A study of the upland and lowland forms of the harvestman mitopus morio

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A STUDY OF THE UPLAND AND LOWLAND FORMS OF THE HARVESTMAN MITOPUS MORIO

by

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being

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C O N T E N T S

INTRODUCTION

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"The geographic variation of the species is the inevitable consequence of the geographic variation of the environment." (Mayr, 1963).

The external environment is continuously variable in climatic factors and in habitat and biotic factors. A species must be adapted to the particular demands of the local environment in the different parts of its range. Every local population is under continuous selection pressure for maximum fitness in the particular locality in which it occurs, and therefore differs from other local populations. The variation in biotic factors and habitat factors are often local, and in a mosaic pattern. Climatic factors however tend to change more slowly over large areas, except where altitude is concerned. This special case is often of particular interest.

The harvestman Mitopus morio (Fabricius) is an extremely widely distributed species, occurring virtually throughout the Palaearctic and Nearctic zones. It ranges from North Africa and Persia to within the arctic circle in Scandinavia and Greenland, and also occurs throughout North America. The habitats it has been found in range from under dead seaweed on the shore, to the sterile alpine zone of high mountains. Between these extremes, it occurs in virtually all habitats. (Stipperberger, 1928; Henriksen, 1938; Bristowe, 1949).

Such a widely distributed species must show great variation in its physiological and ecological adaptation to local environments. M. morio also shows great variety in its morphology. In 1928 Stipperberger wrote of specimens she found in the

North Tyrol:

> "The great amplitude of variation, in body colour and markings, as well as in size, and in the length and armament of the legs, was repeatedly the cause of mistakenly setting up new species."

Before 1923 when Roewer wrote his monograph on the harvestmen, Mitopus had been divided into several species, mainly on the grounds of colouration and size. Roewer grouped all these as subspecies of Mitopus morio. Three varieties of M. morio had been described for the British Isles (e.g. Pickard - Cambridge, 1890). Of these, one was the typical form M. morio which was found throughout the lowland areas, the other two forms were both found in upland areas. The upland forms varied in size and colouration, both from each other and from M. m. morio, M. m. cinerascens being smaller and dull in colour, and M. m. alpinus larger and brightly coloured.

Girling (1969) using M. morio to study the effects of altitude on the ecological characteristics of a widely distributed species, found that the moorland population was not uniform. Having realised that the three different forms were involved, she briefly described a method for separating them based on the leg dimensions.

The life cycle of Mitopus morio has been described by Todd (1949) for lowland specimens from Wytham Woods, Oxford. She found immature specimens from the beginning of April until July, and mature specimens from July until they disappeared in October. She concluded that they overwintered as eggs. This was confirmed for Durham by Phillipson (1959), who found that the times varied with the weather conditions. From hatching to maturity there are seven instars. The first instar occurs mainly within the egg, and moulting to the second instar takes place soon after hatching. Thus the second instar is normally the first one to be caught. Girling (1969) found that the life cycle was essentially the same in both the upland forms, although hatching was slightly later, taking place in May. Because Moor House in the northern Pennines has a severe climate, and Durham a comparatively mild one for the north east of England, the upland forms must be adapted to develop at lower temperatures than the lowland form. Girling also showed that the size difference in the upland forms was not due merely to an added instar in *alpinus* the large form, as both had seven instars.

In this study, the distribution and abundance of the two forms was examined in a variety of upland habitats. These and the morphological and growth characteristics were studied to elucidate the relationships between the two upland forms, and the lowland form. Field work was carried out between the 1st May and 31st July, 1970.

METHODS

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Sampling was carried out by means of pitfall trapping. The traps consisted either of one pound jam jars or of disposable plastic coffee beakers sunk in the ground, with their mouths flush with the ground surface. The traps were filled with water to a depth of about 2 cm., and to this was added a small quantity of detergent, to prevent animals being held in the surface film, and an equal volume of 40% formaldehyde solution to prevent putrefaction in warm weather. The formaldehyde has the added advantage of preventing predation in the trap by killing the animals quickly. The traps were emptied once a week.

The efficiency of pitfall traps for quantitative comparison between traps in different sites has been questioned by Greenslade (1964). He states that although the size of catches depends primarily on the size of the population at risk, and on the level of locomotor activity, species may show differential susceptibility to trapping according to size, behaviour, and the strata in which they are active in the ground vegetation. Also catches of a single species may vary in different types of ground cover, depending on the resistance they present to horizontal movement. However, this last factor was probably not a major factor in the present study, as most of the sampling sites were on well grazed moorland vegetation. Only two sites, one on ungrazed enclosed grassland in Weardale (Site 9), the other at the zoology field station in Durham, showed a marked increase in length and thickness of the vegetation, relative to the other sites.

Sheep presented a problem, in that they frequently lifted pitfall traps out of the ground. This was presumably in search of water, because the number of traps lost each week built up during the dry spell, reaching a peak in the middle of June, when water was very scarce in many areas. The rate of loss was lower in the wetter periods of the summer. No simple method of preventing interference without affecting trapping efficiency was devised. Moles were a minor problem, raising a few traps, and burying others under mole hills.

Later in the study live specimens were collected using a 'Hoover Dustette' vacuum cleaner powered by a portable generator. A coarse gauze across the inflow caught the harvestmen as they were sucked up. Harvestmen were found by separating the tussocks of vegetation in which they lie up during the day.

Mean temperature measurements were made at each of the sites using the sugar inversion technique (Lee, 1969). This method uses the fact that the velocity of a chemical reaction depends on temperature according to the van't Hoff - Arrhenius law:

$$\log k = c_1 - \left(\frac{C_2}{T}\right)$$

where k = velocity coefficient

T = absolute temperature

and C_1 and C_2 are constants.

If k is found, an effective geometric mean temperature for the period can be calculated. The best method, originally introduced by Pallman et al ( ), uses the hydrolysis of sucrose to fructose and glucose, in acid solution. The amount which hydrolyses is measured by the change in optical activity. The solution was put in glass tubes, and left at the ground surface for three weeks. Protection from trampling and also a reduction in direct heating by the sun, was given by lengths of plastic drain pipe driven half way into the ground.

SITES

SITES

Fifteen upland sites were used for sampling. These were selected to give a wide range of altitude, aspect, and substrate. Four sites were at Cow Green in Upper Teesdale, and the remaining eleven were spaced out along the road from St. John's Chapel over the ridge between Weardale and the Langdon Beck (see map). The sites ranged from 1000 to 2000 ft. in altitude, and the substrates ranged from base rich brown earths to base poor acid peat.

Sites A to D were at Cow Green Grid Ref. NY 813303 mainly base rich, being on the sugar limestone or affected by drainage off it.

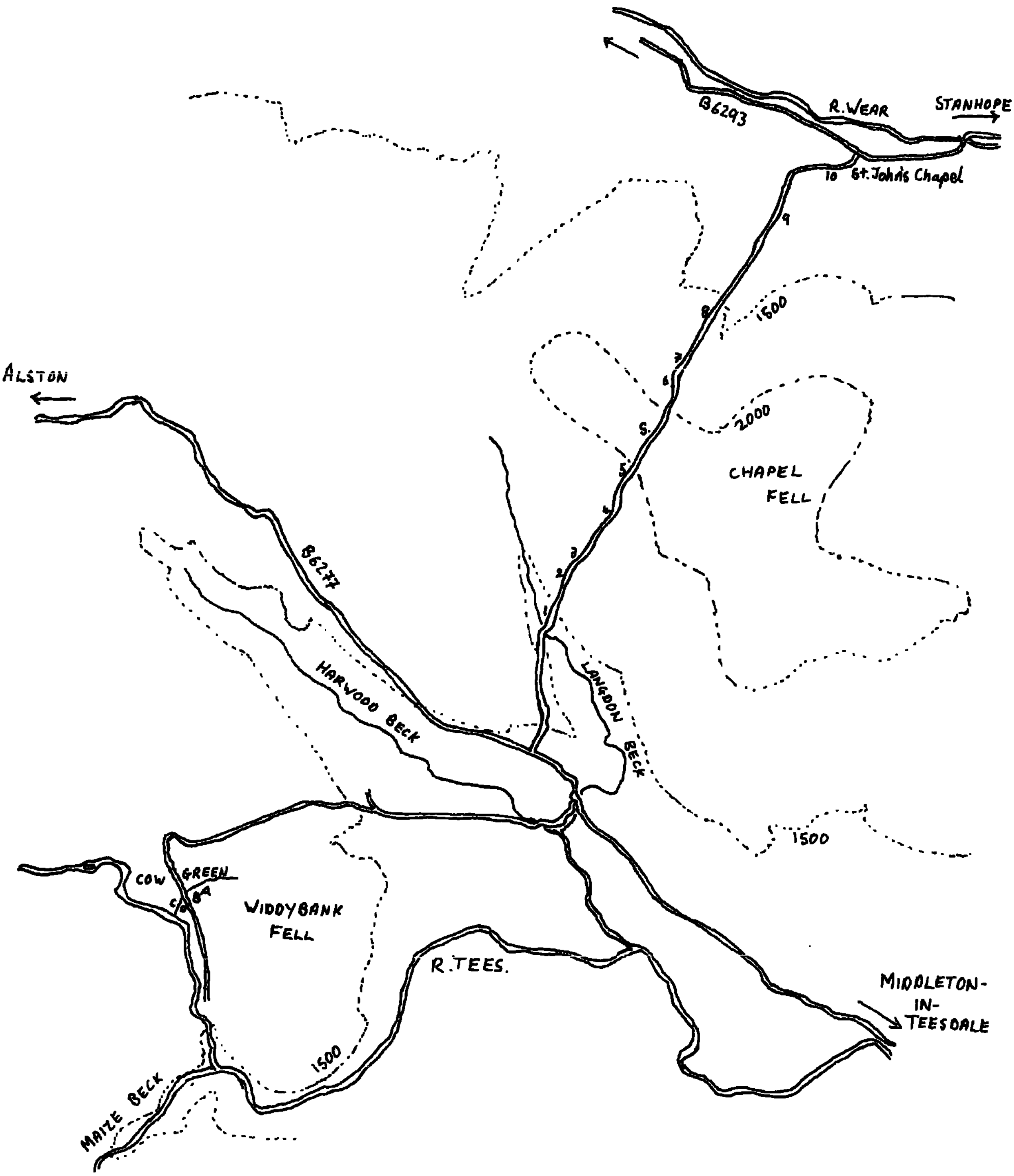
Site A 1600 ft.

