Biological studies on certain forms of the harvestman mitopus morio (FABR.) (opiliones, arachnida)

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How to cite:

Jennings, Amanda Louise (1982) *Biological studies on certain forms of the harvestman mitopus morio (FABR.) (opiliones, arachnida)*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7898/

BIOLOGICAL STUDIES ON CERTAIN FORMS OF THE HARVESTMAN *MITOPUS MORIO* (FABR.) (OPILIONES, ARACHNIDA)

AMANDA LOUISE JENNINGS B.Sc. (Dunelm)

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

1982

ABSTRACT

The harvestman *Mitopus morio* has been studied over a large geographical area in northern Britain, and specimens from other parts of Europe have been examined, to investigate the relationships between the different forms of this species. Previous workers have suggested that *M. morio* has three forms in Britain, two from upland areas (*M. morio cinerascens* and *M. morio alpinus*), and one from lowland regions (*M. morio morio*). The results of this study show that *M. morio cinerascens* and *M. morio morio* are not isolated forms, but that they lie at opposite extremes of a cline of decreasing size with increasing altitude. The form called *M. morio alpinus* is not a variety of *M. morio* but is a distinct British species; it is described in this thesis as *Mitopus ericaeus* sp.n.. The mean lengths of the second femurs of all instars of *M. morio* decrease progressively with increasing altitude. Analyses of specimens of *M. morio* from other parts of Europe show that site altitude and site latitude account for half of the variation in femur length between sites. Body dry weights and lengths of the corpora penes of males also decrease clinally with increasing altitude. The phenology of *M. morio* is similar at all sites, but the date on which a particular mean instar is reached is delayed at the higher altitudes; temperatures are, on average, lower at these upland sites throughout the season. *M. ericaeus* sp.n. is taken at sites above 250m where it co-exists with *M. morio* but is less abundant. *M. ericaeus* sp.n. is larger and more darkly pigmented than *M. morio* at all instars, and adult males differ in their genitalia morphology. *M. ericaeus* sp.n. develops and matures earlier than *M. morio* at the same site, preventing congeneric competition. The two species do not interbreed in the laboratory. The effect of chilling on the egg diapause of both species has been investigated.

ACKNOWLEDGMENTS

I should like to express my gratitude to Dr J.C. Coulson, above all others, for his invaluable guidance, patience and encouragement throughout this study.

I am grateful to Professor D. Barker for providing facilities in the Zoology Department in the University of Durham.

I should like to thank Mr M. Rawes for permission to work on the Moor House National Nature Reserve, and for supplying climatic data for the area; Dr P. Olive for assistance with the chromosome studies; Dr N. Harris for help in using the S.E.M.; and Paul Hillyard for allowing me a free hand with the Natural History Museum's harvestmen collection.

I am indebted to the library staff at the University of Durham for searching out the many ancient and obscure references, and to Nicholas Aebischer for translating the German papers.

Thanks to John Richardson, particularly for caring so diligently for the harvestmen in my absence, and to Eric Henderson for technical assistance; to David Hutchinson for the photography; and to Mrs R.L. Reed for typing the manuscript.

Many thanks also to Graham Rankin and Shirley Goodyer and the other research workers at Durham who have all provided advice, ideas and discussion during the last three years.

Finally, I should like to thank Martin Randall for all his help, but especially for proof-reading the manuscript and for his stalwart encouragement throughout the task of writing up.

This study was financed by a Natural Environmental Research Council research studentship.

CONTENTS

CHAPTER ONE

INTRODUCTION

Wide-ranging species usually exhibit more variation than those having a smaller range (Darwin 1859). Differences between phenotypes may be greatest at the limits of the ecological range of the species, but these phenotypes are gradually connected with one another across the species range. Phenotypic variation is sometimes an expression of climatic adaptation by the species concerned. In the past, incomplete sampling from geographically isolated populations resulted in the proliferation of species and subspecies; many of the first descriptions were made without adequate regard for possible variations. Amongst opilionids, definitions of both species and genera have been made on a basis of colour pattern, dorsal spination, leg spination, tarsal numbers and other structural details; all these characters are subject to considerable variation (Goodnight and Goodnight 1953).

