 1961. Notes on Cumberland & Westmorland Coleoptera. Ent.Mon.Mag. 97 : 15-21.

DAVIES, M.J. 1959. A contribution to the ecology of species of Notiophilus and allied genera (Col., Carabidae). Ent.mon.Mag. 95 : 25-28.

DAVIES, M. 1963. The larvae of some British Notiophilus species (Col., Carabidae). Ent.mon.Mag.99 : 206-209.

DE MIRE, Ph. Bruneau. 1964. Un cas d'hybridation spontanée entre Chysocarabus (Chrysotribax) utilans Dej. et Chrysocarabus (s.tr.) splendens ol. (Col., Carabidae). Bull.Soc.Entomol.France. 69 : 21-25.

DICKER, G.H.L. 1951. Agonum dorsale Pont. (Col., Carabidae), an unusual egg-laying habit and some biological notes. Ent.Mon.Mag. 87 : 33.

EDDY, A., WELCH, D. & RAWES, M. 1968. The Vegetation of the Moor House National Nature Reserve in the Northern Pennines, England. Vegetatio. 16 : 239-284.

EVANS, G.O. 1955. Identification of terrestrial mites, in Kevan, D.K. Mc.E. (ed.), 'Soil Zoology', London : 55-61.

FITCHER, E. 1941. Apparatus for the comparison of soil surface arthropod populations. Ecology, 22 : 338-339.

FOWLER, W.W. 1887. The Coleoptera of the British Islands. Vol.I. London.

FRANK, J.H. 1964. New Northumberland records for Carabidae (Col.) Ent.mon.Mag., 100 : 56.

GANAGARAJAH, M. 1964. Seasonal changes in the gonads, food reserves and neurosecretion in N.brevicollis (F.) Unpublished Ph.D. Thesis. Reading University.

GANAGARAJAH, M. 1965. The neuro-endocrine complex of adult Nebria brevicollis F. and its relation to reproduction. J.Insect.Physiol. 11 : 1377-1387.

GANAGARAJAH, M. 1966. Seasonal changes in food reserves of Nebria brevicollis (Carabidae, Coleoptera). Entomologia exp.appl. 9 : 314-322.

GEIGER, R. 1959. The climate near the ground. Cambridge, Mass.

GILBERT, O. 1952. The natural histories of four species of Calathus (Coleoptera, Carabidae) living in sand dunes in Anglesey, N. Wales. Oikos, 7 : 22-47.

GILBERT, O. 1955. A study of the field life-histories of four species of Calathus (Coleoptera, Carabidae). Unpublished Ph.D. Thesis, University College of North Wales.

GILBERT, O. 1958. Life history patterns of Nebria degenerata (Schaufuss) and N.brevicollis F. J.Soc.Brit.Ent. 6 : 11-14.

GOODIER, R. 1968. Welsh Mountain Beetles - Beetles over 2000ft. Nature in Wales. 2: 1-11.

GREENSLADE, P.J.M. 1963. Daily rhythms of locomotor activity in some Carabidae. Ent.Exp.Appl. 6 : 171-180.

GREENSLADE, P.J.M. 1964. Pitfall trapping as a method of studying populations of Carabidae (Coleoptera). J.Anim.Ecol. 33 : 301-310.

GREENSLADE, P.J.M. 1965. On the ecology of some British Carabid beetles with especial reference to life histories. Trans.Soc.Br.Ent. 16 : 149-179.

GREENSLADE, P.J.M. 1968. Habitat and altitude distribution of Carabidae (Coleoptera) in Argyll, Scotland. Trans.R.ent.Soc.Lond. 120 : 39-54.

GREENSLADE, P.J.M. & SOUTHWOOD, T.R.E. 1962. Relationship of flight and habitat in some Carabidae. The Entomologist. 95 : 86-88.

GRUM, L. 1962. Horizontal distribution of larvae and imagines of some species of Carabidae. Ekol.Polska. Ser.A. 10: 73-84.

HADLEY, M.J. 1966. Biological Studies on Molophilus ater Meigen. (Diptera : Tipulidae). Ph.D. Thesis, Durham University.

HANSEN, V. 1968. Billar XXIV, sandspringere og løbebiller. Danmarks Fauna. 76 : 282-433.

HART, J.F. 1955. British moorlands : a problem in land utilization. (University of Georgia monographs 2). Athens, University of Georgia P.

HAWKINS, A.E. & JEWELL, P.A. 1962. Food consumption and energy requirements of captive British shrews and the mole. Proc.zool.Soc.London. 138 : 137-155.

HEYDEMANN, B. 1956. Uber die Bedentung der 'Formalinfallen ' fur die zoologische Land forschung. Faun.mitt.aus Norddentschl. 6 : 19-24.

HORNUNG, M. 1969. Morphology, mineralogy & genesis of soils of the Moor House National Nature Reserve. Ph.D. Thesis, University of Durham.

HOUSTON, K. Carabidae (Coleoptera) from two areas of the north Pennines. Ent.Mon.Mag. In press.

JEANNEL, R. 1941, 1942, 1949. Coléoptères carabiques. Faune de France. 39, 40, 51, Paris.

JOHNSON, G.A.L. & DUNHAM, K.C. 1963. The Geology of Moor House. Monographs of the Nature Conservancy. Number Two. H.M.S.O.

JOY, N.H. 1932. A practical handbook of British beetles. London.

KEVAN, D.K. 1949. The sexual and other characters of British Nebriini, Notiophiliini and Elaphrini, with special reference to the genus Notiophilus Dum. (Col., Carabidae, Carabinae). Ent.mon.Mag. 85 : 1-18.

KLESS, J. 1961. Tiergeographische elemente in der Kafer -und Wanzen fauna der wutachgebiets und ihrer Ökologischer Anspruche. Z.Morph.Okol. Tiere. 49 : 541-628.

LARSSON, S.G. 1939. Entwicklungstypen und Entwicklungszeiten der Dänischen Carabiden. Ent.Med. 20 : 277-560

LARSSON, S.G. & GIGJA, O. 1958. Zoology of Iceland : Vol.III. Part 46. Coleoptera. Copenhagen & Reykjavik.

LEES, A.D. 1955. The Physiology of Diapause in Arthropods. Cambridge.

LEWIS, T. & TAYLOR, L.R. 1965. Diurnal periodicity of flight by insects. Trans.R.ent.Soc.Lond. 116 : 393-479.

LINDROTH, C.H. 1945, 1949. Die Fennoskandischen Carabidae, eine tiergeographische Studie. Medd.Goteborges Mus.Zool.Arch. 109 : 1-707; 110 : 1-227; 122 : 1-911.

LUFF, M.L. 1968a. New records of Carabidae (Coleoptera) from Northumberland. The Entomologist. 102 : 193-195.

LUFF, M.L. 1968b. Some effects of formalin on the numbers of coleoptera caught in pitfall traps. Ent.Mon.Mag. 104 : 115-116

MACFADYEN, A. 1955. A comparison of methods of extracting soil arthropods. Soil Zoology. Ed. by D.K. McE.Kevan), pp. 315-322. London.

MACFADYEN, A. 1963. Animal Ecology : Aims and Methods. London.

MANI, M.S. 1967. Ecology and Biogeography of High Altitude Insects. Junk.

MANI, M.S. 1962. Introduction to high altitude entomology, London.

MANLEY, G. 1936. The climate of the northern Pennines : the coldest part of England. Quart.J.R.Met.Soc. 62 : 103-15.

MANLEY, G. 1942. Meteorological observations on Dun Fell, a mountain station in northern England. Quart.J.R.Met.Soc. 68 : 151.

MANLEY, G. 1943. Further climatological averages for the northern Pennines, with a note on topographical effects. Quart.J.R.Met.Soc. 69 : 251-261.

McATEE, W.L. 1912. Methods of estimating the contents of bird stomachs. Auk, 29 : 449-464.

MOORE, B.P. 1957a. The British Carabidae (Coleoptera). Part I. A check list of the species. Ent.Gaz.8: 129-137.

MOORE, B.P. 1957b. The British Carabidae. Part II. The county Distribution of the species. Ent.Gaz.8 : 171-180.

MORRIS, R.F. 1960. Sampling insect populations. A.Rev.Ent. 5 : 243-264.

MURDOCH, W.W. 1963. A method for marking Carabidae (Col.) Ent.mon.Mag. 99 : 22-24.

MURDOCH, W.W. 1966a. Aspects of the population dynamics of some marsh Carabidae. J.Anim.Ecol.35 : 127-156.

MURDOCH, W.W. 1966b. Population stability and life history phenomena. Amer.Nat. 100 : 5-11.

MURDOCH, W.W. 1967. The life history patterns of some British Carabidae and their ecological significance. Oikos. 18 : 25-32.

PEARSALL, W.H. 1950. Mountains and Moorlands. London.

PEARSON, R.G. & WHITE, E. 1964. The phenology of some surface-active arthropods of Moorland Country in North Wales. J.Anim.Ecol. 33 : 245-258.

PENNEY, M.M. 1965. Studies on the ecology of *Nebria brevicollis* (F) and *Feronia oblongopunctata* (F.) Ph.D. Thesis, Glasgow University.

PENNEY, M.M. 1966. Studies on certain aspects of the ecology of *Nebria brevicollis* (F.) J.Anim.Ecol. 35 : 505-512

PENNEY, M.M. 1969. Diapause and reproduction in *Nebria brevicollis* (F.) (Coleoptera : Carabidae). J.Anim.Ecol. 38 : 219-233.

POOLE, T.B. 1959. Studies on the food of Collembola in a Douglas fir plantation. Proc.Zool.Soc.Lond. 132, 71-82.

REAY, R.C. 1959. A population study on *Coleophora alticolella* Zell (Lep.) Thesis : Durham University Library.

REITTER, E. 1908. Die Kafer des Deutschen Reiches. Fauna Germanica. Vol.I. Stuttgart.

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

RUDGE, M.R. 1968. The food of the common shrew Sorex araneus L. (Insectivora : Soricidae) in Britain. J.Anim.Ecol. 37 : 565-581.

SCHIØDTE 1867. De Metamorphois Eleutheratorum Observationes : Bidrag til Insekternes Udriklingshistoire. (7 Bidrag) Naturh.Tidsskr.(3) 9p. 227-377.

SCHJØTZ-CHRISTENSEN, B. 1961. Forplantningsbiologien hos Amara infirma Dft. og Harpalus neglectus Serv. Flora og Fauna 67 : 8-18.

SCHØTZ-CHRISTENSEN, B. 1965. Biology and population studies of Carabidae of the Corynephoretum. Nat.Jut. 2 [illegible]

SHAROVA, I.K.H. 1960. Morfo-ekologichestie tyiy lichinok zhuzhelits (Carabidae). (Morpho-ecological types of Carabidae larvae). Zool.Zhur 39 [illegible] : 691-708. 1960. Refferat Zhur., Biol., 1961 (Translation).

SHARP, W.E. 1916. Common Beetles of the British Uplands, London.

SIEW, Y.C. 1966. Some physiological aspects of adult reproductive diapause in Galeruca tanaceti (L.) (Coleoptera : Chrysomelidae).

SKUHRAVY, V. 1959. Potrova polruch strerlikovitych (Die Nahrung der Feld-carabiden). Acta.Soc.Ent.Csl. 56 : 1-18.

SMITH, D.S. 1957. Investigations into loss of flight in beetles. Ph.D. dissertation, University of Cambridge.

SOUTHWOOD, T.R.E. & JOHNSON, C.G. 1957. Some records of insect flight activity in May 1954, with particular reference to the massed flights of Coleoptera and Heteroptera from concealing habitats. Ent.mon.Mag., 93 : 121-126.

SOUTHWOOD, T.R.E. 1962. Migration of terrestrial Arthropods in relation to habitat. Biol.Rev. 37 : 171-214.

SOUTHWOOD, T.R.E. 1966. Ecological methods, with particular reference to the study of insect populations, London.

SPRINGETT, J.A. 1965. An ecological study of moorland Enchytraeidae. Thesis : Durham University Library.

THIELE, H.V. & KIRCHNER, H. 1958. Uber die Korpergrosse der Gebirgs und Flachland populationen einiger Laufkafer (Carabidae). Bom.Zool.Beitr. 9 (2/4) : 294-302.

THIELE, H.V. 1967. Formen der Diapausesteuerung bei carabiden.

THIELE, H.V. 1969. The control of larval hibernation and of adult aestivation in Carabid Beetles. Nebria brevicollis F. and Patrobus atrorufus Strom. Oecologia (Berl.) 2 : 347-361.

THIELE, H.V. & KREHAN, I. 1969. Experimentelle untersuchungen zur larval diapause des carabiden. Pterostichus vulgaris. Ent.exp.& appl. 12 : 67-73.

TIPTON, J.D. 1960. Some aspects of the biology of the beetles *Nebria brevicollis* (F.) and *Feronia caerulescens* (L.) Ph.D. Thesis, Reading University.

TISCHLER, W. 1955. Influence of soil types on the epigeic fauna of agricultural land. In Kevan, D.K. Mc.E. (Ed.), Soil Zoology. London pp.125-136.

VAN DER DRIFT, J. 1951. Analysis of the animal community in a beech forest floor. Tijdschr.Ent. 94 : 1-168.

VAN DER DRIFT, J. 1959. Field studies on the surface fauna of forests - Bigdr. Dierk. 29 : 79-103.

VAN EMDEN, F.I. 1942. A key to the genera of larval Carabidae. Trans.R.Ent.Soc.Lond. 92 : 1-99.

VLIJM, L., HARTSUIJKER, L. & RICHTER, C.J.J. 1961. Ecological studies on carabid beetles. I. *Calathus melanocephalus* (L.) Archs. Neerl. Zool. 14 : 410-422.

WELCH, D. 1967. Communities containing *Juncus squarrosus* in Upper Teesdale, England. Vegetatio 14: 229-240.

WIGGLESWORTH, V.B. 1953. Principles of Insect Physiology, London.

WILDE, J. De., DUINTJER, C.S. & MOOK, L. 1959. Physiology of diapause in the adult Colorado beetle (*Leptinotarsa decemlineata* Say) 1. The photoperiod as a controlling factor. J.Ins.Physiol. 3 : 75-85.

WILDE, De J. 1962. Photoperiodism in insects and mites. An.Rev.Ent. 7 : 1-26.

WILLIAMS, C.B. 1948. The Rothamsted light trap. Proc.R.ent.Soc.Lond. A.23 : 80-85.

WILLIAMS, G. 1958. Mechanical Time sorting of pitfall captures. J.Anim.Ecol. 27 : 27-35.

WILLIAMS, G. 1959. Seasonal and diurnal activity of Carabidae, with particular reference to *Nebria*, *Notiophilus* and *Feronia*. J.Anim.Ecol. 28 : 309-330.

APPENDIX

I. Notes on the breeding biology of the Moor House and Cow Green Carabidae (in alphabetical order)

1. Abax parallelepipedus

In Denmark Larsson (1939) described it as an autumn breeder and larval hibernator; but in England Murdoch (1967) found mature adults from March to September, and in Holland van der Drift (1951) showed that it breeds in spring, summer and autumn.

At Moor House, on the grasslands on the west side of the reserve, a teneral female was taken on 26 May 1966 at 1600 feet, and one female with mature eggs and two mature males at the end of July at 1900 feet. No larvae were found and further information is required to confirm its exact life history at Moor House.

2. Agonum ericeti

Moore (1957b) lists old (post 1854) records from Hampshire, Lancashire, Yorkshire, Cumberland and Durham, and Frank (1964) has since recorded it from Northumberland. It is therefore new to the Westmorland county list of Moore and is a new recent record for the county Durham list.

It is a pronouncedly hygrophilus and brachypterous species, being found only on the very wet areas of the Moor, especially the Valley Bog.

Mature females were taken in the spring and tenerals in the autumn. Three third instars were found : one in a soil core taken at Cow Green on 25 July 1968 which pupated in the laboratory at 10° on 21 August 1968; another at Moor House on 20 August 1968 which pupated in the laboratory at 15° on 26 August 1968; and the third in a pitfall at Cow Green in August.

3. Agonum fuliginosum Figure 11.

This species was most frequently taken on areas of redistributed peat but was not found above 1900 feet on the West side or 2450 feet on the east side of the Reserve.

Mature females were taken in May, June and July; larvae from June to September and teneral adults first appeared in September.

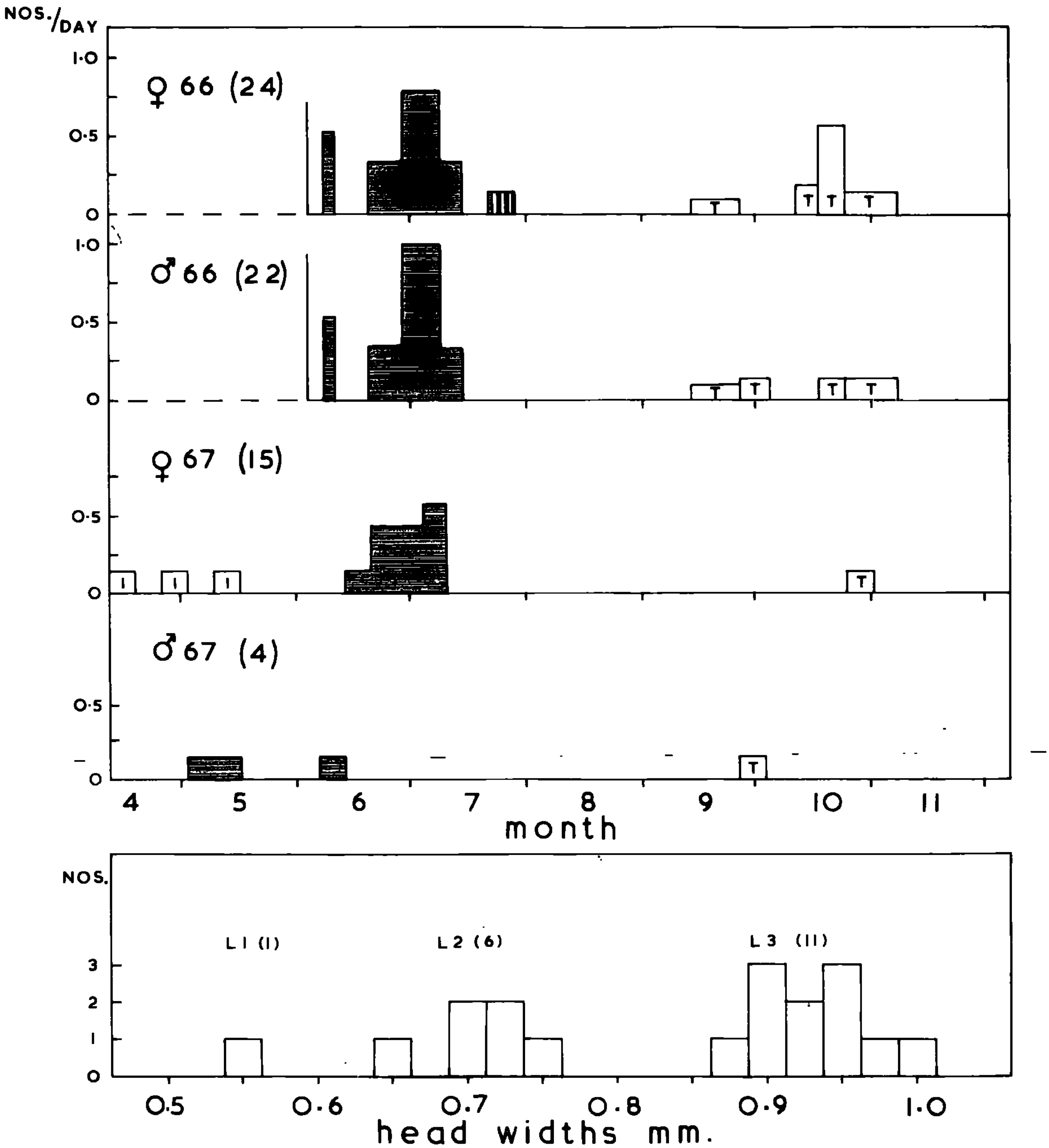
4. Agonum mülleri

This species was only found breeding in a hygrophilous habitat (a mosaic of Juncus squarrosus, J. effusus and Festuca ovina) at 1400 feet on the west side of the Reserve, but adults were taken on adjacent limestone grasslands. Pitfall traps were not in

FIGURE 11a. Agonum fuliginosum. Pitfall trap catches in 1966 on Site 3 and in 1967 on Site 5.

Key as in Fig.6.

FIGURE 11b. Agonum fuliginosum larval head widths.