This is a well drained site on the west slope of Widdybank Fell. The soil is shallow (c. 10 cm.) and overlies the sugar limestone. It is a short mull rendzina, with a large sand fraction, much of which is coarse. The sand comes from weathering of the sugar limestone. The vegetation is calcareous grassland, with some arctic-alpine species.

All plant names are as given in Clapham, Tutin and Warburg (1962).

Festuca ovina
Sesleria caerulea
Koeleria cristata
Carex pulicaris
Minuartia verna
Gentiana verna
Thymus drucei

Figure II. Map to show the positions of the moorland sites.



Site B 1550 ft.

This site is just below site A on the slope of Widdybank Fell, but is very different. The soil is deeper, and has a much higher humus content. It is comparatively base poor and tends to acidity. The vegetation is dominated by *Calluna*.

Calluna vulgaris
Empetrum nigrum
Festuca ovina
Nardus stricta
Viola lutea
Polygala sp.
Campanula rotundi folia

Site C 1525 ft.

This site is flat and poorly drained being in the valley bottom. It is base poor except for a narrow band where a sike carrying calcareous water flows through. The soil is mainly peat. The vegetation is acid grassland except by the sike.

Nardus stricta
Carex nigra
Carex demissa
Juncus squarrosus
Juncus effusus
Sphagnum spp.

By the sike the vegetation is typical of base rich peat.

Carex pulicaris
Carex dioica
Carex lepidocarpa
Festuca ovina
Juncus articulatus

Site D 1535 ft.

This site is wet grassland, but is better drained and has a higher base status than Site C. The soil is peaty and slightly acid.

Sesleria caerulea
Deschampsia caespitosa
Carex pulicaris
Nardus stricta
Ranunculus acris
Trifolium repens
Plantago lanceolatus
Bellis perennis

The remaining eleven sites were mainly on base poor peats or peaty podsols, with rough grass or moorland vegetation. Old mine workings gave some sites a higher base status.

Site 1 Grid reference NY 851331 1450 ft.

This site is comparatively dry and well drained on a south-west slope. The soil is a peaty podsol.

Festuca ovina
Agrostis tenuis
Juncus effusus
Galium saxatile
Trifolium repens
Potentilla erecta
Cirsium palustre

Site 2 Grid reference NY 853335 1625 ft.

This site is very similar to Site 1; but the vegetation is rougher, having some *Nardus*.

Festuca ovina
Nardus stricta
Agrostis tenuis
Juncus effusus
Galium saxatile
Potentilla erecta
Cirsium palustre

Site 3 Grid reference NY 856338 1700 ft.

This site is well drained on a slight south-west slope. It has a higher base status than most of the sites except those on the sugar limestone. Where the soil is shallow over the mine waste there is much *Minuartia*.

Juncus effusus
Festuca ovina
Agrostis tenuis
Nardus stricta
Minuartia verna
Potentilla erecta

Site 4 Grid reference NY 858343 1840 ft.

This site is poorly drained on a slight west slope. The soil is base poor acid peat with a rough grass-rush vegetation, with some degenerating *Calluna* and occasional patches of *Sphagnum*.

Nardus stricta
Festuca ovina
Juncus squarrosus
Eriophorum vaginatum
Sphagnum sp.
Calluna vulgaris
Galium saxatile

Site 5 Grid reference NY 860347 2000 ft.

This site is on an area of mine workings. It is heterogenous with regard to depth of soil, drainage and base status. The vegetation is correspondingly varied with plants characteristic of both base rich and base poor areas. The site is flat, and partly sheltered by spoil tips.

Nardus stricta
Juncus squarrosus
Festuca ovina
Agrostis tenuis
Minuartia verna - base rich
Galium saxatile - base poor
Potentilla erecta
Thymus drucei

Summit NY 862351 2050 ft.

This site is on a flat poorly drained area of blanket peat. The vegetation is mainly *Juncus* - *Nardus*. *Calluna* has been important in the past, because there are many decaying stumps, some regeneration is taking place.

Juncus squarrosus
Nardus stricta
Sphagnum spp.
Polytrichum commune
Calluna vulgaris
Festuca ovina

Site 6 Grid reference NY 865356 1875 ft.

This site is on very wet, poorly drained peat, with a slight north-east slope. Being on the dip slope it receives little sun especially in winter when it retains snow cover late. The vegetation is dominated by *Sphagnum*.

Sphagnum spp.
Juncus squarrosus
Polytrichum commune
Festuca ovina
Galium saxatile

Site 7 Grid reference NY 866358 1700 ft.

This site is on damp peat on a north-east slope. It is similar to Site 6, but being warmer and drier has much less Sphagnum.

Juncus squarrosus
Festuca ovina
Molinia caerulea
Galium saxatile
Potentilla erecta
Polytrichum commune
Sphagnum sp.

Site 8 Grid reference NY 869364 1525 ft.

This site is similar in general to the preceding two, and is intermediate in wetness, and ease of drainage.

Juncus squarrosus
Sphagnum sp.
Polytrichum commune
Festuca ovina
Molinia caerulex
Galium saxatile
Potentilla erecta

Site 9 Grid reference NY 876373 1250 ft.

This site is on flat enclosed grassland, on the north side of a wall. It has in the past been improved by fertilizing, ploughing and reseeding. The soil is a leached brown earth. The vegetation is a mixture of grasses with clover and weeds. It was neither grazed nor mown during the study.

Dactylis glomerata
Cynosurus cristatus
Alopecurus pratensis
Poa trivialis
Trifolium repens
Juncus effusus
Ranunculus sp.
Rumex sp.
Urtica dioica

Site 10 Grid reference NY 882378 1050 ft.

This site was on recently reseeded enclosed grassland. It is flat and well drained, the soil is a brown earth. The edges of the field where many broad leaved weeds were present was treated with a selective weedkiller. The grass was mown for hay in mid-June. This was the most unnatural site.

Dactylis glomerata
Cynosurus cristatus
Alopecurus pratensis
Tritolium repens
Ranunculus sp.
Rumex sp.
Urtica dioica

Lowland specimens of Mitopus morio were collected at the Zoology Field Station in Durham.

Zoology Field Station Grid reference NZ 274406 250 ft.

This site is on a brown earth, well drained, sloping south-west. The vegetation is one resulting from ungrazed pasture. It has an uneven, tussocky composition of grasses remaining from the pasture interspersed with herbs which have entered since grazing ceased.

Dactylis glomerata
Lolium perenne
Rubus sp.
Rumex acetosa
Cratageus monogyna
Phleum prateuse
Plantago lanceolata
Urtica dioica
Achillea millefolium
Potentilla erecta

DESCRIPTION AND SEPARATION OF FORMS

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Most of the recent work on *Mitopus morio* has been carried out on lowland specimens. Todd (1949) included it in her study of the harvestmen of Wytham Wood, and Phillipson (1959, 1960a, 1960b, 1962) used it for life cycle, feeding, and energetics studies. Other works on the ecology and distribution of the British harvestmen include *Mitopus* (Bristowe, 1949; Heighton, 1964; Hull, 1926, 1930; Pearson and White, 1964; Sankey, 1949; Savory, 1962), but only Hull mentions the existence of different forms, and goes so far as to suggest that they really are separate species.