Mitopus morio (Fabricius) is one of the most wide-ranging species of harvestmen, occurring across all Europe from Iceland and Spitzbergen to North Africa, Siberia, China, Persia and North America (Sankey and Savory 1974). It is the only harvestman occurring in Greenland (Savory 1962, Meinertz 1973). It is widely distributed and frequently abundant over a broad range of habitats, particularly low herbage vegetation types.

Previous studies on the harvestman *M. morio* have concentrated on specimens collected from localities which were frequently widely separated, geographically. This study arose from the considerable confusion over the taxonomy of *M. morio*. In his monograph on the British species of harvestmen, Pickard-Cambridge (1890) listed three closely related species of *Mitopus* (then in the genus *Oligolophus*): the intermediate-sized lowland *Oligolophus morio* (Fabr. 1799), and two upland species: the small

O. cinerascens (C.L.Koch 1839), and the large *O. alpinus* (Herbst 1799). Twenty two years later, all these species were synonymised by the German arachnologist Roewer (1912, 1923) under the name of *Mitopus morio*. Roewer was of the opinion that *M. morio* was a highly variable, widely distributed, but single species, and this opinion has remained unchallenged to the present time. In the most recent key to the British harvestmen (Sankey and Savory 1974), the authors mention the existence of three British forms of *M. morio* which had been identified by Girling and Stallybrass (unpublished dissertations, University of Durham). These corresponded in characteristics to the species mentioned by Pickard-Cambridge. Since the previous studies had concentrated on geographically and altitudinally separated populations of *M. morio*, the aim of this investigation was to examine both these populations and those from the intermediate regions, by more extensive sampling, in order to see whether or not the three populations overlapped in their distributions, or whether a true hybrid zone existed. Sites were therefore chosen at a wide range of altitudes in northern Britain.

Various references have been made in the past to the "varieties" or "forms" of *M. morio*. The International Code of Zoological Nomenclature (1964) determines that, before 1961, the use of either of these terms cannot be interpreted as a statement of either subspecific or infra-subspecific rank. Throughout this thesis, references will be made to the "upland form" or "lowland form" of *M. morio*, for example "the upland form *cinerascens*", despite the fact that the term has no taxonomic validity. The upland form of *M. morio*, *cinerascens*, is that referred to as *Oligolophus cinerascens* by Pickard-Cambridge (1890); and the lowland form, *morio*, as *O. morio* (Pickard-Cambridge *loc. cit.*).

In this thesis, the large upland form of *M. morio* mentioned by Sankey and Savory (1974) as the form *alpinus* will be shown to be a distinct species of *Mitopus* and not simply another variant of *M. morio*. It is described as a new species for Britain, since in past publications (Koch 1848, Thorell 1876, Simon 1879, Pickard-Cambridge 1890) it has been incorrectly assigned to the taxon *M. alpinus*. It will also be shown that *M. morio* displays a well-marked gradation of characters, which extend without a break over a wide altitudinal range. The forms *morio* and *cinerascens* lie at opposite ends of this gradient.

Other examples of *M. morio* have been examined from sites separated both altitudinally and latitudinally from the main sites in northern Britain. These have included specimens from a range of altitudes on Cairn Gorm, Inverness-shire; St Kilda; Pembrokeshire; Iceland; Norway and Austria.