NOS./DAY
♀ 66 (24)
♂ 66 (22)
♀ 67 (15)
♂ 67 (4)
month
NOS.
L1 (1)
L2 (6)
L3 (11)
head widths mm.

continuous use in this area but mature females and five third instar larvae were taken in July; one teneral female in September and another in October.

5. Amara aulica

This species was only found in the Meadow. A mature male and a mature female (both micropterous) were taken at the beginning of August; one second instar in the second week and two third instars in the fourth week of September.

Lindroth (1949) recorded this species as constantly macropterous and capable of flight; a constant larval hibernator with a biennial life cycle and found in mesophilus habitats. At Moor House it resembles an autumn breeder with winter larvae but, although likely, there is no evidence that it has a biennial life cycle.

6. Amara lunicollis (an occasional species)

Only two females were taken : one at 2400 feet on the west side of the Reserve and one from the east side near the field station on a wet habitat. They were macropterous with well developed wing muscles. There is no evidence that it breeds on the Reserve but Lindroth (1949) described it as a spring breeder and adult hibernator.

7. Bembidion atroviolaceum (an occasional species)

One female was found in the stomach of a frog taken on 29 July 1966 on redistributed peat on the east side at 2000 feet, and two teneral females in the stomach of a frog taken on 2 August 1966, also on redistributed peat, but near the field station. All three specimens were macropterous. No larvae were found and little is known about its status at Moor House. The two tenerals taken in August suggest that it has summer larvae, but there is no evidence that it breeds at Moor House.

8. Bembidion bruxellense (an occasional species)

One macropterous male was taken at the beginning of June on redistributed peat at 2450 feet.

In Denmark Larsson (1939) describes it as a spring breeder and adult hibernator and Greenslade (1968) records it as a lowland species in Scotland. Although widely distributed in Britain there is no evidence that it breeds on the Reserve and it is probably an immigrant from lowland areas.

9. Bembidion lampros (an occasional species)

One mature macropterous female was found on the redistributed peat at 2450 feet in June.

Lindroth records it as a wing dimorphic species, with the macropterous form capable of flight, and a constant imago hibernator with summer larvae on mesophilous habitats. There is no evidence that it breeds on the Reserve and, like B.bruxellense, it is probably an immigrant from lowland areas.

10. Bembidion nitidulum (an occasional species)

One immature male was taken on 18 April 1967, one teneral male on 5 August 1968, one teneral female on 5 September 1968 and one teneral male in the second week of October. The first three were found under stones on made ground, while the fourth specimen was taken from an area of Calluna on made ground, all at Bog End at the edge of standing water. They were macropterous.

Lindroth (1949) records it as a wet species capable of flight, a spring breeder and an adult hibernator. There is no evidence that it breeds at Moor House, but as all four specimens were taken within a few yards of each other, it is probable, and a similar life history would be expected.

11. Bradycellus harpalinus (an occasional species)

Only three macropterous females were taken; two on the Limestone grassland in October and one on the Alluvial grassland on 27 March 1966 near the Moor House field station.

Lindroth (1949) describes this species as slightly xerophilus and wing dimorphic, with predominantly winter larvae. There is no evidence that it breeds at Moor House.

12. Bradycellus ruficollis (an occasional species)

Two males only were found; one on Alluvial grassland in March and the other in the Meadow in September.

There is no evidence that it breeds at Moor House. Lindroth (1949) describes it as a mesophilus and macropterous form with summer larvae and adults during the winter.

13. Calathus fuscipes (an occasional species)

One female was taken at 1400 feet on the western boundary of the Moor House Reserve, in a pitfall at the beginning of July.

There is no evidence that it breeds on the Reserve, but as it is a brachypterous species it is probable. Lindroth (1949) describes it as a constantly brachypterous and mesophilus species and a predominant larval hibernator.

14. Calathus melanocephalus Figure 12b.

At Cow Green this species was common on the non-wet habitats and was frequently taken on Sites 7 and 8. At Moor House it was scarce and was only taken on the west side on non-wet habitats. One apterous female was taken on the top of Great Dun Fell.

Lindroth (1949) records this species as mesophilus and wing dimorphic, but during this study it was only taken on the non-wet habitats and only one + winged specimen was found.

It has been described as a summer/autumn breeder with winter larvae (Larsson 1939; Lindroth 1945; Gilbert 1956; Vlijm et al 1961; Greenslade 1965) and that the adults might breed a second year (Gilbert 1956; Skuhravy 1959; Greenslade 1965). In the north of Sweden Lindroth (1949) recorded teneral adults in July and August. He also noted that this species shows a definite tendency to change from larval to imaginal hibernation in the more continental climate of eastern Fennoscandia.

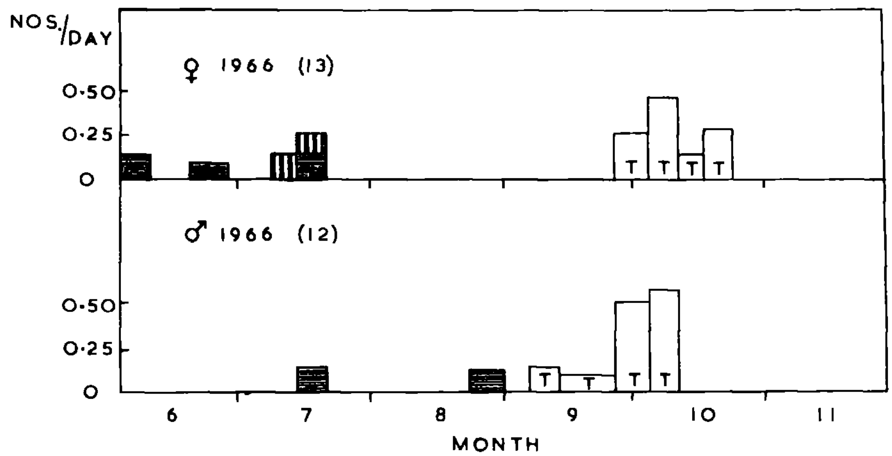
Overall at Moor House and Cow Green, mature females were taken in June, July and August and spent females in August, September and October. No larvae were found but teneral adults were taken at the end of September and in October. Figure 12 gives details of pitfall captures at Cow Green. There is insufficient evidence to confirm a biennial life cycle, but if the emergence of the tenerals taken in September and October are typical, it is unlikely that the immature stages could develop

FIGURE 12a. Calathus micropterus. Pitfall trap catches in 1966 on Site 2.

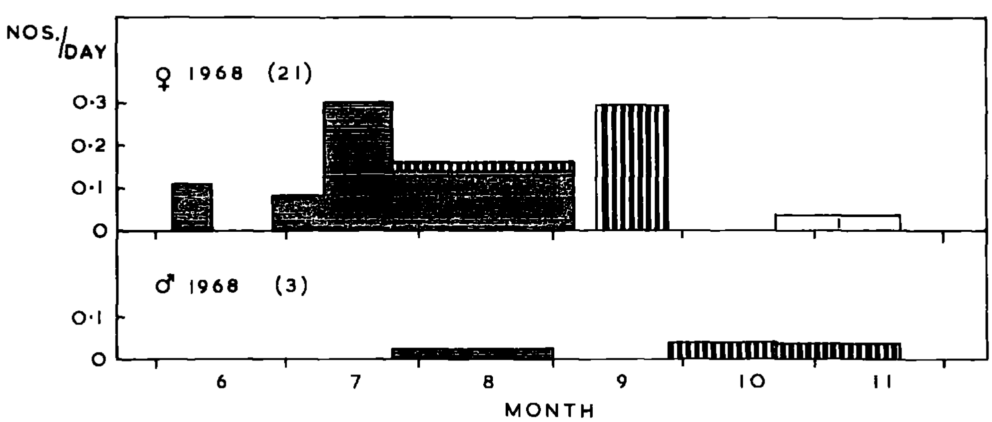
Key as in Fig.6.

FIGURE 12b. Calathus melanocephalus. Pitfall trap catches in 1968 on Sites 7 and 8.

Key as in Fig.6.



NOS./DAY
♀ 1966 (13)
0·50
0·25
0
T T T T
♂ 1966 (12)
0·50
0·25
0
T T T T
6 7 8 9 10 11
MONTH



NOS./DAY
♀ 1968 (21)
0·3
0·2
0·1
0
♂ 1968 (3)
0·1
0
6 7 8 9 10 11
MONTH

quicker than lowland populations and a biennial life cycle is indicated. Adults and larvae would therefore overwinter which could give the impression of a change from larval to imaginal hibernation.

15. Calathus micropterus Figure 12

At Moor House this species was widely distributed but scarce and was found mainly on the drier areas of the Moor. On these areas there are occasional well drained patches where Bilberry (Vaccinium myrtillus) and Calluna are the dominant plants and C.micropterous adults are frequently taken. This habitat is rather similar to Site 8, the Calluna grassland, where adults were also frequently taken. The larvae, however, were only found on the wet habitats.

In Denmark Larsson (1939) recorded it as having winter larvae, but in Scandinavia it is an adult hibernator.

Figure 12a shows the results of the main pitfall captures at Moor House. But overall at Moor House and Cow Green developing females were taken at the beginning of June, mature females in June and July, and spent females in July and August. First instar larvae were taken in the second half of June and third instars from the end of June to the end of August. Two third instars taken on 25 July 1968 and one on 20 August 1968, pupated a few days after being brought into the laboratory. Teneral adults were taken from the last week in September to the end of October.

This species has been found breeding in the autumn in lowland areas in Northumberland on non-wet habitats (Luff, pers. comm.)

As the adults are found mainly on the drier habitats, even on the Mixed Moor, non-wet habitats and subsequent autumn breeding are probably characteristic of this species. The spring/summer breeders on wet habitats may be a separate race to the autumn breeders, formed perhaps as a result of competition with C.melanocephalus, but the factors controlling their life cycles (e.g. photoperiod and temperature) obviously requires investigation.

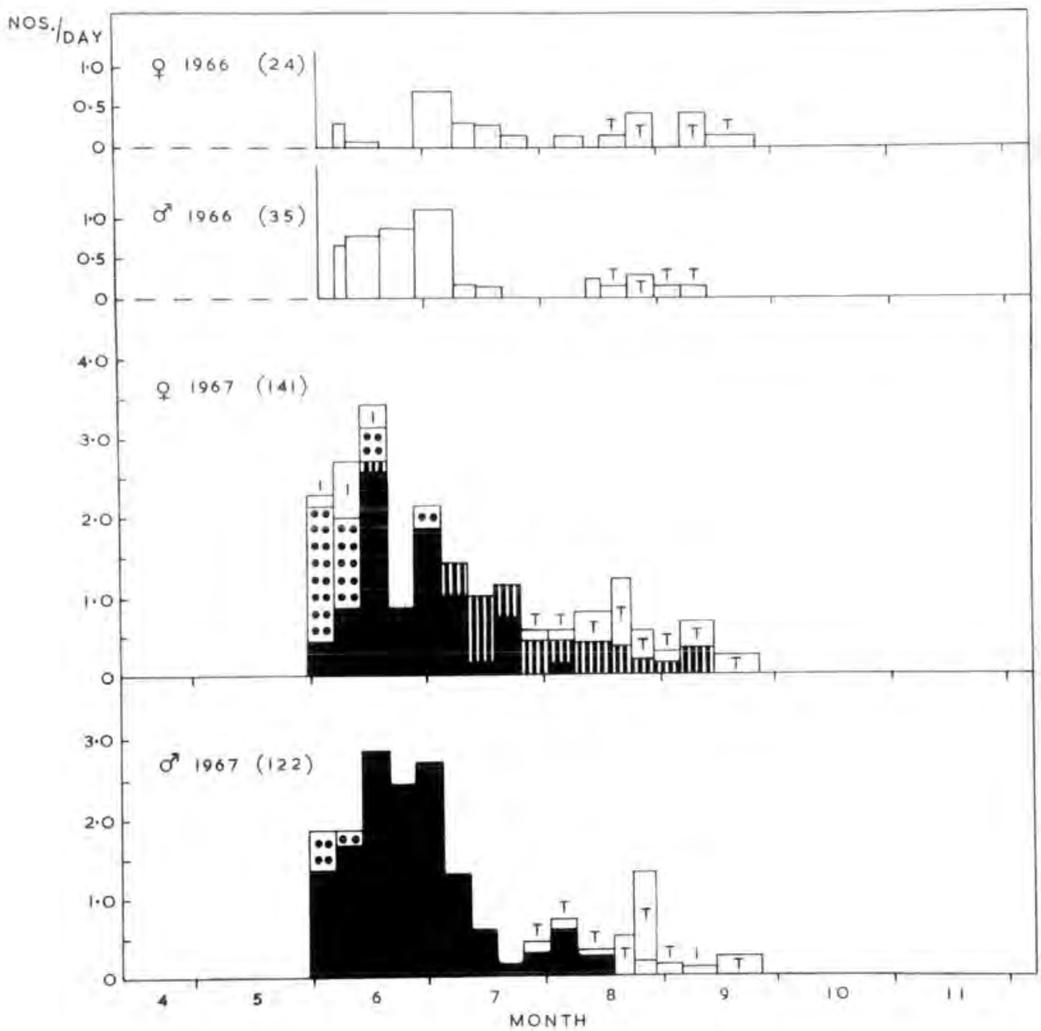
16. Carabus glabratus Figures 6, 7, 13.

This species was abundant on the Blanket Bog, scarce on the redistributed peat, and rarely found elsewhere. Lindroth describes it as a mesophilus and predominantly-forest species. Its association with the Blanket Bog may therefore be due partly to the plant cover afforded by this type of vegetation.

At 1800 feet on the east side of the Reserve it breeds in the summer (Figure 13). First instar larvae were taken at the end of July and in August; second instars at the end of August and in September; third instars in October and November. Third instars, together with the adults, overwinter and the new generation adults emerge in July to September. It thus has a biennial life cycle. Using the mandibles and the ovaries as a guide to the age of the adults (Section V.9) there is an

FIGURE 13. *Carabus glabratus*. Pitfall trap catches in 1966 on Sites 1 and 2, and in 1967 on Sites 4 and 5.

Key as in Fig.6.



NOS./DAY
♀ 1966 (24)
♂ 1966 (35)
♀ 1967 (141)
♂ 1967 (122)
MONTH

indication that some survived for two years and had two breeding seasons, while a few may survive to breed in a third year.

17. Carabus problematicus Figures 8, 9, 14.

The adults were abundant on the wet and non-wet habitats, but most of the larvae were taken on grasslands and redistributed peat. They were rarely found on the Blanket Bog.

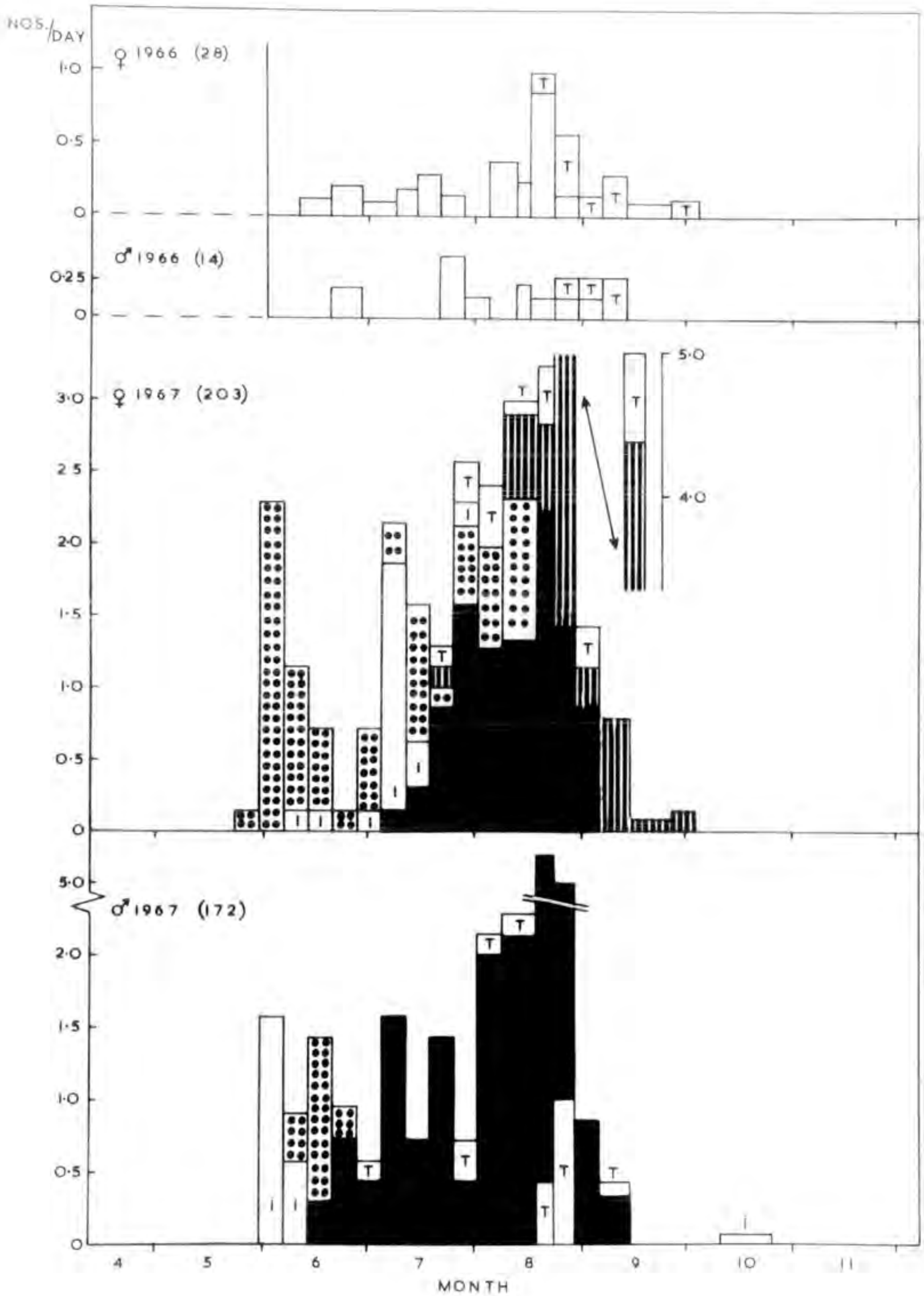
At 1800 feet on the east side of the Reserve it breeds in the autumn (Figures 8, 9, 14). First instar larvae were taken at the end of September and in October; second instars from the end of September until November; third instars from the middle of September until the end of June. The majority of the third instars were found in the last week of May and the second week of June. No pupae were found but teneral adults first appeared at the end of July and were found until the middle of September. Like C. glabratus, the adults may survive for several years (Section V.9).

18. Carabus violaceus

The adults and larvae were taken, in small numbers, mainly on the non-wet habitats, but never on the very wet areas of the Blanket Bog.

FIGURE 14. *Carabus problematicus*. Pitfall trap catches in 1966 on Sites 1, 2 and 3, and in 1967 on Sites 4, 5 and 6.

Key as in Fig.6.


NOS./DAY
♀ 1966 (28)
♂ 1966 (14)
♀ 1967 (203)
♂ 1967 (172)
MONTH

The life history is similar to C.problematicus but the breeding season is slightly earlier. Immature females were taken in May and the beginning of June; developing females at the beginning of June; mature females in June and July; first instar larvae in July and August; one second instar in September; third instars from September to November; tenerals at the end of July and in August. It thus has a biennial life cycle and like C.glabratus and C.problematicus it may breed in more than one year.

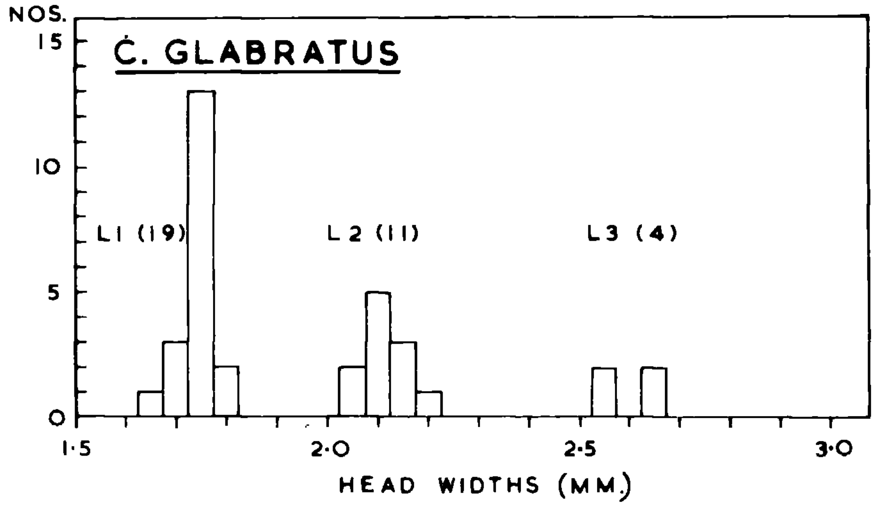
19. Clivina fossor (an occasional species)

A burrowing form and specimens were obtained (but only from soil cores and by hand collecting) at Cow Green and on both sides of the Reserve up to about 2000 feet on redistributed peat and slightly flushed grasslands.