> "*M. morio* is by far our most abundant species, but in upland regions, it is largely replaced by *M. alpinus*. The latter is usually regarded as a mere upland variety of *morio* simply because the females cannot easily be distinguished; but there are two other continental forms *palliatus* (Latr.) and *glacialis* (Koch) belonging to the same group, which with a similar distribution to that of the genus *Erigone* of spiders, exhibits a like tendency to variation, and a close relationship of species." (Hull, 1926).

The majority of authors tended to lump the forms together. Pickard - Cambridge (1890) gave detailed descriptions of the adults of all three forms, but stated that in his opinion, *morio* and *alpinus* were the same species. Falconer (1910) allowed them to stand as species, but quoted Kulozynski, who stated that *cinerascens* is merely immature *alpinus*, which is itself only an alpine form of *morio*. After Roewer (1923) had

had united them in one species, morio, this became accepted until Girling (1969) found all three forms, and described a method of separation applicable to all instars. This is based on the length of the femur of the second walking leg, and the ratio of the length to the width of the femur.

In the current study, this method was not adequately confirmed, because very few early instars of alpinus were caught. The fifth instar of alpinus, and the seventh instar of cinerascens have a similar femur length. These are clearly separable by the fact that the seventh instar cinerascens are adult, with the genital plate free at the anterior end, and the penis or ovipositor protrusible. Fifth instar alpinus are immature, with the genital plate sealed. When Girling's method was used, the separation was not completely satisfactory, as there was some overlap of the ratio of femur length to width, between the two forms (see Figure 2).

TABLE 1

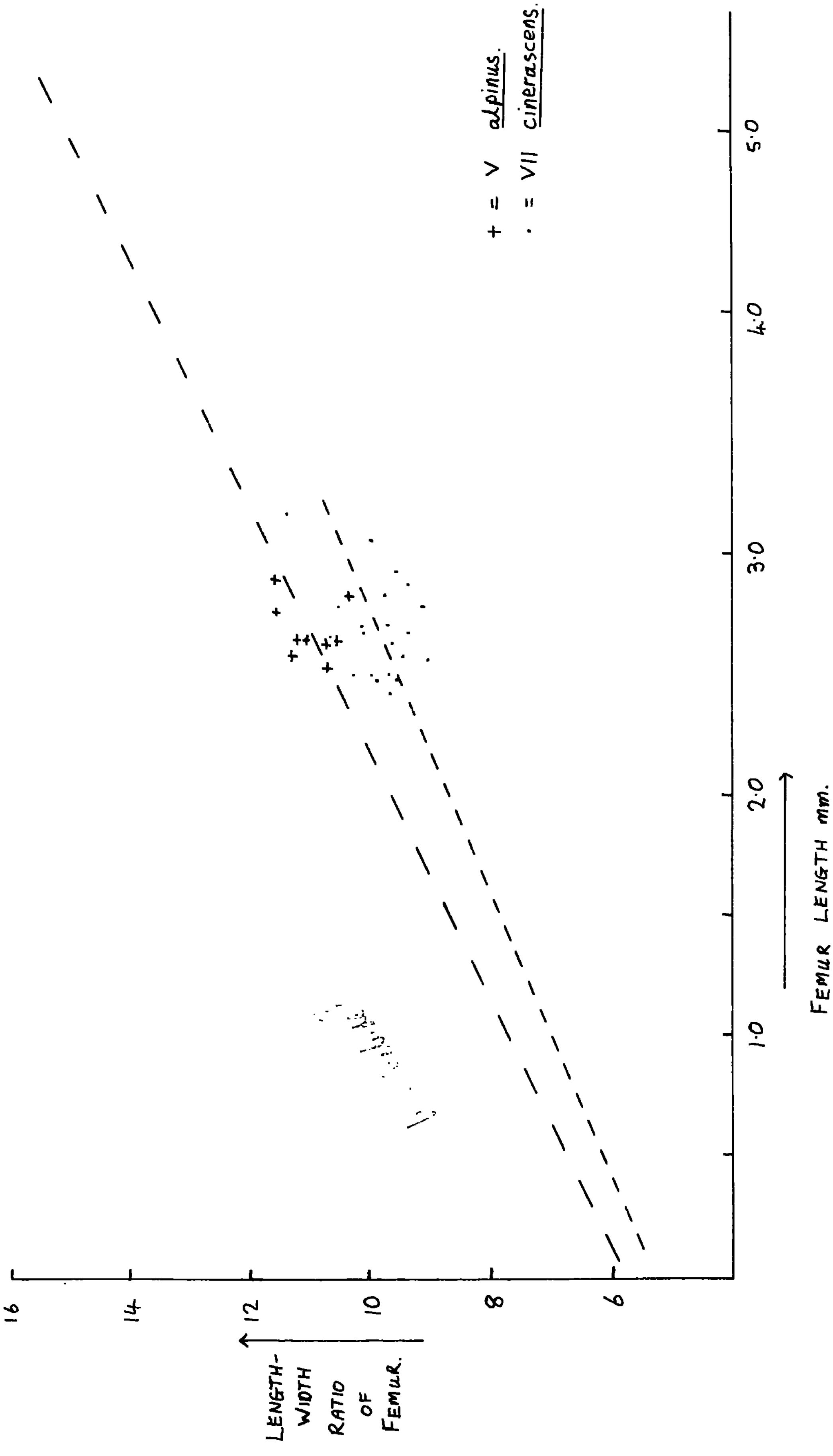
The mean femur length and mean ratio of femur length to width for V alpinus and VII cinerascens

Instar	No. in sample	Mean femur length (mm)	SD	Mean ratio	SD
V alpinus	8	2.69	0.12	10.93	0.49
VII cinerascens	48	2.65	0.19	9.86	0.19

From this it seems that Girling's method will separate the bulk of a population but that individual specimens would present problems.

Colouration, and the degree of armament on the chelicerae, tibiae and femorae, give an indication of which form is involved, but are sufficiently variable to prevent confidence in ascribing individuals to a particular form. The following descriptions

Figure 2. Femur length against length-width ratio for V alpinus and VII cinerascens to show overlap.



give the general external appearance of the three forms.

Mitopus morio morio. This form is whitish yellow with a brown or black dorsal mark shaped like an hour glass. This mark is often divided longitudinally by a pale stripe, and bordered by a narrow white margin. Its denticulae are small which gives it a smooth appearance. The trident is small with three main spines, sometimes with further smaller irregular spines. The ocularium is small and backward sloping. The legs are long, the second pair being longest, followed by the fourth, first and third pairs. They are quite strong, and often of a duller colour than the body, and are armed with spines. The pedipalp has a small hairy apophysis on the femoral joint. The sexes are distinguishable, the male being smaller, darker and more square with longer legs, whiter denticulae and heavier armament.

M. m. alpinus. This form is larger and more richly coloured than M.m. morio. The abdominal band is deep yellow brown, pale along the middle, broadly margined in black and surrounded with a distinct whitish yellow border. The denticulae and the armament of the legs are stronger.

M. m. cinerascens. This is the smallest form. It is greyish yellow with the colour of the hour glass shape varying from pale to almost black, divided by a pale or reddish stripe, and bordered by white. The denticulae are smaller and fewer in number. The legs are shorter, stouter and almost devoid of armament.

The shape and proportions of the penis are good diagnostic characteristics in the harvestmen, and have been used for the separation of the similar species Opilio saxatilis and O. parietinus (Bristowe, 1949; Sankey, 1949). Girling (1969) examined the penes of the three forms, and noticed differences in the degree of pigmentation; cinerascens being almost unpigmented, alpinus having a considerable degree of pigmentation, morio being intermediate in the degree of pigmentation.

Harvestmen have a penis with a characteristic structure, consisting of three sections (see Figure 3), the corpus, the glans penis, and the distal tube. The penes of the three forms are of a generally similar shape. A series of four measurements were made on penes from each of the forms, ten each of morio and cinerascens, and seven of alpinus of which only seven adult males were caught. The mean values of these measurements are shown in Table 2.