In the past, reference has been made to another form of *Mitopus* which was described as a variety of *M. alpinus*, named *borealis* (Thorell 1876). Specimens of this variety (*sic*) came from Alpine Switzerland and the island of Maasöe in Norway. Thorell described *borealis* as a more spiny form of *alpinus*, with the legs in particular being densely denticulated. The definitive characteristics given by him were very vague however, and he stated that the females could not be distinguished from those of *M. alpinus* except in the palp patellae and tibiae which were somewhat shorter. The only other reference to this variety has been made by Sankey and Savory (1974) in which they suggest that *M. morio borealis (sic)* may occur in the extreme north of Britain and on coastal islands around Scotland. They give no evidence to support this statement. During this research, specimens of *M. morio* examined from Iceland were found to be more spiny than samples of *M. morio* from other regions, but it will be shown that they do not differ significantly from them in other ways. Thus the form *borealis*, like *cinerascens*, may be distinguishable when specimens are collected from an isolated area; but when placed amongst the whole spectrum of variants of *M. morio* from widely differing geographical regions, they only serve as further evidence for the tremendous variability and adaptibility of *M. morio* as a single species.

The phenological development of the upland form of *M. morio* and that of the form previously referred to as *alpinus*, have been studied from the early nymphal stages to maturity in the field. Finally, the egg development and early nymphal stages have been studied in the laboratory; both to determine the number of instars of *M. morio* over different parts of its range; and to attempt to elucidate the mechanism bringing about synchronisation of the life cycle, through the egg diapause.

CHAPTER TWO

SAMPLE SITES AND GENERAL METHODS

2.1 The location of the sample sites

Sites were chosen at a wide range of altitudes in northern Britain; their locations are marked in Figure 2.1. The altitude of each sample site was measured using an aneroid barometer calibrated from Ordnance Survey data. The bulk of the sampling was done in northern England during the three field seasons (1979 to 1981); in 1980 pitfall catches were also taken along an altitude transect on the north-west aspect of Cairn Gorm, Inverness-shire.

2.1.1 The main sites

The seven main sites are listed in Table 2.1. In 1979, there were five main sites, three on Muggleswick Common, Co. Durham, one at Bog End on the Moor House National Nature Reserve, Cumbria, and one at the Durham University Field Station. All seven sites were sampled in 1980.