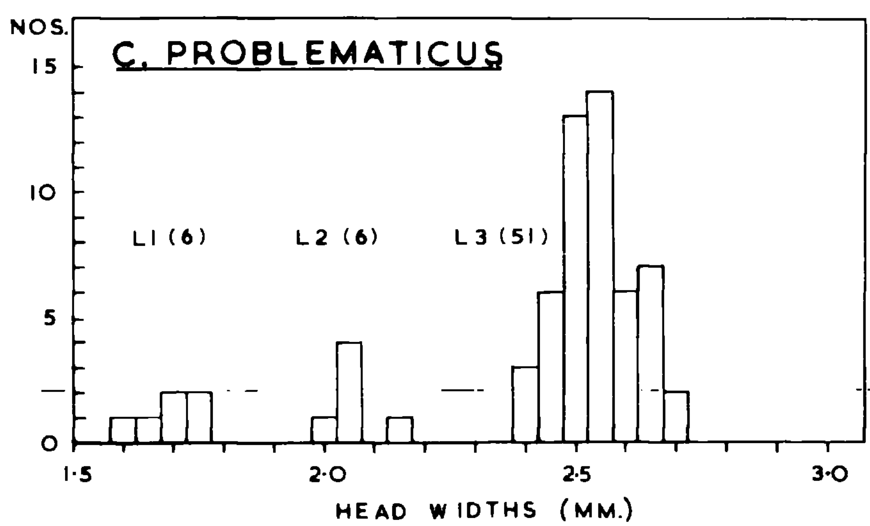
One teneral - winged, female was taken on 27 September 1968 at Cow Green and eight mature males from May to July. The one female indicates that it breeds at Cow Green and probably has summer larvae, but further specimens are required to confirm its life history.

Lindroth records peak activity in June and Tipton (1960) describes it as a spring breeder and adult hibernator.

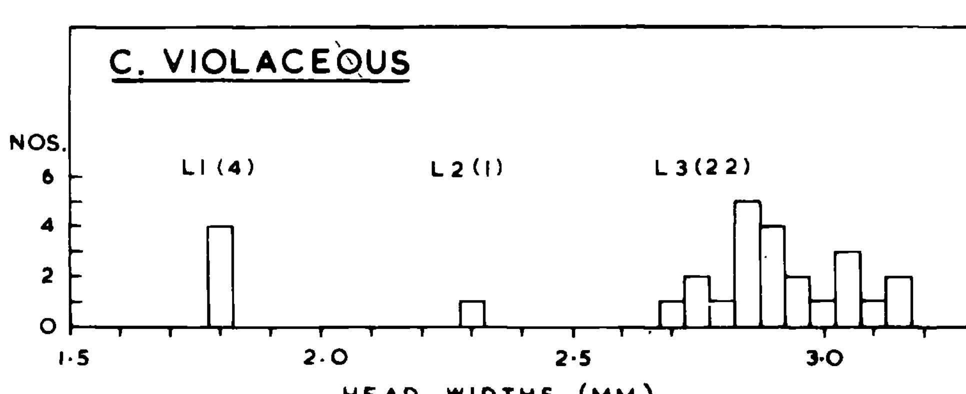
FIGURE 15. _Carabus glabratus_, _C. problematicus_, and _C. violaceus_ : larval head widths.



C. GLABRATUS
NOS.
15
10
5
0
L1 (19)
L2 (11)
L3 (4)
1·5
2·0
2·5
3·0
HEAD WIDTHS (MM.)



C. PROBLEMATICUS
NOS.
15
10
5
0
L1 (6)
L2 (6)
L3 (51)
1·5
2·0
2·5
3·0
HEAD WIDTHS (MM.)



C. VIOLACEOUS
NOS.
6
4
2
0
L1 (4)
L2 (1)
L3 (22)
1·5
2·0
2·5
3·0
HEAD WIDTHS (MM.)

20. <u>Cychrus caraboides</u>

A scarce species, found on the wet habitats at Moor House, but the Limestone grassland at Cow Green. Mature females were taken at the end of July and in August; first instar larvae in August and in September; second instars in September; third instars in September and October. Like the <u>Carabus</u> species it probably has a biennial life cycle.

21. <u>Dyschirius globosus</u>

A burrowing form found only on the Sugar Limestone Grassland at Cow Green.

Developing females were found at the end of April and the beginning of May; mature females at the end of May and in June; teneral adults in October. No larvae were found, but only new generation adults were present in soil cores in December. The life history is similar to that found by Larsson and Lindroth.

22. <u>Elaphrus cupreus</u>

Only found on wet habitats at Cow Green. Mature adults were taken at the end of May, beginning of June; tenerals in September. No larvae were found. Larsson describes it as a spring breeder and adult hibernator capable of flight. If it breeds at Cow Green a similar pattern is indicated.

23. <u>Leistus rufescens</u> Figure 16

Taken most frequently on the east side on the wet habitats. The adults were able to avoid the pitfall traps, but the larvae were readily taken.

The larval head widths and times of occurrence of the adults and larvae at Moor House are shown in Figure 16. This species has a similar life history pattern in the south of England (Murdoch 1967), Denmark (Larsson 1939), and Sweden (Lindroth 1949).

At Cow Green it was also found breeding on non-wet habitats, e.g. <u>Calluna</u> grassland, but mature females were not found until September.

24. <u>Loricera pilicornis</u> Figures 17 and 18

A common species at all altitudes up to 2500 feet. Taken most frequently on the redistributed peat, the well drained areas of the Blanket Bog and in the Meadow.

Details of the activity of the adults are shown in Figure 17 and head widths and the occurrence of the larvae in 1967 in Figure 18. It is a typical spring/summer breeder with summer larvae.

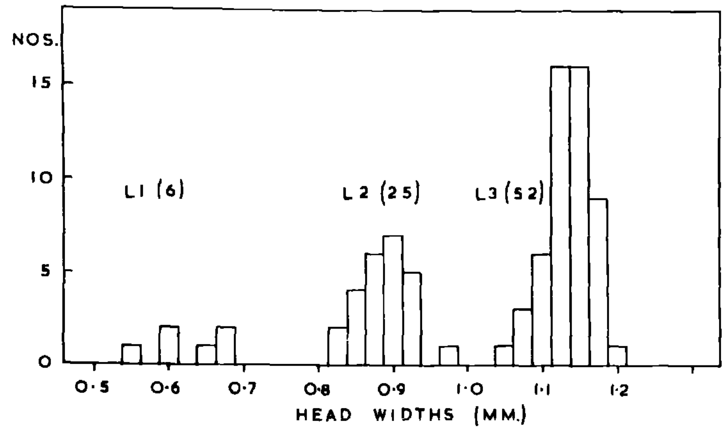
FIGURE 16a. Leistus rufescens : larval head widths.

FIGURE 16b. Leistus rufescens :

i. Temporal distribution of the 1966 generation larvae

ii. Pitfall trap catches of adults in 1966 on all sites c.1800 feet, and in 1967 on Site 4.

Key as in Fig.6.


NOS.
15
10
5
0
L1 (6)
L2 (25)
L3 (52)
0·5
0·6
0·7
0·8
0·9
1·0
1·1
1·2
HEAD WIDTHS (MM.)

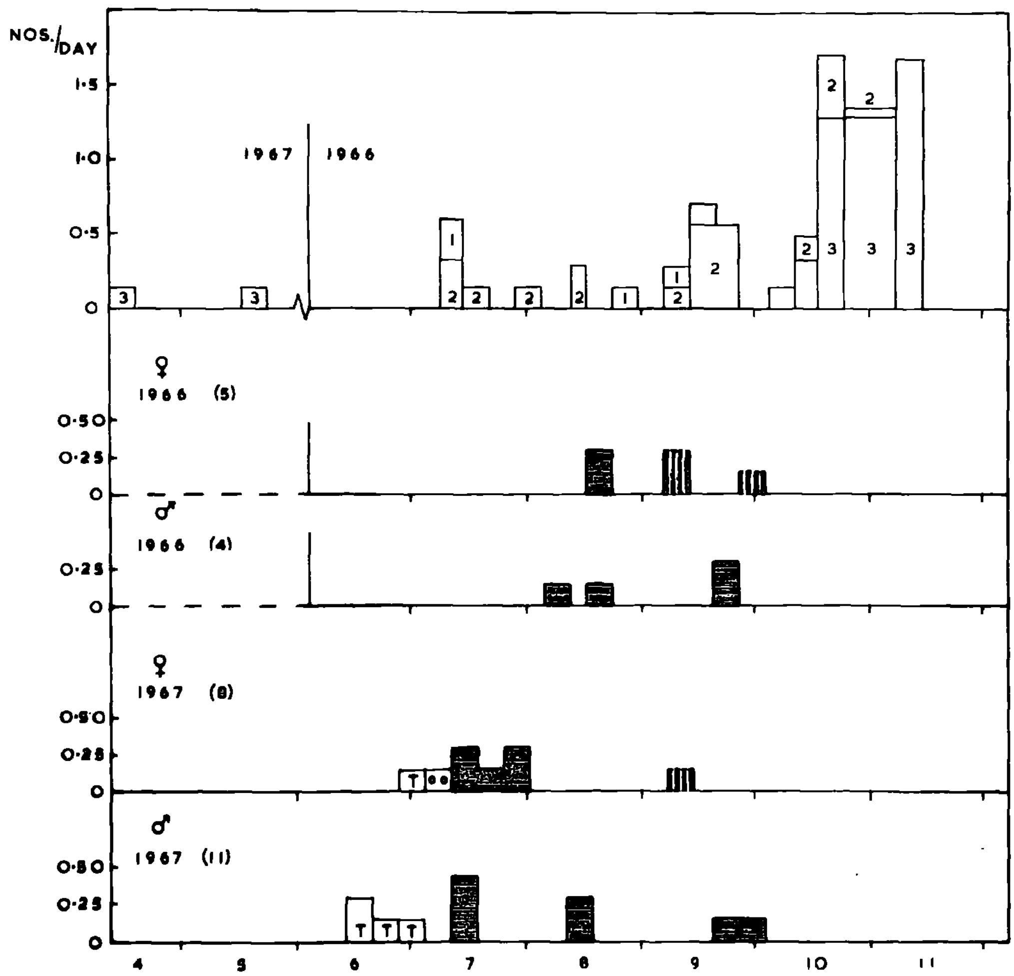

NOS./DAY
1·5
1·0
0·5
0
1967
1966
1966 (5)
0·50
0·25
1966 (4)
1967 (8)
1967 (11)
4
5
6
7
8
9
10
11

FIGURE 17. _Loricera pilicornis_ : pitfall trap catches in 1966 on Sites 1, 2 and 3, and in 1967 on Sites 4, 5 and 6.

Key as in Fig.6.

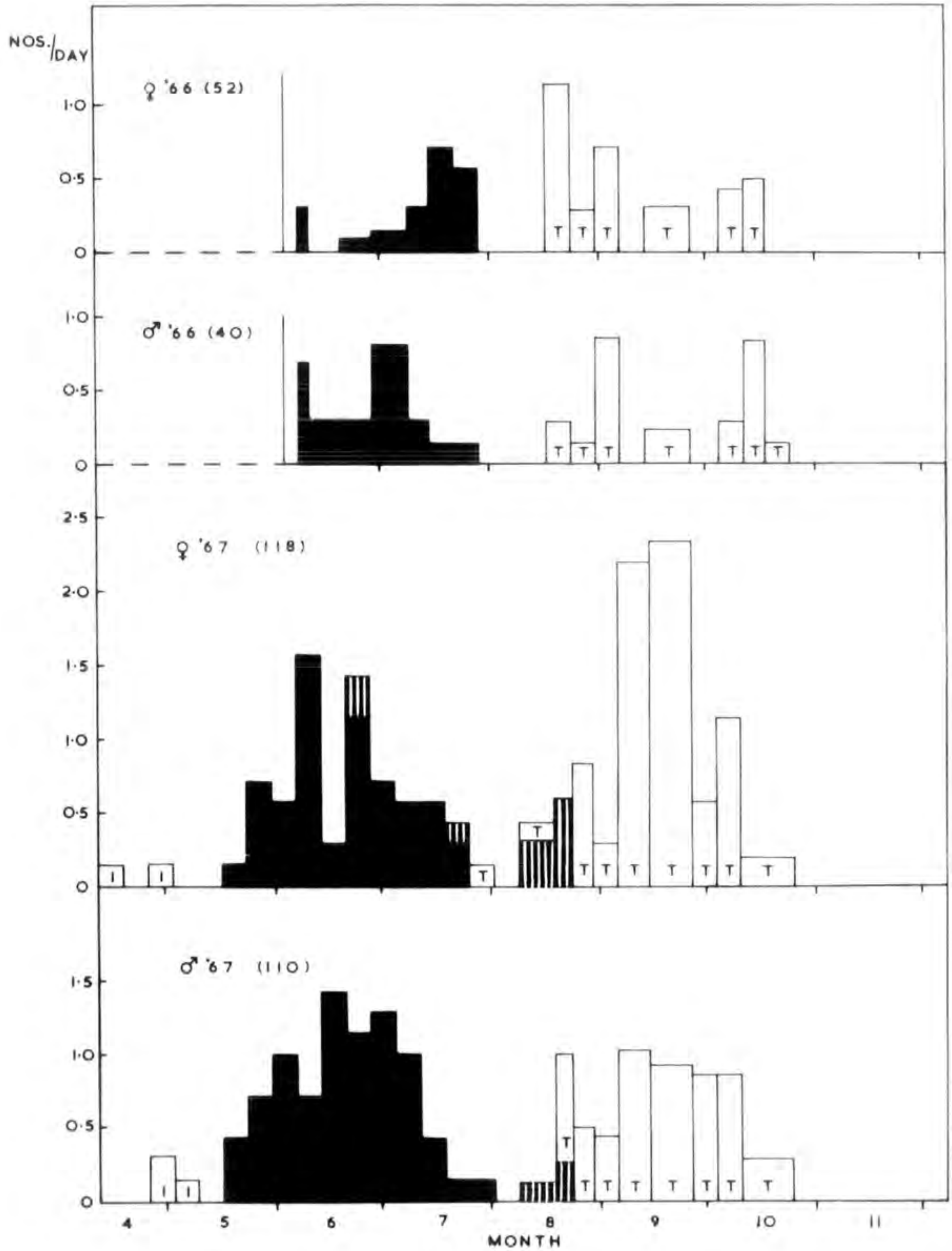
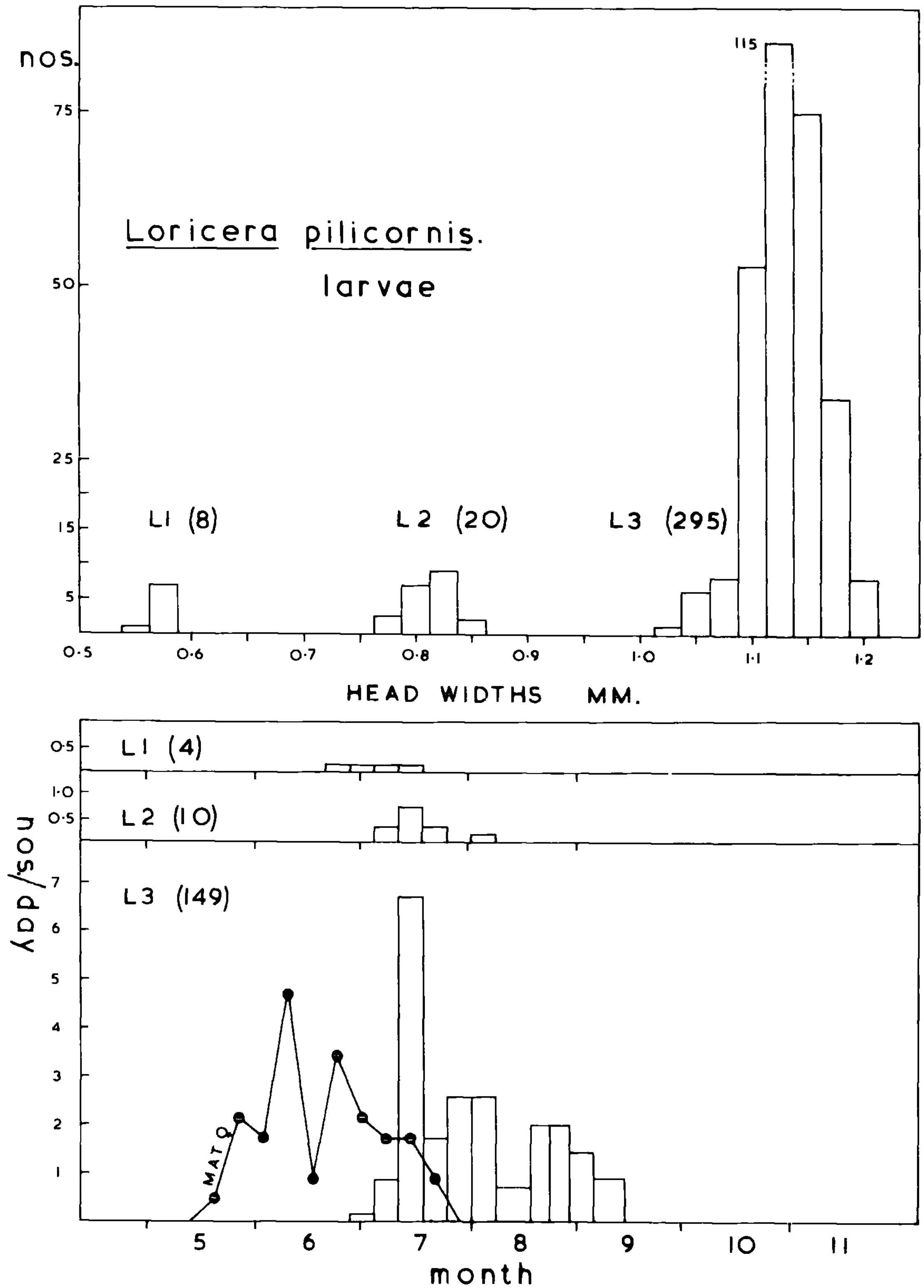

NOS./DAY
♀ '66 (52)
♂ '66 (40)
♀ '67 (118)
♂ '67 (110)
1·0
0·5
0
2·5
2·0
1·5
T
I
4
5
6
7
8
9
10
11
MONTH

FIGURE 18a. Loricera pilicornis : larval head widths

FIGURE 18b. Loricera pilicornis : temporal distribution of larvae in 1967. L1,2,3 = first, second and third instars respectively.


nos.
75
50
25
15
5
115
Loricera pilicornis.
larvae
L1 (8)
L2 (20)
L3 (295)
0·5
0·6
0·7
0·8
0·9
1·0
1·1
1·2
HEAD WIDTHS MM.
nos./day
0·5
L1 (4)
1·0
0·5
L2 (10)
7
6
5
4
3
2
1
L3 (149)
MAT ♀
5
6
7
8
9
10
11
month

25. <u>Miscodera arctica</u> (an occasional species)

One first year female, with developing ovaries, was taken in May and two females with mature eggs in the first half of June, from pitfall traps on a wet habitat at 2450 feet on Great Dun Fell. No larvae were taken, but these three specimens indicate that it is a spring/summer breeder.

Larsson regards <u>Miscodera arctica</u> as an autumn breeder, whereas Lindroth (1945, 1961) is of the opinion that it hibernates as an adult, but that the life cycle may take two years in the northernmost part of Fennoscandia.

26. <u>Nebria brevicollis</u> (an occasional species)

In the lowlands this is a common species and is one of the most widely studied carabids in this country (Gilbert 1958; Tipton 1960; Greenslade 1964; Ganagarajah 1964, 1965; Penny 1964, 1965, 1969).

It was scarce at Moor House and was only taken at 1400 feet on the west side of the Reserve. Three adults and four larvae were found at Cow Green.

Mature females were taken in August and September; first instars in October and November; one third instar on 5 June 1968. There is no evidence that the life history is significantly different from that found by other authors.