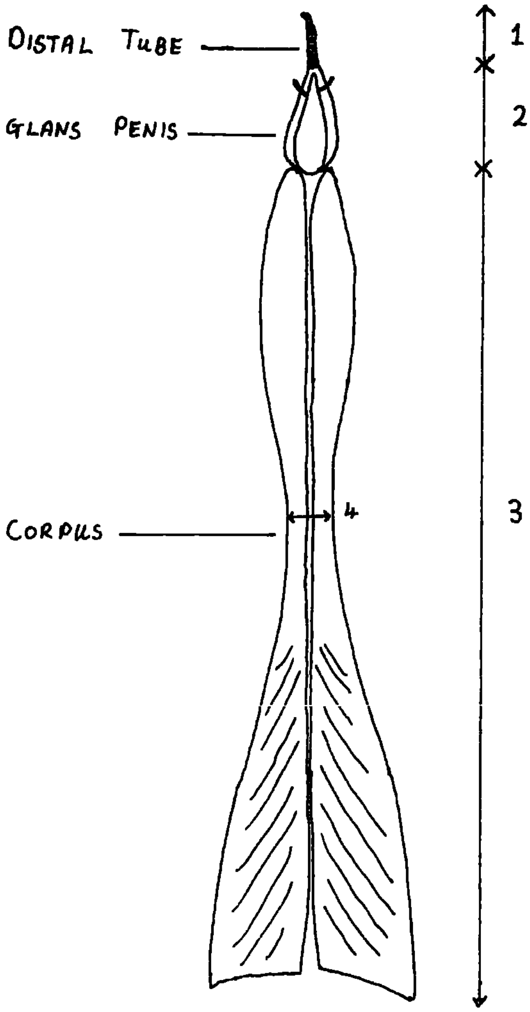
TABLE 2

Mean values for the penis measurements for each of the forms of Mitopus

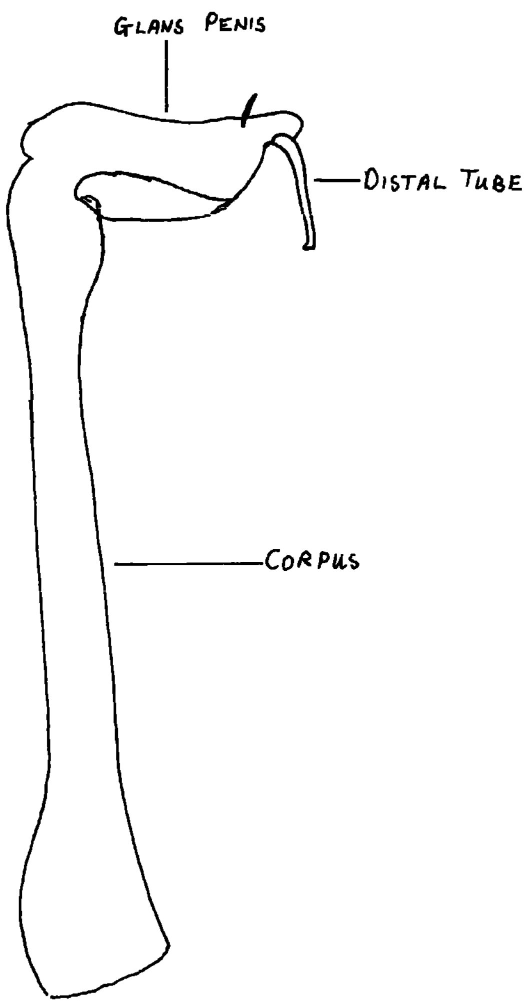
	alpinus		morio		cinerascens	
	Mean (mm)	SD	Mean (mm)	SD	Mean (mm)	SD
Length of distal tube (1)	0.2019	0.006	0.1863	0.005	0.1835	0.010
Length of glans (2)	0.4193	0.023	0.3298	0.011	0.2334	0.011
Length of corpus (3)	2.8224	0.14	2.1447	0.084	2.0438	0.071
Minimum width of corpus (4)	0.1245	0.004	0.1189	0.005	0.1039	0.008

These measurements show that there are marked differences in the proportions of the penes of the forms, despite the overall similarity in shape. The length of the distal tube (1) is very similar in all three forms. The most marked differences are in the lengths of the glans penis (2). When measurement 2 is plotted against measurement 3, the length of the corpus, there is separation into three groups (Figure 3a), cinerascens and morio giving compact groups, but alpinus showing rather

Figure 3. The penis of Mitopus.

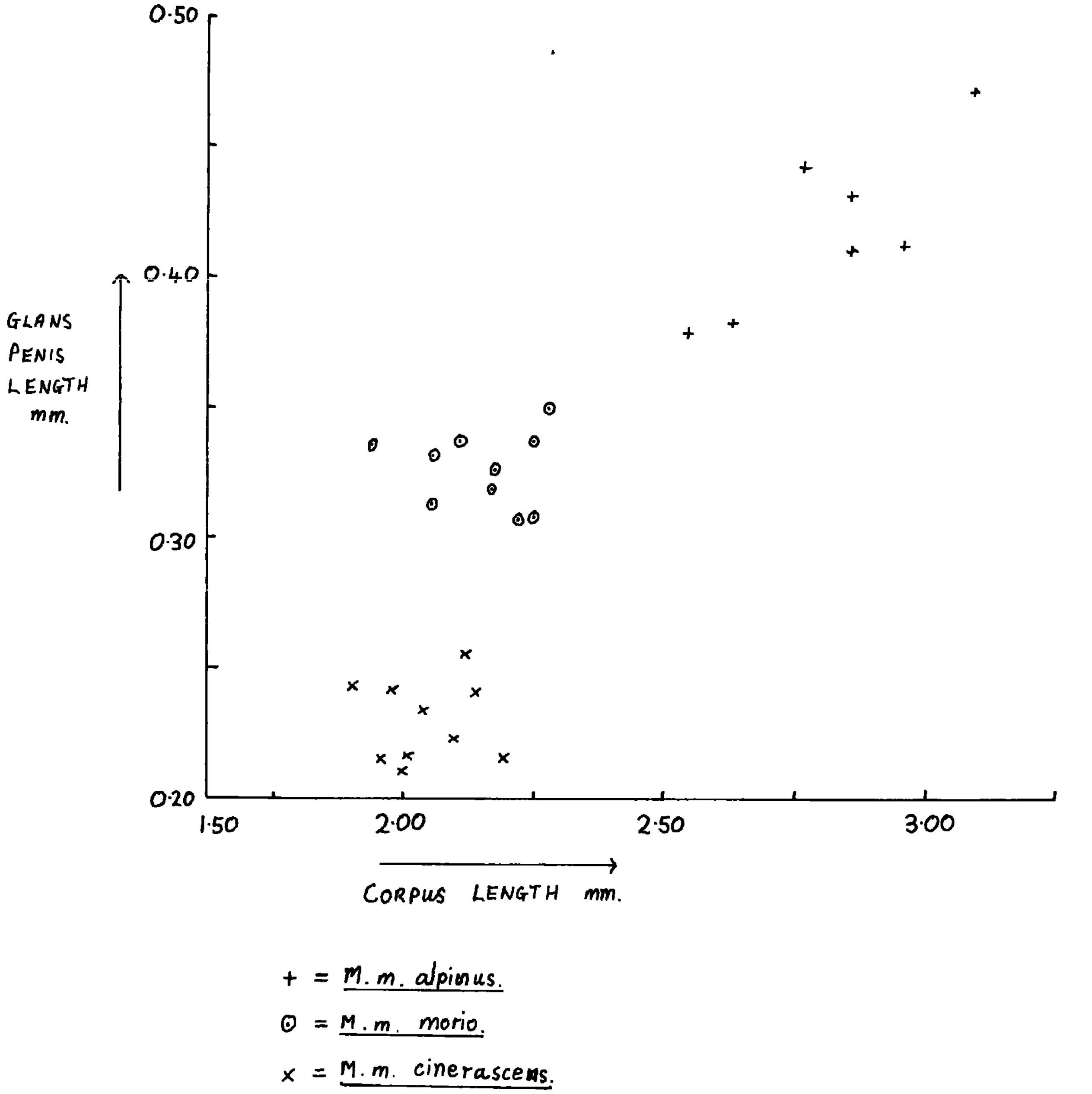


a) Ventral view.



b) Lateral view.

Figure 3a. Glans penis length against corpus length, showing separation of the three forms of Mitopus.



more scatter. (One of the low figures came from an unusually small adult of alpinus, which was in poor condition, having only four of its eight legs remaining. Harvestmen autotomize their legs readily, but unlike spiders and other arachnids, they do not have the ability to regenerate them. Loss of one or two legs does not appear to have serious effects, but specimens with fewer than six legs tend to be smaller in size).

The structure of the ovipositor of the female is not a satisfactory characteristic, because the organ is highly protrusible, and the shape varies with the degree of protrusion. The degree of pigmentation, and the size of the ovipositor vary between forms, that of cinerascens being small and lightly pigmented, whilst that of morio is intermediate with regard to both characters.

A population of Mitopus can be assigned to one or other of the forms by these means, although occasional individuals may present some problems. Kulczynski's statement that cinerascens consists merely of immature alpinus is clearly incorrect, as adults, both male and female, occur in both size forms. Also fifth instar immature alpinus are the same size as mature cinerascens, and sixth instar alpinus still immature, are larger than adult cinerascens.

DISTRIBUTION AND ABUNDANCE

DISTRIBUTION AND ABUNDANCE

Mitopus morio morio is the only form of Mitopus found in Durham, and is not found in the upland areas. Similarly, M. m. cinerascens and M. m. alpinus are restricted to the upland areas, and are not found in Durham. From the present study, the upland forms extend down to at least 1050 ft. (320 m.) on a north facing slope. The point at which the change from upland to lowland forms takes place would be of great interest. Girling (1969) had trapped from 1700 ft. upwards, hence in the present study, trapping was concentrated between 1,000 and 1,700 ft., in an attempt to find the point of change. However this point was not found despite the fact that the lowest sites, 9 and 10 were below the level at which open moorland ends, and the vegetation becomes that of enclosed farmland.