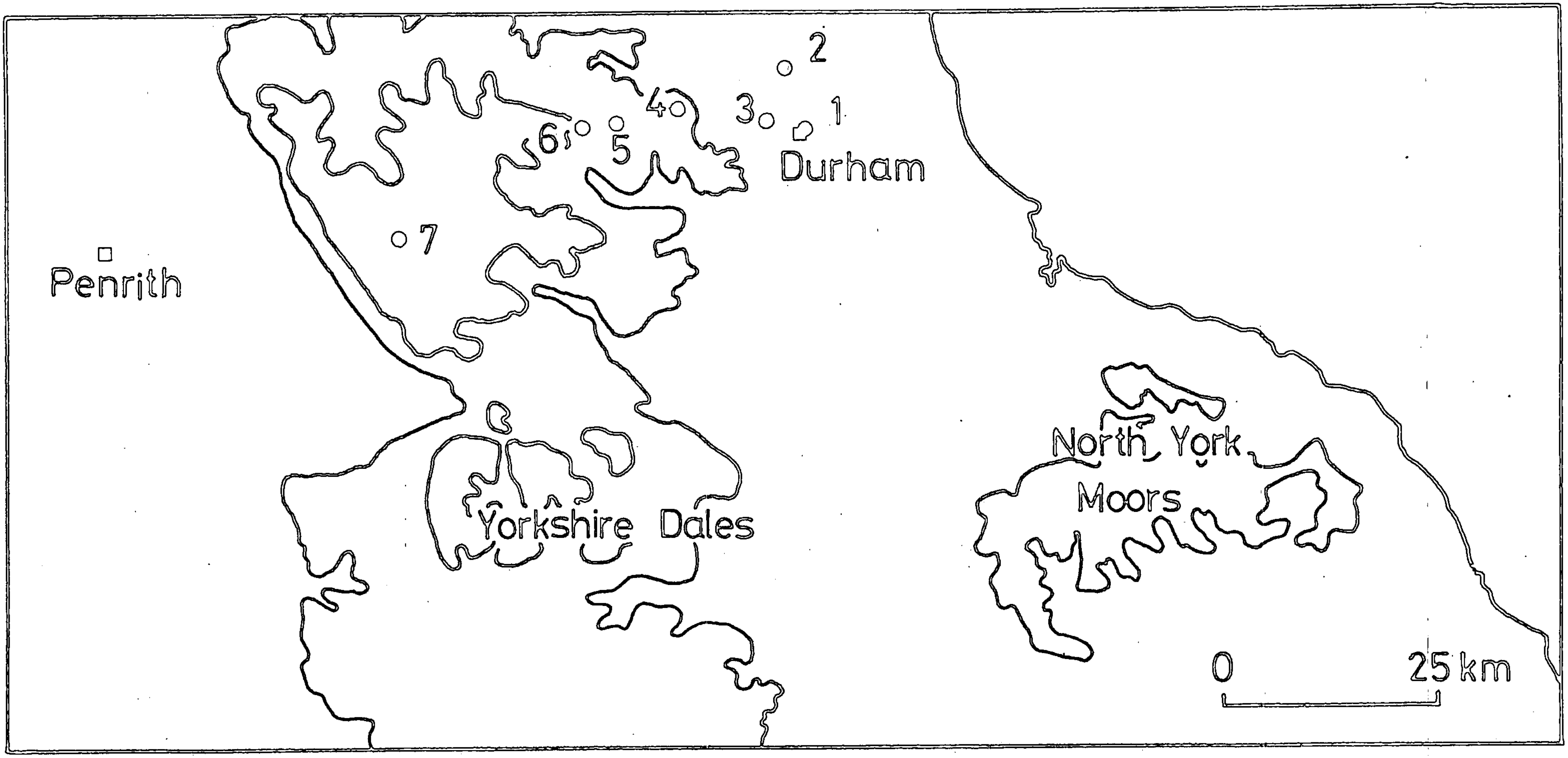
Table 2.1 Main sample sites in 1979 and 1980

Site	Altitude (m)	National Grid Reference
Field Station	76	NZ 274406
Waldridge Fell	137	NZ 243493
Esh Winning	152	NZ 195416
Muggleswick 1	260	NZ 029494
Muggleswick 2	411	NZ 014447
Muggleswick 3	476	NZ 004440
Bog End	549	NY 764329

Figure 2.1 : The main sample sites

1. 76m Durham University Field Station
2. 137m Waldridge Fell
3. 152m Esh Winning
4. 260m Muggleswick Common
5. 411m Muggleswick Common
6. 476m Muggleswick Common
7. 549m Bog End

The thin contour shows land over 244m; the thick contour, land over 488m.


2
4
3
1
6
5
Durham
7
Penrith
North York
Moors
Yorkshire Dales
0
25 km

The nature of the vegetation at the upland moorland localities varied from the lower, drier, grazed heath-like sites where *Calluna vulgaris* (L.) Hull was dominant, and *Vaccinium myrtilis* L. and *Pteridium aquilinum* (L.) Kuhn also occurred (Muggleswick 260m), to the highest sites on blanket bog (Moor House 549m) where *Calluna* and *Eriophorum vaginatum* L. are co-dominant. The lower altitude sites were not all on moorland. The 76m site at the Durham University Field Station was sampled in all three field seasons. Few specimens were obtained from pitfall traps since material was lost as a result of interference by badgers. The vegetation at this site comprised tussocky grasses (*Dactylis glomerata* L., *Lolium perenne* L. and *Phleum pratense* L.), with brambles (*Rubus* spp.), under a canopy of mixed deciduous trees.

The area chosen on Waldridge Fell 137m was dominated by tall *Calluna*. The adjoining vegetation also included *Epilobium angustifolium* L. and tussocky grasses.