27. Nebria rufescens

A very abundant species on the Fell Top Podzols and the Limestone grassland above about 2400 feet, and common on the Blanket Bog at about 2400 feet. Its abundance decreased with a decrease in altitude and at about 1800 feet on the east side it was scarce. No specimens were taken below about 1900 feet on the west side.

It was found breeding mainly on non-wet habitats and drier parts of the wet habitats, but not if N.salina or N.brevicollis were present.

At 2780 feet, developing females were taken in April and May; mature females in May, June and a few in July; first instars in July, August and September; second instars in August and September; third instars from August to May, and tenerals in July. At 2780 feet this species has a biennial life cycle and adults may breed at least in a second year.

At 1800 feet near the field station, immature and developing females (some with no corpora lutea) were taken in April; mature females in May, June and July; spent females in September; first instars at the end of July and in August and September; second instars in August and September; third instars at the end of September and in October, April and May; tenerals in June and July.

Some immature and developing females with no corpora lutea (indicating that they had not produced eggs) were taken in April. They were not teneral and their mandibles were worn, suggesting that they had emerged the previous year but had not bred. There is no evidence that females breed the same year that they emerge and a biennial life cycle at 1800 feet is also indicated.

In Iceland, Larsson & Gigja (1958) describe a similar life history pattern, except that adults emerge in the spring and early summer, and they consider that as a rule the life cycle is annual.

28. Nebria salina

Common on the grasslands below 1900 feet; never found on wet habitats. Developing females were taken in July; mature females in August, September and October; first instars in September and October, and third instars in November and April. The life history is similar to that found by Gilbert (1958).

29. Notiophilus aestuans

Four females and one male, all + winged, were taken on the Sugar Limestone Grassland at Cow Green. Previously this species has been recorded only from Hampshire (on sandy soils) and the east highlands of Scotland (Moore 1957b).

In Denmark, Larsson recorded peak numbers in June and July, larvae in July and August, pupae and teneral adults in August and the beginning of September, indicating that it was a summer breeder and imago hibernator. In Sweden, however, Lindroth found that it was normally a larval hibernator.

Of the specimens taken at Cow Green, one immature female was taken in July; two mature females and one mature male in October; and one female, with its abdomen missing, in September. No larvae were identified but, if it breeds on the Sugar Limestone Grassland, an autumn breeder and larval hibernator would be expected.

30. Notiophilus aquaticus

A wing dimorphic species, but only the - winged form was found.

Mature females were taken in June, July and August and the first half of September. No larvae were identified but one pupa, taken near the Moor House Field Station on 27 July 1968, emerged at 15^{o} on 3 August 1968. Immature females, with corpora lutea, and tenerals were taken at the end of October and from soil cores during February.

In Denmark, Larsson recorded peak numbers in August and September and larvae in June, the end of July and the beginning of August; in the Welsh mountains, Pearson & White (1964) recorded a peak in April and May and another in September and October; and in Sweden, Lindroth considers that the adults overwinter with subsequent spring breeding. At Moor House and Cow Green summer larvae are indicated, but the life history patterns may be similar to that of Notiophilus biguttatus, as mature females were also found on the non-wet habitats in August and the first week of September.

31. Notiophilus biguttatus Figure 19

Common and widely distributed throughout the Reserve, except on the fell tops. Found most frequently on the re-distributed peat and the well drained area of the Blanket Bog.

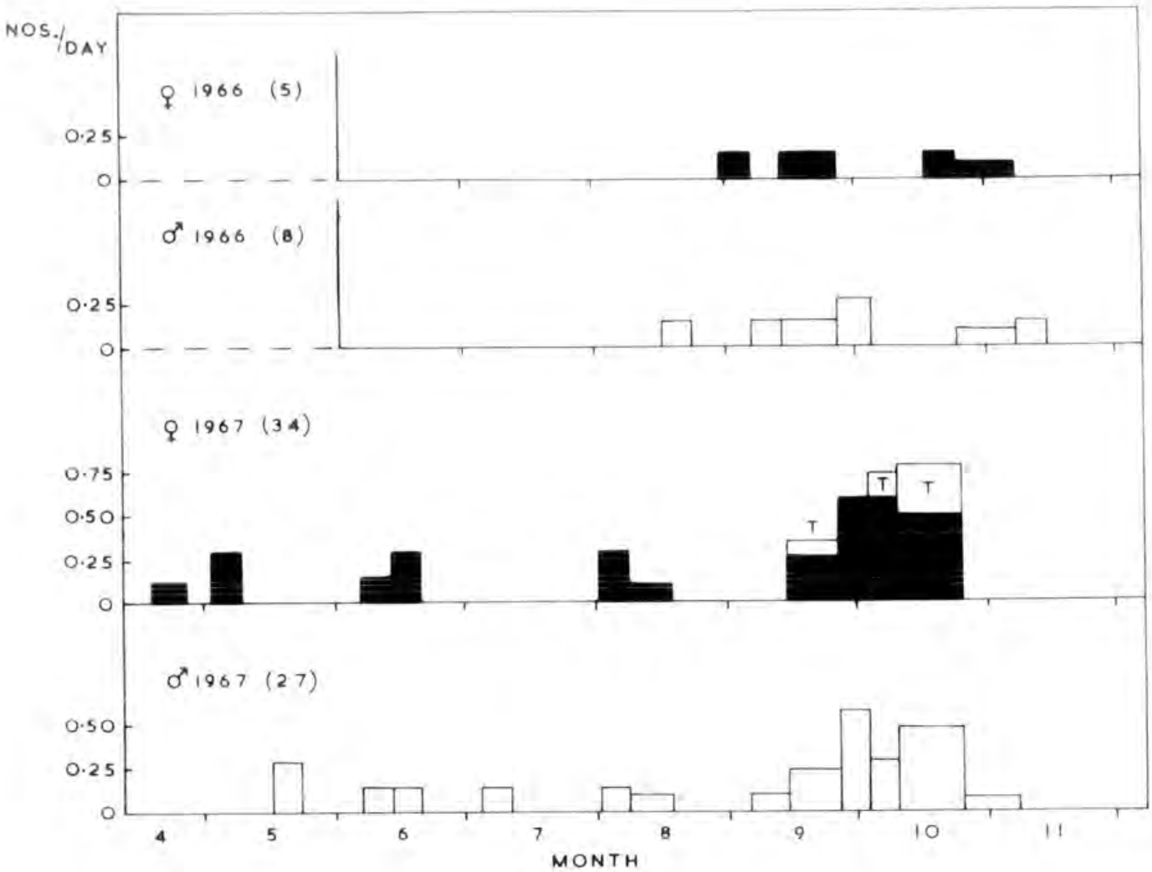
In Denmark (Larsson 1939), Sweden (Lindroth 1949), Iceland (Larsson & Gigja 1958) and the south of England (Davies 1959; Greenslade 1965), this species is a spring breeder with summer larvae. The latter author recorded that a minor peak in the autumn was due to the emergence of the new generation adults.

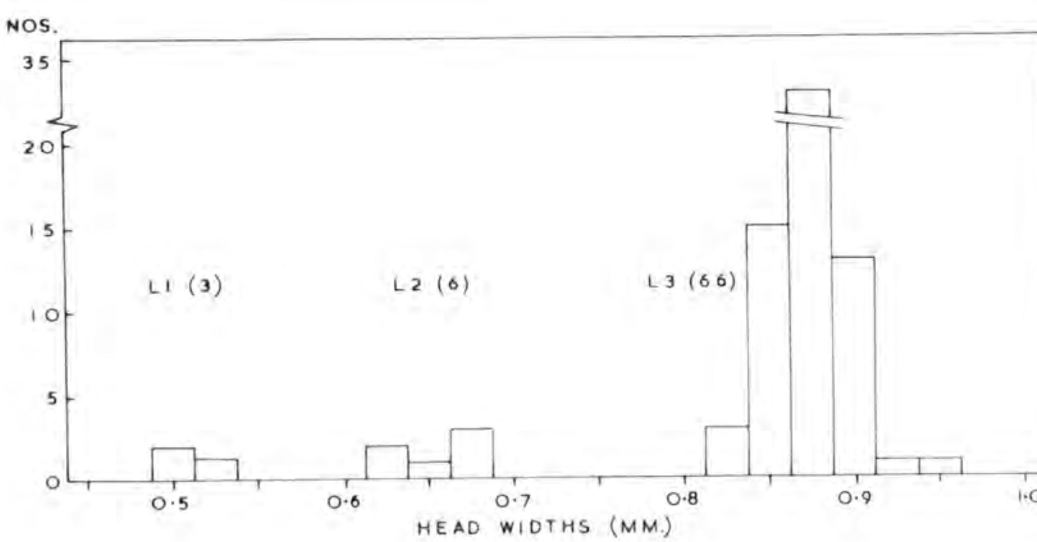
At Moor House, however, on both wet and non-wet habitats, the major peak was found in the autumn (Figure 19) and included mature females and others developing eggs for the first time. Another smaller peak was found in May and June, but all the immature and developing females had corpora

FIGURE 19a. <u>Notiophilus biguttatus</u> : pitfall trap catches in 1966 on all sites c.1800 feet, and in 1967 on Sites 4, 5 and 6.

Key as in Fig.6.

FIGURE 19b. <u>Notiophilus biguttatus</u> : larval head widths


NOS./DAY
♀ 1966 (5)
0·25
0
♂ 1966 (8)
0·25
0
♀ 1967 (34)
0·75
0·50
0·25
0
T
T
T
♂ 1967 (27)
0·50
0·25
0
4
5
6
7
8
9
10
11
MONTH


NOS.
35
20
15
10
5
0
L1 (3)
L2 (6)
L3 (66)
0·5
0·6
0·7
0·8
0·9
1·0
HEAD WIDTHS (MM.)

lutea indicating that they had already produced eggs, probably in the previous autumn.

First instar larvae were found from the end of October to the first half of July. (One on 24 October 1965; two on 14 February 1967; one on 27 March 1966; two on 22 April 1966; one, newly emerged from an egg, on 16 May 1966; two in pitfalls on 13 - 20 June 1967; two in pitfalls on 11 - 18 July 1967). One second instar was taken in the middle of July while third instars were taken from the middle of June (26 individuals), in July (45), August (14), and the beginning of September (2). Teneral adults were taken in July, September and October.

Except for the autumn breeding season and some over-wintering first instar larvae (and perhaps eggs ?), this species exhibits the life history pattern of a spring breeder with a summer larvae as found by other authors. This species is also discussed in Section V. 4. iii. on life history patterns.

As Notiophilus adults are able to avoid pitfall traps, an indication of its breeding season by noting peak numbers may not be reliable. In this study only dissection could confirm that the females first developed their eggs in the autumn.

32. Notiophilus germinyi

At Moor House it was abundant on the Fell Top Podzol of Great Dun Fell and also the Limestone grasslands at 2400-2500 feet. Except for one third instar larva in the Meadow, it was not taken elsewhere on the Reserve.

Larsson and Lindroth record it as an autumn breeder and larval hibernator with peak numbers in July and August.

At Cow Green, mature females were found in September and the beginning of October, but at 2780 feet on the Fell Top Podzol it is a spring/summer breeder. Immature females were taken in May and June; developing females in June, mature females in June and July; spent females in September; first instar larvae in August and September; overwintering second and third instars, together with immature adults, were found in soil cores taken in January and February; second and third instars were also found in May and June and a few third instars in July; tenerals at the end of August and in September. At 2780 feet it thus has a biennial life cycle.

The larvae of this species found at Moor House are distinctly different from the description given by Davies (1963). He took N.biguttatus as the type larval species as he considered that it had the full complement of cercal setae (five in the first instar and seven in the second and third instars). However, Moor House N.germinyi first instars had six cercal setae while the second and third instars had eight. The extra seta is situated dorsally between the terminal seta and the terminal dorso-lateral seta and clearly distinguishes this species.

Also contrary to his key, the head of the Moor House specimens have a prominent setiferous tooth at the hind angle.

As a key to the British Notiophilus species is in preparation (Luff, pers.comm.), no attempt has been made to publish a description.

33. Odontonyx rotundatus (an occasional species)

A scarce species, taken mainly on the alluvial grasslands. Lindroth records it as a predominantly larval hibernator, but insufficient specimens were obtained to confirm its life history at Moor House.

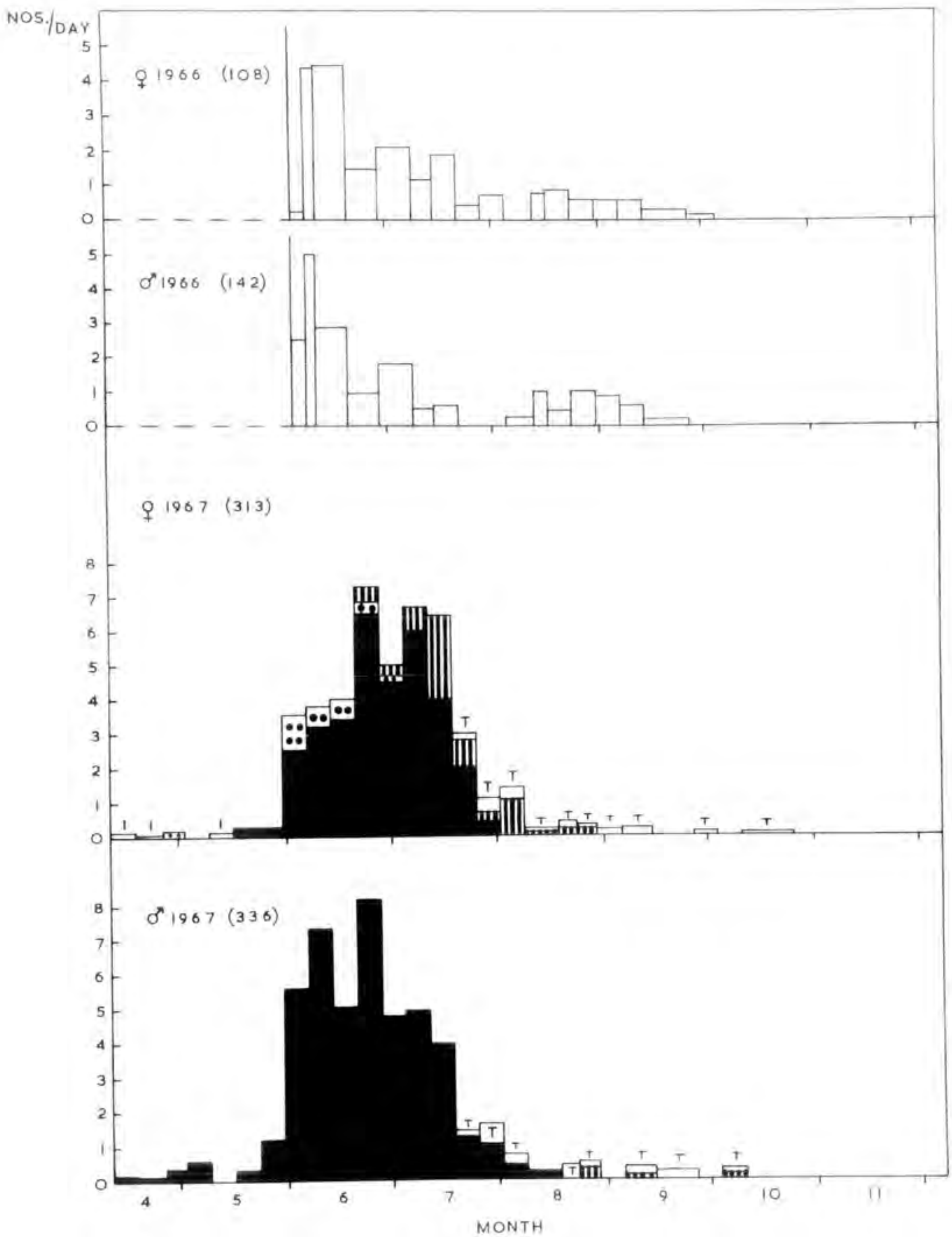
34. Patrobus assimilis Figures 20 and 21

Patrobus assimilis was common and widely distributed throughout the Reserve. The life cycle at 1800 feet, where it breeds on the wet habitats, is shown in Figure 20 (adults) and Figure 21 (larvae).

At 2780 feet adults and larvae were found throughout the year, but during the winter months they were obtained only from soil cores. Immature females were taken in April, May and June. They were either young beetles with only slightly worn mandibles and no corpora lutea, or else they had well worn mandibles and ovaries with corpora lutea indicating that they had passed through at least one breeding season. Two mature females were found in soil cores taken on 2 May 1968 but all

FIGURE 20. Patrobus assimilis : pitfall trap catches in 1966 on Sites 1, 2 and 3, and in 1967 on Sites 4, 5.

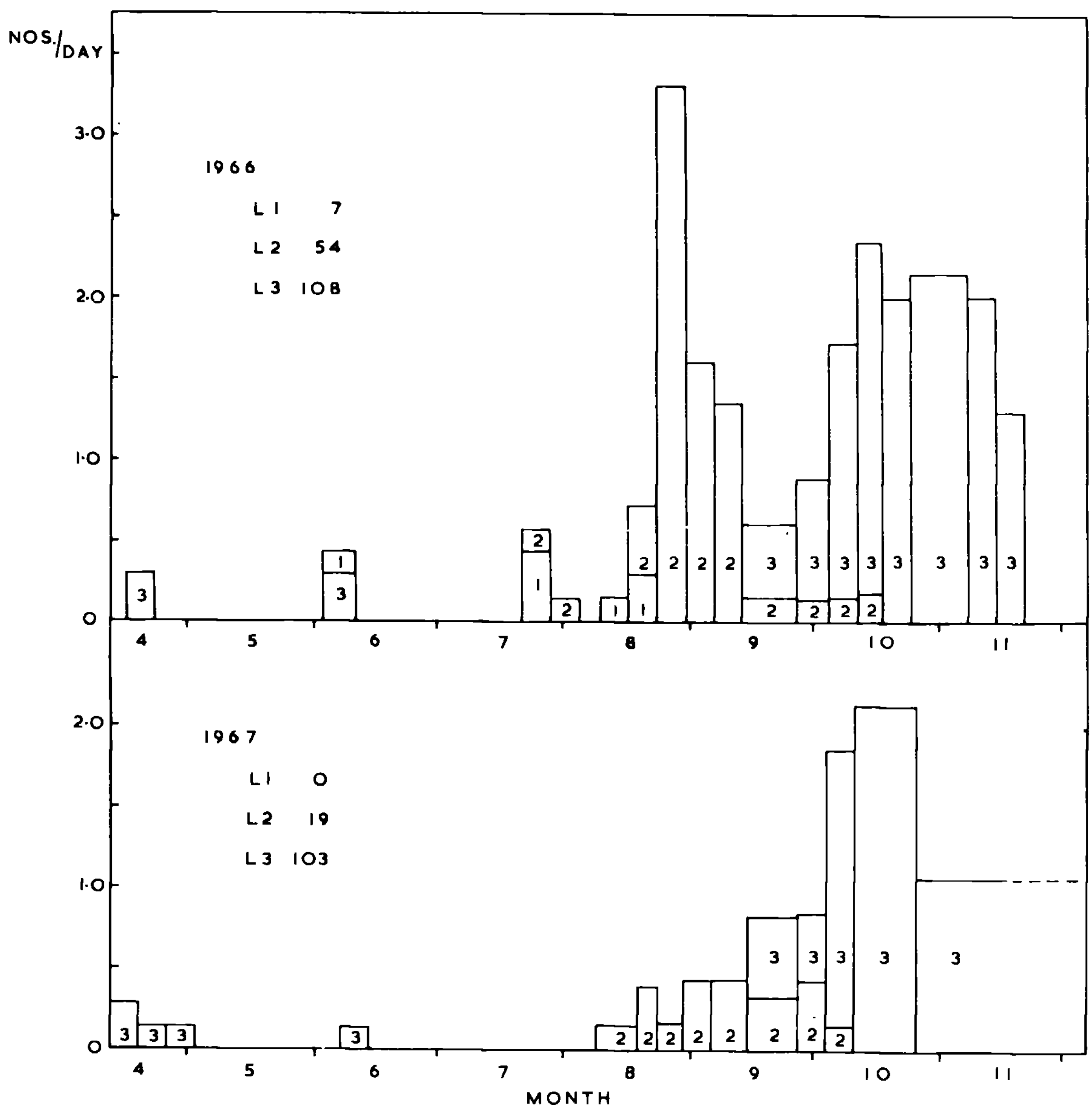
Key as in Fig.6.



NOS./DAY
♀ 1966 (108)
♂ 1966 (142)
♀ 1967 (313)
♂ 1967 (336)
MONTH

FIGURE 21. *Patrobus assimilis* : captures of larvae in 1966 and 1967 at c.1800 feet.