Throughout the discussion of the distribution and abundance of the forms, the mean number of Mitopus caught per trap week is used, rather than the total numbers caught. This is because different numbers of traps were used at some sites, and also because different sites suffered different degrees of interference by sheep.

When the trapping results for sites on a single hillside are considered, there is some tendency towards decreasing numbers of Mitopus with decreasing altitude (Table 3). This trend is not clearly marked when compared to the results obtained by Pearson and White (1964) in North Wales (Table 4), but the heterogeneity of the sites in the present study may account for some of this, e.g. Site 5 is on mine waste not moorland.

TABLE 3

Numbers of harvestmen caught per trap week at sites at different altitudes on a hillside

Site	Altitude (ft.)	Nos. per trap week	
		Mitopus morio	Other species
(a) On south facing hillside			
Summit	2050	3.41	0.00
5	2000	0.48	0.00
4	1840	4.10	0.15
3	1700	2.22	0.28
2	1625	1.89	0.11
1	1450	0.48	0.15
(b) On north facing hillside			
Summit	2050	3.41	0.00
6	1875	0.15	0.00
7	1700	1.08	0.00
8	1525	2.33	0.03
9	1240	2.05	0.23
10	1050	0.42	0.11

TABLE 4

Numbers of harvestmen caught at four sites at different altitudes in North Wales (Adapted from Pearson and White, 1964)

Altitude		Nos. caught	
(m)	(ft.)	Mitopus morio	Other species
530	1750	2179	28
450	1425	283	268
360	1200	16	257
240	800	1	352

Pearson and White did not distinguish any forms of Mitopus, but were probably dealing with the upland forms. If this is the case, their results are of interest in that they suggest that the change from upland to lowland forms, may take place in an area of low Mitopus populations.

Mitopus morio is the only abundant species in the upland areas, and forms by far the greater part of the total harvestman population, averaging 94% over fifteen sites. At the field station in Durham, however, Mitopus morio is merely one of eleven species, and forms a much smaller part, 9% of the total number of harvestmen. Comparison of the numbers caught per trap week between Durham and the moorland sites is liable to error because of the differences in vegetation. The thick rank grass, ungrazed for five years, which is present at the field station, presents a greater resistance to horizontal movement than well grazed moorland vegetation and this reduces the catching efficiency of these pitfall traps below that of the moorland traps.

The mean catches per trap week of Mitopus morio and of all harvestmen, are shown in Table 5. From these figures, it is clear that even allowing for reduced trap efficiency in Durham, Mitopus is more abundant in many of the moorland sites than it is in Durham. The most likely explanation for this is that Mitopus is the only species able to thrive under the harsh climatic conditions of the Northern Pennines and thus is freed from competition by other species. This allows Mitopus to exploit a wider niche, and thus be more abundant. At the Zoology Field Station, which has a comparatively mild climate, 11 species are found, and Mitopus is probably restricted to a much narrower niche, and is therefore reduced in abundance.

TABLE 5

Mean catch per trap week of Mitopus morio and of all harvestmen at each site

Site	Mean catch per trap week		
	Mitopus morio	All harvestmen	% M. morio
A	0.31	0.31	100
B	0.69	0.72	96
C	0.65	0.65	100
D	1.27	1.27	100
1	0.48	0.64	76
2	1.89	2.00	94
3	2.22	2.50	89
4	4.10	4.25	97
5	0.48	0.48	100
Summit	3.41	3.41	100
6	0.15	0.15	100
7	1.08	1.11	98
8	2.33	2.33	100
9	2.04	2.27	90
10	0.42	0.53	79
Durham	0.44	5.11	9

This agrees well with the general statement that a harsh environment is species poor, but that those species present often occur in comparatively large numbers. Comparison of arctic faunas with those of temperate or tropical regions, is often given as an example of this. It is thus interesting to note that the climate of the North Pennines is sub-arctic, and in many ways comparable to that of South Iceland at sea level (Manley, 1936).

The distribution of Mitopus in moorland areas is far from uniform. It was found in all of the sites, but the abundance, as measured by the mean number caught per trap week, ranged from 0.15 to 4.10 (Table 5), a ratio of 1 : 27. The difficulty in explaining this is that a wide range of factors may affect the abundance, and owing to shortage of time it was difficult to quantify these. The factors studied were altitude, temperature, humus content of the soil, wetness of the soil, and base status. As the results were not quantitative, they were ranked and compared to the ranks of abundance of Mitopus using Spearman's rank correlation. The results of this are given in Table 7. This ranking method is not wholly satisfactory, because one difference in rank number can mean either a small or a large difference in the factor being ranked.

TABLE 6

The order of ranking used for correlation of factors using Spearman's ranking method

No. per trap week	Altitude	Wetness	Temperature	Humus	Base status
High rank 1	High 1	Wet 1	Low 1	High 1	Poor 1
Low rank 15	Low 15	Dry 15	High 15	low 15	Rich 15

TABLE 7

R values from Spearman's rank correlation

Factor	R value	Significance
Altitude	0.14	NS
Wetness	0.23	NS
Temperature	0.33	NS
Humus content	0.14	NS
Base status	0.40	NS

As shown earlier (Table 3) there appears to be some effect of altitude, with lower numbers, with decreasing altitude. This is partly obscured by other effects, even when a single slope is considered, and when all sites are compared, a very low correlation value is obtained. This may be because of heterogeneity with regard to the other factors, but equally the altitude effect may be an artefact.

Temperature is in part affected by altitude but also by aspect, and as the ground level temperature was measured, it is also affected by the vegetation, the maximum temperatures being reached above the ground surface. The figures for mean temperature obtained were not wholly satisfactory because several of the samples were lost by interference in each of the two three-week periods considered. There is some correlation between temperature and abundance, low temperatures apparently favouring high numbers. This might seem unexpected, but is probably due to the need of harvestmen for a high relative humidity. The relative humidity at a site depends on the temperature and on the availability of water. A cool damp site is more likely to maintain a high relative humidity than a warm dry site. This supposition is supported by the fact that there is some correlation between damp sites and high abundances of Mitopus.

The humus content is one of the main factors affecting the wetness of the site, the others being rainfall and the ease of drainage. Humus content was estimated on the basis of soil colour and ranged from the very low humus content of the shallow rendzina overlying the sugar limestone to the almost pure humus of the blanket peat. In view of the importance of water retention in maintaining humidity, the low correlation between humus and numbers is unexpected.

Base status shows the greatest rank correlation, low base status being correlated to high abundances of Mitopus. There is no obvious reason why low base status should be favourable and it is possible that it is in part due to the fact that the base rich sites are mainly those which are unfavourable for another reason, e.g. Site A is liable to drought.

In conclusion, it seems that a base poor site which is damp and cool is the most favourable site for the upland forms of Mitopus. However, not all of the sites fulfilling these conditions are as favourable as Sites 4 and the summit, Site 6 has the lowest numbers of all. This site is the coldest and also very wet, but these are not very much greater than on the favourable sites. The difference may be that in winter, Site 6 on the dip slope facing north-east is sheltered from the sun, and thus retains its snow cover late. Mitopus overwinters in the egg and the presence of suitable oviposition sites, and the environmental conditions needed for overwintering, may be as important as the factors the active animal meets in determining abundance.

Similar difficulties are found in attempting to explain the differences in abundance of the two moorland forms, cinerascens and alpinus. Cinerascens is the most abundant species and forms the bulk of the population at most sites, but at one site, the summit, alpinus is the dominant form, comprising 94% of the catch (Table 8). This result is important as it suggests that alpinus is not merely a recessive form of the same species.

TABLE 8

The numbers of each form of Mitopus morio and the percentage of cinerascens caught at each upland site

Site	Nos. caught		% Cinerascens
	Alpinus	Cinerascens	
A	4	28	87.5
B	14	56	80
C	0	39	100
D	0	105	100
1	0	16	100
2	0	51	100
3	14	66	82.5
4	25	139	85
5	10	9	47
Summit	109	7	6
6	0	7	100
7	5	34	87
8	15	62	81
9	14	76	84
10	7	12	62

Amongst the sites with a high catch (>70) the distribution falls into three groups, sites with 100%, 80-85% and 6% cinerascens. These results were compared statistically to find the probability that all these samples are drawn from the same population. The results (Table 9) show that Site D (100%) and the summit site (6%) are highly significantly different ($p < 0.001$) from each other, and from 80-85% group. The

80-85% group (Sites 3, 4, 8, 9) are unlikely to be drawn from different populations ($p > 0.1$).