The vegetation at Esh Winning 152m was a mixture of tussocky grass with scattered *Calluna* plants, under a canopy of mixed deciduous trees.

2.1.2 Additional sites in northern England

In 1979, harvestmen were also collected by hand from sites at a wide range of altitudes in the North Yorkshire Moors and Yorkshire Dales. The sites chosen (listed in Appendix 1) had been previously sampled during another study (Coulson and Butterfield in a Report to the Nature Conservancy Council 1980) in which they are more fully described. Pitfall-trapped specimens from this previous survey were also made available to me.

During the 1981 field season, pitfall traps were laid at a greater number of sites at lower altitudes in Co. Durham than in the previous years. Further specimens were also made available to me from M. Coulson. The sites are listed in Table 2.2.

Table 2.2 Additional sample sites in 1981

Site	Altitude (m)	National Grid Reference
Bear Park	91	NZ 243440
Hurworth	122	NZ 426338
Wheatley Hill	152	NZ 358388
Sunbiggin Road	183	NY 701157
Hoff Wood	198	NY 661169
Sunbiggin Fen	254	NY 673077
Sun Peak Butts	274	NY 680083
Hamsterley	310	NZ 062279

2.1.3 The Cairn Gorm transect

Sites were chosen to cover a wide altitude range from 213m to 1189m. The vegetation varied from site to site as a consequence of the increasing altitude:

a. 213m (NH 942163)

The vegetation at this site largely comprised *Vaccinium myrtilis* and *Calluna vulgaris* with sphagnum moss.

b. 305m (NH 952104)

This site lay on the edge of coniferous woodland, with *Vaccinium myrtilis* dominant.

c. 454m (NH 986076)

This site was on a steep bank, sparsely vegetated by *Calluna* and lichens. There was a very dense *Calluna* sward nearby.

d. 576m (NH 988072)

A wet site, with a stream nearby. The *Calluna* fairly tall, but open.

e. 665m (NH 992059)

A drier site, with short *Calluna* dominant.

f. 768m (NH 996052)

A wet peaty site, on a slight incline.

g. 972m (NJ 000046)

Very short *Calluna* and *Vaccinium* on a slight gradient.

h. 1137m (NJ 004048)

A very exposed site, largely bare rock and gravel, with patches of moss and very short *Festuca*.

i. 1189m (NJ 006044)

A very short turf of *Vaccinium, Carex* and *Festuca* with scattered rocks.

2.2 General Methods

2.2.1 Fieldwork

Hand Collection

Harvestmen were collected by hand throughout the season. Early instars were caught by pulling back the tussocks of vegetation to reveal the harvestmen, and then sucking the animals into a large pooter. These early instars frequently occurred in aggregations, so that several individuals were often caught together by this method. Speed of capture was essential, since all instars moved very rapidly, the larger ones in particular. No more than about ten animals could be kept together in the pooter without cannibalism occurring, so that frequent emptying of the pooter was necessary. Older instars, too large for a pooter, were caught by picking them up one by one by their legs and placing each into an individual tube, to avoid cannibalism.

Pitfall Trapping

Most specimens were obtained from the main sites by pitfall trapping. In 1979, the pitfall traps used were polythene screw-top bottles (5cm by 12cm); in 1980, these were replaced by vending machine plastic cups (7cm by 8cm). Both had the advantage that they did not endanger grazing sheep if accidently trodden on. Traps were filled to a depth of about 3cm with a 2% solution of formalin to kill and preserve specimens, with a few drops of detergent to reduce the surface tension.

Traps were placed along a transect 2m apart. In 1979, traps were placed at each of the four main sites. In 1980, there were seven main sites and the number of traps was increased at some of these, in order to increase the catch.

A few specimens were also obtained from the Durham University Field Station in 1979, during an undergraduate project (G. Downs).