1, 2, 3 = first, second and third instars respectively.



NOS./DAY
3·0
2·0
1·0
0
1966
L1 7
L2 54
L3 108
1967
L1 0
L2 19
L3 103
4
5
6
7
8
9
10
11
MONTH

other mature females were taken between the last week of May and the second week of July. Spent females were taken at the end of June and in July and August. Females which had no mature eggs, but had recently laid eggs and were absorbing their immature eggs, were found at the beginning of July. First instar larvae were found in July and August; second instars in August; third instars from the middle of September until the middle of June; teneral adults at the end of July and in August. At this altitude this species therefore has a biennial life cycle and adults may live for more than one year.

The life history is discussed in Section V. 4.b. iii. and their habitat distribution in Section V. 4.c. A key to the adults and larvae of the British species of the genus Patrobus is given in the Appendix : Section II.

35. Patrobus atrorufus

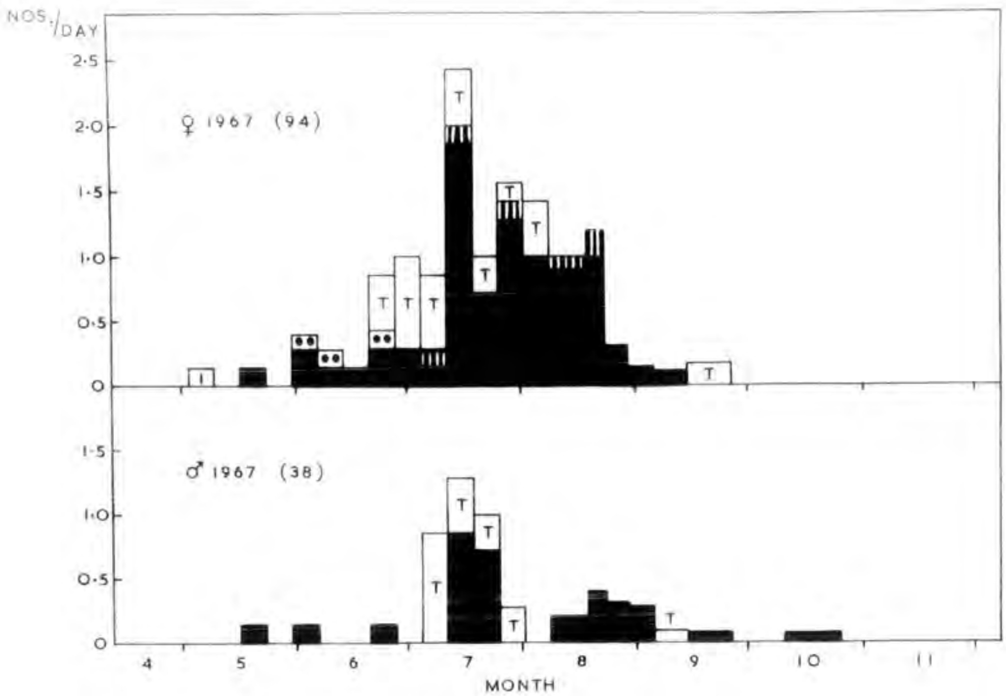
A common species in the lowlands, but at Moor House it is probably approaching the limits of its range.

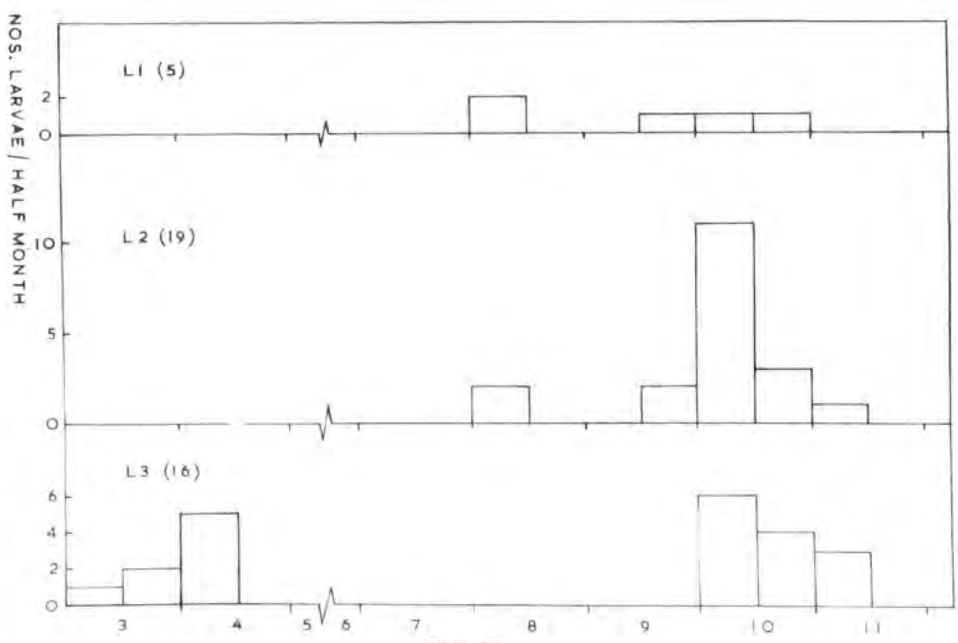
In Denmark, Larsson describes it as an autumn breeder with winter larvae; the new generation adults emerging in the spring. In the south of England Murdoch (1967) describes a similar life history with mature adults occurring between July and October and newly emerged adults in May and June.

FIGURE 22a. *Patrobus atrorufus* : pitfall trap catches in 1967 on the Meadow (Site 6).

Key as in Fig.6.

FIGURE 22b. *Patrobus atrorufus* : captures of larvae in 1966 and 1967 at c.1800 feet.


NOS./DAY
♀ 1967 (94)
♂ 1967 (38)
T
MONTH


NOS. LARVAE / HALF MONTH
L1 (5)
L2 (19)
L3 (16)
MONTH

In the Meadow at Moor House the generations overlap and some individuals have a biennial life cycle. Details of the adults taken in the Meadow in 1967 and the occurrence of the larvae throughout the year are given in Figure 22.

Detailed examination indicated that most females laid eggs in the same year that they emerged, but a few did not breed until the following year and thus had a biennial life cycle. The cause of the significant difference of the sex ratios of the Meadow pitfall catches in 1967 ($\chi^2 = 11.9$ 1 d.f. $P < .001$) is not known.

The peak of the breeding season in the Meadow is earlier than on the alluvial and Limestone grasslands and in the lowlands. The earlier breeding season in the Meadow is possible as the effect of the ungrazed vegetation results in a high summer humidity. On the other habitats, the short vegetation and resulting dry conditions in summer probably delay the breeding season.

The species habitat distribution in relation to their life histories is discussed in Section V. 4.c. A key to the adults and larvae of the genus Patrobus is given in the Appendix, Section II.

36. Pterostichus adstrictus   Figure 23

Taken primarily on areas of redistributed peat and peaty gleys. It is a spring breeder with summer larvae (Figure 23). One teneral male was taken on 9 May 1967 at 1800 feet indicating that it had probably overwintered as a larva. At higher altitudes it may regularly overwinter as a larva and even have a biennial life cycle.

37. Pterostichus aethiops

Only taken on the west side of the reserve below 2100 feet on flushed grasslands or well drained areas of Juncus squarrosus. Mature females were taken at the end of June and in July, and one third instar in February. It probably has a biennial life cycle similar to P.madidus (see below).

38. Pterestichus diligens   Figure 24

A pronouncedly hygrophilous species, being found entirely on wet habitats. Lindroth records it as a wing dimorphic species, but only brachypterous specimens were taken at Moor House and Cow Green.

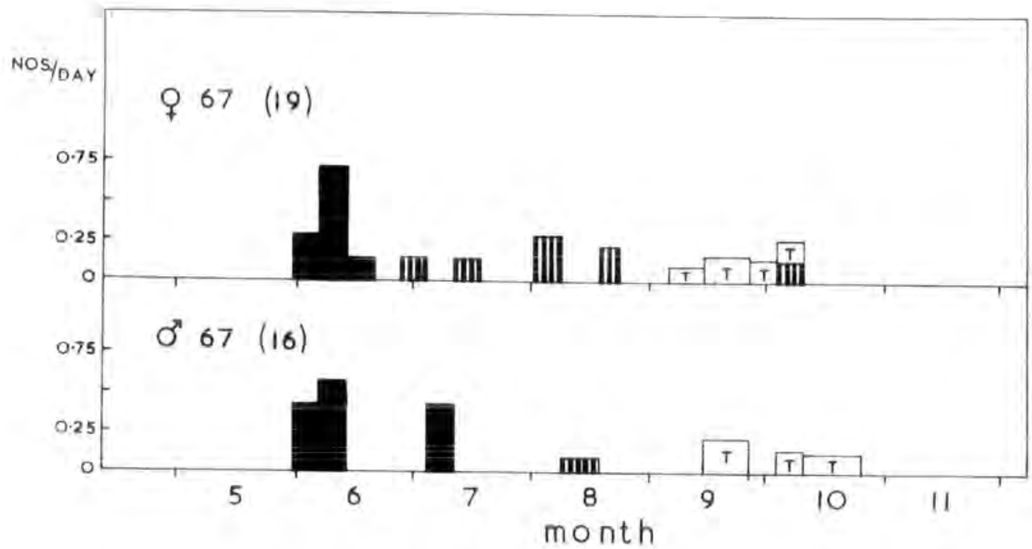
Details of pitfall trap catches of adults are shown in Figure 24. It is a spring breeder with summer larvae and overwintering adults.

FIGURE 23a. *Pterostichus adstrictus* : pitfall trap catches in 1967 on Sites 4 and 5.

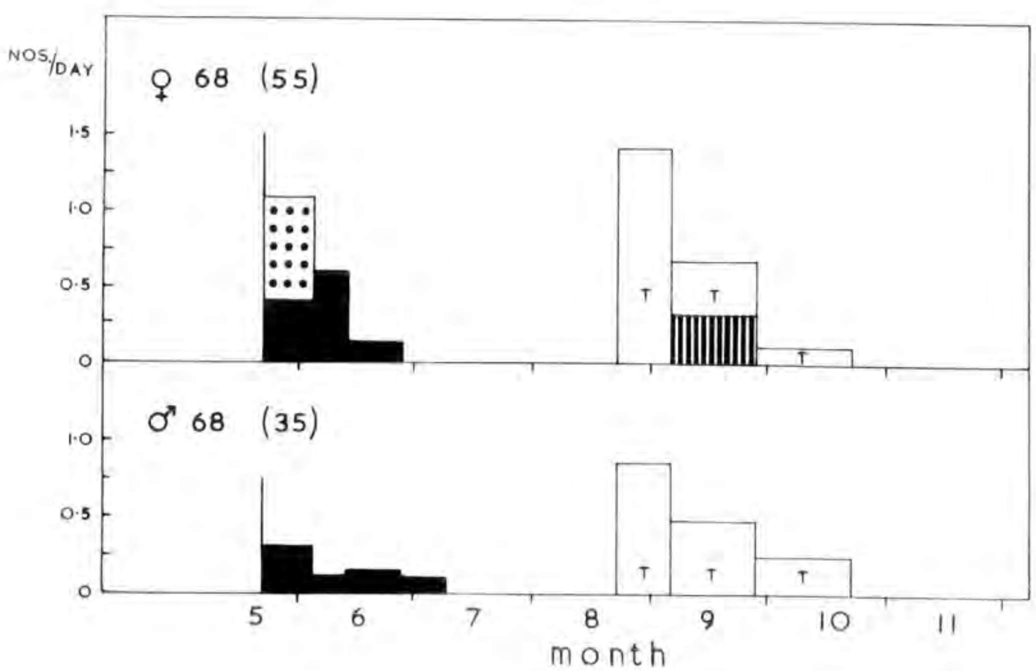
Key as in Fig.6.

FIGURE 23b. *Pterostichus madidus* : pitfall trap catches in 1968 on Sites 7 and 8.

Key as in Fig.6.



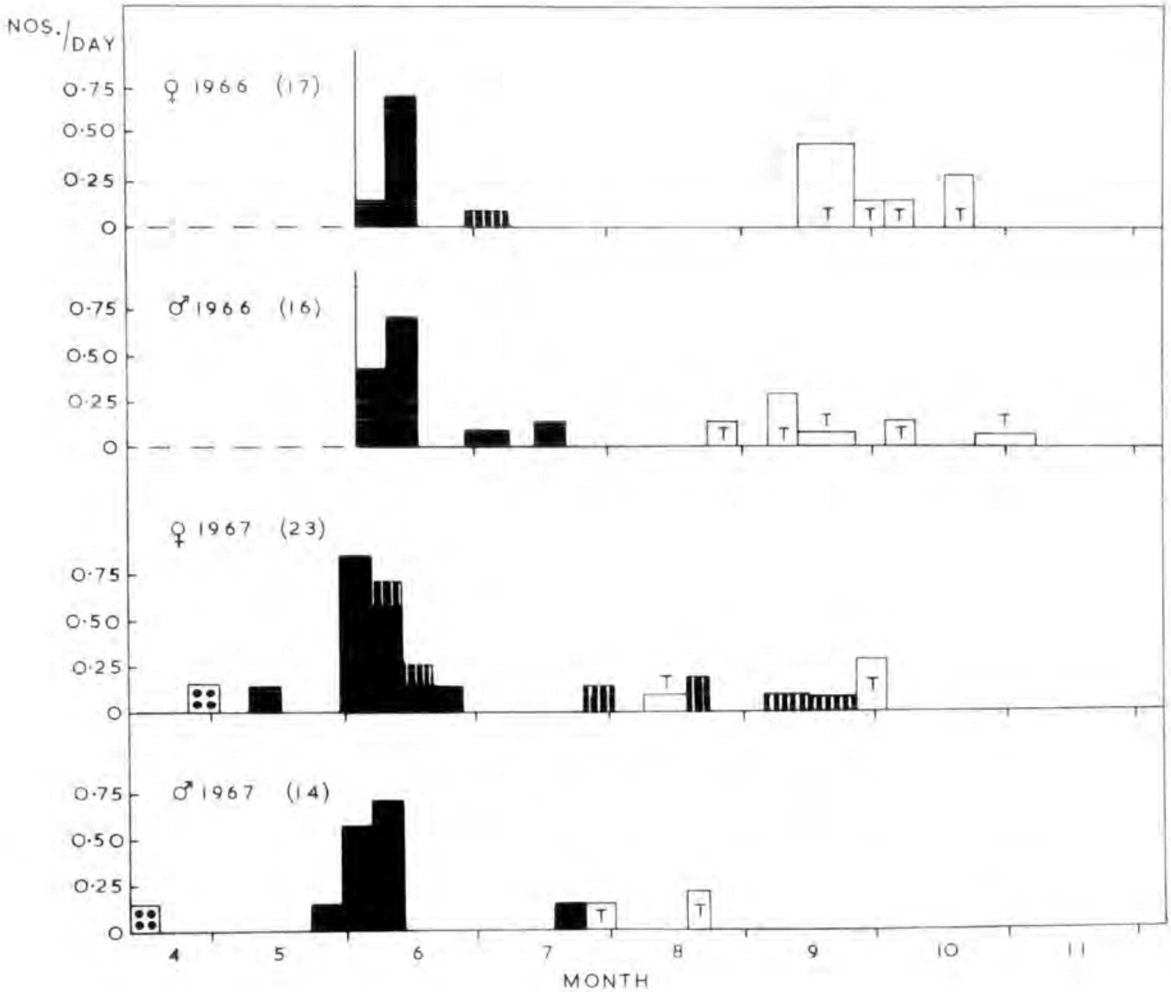
NOS/DAY
♀ 67 (19)
0·75
0·25
0
♂ 67 (16)
0·75
0·25
0
5
6
7
8
9
10
11
month



NOS/DAY
♀ 68 (55)
1·5
1·0
0·5
0
♂ 68 (35)
1·0
0·5
0
5
6
7
8
9
10
11
month

FIGURE 24. Pterostichus diligens ; pitfall trap catches in 1966 on Sites 1, 2 and 3, and in 1967 on Sites 4 and 5.

Key as in Fig.6.



NOS./DAY
♀ 1966 (17)
♂ 1966 (16)
♀ 1967 (23)
♂ 1967 (14)
0·75
0·50
0·25
0
T
4
5
6
7
8
9
10
11
MONTH

39. <u>Pterostichus madidus</u> Figure 23b

This species was frequently taken at Cow Green on non-wet habitats and details of dissections of pitfall trap catches from Sites 7 and 8 are given in Figure 23b. Dissection of material from the west side of the Moor House Reserve reveals a similar pattern. Information from the adults only, suggests that it has "summer" larvae and an annual life history. However, it has a biennial life cycle. Although no first instars were found (probably because of their burrowing habit), second instars were taken in August, September and October, and third instars in October, November, and older specimens in May and June. A few females in the spring of 1967 had developing ovaries with corpora lutea and very worn mandibles, indicating that they were entering at least their second breeding season.

40. <u>Pterostichus melanarius</u>

Taken only on the west side of the Moor House Reserve, mainly on flushed grasslands.

In the lowlands Briggs (1957) recorded that eggs were laid in August and September (but Murdoch 1967; July - October) and the new generation adults appeared the following June. Although primarily a larval overwintering species, some adults may also hibernate.

At Moor House immature females were taken in May; mature females in June and July, and one spent female in September. No teneral adults or larvae were found, but the life cycle is probably biennial and similar to P.madidus.

41. Pterostichus nigrita Figures 25 and 26a

Widely distributed and common, especially on the east side of the reserve, on wet habitats.

Pitfall trap catches of adults in 1966-67 are shown in Figure 25. First instar larvae were taken in June, second instars in June, July and August, and third instars in July and August. The larval head widths are given in Figure 26a.

42. Pterostichus strenuus Figure 26b

Found mainly on the flushed grasslands, but a very local species.

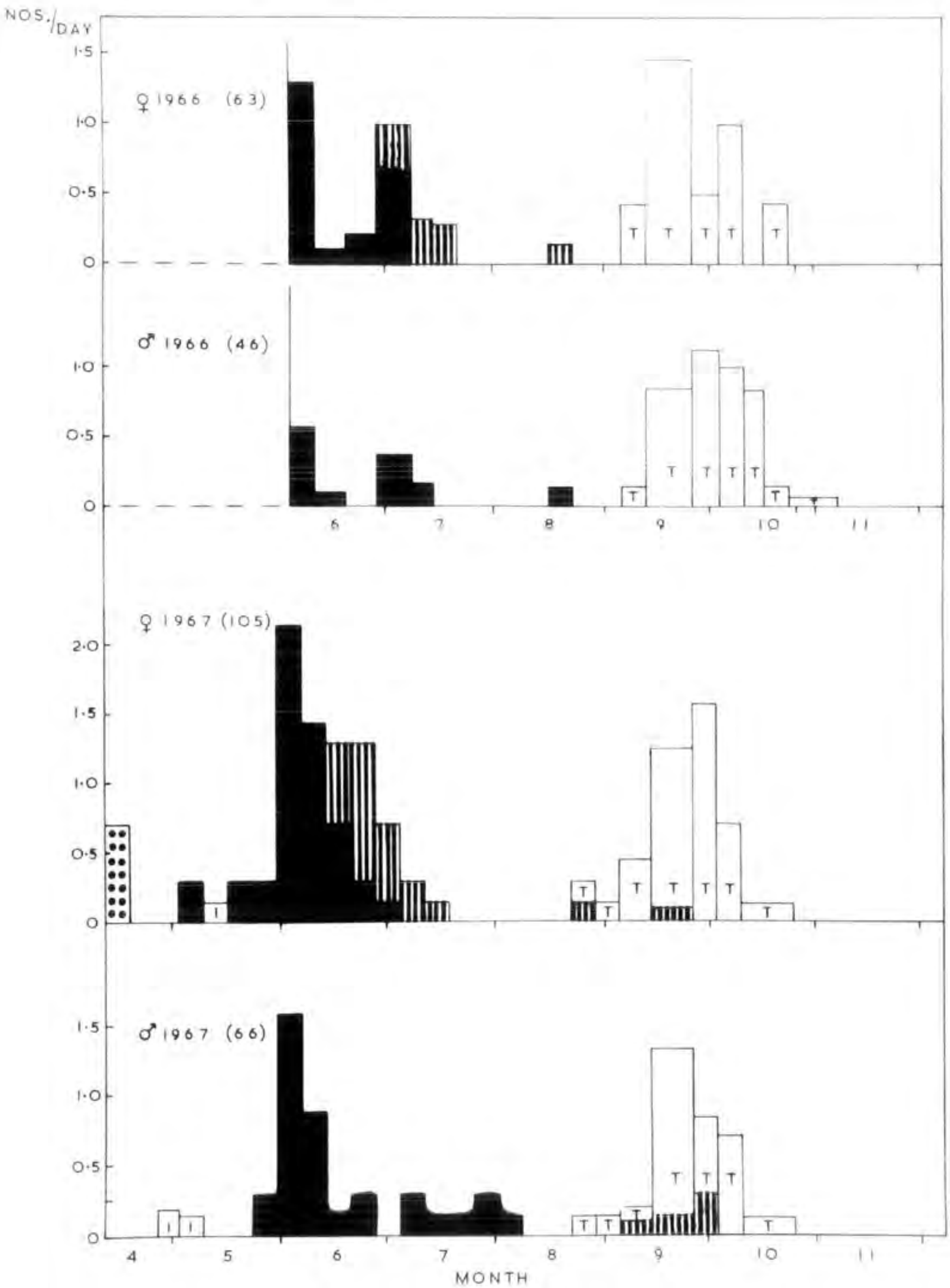
Pitfall trap catches are shown in Figure 26b. Third instar larvae were taken in August.