TABLE 9

Results of statistical test to show the probability of sites with 100%, 80-85% and 6% cinerascens, being samples of the same population

%s tested		d	p
100	6	13.96	$\ll 0.001$
100	85	4.20	< 0.001
100	80	4.71	< 0.001
85	6	15.78	$\ll 0.001$
80	6	10.58	$\ll 0.001$
85	80	0.82	> 0.1

The distribution of the two forms in relation to the environmental factors was studied using Spearman's rank correlation. The results of this are shown in Table 10. This shows up considerable differences between the habitat preferences of the two forms, cinerascens preferring sites at lower altitude, which have a lower humus content, and are drier. Alpinus prefers sites at higher altitude which are cooler and base poor. The correlations are low, however, and may be due in part to random events. The apparent effect of altitude may be given as an example of this. In the present study, the highest sites, 5, 6 and the summit, had low numbers of cinerascens, but Girling (1969) found cinerascens to be abundant at higher altitudes, than the sites used in the present study, on Dun Fell and also found that cinerascens formed the bulk of the catch even at these high altitude sites.

TABLE 10

R values for Spearman's rank correlation when alpinus and cinerascens are considered separately

Factor	Alpinus		Cinerascens	
	R	P	R	P
Altitude	0.32	NS	-0.52	NS
Wetness	0.05	NS	-0.12	NS
Temperature	0.42	NS	0.13	NS
Humus content	0.04	NS	-0.20	NS
Base status	0.32	NS	0.10	NS

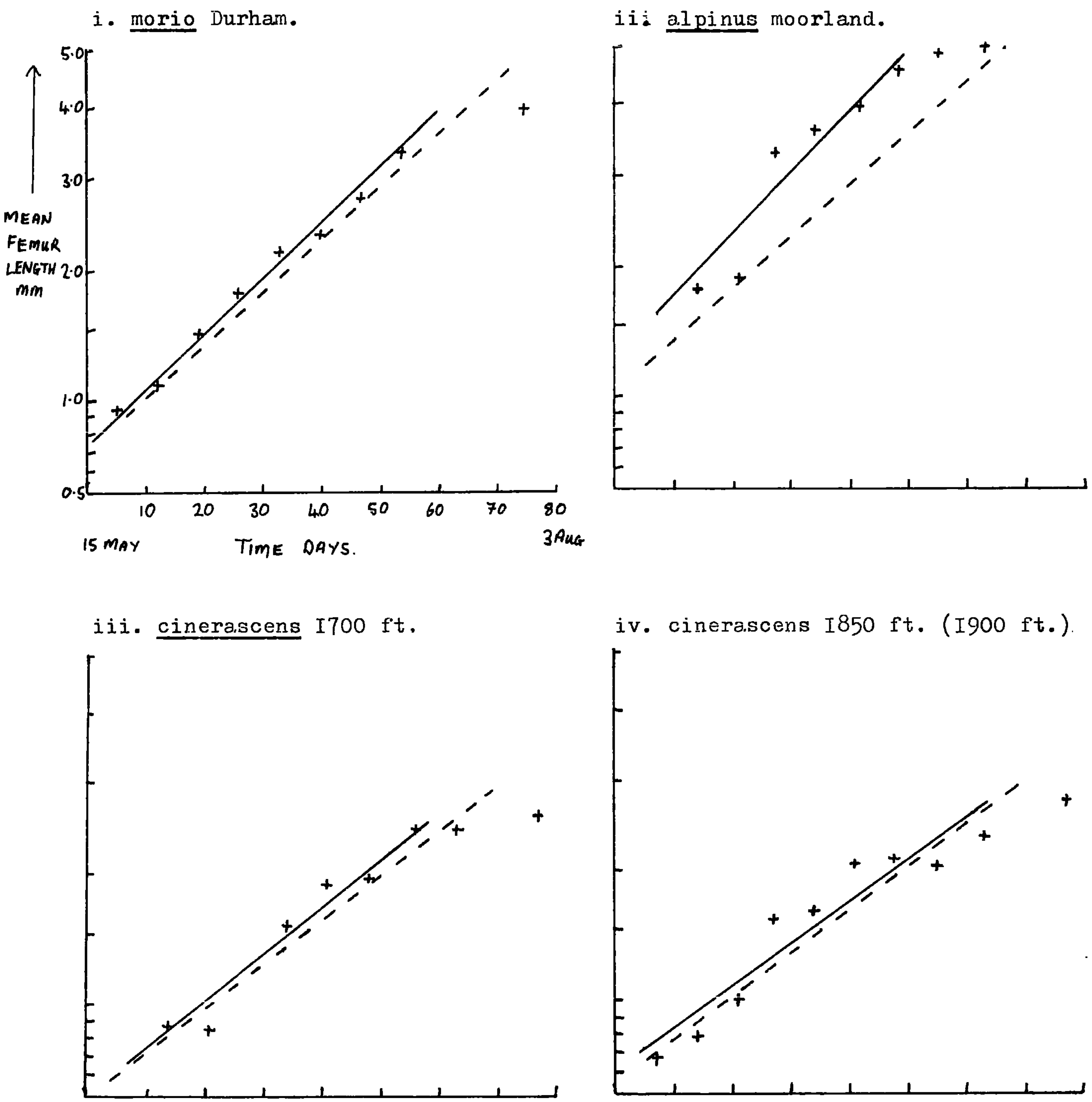
DEVELOPMENTAL HISTORY

DEVELOPMENTAL HISTORY

Girling (1969) studied the developmental history of all three forms of *Mitopus morio*, basing her conclusions on the analysis of the pitfall samples. She found the mean femur length and the mean instar of the sample for each trapping period at each of the sites. She then plotted these against time. Comparable sites were treated in the same way for the results of the present study, and are plotted in Figures 4 and 5, with the results for 1969 shown for comparison. The figures for *morio* in Durham are exactly comparable, because trapping was carried out on the same site in both 1969 and 1970. The other figures are less exactly comparable, but the 1700 ft. site on Dun Fell and Site 3 are both at the same altitude, and both on western slopes. The 1900 ft. Dun Fell site is compared with Site 4. This site is 50 ft. lower, but is more exactly comparable in vegetation. The 1969 figures used for *alpinus* were aggregate figures, which makes it difficult to know which site from the present study to use in comparison. Therefore the aggregate of the moorland catches for *alpinus* was used for the 1970 results.

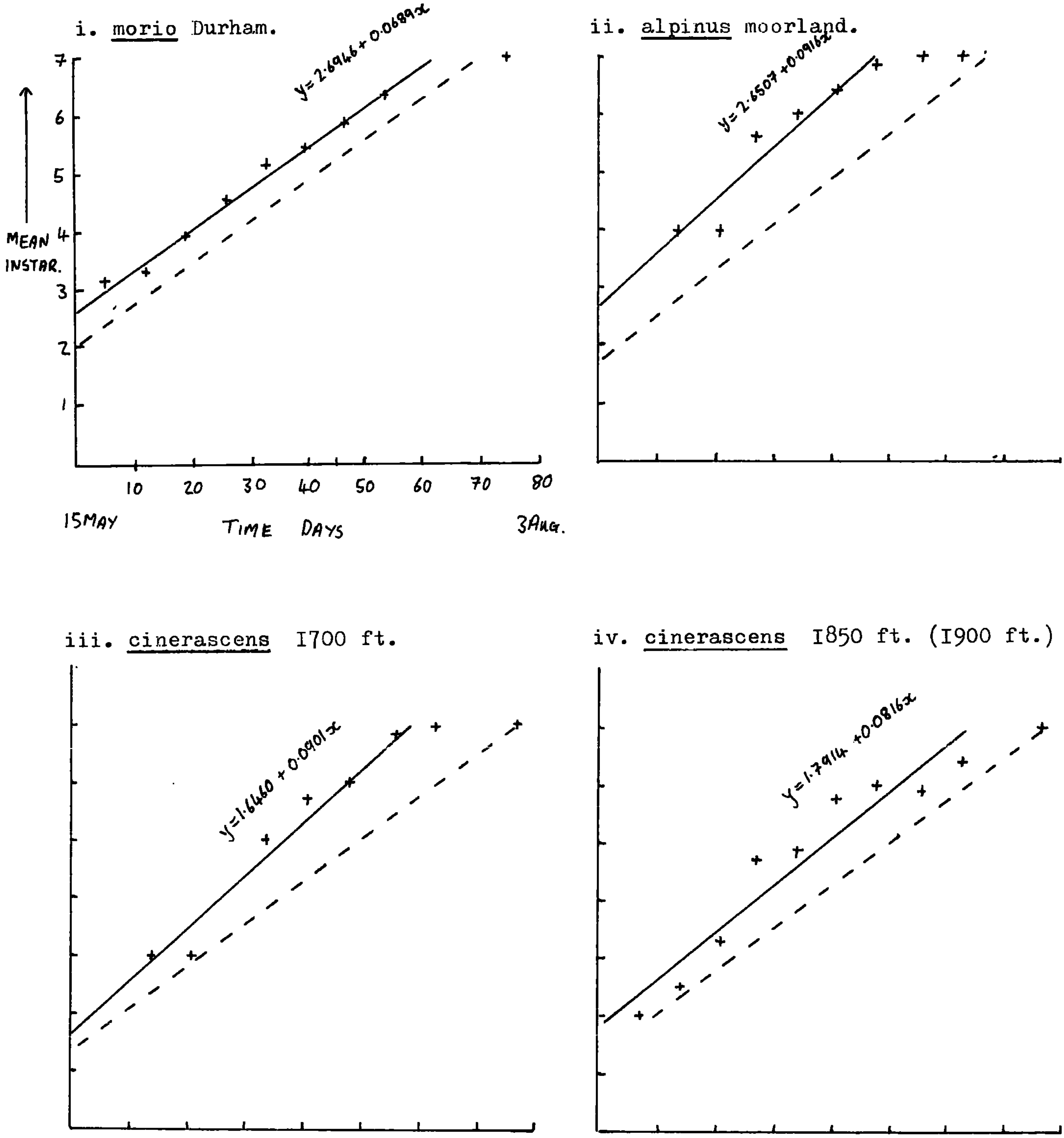
From the graphs of mean femur length, and mean instar against time, it can be seen that there was much similiarity between the two years. However the harvestmen were in a later instar in 1970 than at the same time in 1969. This means that *Mitopus* hatched earlier in 1970. After hatching, this advantage was maintained at Durham, but there was some tendency to increase the advantage on the moorland sites which can be shown by the number of days earlier the harvestmen reached the