Vacuum Sampling

In 1979, attempts were made to collect harvestmen using a D-vac, a method which has been successful for spider collection (Taylor 1958, Duffey 1974). This method, however, was found to be very inefficient for harvestmen, probably because the animals either clung very tightly to the vegetation, or buried themselves into the moss layer. Duffey *(loc. cit)* found the efficiency of sampling decreased with increasing vegetation height and that the technique was unsuitable in vegetation taller than 30cm. The vegetation at several of the sites used in this study was taller than 30cm. The few specimens which were vacuumed up frequently suffered from loss of legs as a result, and had to be discarded.

2.2.2 Laboratory work

Specimens were preserved in 70% ethanol or 10% formalin solution. The latter was used to preserve specimens which were later dehydrated to obtain dry weights.

All body measurements (mm) were made using a microscope graticule calibrated to three decimal places.

Live animals were kept in a variety of containers. Individuals were maintained in plastic screw-top jars, 6cm by 4cm and 9cm by 8cm. Harvestmen are susceptible to changes in humidity (Todd 1949), particularly the younger instars. A suitable humidity must be maintained for successful culture, otherwise desiccation or fungal attack ensue, and the cuticles of newly moulted animals do not harden properly. Consequently, both types of culture jar were lined with a thin (0.5 - 1.0cm) base-layer of Plaster of Paris and a piece of filter paper, both of which were kept damp but not wet. Groups of immature animals and breeding pairs were maintained in plastic fish tanks, also with a base-layer of damp Plaster of Paris to maintain humidity. Tanks were covered with muslin or plastic lids with holes pierced for ventilation, and kept in 10°C or 15°C constant temperature rooms.

The harvestmen were fed at frequent intervals. The food offered was varied: *Mitopus* is omnivorous in its laboratory diet. Younger instars were offered dead *Drosophila*. In addition to these, older animals were given small pieces of fresh liver, or, for convenience, powdered standard animal feed pellets mixed to a paste with water.

2.2.3 Determination of the instars

The instars of *M. morio* and other harvestmen may be separated on femur length measurements using a technique developed by Heighton (1964). Measurements were made of the lengths of the femurs of the second walking legs (left or right) for all specimens collected. Data for each altitude site and year were kept separate. Each instar fell into a discreet-size class frequency on a basis of these measurements. A femur length frequency plot for each of the main sites results in a series of polymodal frequency histograms. Figures 2.2 and 2.3 are femur length frequency plots for the upland form *cinerascens* from four of the main sites in 1980. The results were similar in 1979. Each peak represents the size class frequency of a particular instar. The data for Muggleswick 476m provide the most complete picture, with five distinct peaks for the juvenile stages, representing five instars. First instar animals are not found in the field, since a few minutes after hatching the first instar nymphs moult to the second instar whilst still clinging to the eggshell (Sankey and Savory 1974). Field collections of animals therefore provided specimens from the second instar onwards. The upland *cinerascens* has seven instars between hatching from the egg and adulthood. This confirms the conclusion in the unpublished work by Heighton (1964) on the lowland *M. morio*. Slagsvold (1976) found the same number of instars for *M. morio* in Norway. The adult stage is the final instar, and is the only stage when the two sexes may be readily distinguished from one another, since the genital operculum remains closed until the seventh and final instar. Male specimens tend to have the longer legs, but there is some overlap between the lengths of the second femurs of males and females at all the sites.