43. Trechoblemus micros (an occasional species)

Only two specimens were caught. One, a male, at the end of June at 2500 feet, the other, a callow female, in August. Both specimens were apterous, but Lindroth described this species as + winged and capable of flight.

FIGURE 25. Pterostichus nigrita : pitfall trap catches in 1966 on Sites 1, 2 and 3, and in 1967 on Sites 4 and 5.

Key as in Fig.6.



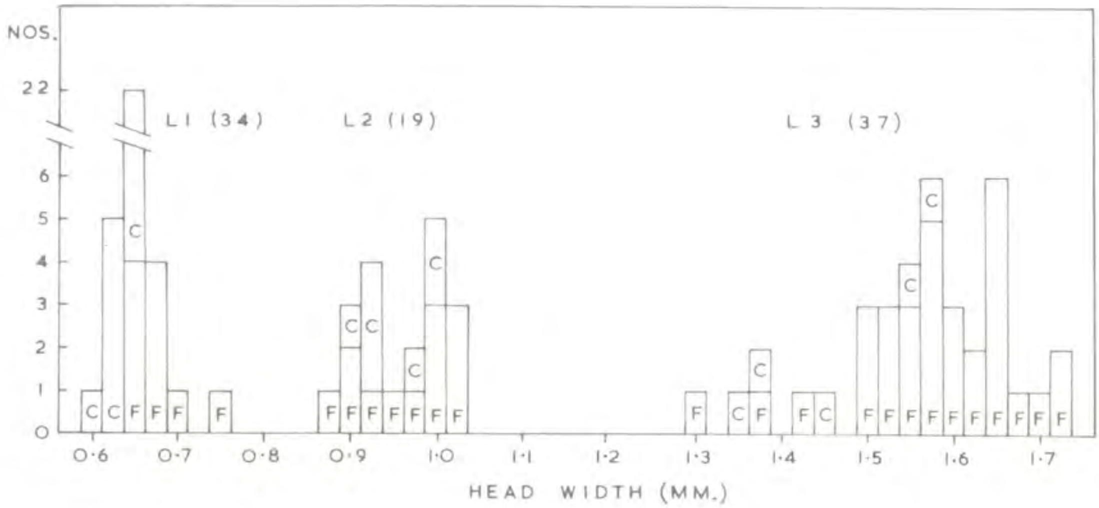
NOS./DAY
♀ 1966 (63)
♂ 1966 (46)
♀ 1967 (105)
♂ 1967 (66)
MONTH

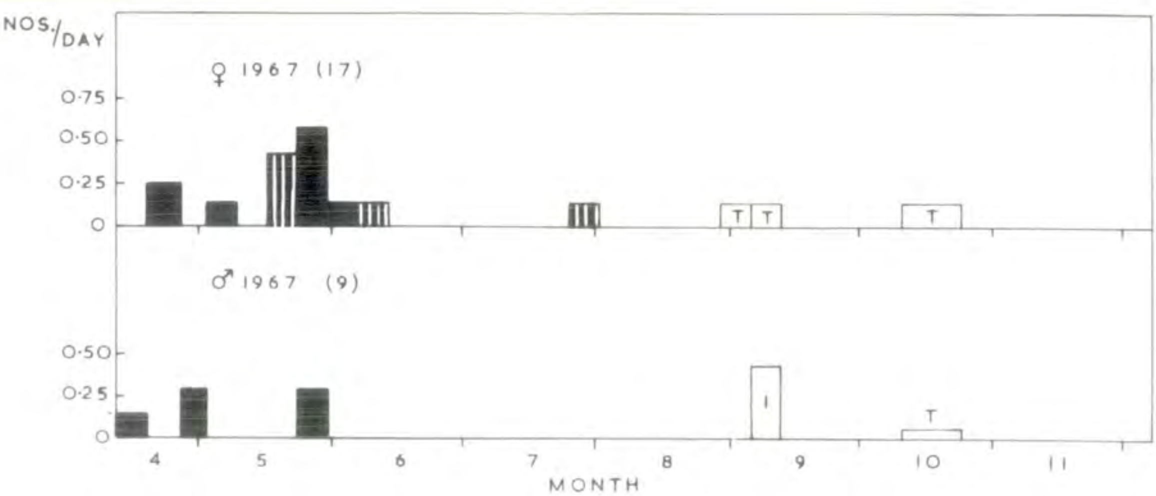
FIGURE 26a. Pterostichus nigrita : larval head widths.

C = specimens bred in the laboratory.

F = specimens caught in the field.

FIGURE 26b. Pterostichus strenuus : pitfall trap catches in 1967 on the Meadow (Site 6).


NOS.
22
6
5
4
3
2
1
0
L1 (34)
L2 (19)
L3 (37)
0·6
0·7
0·8
0·9
1·0
1·1
1·2
1·3
1·4
1·5
1·6
1·7
HEAD WIDTH (MM.)


NOS./DAY
♀ 1967 (17)
0·75
0·50
0·25
0
♂ 1967 (9)
0·50
0·25
0
4
5
6
7
8
9
10
11
MONTH

In Denmark it is a spring breeder and adult hibernator, but its status at Moor House is uncertain.

44. Trechus obtusus Figure 27

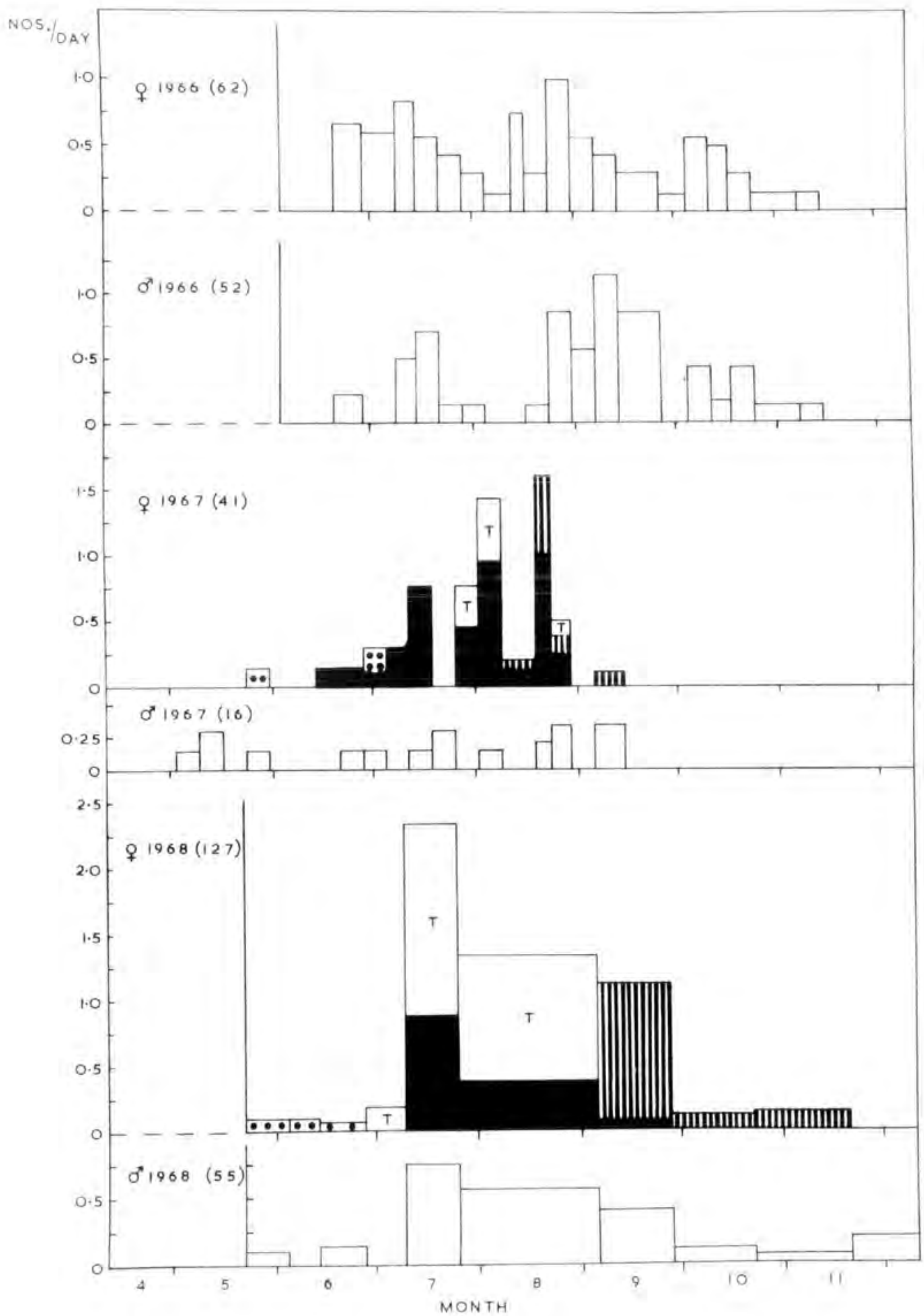
Widely distributed, not uncommon on the Blanket Bog, but found more frequently on the drier habitats.

Adult pitfall trap catches at Moor House and Cow Green are shown in Figure 27.

Numerous Trechus larvae were found, but it was not possible to identify them with certainty to species. Boldori's (1951) key uses the shape of the nasale as the diagnostic character, but the nasale were worn and this character is not considered reliable. However, the dates the Moor House and Cow Green larvae were taken indicated an adult that was an autumn breeder, and most were from areas where only T.obtusus was found.

T.obtusus was the only common Trechus species and their larvae were bred through to adults. Larvae of the other species could not be obtained and the identification of the Trechus larvae, as T.obtusus, is partly inferred. First instars were taken in August and October; second instars in August, October, February, March (and at 2780 feet in June); third instars from October to June, and pupae in June. Females with well worn mandibles were found at all altitudes

FIGURE 27. <u>Trechus obtusus</u> : pitfall trap catches in 1966 on Sites 1, 2 and 3, and in 1967 on Sites 4 and 5, and in 1968 on Sites 7 and 8.


NOS./DAY
♀ 1966 (62)
♂ 1966 (52)
♀ 1967 (41)
♂ 1967 (16)
♀ 1968 (127)
♂ 1968 (55)
T
MONTH

in the spring and early summer. Some had corpora lutea and were preparing to breed for at least a second time, whilst those without corpora lutea were preparing to breed for the first time and therefore had a biennial life cycle.

45. Trechus quadristriatus (an occasional species)

A scarce species, taken almost entirely in the Meadow in August, September and October, but mature females only in August. Lindroth records it as slightly xerophilus, and Larsson as an autumn breeder and larval hibernator. If it breeds at Moor House a similar life cycle is indicated.

46. Trechus rubens (an occasional species)

One immature female was found in a frog's stomach on 3 July 1966, one mature female (which had laid eggs) in another stomach on 3 July 1966, one teneral female on 25 July 1968, and a male and a female, both teneral, at the beginning of October. The frogs and the other three specimens were caught on redistributed peat and the frogs' stomach contents were typical of redistributed peat fauna.

Larsson & Gigja (1958) state that it has special swarming periods and some individuals may be carried far from their original breeding site (biotopes well protected against sudden desiccation, preferably with luxuriant vegetation.)

In Iceland it is a spring breeder with summer larvae and overwintering adults, but Larsson notes that the stability usually characterising the developmental cycle of ground beetles seems to be lacking.

No larvae were identified and it remains uncertain whether it breeds at Moor House.

47. <u>Trechus secalis</u> (an occasional species)

Only two females were taken; one from a frog's stomach taken on the redistributed peat, the other a teneral from an alluvial grassland soil core cut on 20 June 1967. Two males were caught on Site 9. No larvae were identified, but as it is flightless, it probably breeds at Moor House and Cow Green. Larsson and Lindroth record it as an autumn breeder and larval hibernator.

48. <u>Trichocellus cognatus</u> (an occasional species)

Single specimens were taken throughout the Moor House Reserve on wet and slightly wet habitats.

Mature females were taken at the beginning of July and one teneral female in October. There is no evidence that it breeds at Moor House, but at Waldridge Fell (a <u>Calluna</u> heath a few miles to the north of Durham City) mature females were taken in March, April and the beginning of May, and Lindroth also records it as a spring breeder and imago hibernator.

APPENDIX

II. A guide to the British species of the genus *Patrobus* Col., Carabidae)

The genus *Patrobus* was erected by Stephens in 1827, and Moore (1957a) lists three species from the British Isles. The adults can be identified using the keys of Fowler (1887) and Joy (1932). The brachypterous *Patrobus assimilis* and *P.atrorufus* can be difficult to separate without reference to the genitalia but *P.septentrionis* is readily distinguished by its larger size and macropterous condition.

Fowler states that the *P.atrorufus* adult has a smooth forehead whereas that of *P.assimilis* is tranversely wrinkled and uses this character to separate the species. However, specimens of *P.atrorufus* with distinctly wrinkled foreheads and of *P.assimilis* with almost smooth foreheads have been found and this character is not considered reliable.

Joy uses the shape of the antennae to separate *P.assimilis* and *P.atrorufus*. This character, although reliable, is often difficult to see and can be missed if the antennae are not viewed from the correct aspect. *P.atrorufus* could thus be mistaken for *P.assimilis*.

The apex of the aedeagus and the stylus of the ovipositor of all three species are characteristic and can often be seen in situ. The sexual and other characteristics of the adults of the three species are given below and the larvae are also described.

ADULTS

P.septentrionis Dejean

Length 8-10mm, male usually smaller than the female; macropterous; head and thorax pitchy to pitchy red, elytra often lighter, legs reddish; the striae of the elytra continued to the apex and the puncturation feint. The aedeagus (Figure 28h) and the stylus of the ovipositor (Figure 28c) are characteristic.

In England it has been found in Lancashire, Yorkshire, ? Cumberland and Northumberland; in Scotland in the east and west highlands (Moore 1957a).

P.assimilis Chaudoir

Length 6.5-8mm, the male usually smaller than the female; brachypterous; head, thorax and elytra pitchy black to reddish, legs reddish; the striae and puncturation of the elytra variable, often evanascent at the apex and the puncturation at the base strong; antennal segments rounded (Figure 28d); forehead usually distinctly transversely wrinkled but almost smooth forms do occur.

The aedeagus (Figure 28f) is distinctly rounded with a pointed apex which readily distinguishes this species from P.atrorufus. The stylus of the ovipositor (Figure 28a), about 1.5 times as long as broad, is characteristic of this species.

In Britain it is found in the upland areas of northern England, Wales and Scotland, although in the north of Scotland it may be found at sea level.

P.atrorufus Ström.

Length 7-9mm, male usually smaller than the female; brachypterous; head, thorax and elytra pitchy to reddish, legs reddish; the striae of the elytra visible to apex but puncturation feint; antennal segments slightly flattened and sides not evenly rounded (Figure 28e); forehead generally smooth but slightly transversely wrinkled forms do occur.

The aedeagus (Figure 28g) is straight and the apex squarish which readily distinguishes this species from P.septentrionis and P.assimilis. The stylus of the ovipositor (Figure 28b) more than twice as long as broad, is similar to P.septentrionis but smaller.

This species is widely distributed throughout Britain (Moore 1957b).

FIGURE 28. Diagnostic features of *Patrobus* adults.

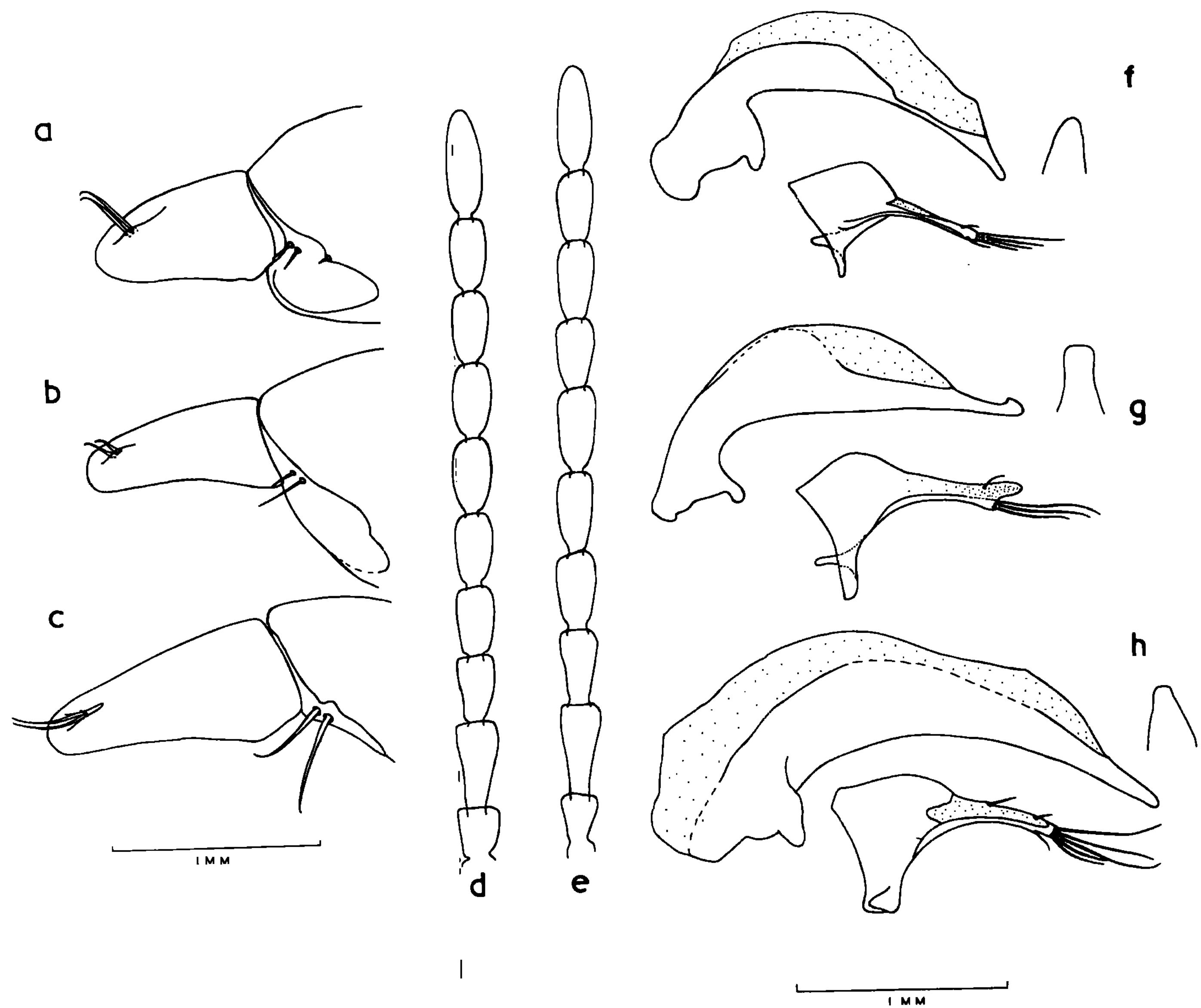
a-c Left stylus of ovipositor, ventral view.

a. *assimilis* b. *atrorufus* c. *septentrionis*

d,e Antenna d. *assimilis* e. *atrorufus*

f-h Lateral view of the aedeagus and right paramere, and dorsal view of the tip of the aedeagus (not on the same scale)

f. *assimilis* g. *atrorufus* h. *septentrionis*



a
b
c
1 MM
d
e
f
g
h
1 MM

LARVAE

The larvae can be identified to genus using the keys of Boving & Craighead (1930) and van Emden (1942). Schiødte (1867) described Patrobus atrorufus larvae and Larsson (1968) published a key to the three species. He separates P.assimilis from the other two species using the relative lengths of the maxillary palpal segments, while P.atrorufus and P.septentrionis are separated on the form of the nasale. Although the nasale for each species is characteristic, it is invariably broken or worn, often making identification using this character impossible. The difference in the form of the maxillary palp of the specimens examined was slight and other characters have therefore been used.