Figure 4. Mean femur length against date, with results from 1969 shown for comparison.



Key to [illegible]

Figure 5. Mean instar against time, with results from I969 shown for comparison.



third and sixth instars in 1970 (Table 11).

TABLE 11

The number of days earlier that the III and VI instars of each form were reached in 1970 compared to 1969

Form	Site 1969	Site 1970	Instar	No. of days earlier
morio	Field station, Durham		III	8
			VI	7
alpinus	Moor House, N. Pennines		III	14
			VI	17
cinerascens	1700 ft. Dun Fell	3	III	8
			VI	15
cinerascens	1900 ft. Dun Fell	4	III	7
			VI	11

These differences can be explained in general terms by the weather. The year 1969 had a cold late spring, which was followed by fine weather in early summer. Spring was earlier in 1970, and the early summer was exceptionally fine and dry.

The size differences are not so marked, despite the harvestmen developing earlier in 1970, this was because the sizes of the instars were generally smaller than in 1969. (Some of the 1969 material was measured as a check to ensure that the same length was measured in both studies). This difference in size was clearly marked in the Durham collections, and as these results are directly comparable, they are given as an example (Table 12). The cause of the smaller size in 1970 is not clear, but as the earliest instars were involved, it is likely that conditions when the eggs were laid the previous autumn may have been involved.

TABLE 12

The mean femur length for each instar in collections made at the Zoology Field Station, Durham in 1969 and 1970

Instar	1969		1970	
	Mean femur length (mm)	SD	Mean femur length (mm)	SD
2	0.71	0.04	0.625	0.04
3	1.09	0.06	0.94	0.10
4	1.59	0.05	1.45	0.10
5	2.25	0.01	2.07	0.15
6	3.09	0.13	2.86	0.20
7	4.62	0.36	3.95	0.30

Despite this size difference, the growth increment at each moult was very similar in each year. A measure of the growth increment is obtained by dividing the mean femur length for each instar by that of the previous instar. Results for 1969 and 1970 are compared in Table 13. The differences are not significant, for alpinus the most different, t = 0.5 with 1° freedom.

TABLE 13

The growth increments between each moult for comparable collections in 1969 and 1970

Instar	morio	Durham	alpinus		cinerascens 1700 ft.		cinerascens 1850-1900ft.	
	1969	1970	1969	1970	1969	1970	1969	1970
2								
	1.52	1.50	1.43	1.45	1.38		1.49	1.37
3								
	1.46	1.54	1.43	1.57	1.35	1.43	1.21	1.47
4								
	1.41	1.42	1.32	1.46	1.30	1.34	1.40	1.30
5								
	1.37	1.39	1.48	1.35	1.35	1.23	1.32	1.28
6								
	1.50	1.38	1.35	1.36	1.32	1.32	1.35	1.23
7								
Mean growth increment	1.45	1.45	1.40	1.44	1.34	1.33	1.35	1.33

Because of the apparent effect of weather on the growth of harvestmen, correlation coefficients were calculated for the weekly growth increments at the Cow Green sites, and the weekly mean temperature, and weekly rainfall as measured at the Cow Green meteorological station. These gave very low correlation, $r = +0.02$ for mean temperature, and $r = -0.04$ for rainfall. This shows that growth is not directly correlated to weather, however, good weather may increase the availability of food and thus increase the growth rate.

The growth characteristics for each form were very similar in 1969 and 1970. The date of hatching appears to be related to the onset of warmer weather in spring (as previously suggested by Stipperberger, 1928 and Heighton, 1964). Once the animals have hatched, there is no direct correlation with weather, but this may affect the growth rate indirectly through such effects as the availability of food.

SEX RATIO

SEX RATIO

The sex ratios of both of the upland forms of *Mitopus* were worked out from the pitfall samples. In both forms, the ratio differed significantly from 1 : 1. The mean ratio being 10 females : 1 male in *alpinus* and 3 females : 1 male in *cinerascens*. The difference between these ratios is highly significant.

TABLE 14

χ^2 values for the difference between the sex ratio for each form and 1 : 1, and for the difference between the two ratios

	χ^2	°freedom	Probability
alpinus 1 : 1	44	1	0.001
cinerascens 1 : 1	40	1	0.001
alpinus : *cinerascens*	9	1	0.01

These catches may represent the true sex ratios, but any difference in activity or behaviour patterns between the sexes is likely to affect the proportions of each sex caught. If the sex ratio is the same in catches by two different methods, it might be expected that this was the true sex ratio, Insufficient adults were caught by hand for these to provide a check.

When the pitfall catches for each trapping period are separated (Table 15) it can be seen that *alpinus* has a similar sex ratio throughout, whilst *cinerascens* shows a decline in the proportion of females.

TABLE 15

The numbers of males and females of the two upland forms of Mitopus caught in each trapping period

Form	Sex	Nos. in each trapping period					
		11-18 June	18-25 June	25 June-2 July	2-10 July	10-17 July	17-31 July
alpinus	M	0	0	2	2	3	0
	F	2	14	5	12	25	15
cinerascens	M	0	0	0	1	8	36
	F	0	1	4	24	41	71

This change in the proportion of female cinerascens is not statistically significant, $\chi^2 = 3.1$ with 2^o of freedom. However, if the change is real, it might be caused by males maturing later than females. Many of the cinerascens caught in the period 2-10th July were immature, fewer of those caught from the 10-17th July were immature, and almost all specimens caught in the final period were mature. This is the most likely cause, though changes in relative activity of the sexes, or death of females after oviposition could also have an effect.

The sex ratio of the Durham form was not satisfactorily determined because only nine adults were trapped. These were in the ratio of 8 females to 1 male. A catch by hand on 14th August yielded 10 males and only 4 females. This gives a mean ratio of approximately 1 : 1. These results may be showing a decline in the proportion of females similar to that of cinerascens but are likely to be due to chance effects in two small samples.

POLYMORPHISM

POLYMORPHISM

If the two moorland forms are conspecific, polymorphism is occurring. Polymorphism can be either transient, with one morph replacing another, or balanced, with the proportions of the morphs being maintained by selection pressure. In cases of balanced polymorphism, the proportions of the different morphs are generally either the same over large areas, or show a wide range of variation depending on the action of selective pressures in a particular site.

In the case of *alpinus* and *cinerascens*, transient polymorphism is unlikely, because both forms have been known for over 130 years.

Balanced polymorphism of the widespread type is unlikely to be occurring. This requires that the population should be homogenous. In the present study, there is very little chance that the samples are drawn from an homogenous population. Even when the sites at which both forms coexist are considered, and when the summit site which has an unusually high proportion of *alpinus* is excluded, there is little chance of these samples being from an homogenous population. Brandt and Snedecor's ^{2} test for homogeneity gives a value of 48.22 with 9 degrees of freedom. This is highly significant, and means that there is less than a one in a thousand chance that the samples are from an homogenous population, and thus that there is unlikely to be balanced polymorphism over a large area.

When the proportion of the morphs present varies between sites, it is produced by differences in selective pressure on the morphs. In such cases a wide range of proportions is expected. In the present case however the bulk of the samples have 100% or 80-85% of cinerascens but none in the 20-40% which would be expected. This fact and the absence of any obvious change in the selection pressure on the forms between sites, suggests that this type of polymorphism is not occurring.