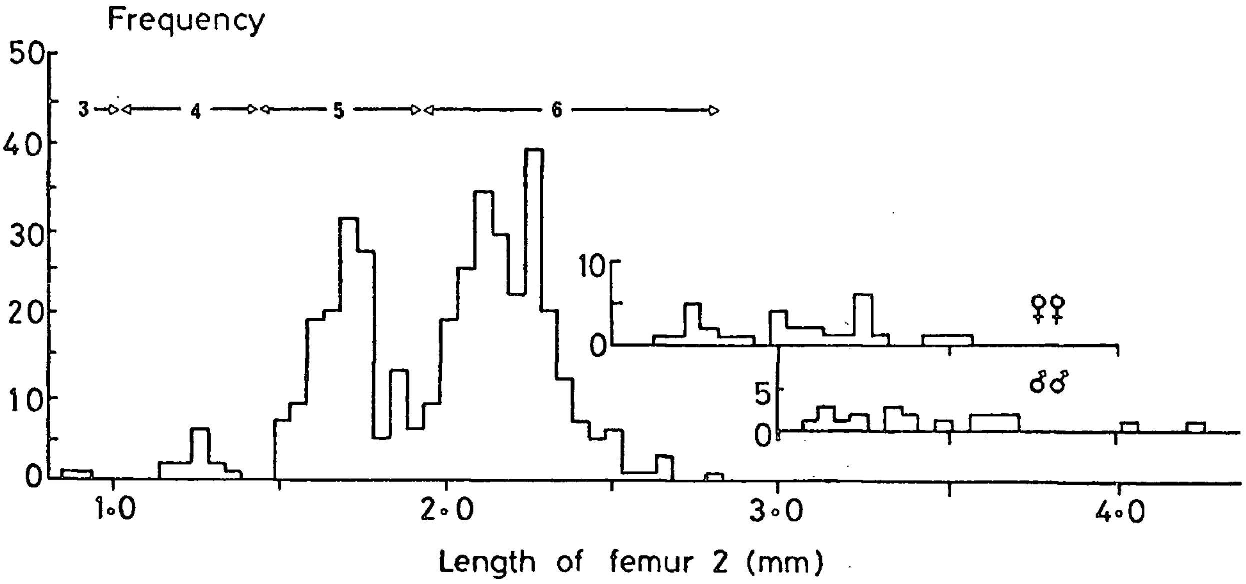
The estimated range of the lengths of the second femurs for each instar were determined from these histograms, and the mean femur length of each instar at each altitude was calculated for the two years. It is possible to calculate the range using a cumulative frequency plot on arithmetic probability paper (Harding 1949). This was done for the specimens taken in 1980 from Bog End 549m; the calculated ranges obtained

Figure 2.2 : Polymodal frequency plots of the lengths of the second femurs (mm) of instars of *Mitopus morio* in 1980. (Specimens from hand and pitfall collections.)

a. *M. morio* from Muggleswick 260m

b. *M. morio* from Muggleswick 411m

a


Frequency
50
40
30
20
10
0
3
4
5
6
10
0
♀♀
5
0
♂♂
1·0
2·0
3·0
4·0
Length of femur 2 (mm)