No P.septentrionis second instar was available and only one first and one third instar was studied. The third instar was not of British origin. All instars of the other two species were numerous and specimens have also been bred ex ovo.

The first instars are readily distinguishable by their head widths (Table 34, Figure 29), the presence of egg bursters (Figure 30b, e, h) and the presence of only five large cercal setae. Although egg bursters persist into the second instar on some species of carabid, there was no evidence of this amongst the Patrobus specimens examined. In all instars the setae on the inner side of the maxilla (Figures 30 o,p,q and 31 a,b,c) and, if not worn, the shape of the nasale (Figure 30 a-h) can be used to separate the species.

P.assimilis second and third instars are also readily distinguished from the other two species by the number of cercal setae and from P.atrorufus by the colour of the cerci (Table 34).

No second instar P.septentrionis larva was available but it would be expected to be similar to the third instar.

The third instars of P.septentrionis and P.atrorufus are readily separated by the form of the maxillae (Figure 30, o,p,q). The head width alone would probably separate off the third instars of P.septentrionis, but more specimens are required to determine the reliability of this character. The same applies to the colour of the cerci.

A few specimens of the genus Patrobus were taken at Moor House which showed features characteristic of both P.assimilis and P.atrorufus. They were only found on the alluvial and limestone grasslands where adults of both species occur, but with the above exceptions, where only the characteristic P.atrorufus larvae were found. The form of the nasale and the number of cercal setae varied, but the maxillae had about one and a half rows of stout setae on the inner side and appeared to be a variation of P.assimilis. The cerci were sometimes bi-coloured, but not as dark as P.assimilis.

These larvae were not found where only P.assimilis adults were taken or in lowland areas where only P.atrorufus adults were taken, as might be expected if they were a variety of one or the other.

There is no laboratory evidence that the above two species interbreed, but crosses between carabid species have been recorded (De Miré 1964), and these larvae may be the result of interbreeding.

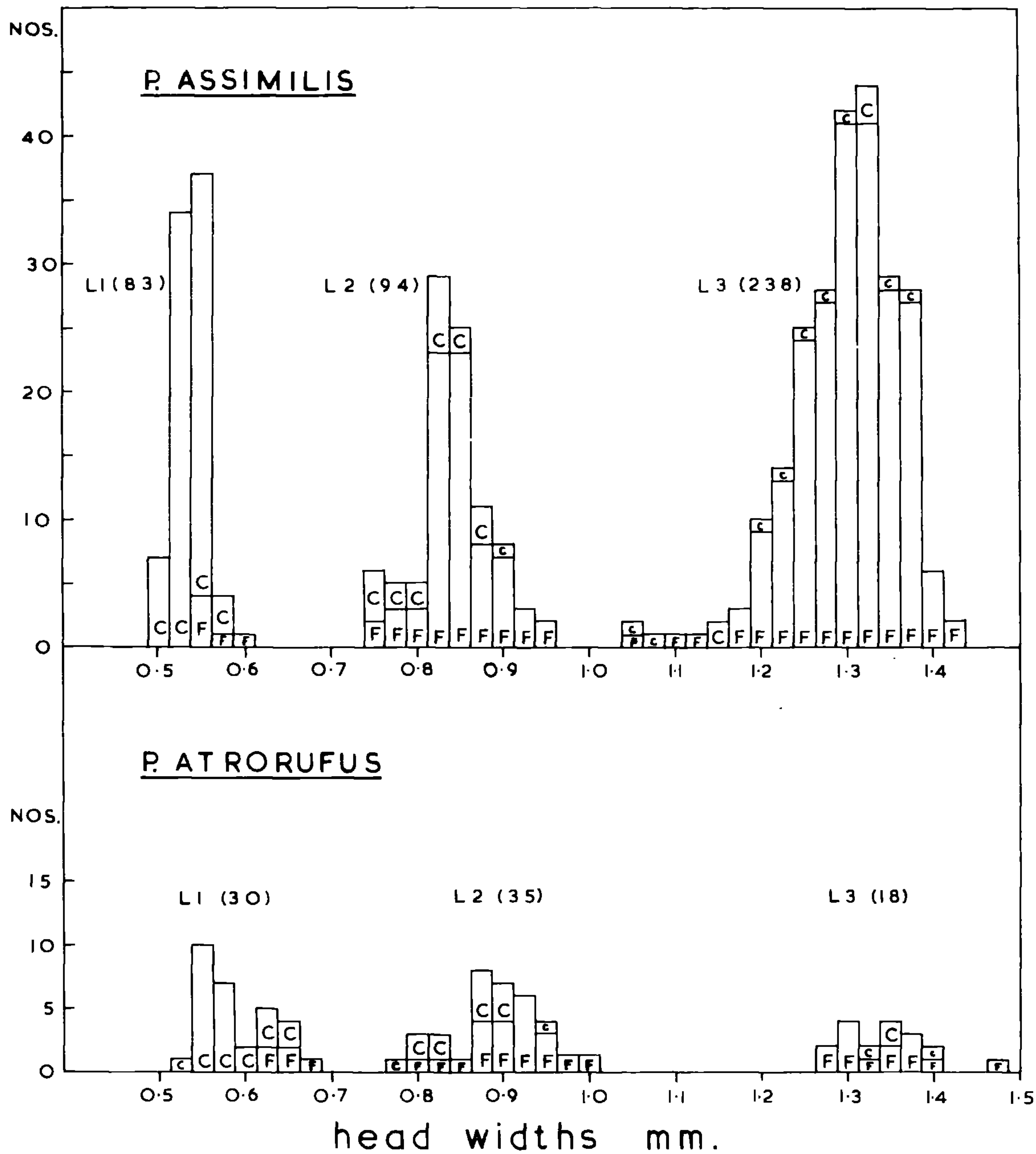
TABLE 34. DETAILS OF PATROBUS LARVAE

		Nos. studied	Head widths (mm) min.	mean	max.	Cerci colour	Nos. of setae
P.septentrionis							
	L1	1	-	0.65	-	uniformly light	5
	L2	0	-	-	-	-	-
	L3	1	-	2.25	-	bicoloured, end 1/3 darker	6
P.assimilis							
	L1	83	0.50	0.54	0.60	uniformly light	5
	L2	94	0.75	0.84	0.95	bicoloured, end 1/2 darker	7
	L3	238	1.05	1.30	1.43	bicoloured, end ½ darker	7
P.atrorufus							
	L1	30	0.53	0.59	0.69	uniformly light	5
	L2	34	0.78	0.89	1.00	uniformly light	6
	L3	16	1.28	1.35	1.48	uniformly light	6

FIGURE 29. Patrobus assimilis and P.atrorufus : larval head widths.

C = specimens bred in the laboratory

F = specimens caught in the field



NOS.
P. ASSIMILIS
L1 (83)
L2 (94)
L3 (238)
0·5
0·6
0·7
0·8
0·9
1·0
1·1
1·2
1·3
1·4
P. ATRORUFUS
NOS.
L1 (30)
L2 (35)
L3 (18)
1·5
head widths mm.

FIGURE 30. Diagnostic features of *Patrobus* larvae.

a-h Nasales :

a L3, b L1 of *septentrionis*

c L3, d L2, e L1 of *assimilis*

f L3, g L2, h L1 of *atrorufus*

1-m Left antenna of third instar larvae

1 *septentrionis*

m *assimilis*

n *atrorufus*

o-p Left maxilla, dorsal view, third instar larvae

o *septentrionis*

p *assimilis*

q *atrorufus*

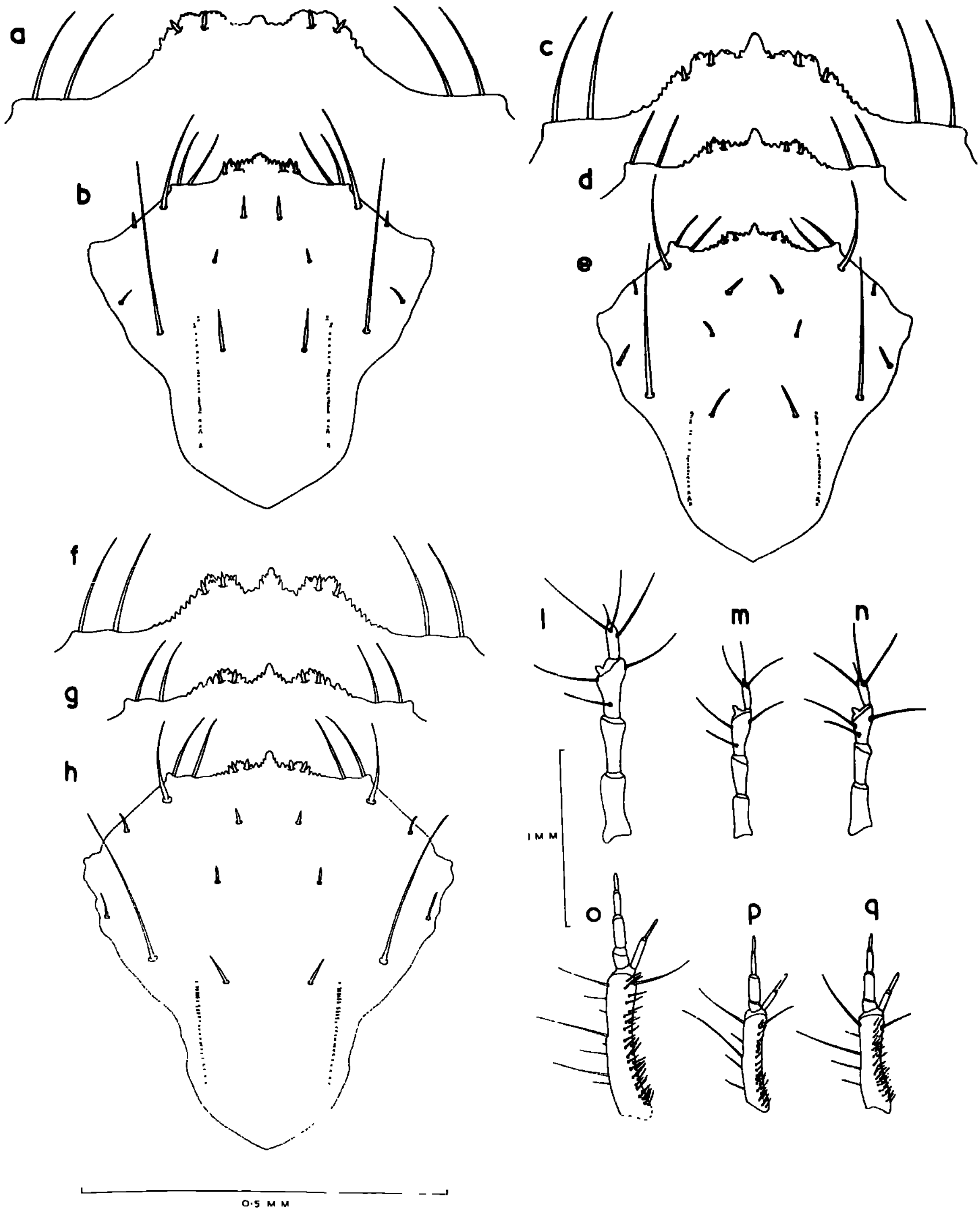

a
c
b
d
e
f
g
h
l
m
n
1 MM
o
p
q
0·5 MM

FIGURE 31. Diagnostic features of Patrobus larvae

a-c Left maxilla, dorsal view, of the first instar larvae

a septentrionis

b assimilis

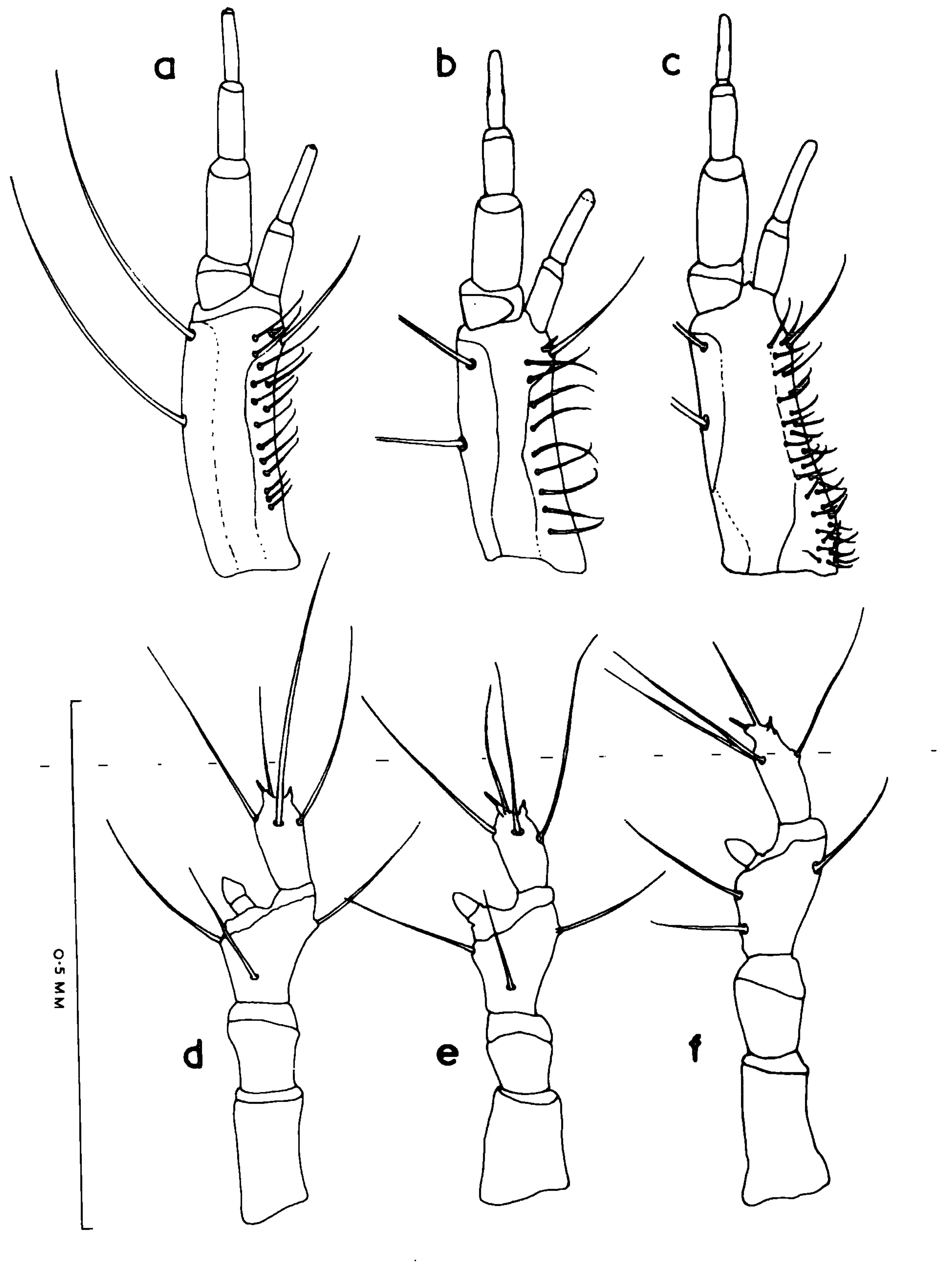
c atrorufus

d-f Left antenna, dorsal view of the first instar larvae.

d septentrionis

e assimilis

f atrorufus


a
b
c
d
e
f
0·5 MM

<u>Patrobus</u> larvae; key to the British species

1. Egg bursters present; cerci with 5 large setae (1st instars) 2

- No egg bursters; cerci with more than 5 large setae (2nd and 3rd instars) 4

2. Stipes of maxillae with 2 - 3 rows of setae (Fig.31c) <u>atrorufus</u> L1

- Stipes of maxillae with less than 2 rows of setae Fig.31a&b) 3

3. Setae of maxillae as in Fig.31a <u>septentrionis</u> L1

- Setae of maxillae as in Fig.31b. A few extra setae may be present at the base as found in the 2nd and 3rd instars (Fig.30p). Nasale with central tooth prominent (Fig.30e) <u>assimilis</u> L1

4. Cerci with seven large setae and bi-coloured (end half dark). Maxilla as in Fig.30p; nasale, unless worn, with central tooth prominent (Fig.30c&d) <u>assimilis</u> L2 or L3

- Cerci with six large setae 5

5. Maxillae with three variable rows of setae (Fig.30q);
Cerci unicoloured - uniformly light

atrorufus L2 or L3

- Maxillae very elongate with more or less two rows of setae (Fig.30o)

septentrionis (L2) & L3

APPENDIX

III. Taxonomic observations on Nebria larvae

Three of the five species of Nebria found in Britain, (N.brevicollis, N.salina, and N.rufescens), (Moore 1957a), occur at Moor House and Cow Green (Houston, in press).

N.nivalis, Blair (1950) has been found at high altitudes in the Cairngorms and on Ben Nevis, Scotland, and N.livida on the east coast of England on clay cliffs and in Staffordshire. No second instar N.livida and no N.nivalis larvae or details concerning them were available, and they are therefore not included here.

The larvae can be identified to genus using Van Emden's key (1942).

The characters used to separate N.brevicollis, N.salina and N.rufescens, in this present study, are shown in Table 35 and Figure 32. Characters for N.livida are included for comparison. This is not intended to be a comprehensive key as one is in press (Luff, pers.comm.).

The head widths were measured at the widest part behind the eyes. The length of the second antennal segment characterises each species, but as each specimen varied slightly in size, the ratio of the width to the length is used. The average width of the segment, generally that at the middle, was measured from the dorsal view. (The shape of the second antennal segment of N.nivalis is not known.)