From the results of this study there is nothing to suggest that the two forms are merely morphs of the same species.

ICELANDIC SPECIMENS

ICELANDIC SPECIMENS

Mitopus morio is the only common harvestman in Iceland, where it is found throughout the island in almost all habitats (Henriksen, 1938).

Girling (1969) put forward the hypothesis that M. m. cinerascens and M. m. alpinus occupied separate food niches, cinerascens taking smaller prey and alpinus larger animals. She further suggested that in lowland areas where there was competition from other species of harvestmen, these forms were replaced, alpinus by a more efficient morio, and cinerascens by other smaller species more efficient in the lowland environment. If this is the case, it may be expected that in Iceland in the absence of competition, alpinus and cinerascens might be found in the lowlands as well as in upland areas.

In order to test this hypothesis, some harvestmen were obtained from Iceland. Only a small sample was available, but this contained representatives of all instars from the third to the seventh. Specimens were caught at sites from sea level to 350 m. Only one size form was present, and this was not assignable to any of the three forms studied in England. In size, the Icelandic specimens were nearest to the lowland M. morio, but the early instars were larger. The adult Icelandic specimens were smaller than adult morio because of the lower growth increment of the Icelandic form, 1.31 compared to 1.45 for morio. The Icelandic specimens were always larger than cinerascens and smaller than alpinus (see Table 16).

TABLE 16

Mean femur lengths of the 2nd to 7th instars of Mitopus from various areas

Instar	morio Durham	cinerascens N. Pennines	alpinus N. Pennines	morio Iceland
2	0.64	0.63	0.96	
3	0.94	0.89	1.32	1.22
4	1.45	1.31	2.10	1.47
5	2.07	1.64	2.53	1.98
6	2.86	2.10	3.75	2.64
7	3.95	2.57	4.79	3.53

The shape and structure of the penis of the Icelandic form is very similar to that of the other forms. It is, however, well pigmented and the proportions are different (Tables 2, 17).

TABLE 17

Lengths of the different parts of the penis of Mitopus morio from Iceland

	Mean length in mm.
Length of distal tube	0.1709
Length of glans	0.3846
Length of corpus	2.4769
Minimum width of corpus	0.1350

Further to these measurable differences, the Icelandic specimens were very dark in colouration, and were very heavily armoured, with the armament being deeply pigmented. The armament was heavier than any seen on the most heavily armed British form alpinus. From this it seems that Mitopus in Iceland belongs to a separate geographic race, and is probably that described as M. morio borealis.

The Icelandic specimens do not throw any light on the relationships of the British forms of Mitopus morio. Because only one form is found, and that a different race to those found in England, do they provide evidence for or against Girling's hypothesis that alpinus and cinerascens are restricted to upland areas where there is little competition from other species of harvestmen.

GENERAL DISCUSSION

GENERAL DISCUSSION

Two forms of Mitopus morio are present in upland areas, and differ from the lowland form. These differences, which are present in all stages both immature and adult, show clearly in size, as measured by femur length, and in penis proportions. They show less clearly in the length-width ratio of the femur, and in colouration, and the degree of armament.

The differences can be explained either by two distinct species being present in the upland areas, or by Mitopus morio showing polymorphism in the upland areas, with both upland morphs differing from lowland populations. If distinct species are involved, there may be two or three species, one of the upland forms being merely morio which has undergone character displacement if only two species are present. Alternatively, all three forms may be distinct species. If the upland forms are morphs of the same species, it is unlikely that the upland and lowland forms are separate species, because the differences between the two upland forms alpinus and cinerascens are greater than the differences between these and morio the lowland form.

To be considered morphs of the same species, the two upland forms must interbreed. No intermediates were found. Thus if interbreeding was taking place, the size difference is in all probability due to a single gene. One of these genes must be dominant. Of the upland forms of Mitopus, the small form is the most frequent on all but one of the sites. It is thus likely that if both forms interbreed, the gene for small size is dominant. But there is one site on which the large form alpinus is very markedly the most abundant. This is extremely unlikely to be due to chance. The other explanations for alpinus being most frequent are either that there is strong selection pressure against small size at this site, or that the gene for small size is in the process of replacing the gene for large size. Neither of these explanations is likely. The site at which alpinus is abundant is not sufficiently different from the other sites to account for such a dramatic change in selection pressure. The fact that both forms have been known for over 130 years reduces the likelihood that cinerascens is replacing alpinus.

If polymorphism is occurring, it is not balanced over the whole area, because the samples are highly heterogenous with regard to the proportions of the forms. Therefore the proportions of each form would have to be controlled by differences in selection pressure between the sites. In the present study, there is no obvious factor to provide different degrees of selection for or against a morph at different sites. Furthermore, in this type of polymorphism, a wide range in the proportions of the different morphs is expected. In this case most sites have 80% or 100% of cinerascens and none have between 20 and 40%. Thus there is no evidence to suggest that polymorphism is the explanation of the two moorland forms.

For two similar species to coexist in the same area, there must be sufficient differences in their ecology for each species to have a refuge, i.e. the niches of the two species must not overlap completely. The difference between the forms most likely to produce a niche separation is that of size. If the size of the harvestman is related to the size of prey consumed, there could be sufficient difference to provide each species with a food refuge. The linear size difference necessary in these circumstances has been determined empiracally to be in the ratio of 1 : 1.3. Bossert (quoted in MacArthur and Wilson, 1967) calculated the difference on theoretical grounds, arriving at the conclusion that the difference between the means for each species of an isolating character needed to be between 30 and 50% of the common mean for that character to reduce the 'error' to a very low level. The 'error' is either the frequency of hybrid matings in the case of an imperfect prezygotic isolating character, or, as is relevant in this case, the % contacts of an interspecific nature resulting to damage to both species, in the case of an imperfect ecological difference separating two competing species. The differences between the means of the femur lengths for corresponding instars of the two forms averages 44% of the common mean. This size difference is increased during development by the faster growth rate of alpinus. The size difference is sufficient to provide separate niches if prey size is related to the size of the harvestman.

Hutchinson (1959) pointed out that if such a niche separation based on food size is to work, all individuals of the large form must always be larger than those of the small form. He made the point in relation to Corixidae and generalised to hemimetabolous insects with annual life cycles involving relatively long periods of growth. Harvestmen though not insects, are hemimetabolous and have an annual life cycle with a long growth period. Thus to allow food niche separation on the basis of size, alpinus would always have to be larger than cinerascens. This is shown clearly; for a given instar alpinus is always markedly larger than cinerascens. Furthermore alpinus hatches at about the same time or earlier than *cinerascens*, and once hatched, *alpinus* grows faster. All these tend to keep the size difference at a maximum.

The size difference as expressed in the size of the penis could equally provide a barrier to mating. This is likely to be further strengthened by cannibalism, an individual of the small form attempting to mate with one of the large form might well be eaten. This was not tested directly, but when individuals of different instars are kept together, the larger individuals rapidly consume the small ones. Cannibalism has also been recorded in the field (Bristowe, 1949).

There are apparently sufficient differences at all times, between the two forms, to allow two species to coexist. Thus in the absence of evidence suggesting polymorphism, it is likely that two species are involved in the upland areas. To confirm this, breeding experiments should be carried out, the possibility of niche separation should be clarified by food analyses and the possible existence of differences in oviposition sites should be considered.

The relationships between the two moorland forms *alpinus* and *cinerascens*, and the lowland form *morio* are less easily determined as they are allopatric. Either *alpinus* or *cinerascens*, could be conspecific with *morio*, but have undergone character displacement in the presence of a species of similar ecology. To clarify this, breeding experiments should be carried out to show if lowland *morio* will breed with either of the upland forms.

On the basis of this study I suggest that the two upland forms are separate species as originally described. Further studies, especially breeding experiments, are desirable before this is stated conclusively, and before the relationship of the upland forms to the lowland form can be determined.

SUMMARY

SUMMARY

Mitopus morio exists in three distinct forms in England. Two of these are restricted to upland areas, and one is restricted to lowland areas.

The three forms are clearly separable by femur length in all instars and by the proportions of the penis in the adult male. There are also differences in colouration and the degree of armament but these are more variable.

The distribution and relative abundance of the moorland forms is not clearly correlated with environmental factors acting on the active animal during the summer months. Oviposition sites, and the factors affecting the overwintering eggs may be of more importance.

The sex ratios of the moorland forms as found in pitfall samples differ from 1 : 1, showing a preponderance of females. The sex ratio of the two moorland forms differ significantly from each other.

The growth increments of the three forms were closely similar in both 1969 and 1970. Hatching was earlier in 1970. The date of hatching may be related to the onset of warm weather in spring. Weather does not appear to be closely correlated to growth rate.

There is no evidence to suggest that the two moorland forms are morphs of the same species.

The size difference between the upland forms is sufficient to allow each form a food refuge based on prey size.

It is suggested that the two upland forms are separate species.

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