TABLE 35. **DETAILS OF <u>NEBRIA</u> LARVAE**

Figures in brackets indicate the number of specimens measured for each character.

		head widths (mm) min	mean	max		2nd antennal segment shape	ratio width: length		Cerci length (mm)	Length of cerci/head width	
brevicollis	L1	-	0.95	-	(3)	quadrate	1:1	(6)	1.81	1.9	(3)
	L2	-	1.25	-	(1)	quadrate	1:1	(9)	2.5	2.0	(3)
(all ex ovo)	L3	1.6	1.71	1.79	(4)	elongate	1:1.2	(4)	3.75	2.12	(3)
salina	L1	0.80	0.86	0.88	(8)	transverse	1:0.58	(11)	1.6	1.87	(11)
	L2	-	1.03	-	(1)	transverse	1:0.75	(4)	2.42	2.35	(1)
	L3	-	1.63	-	(1)	slightly elongate	1:1.01	(4)	3.08	1.93	(1)
rufescens	L1	0.88	0.9	0.95	(8)	elongate	1:1.16	(8)	1.52	1.68	(2)
	L2	1.1	1.18	1.23	(24)	elongate	1:1.54	(20)	2.16	1.91	(4)
	L3	1.48	1.55	1.63	(35)	elongate	1:1.85	(20)	2.43	1.88	(4)
livida	L1	-	1.03	-	(1)	very elongate	1:2.14	(1)	1.98	2.02	(1)
	L2	-	-	-		-	-	-	-	-	-
	L3	-	2.06	-	(1)	very elongate	1:3.0	(1)	4.43	2.15	(1)

FIGURE 32. Nebria larvae. Diagrams of the right, seventh, abdominal tergite, of the first, second and third instar larvae of

a N.salina

b N.rufescens

c N.brevicollis

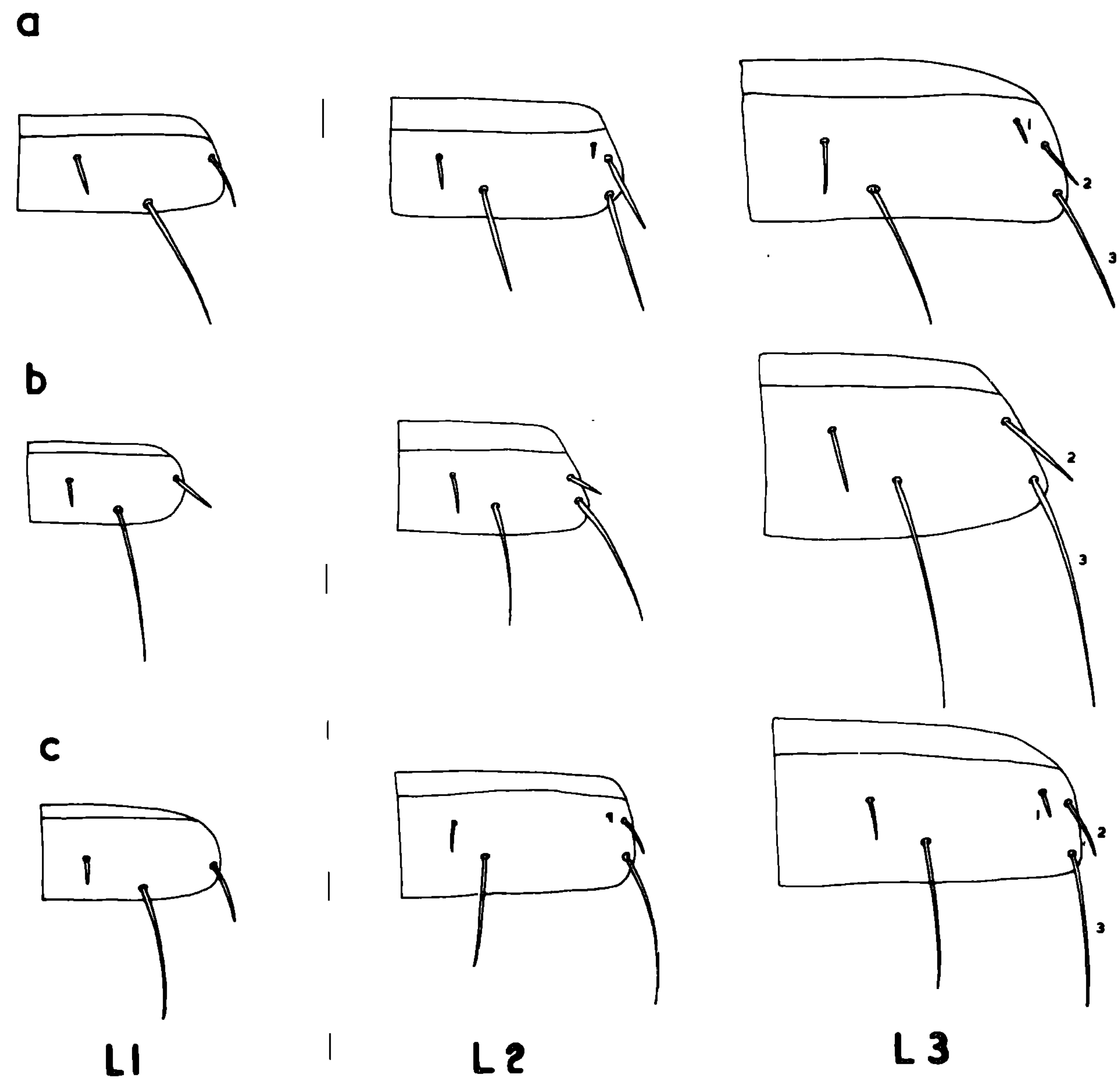

a
b
c
L1
L2
L3
1'
2
3
1

Figure 32 shows diagrammatically the position of the large setae on the right seventh abdominal tergite of each instar. (Other tergites are similar.) In the third instars, N.brevicollis and N.salina have five and N.rufescens only four. N.livida has an extra one between the setae labelled 2 and 3, but the position of these three setae is very variable. N.brevicollis and N.salina can be further separated by the position of setae labelled No.1. The angle between 1 to 2 and 3 to 4 is less obtuse in N.salina. The angle does vary and this character should not be used alone. In the second instar of these two species, setae No.1 is sometimes missing.

APPENDIX

IV. A mechanical time sorting pitfall trap

INTRODUCTION

A method is often required which will record, in the field, the diel activity of certain terrestrial arthropods. Williams (1958) described a piece of apparatus for the mechanical time sorting of pitfall captures, and the literature concerning trapping methods was reviewed by Southwood (1966).

This section describes an apparatus which is a modification of Williams' (1958) method. It was designed to separate the captures of Carabidae into predetermined periods of each day and which, if required, could be left to run unattended for 8 days.

The apparatus was used in conjunction with a length of gutter, as previously employed by Schjøtz-Christensen (1965), to increase the numbers of individuals captured.

Description of apparatus

The apparatus, whose details are shown in Figures 33 & 34, consists of a chute, which collects Carabidae and other arthropods falling through the outlet pipe of the gutter, and which is revolved once per day by a 24hr clock. Surrounding the clock and below the circle described by the chute outlet is a container

FIGURE 33. The mechanical time sorting pitfall trap : essential features of the apparatus.

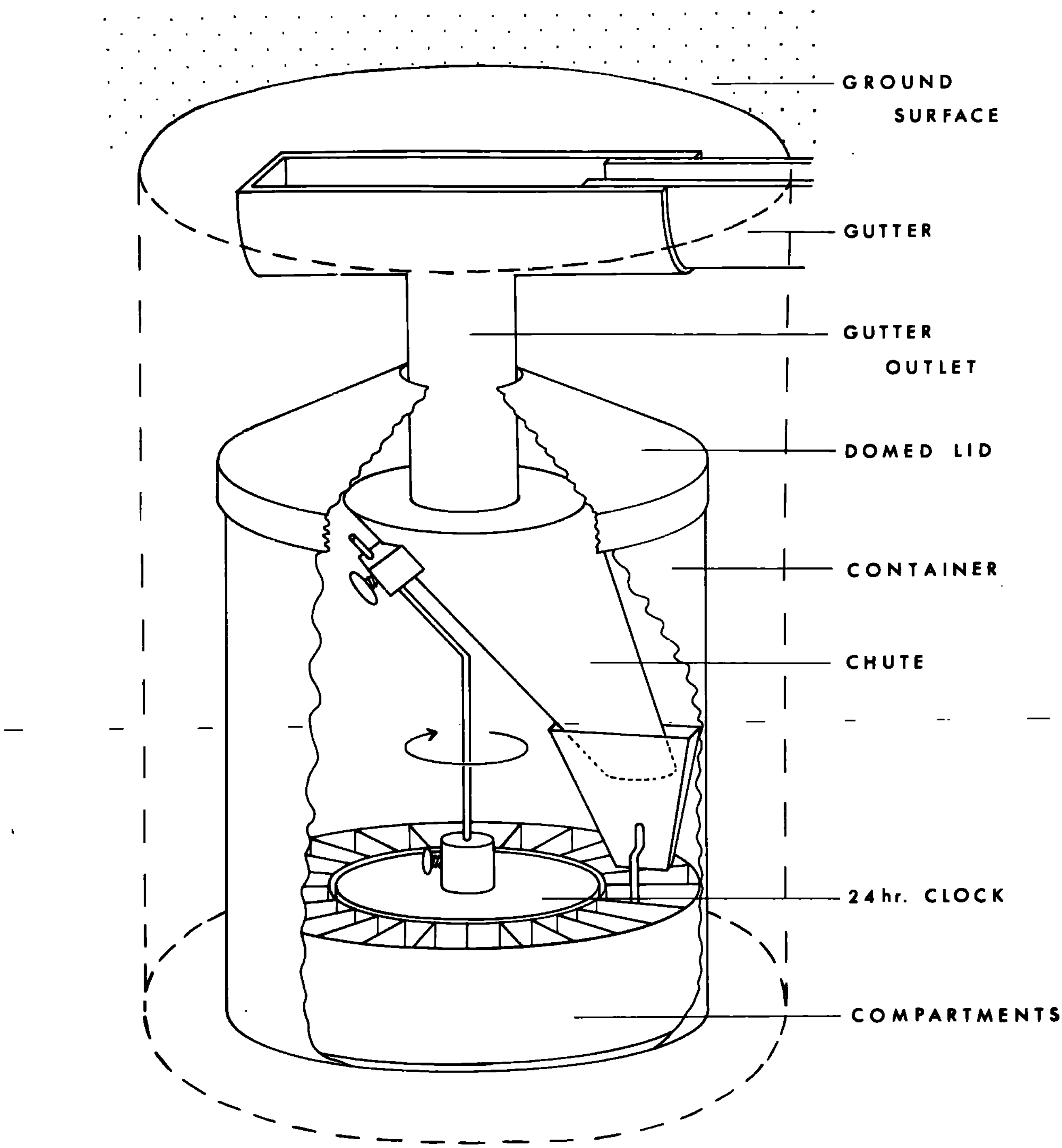
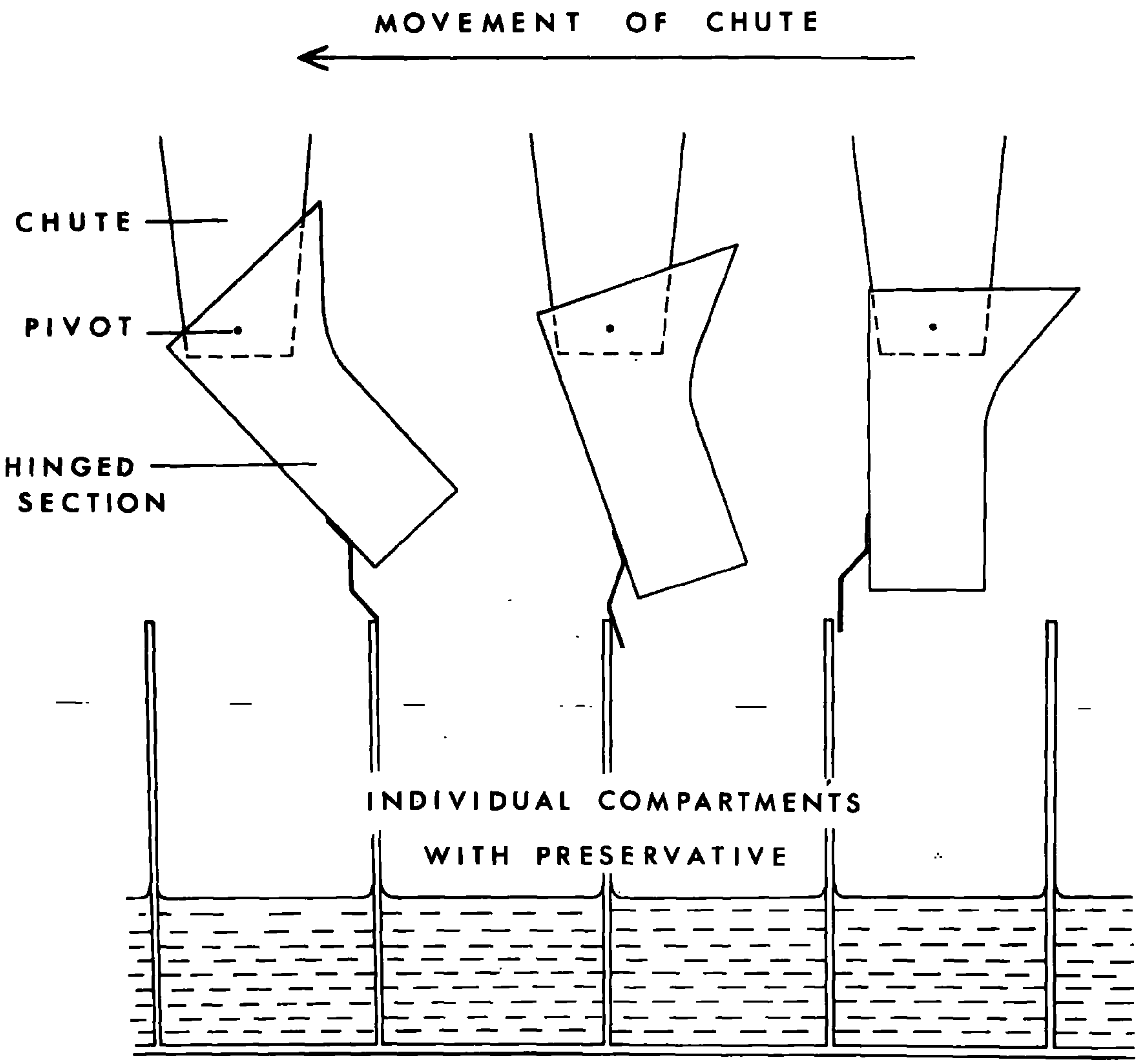

GROUND SURFACE
GUTTER
GUTTER OUTLET
DOMED LID
CONTAINER
CHUTE
24 hr. CLOCK
COMPARTMENTS

FIGURE 34. The mechanical time sorting pitfall trap : mode of action of the hinged section.


MOVEMENT OF CHUTE
CHUTE
PIVOT
HINGED
SECTION
INDIVIDUAL COMPARTMENTS
WITH PRESERVATIVE

outer diameter 22cm divided into 24 individual numbered compartments which can be filled with preservative.

The end of the chute was provided with a hinged section (see Figure 34) to ensure that any Carabidae falling into the chute would be directed into the compartment appropriate for that time of the day. The angle of the chute was 50^{o} to the horizontal and the surface sprayed with Polytetrafluoroethylene to reduce the chance of an insect sticking to it.

The whole apparatus was enclosed in a large watertight container, with a hole in the domed lid to take the gutter outlet, and sunk into the ground below the level of the gutter.

The chute and the compartments were constructed from sheet metal. The compartments were removable as one block to facilitate emptying and cleaning.

A 2m length of plastic roof-gutter, semi-circular in cross section, 5cm radius, was placed with its top edges flush with the ground surface and with a removable outlet end positioned over the chute in the container. It is important that there is no gap between the gutter and the ground surface, otherwise many arthropods will not fall into the gutter.

The delay between an insect falling into the gutter and entering the time sorting apparatus must be taken into consideration when assessing the results. Large species, e.g.

Carabus problematicus Hbst., often fell through within a minute, but small species, e.g. *Trechus obtusus* Er., sometimes took longer - especially if there was litter on the floor of the gutter.

To prevent rainwater filling the trap, a section of the floor of the gutter at both ends was removed and replaced with a piece of fine gauze. Owing to the very slippery nature of the plastic when clean, the floor of the gutter was rubbed with an abrasive to allow unimpeded movement of the arthropods. The walls were left smooth and kept clean to prevent specimens crawling out. A piece of chicken wire was placed over the gutter to keep out litter, frogs and small mammals.

To ensure accuracy of the sorting mechanism into hourly periods it is important that the tops of the walls dividing each compartment are on the same plane and equally spaced, and that the axis of movement of the chute is perpendicular to this plane and in the centre of the compartments. Accuracy to within $\pm$ 5 minutes was considered satisfactory.

APPENDIX

V. A reliable and permanent method for marking Carabidae (Col.)

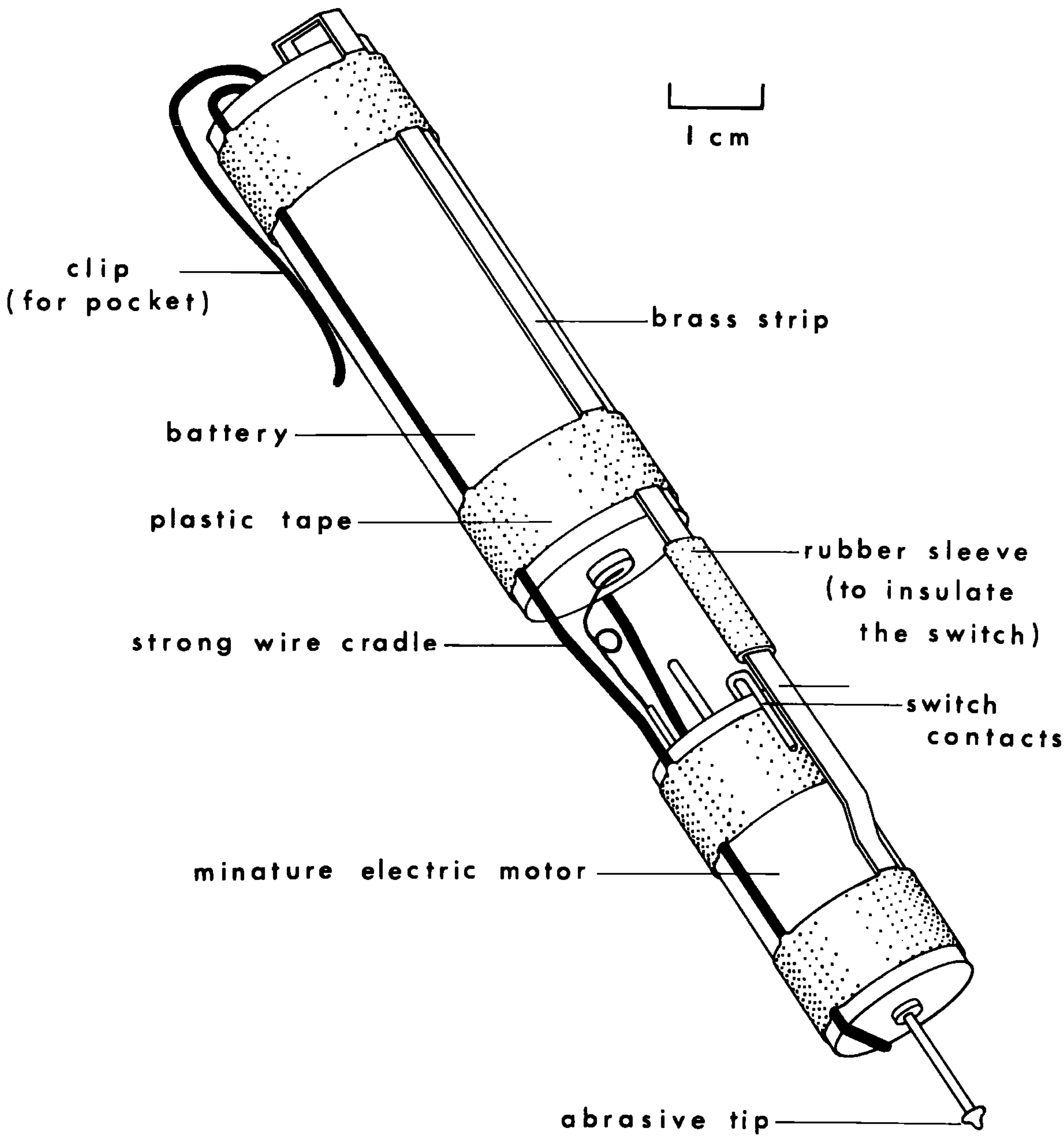
A method for marking insects is often required which is cheap, permanent, individual and easily recognisable, causes no detrimental effect to the specimen and can be quickly and easily applied in the laboratory and in the field.

Numerous notes and papers have been published concerning marking methods and Southwood (1966) reviewed the literature. Various methods were tried for marking Carabidae, including clipping off parts of the elytra (Gilbert 1952), paints (Greenslade 1963), and micro-cautery (Schjøtz-Christensen 1965), but a simple, reliable and permanent method of individually marking Carabidae in the field was still wanting. The following method and apparatus was therefore devised.

METHOD

Figure 35 shows details of the apparatus. A chip of fine carborundum was stuck, using an epoxy resin, onto the end of the armature of a miniature 1.5-6 volt D.C. electric motor. This piece of carborundum was then carefully ground down against the rest of the carborundum stone, using the motor as a lathe, until it was the required shape. Various shapes were tried, but the most useful was as shown in Figure 35. The chip was about 3mm long and 2mm diameter at the base. The point of

FIGURE 35. Diagram of the marking apparatus.


1 cm
clip
(for pocket)
brass strip
battery
plastic tape
rubber sleeve
(to insulate
the switch)
strong wire cradle
switch
contacts
minature electric motor
abrasive tip

the tip was ground away until it was approximately 150μ diameter. The tip of the abrasive was used for making small marks (approx. 200μ diameter) on the surface of the cuticle, usually on small beetles, e.g. Notiophilus germinyi, while the shoulders were used for making larger marks (approx. 500μ diameter) usually on the larger beetles, e.g. Carabus glabratus. It is important that the tip is not sharp otherwise a hole is easily drilled right through the cuticle.

On N.germinyi it was possible to place marks in at least seven different positions on each elytra and five on the thorax. On larger beetles a much greater number of positions was possible. These marks could be applied and recognised in the field but it was necessary to use a magnifying glass when dealing with the smaller species. It sometimes proved difficult to mark the elytra of teneral specimens, but this was overcome by marking the edge of the thorax. With practice a beetle could be marked and identified within a minute.

The motor was further modified so that the armature could move freely along its axis for about 3mm. This helped to avoid excess pressure applied during marking. A pressure switch, which could be operated by the forefinger, was attached to the motor.

Sections through the thorax of marked beetles showed no damage to the tissue beneath the cuticle, as was often the case when using the micro-cautery method. Numerous marked species were kept in the laboratory, some for over a year, with no apparent effect on their behaviour or longevity.