b

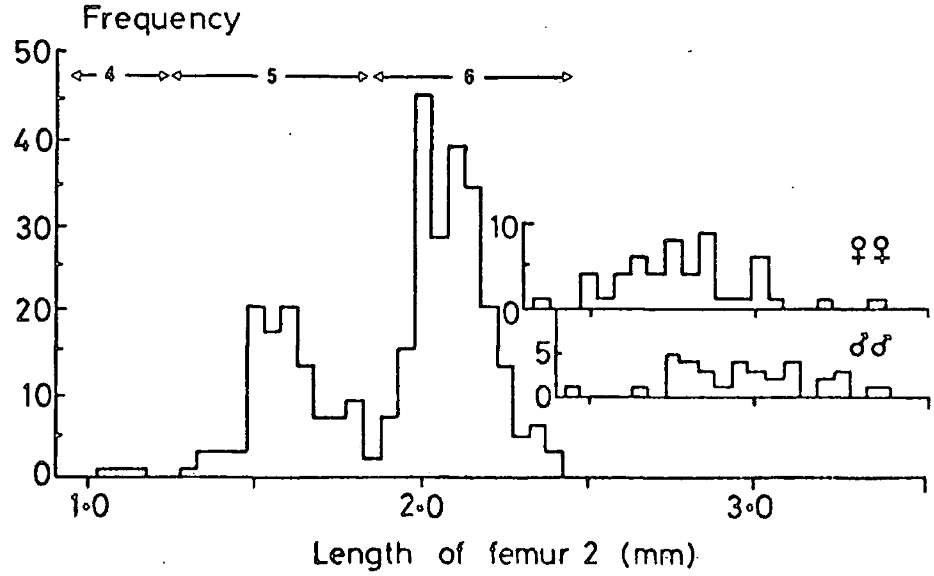
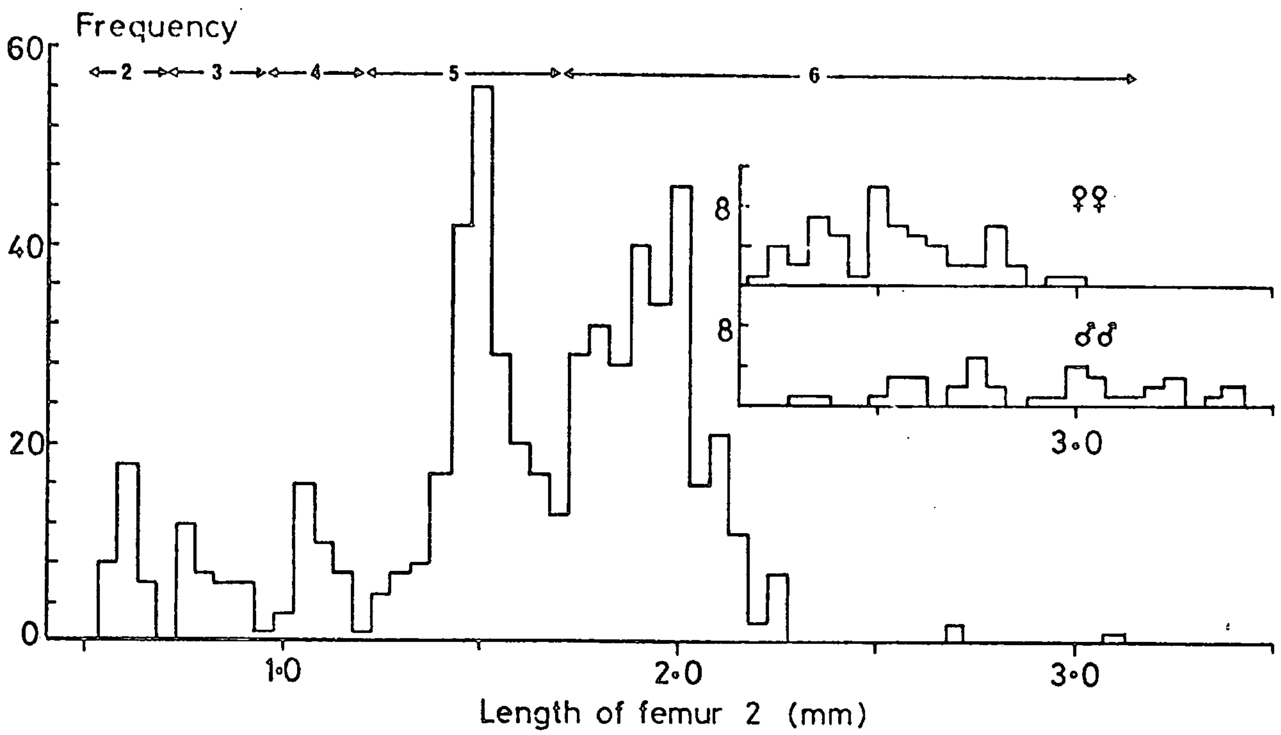

Frequency
50
40
30
20
10
0
4
5
6
10
0
♀♀
5
0
♂♂
1·0
2·0
3·0
Length of femur 2 (mm)

Figure 2.3 : Polymodal frequency plots of the lengths of the second femurs (mm) of *Mitopus morio* in 1980. (Specimens from hand and pitfall collections.)

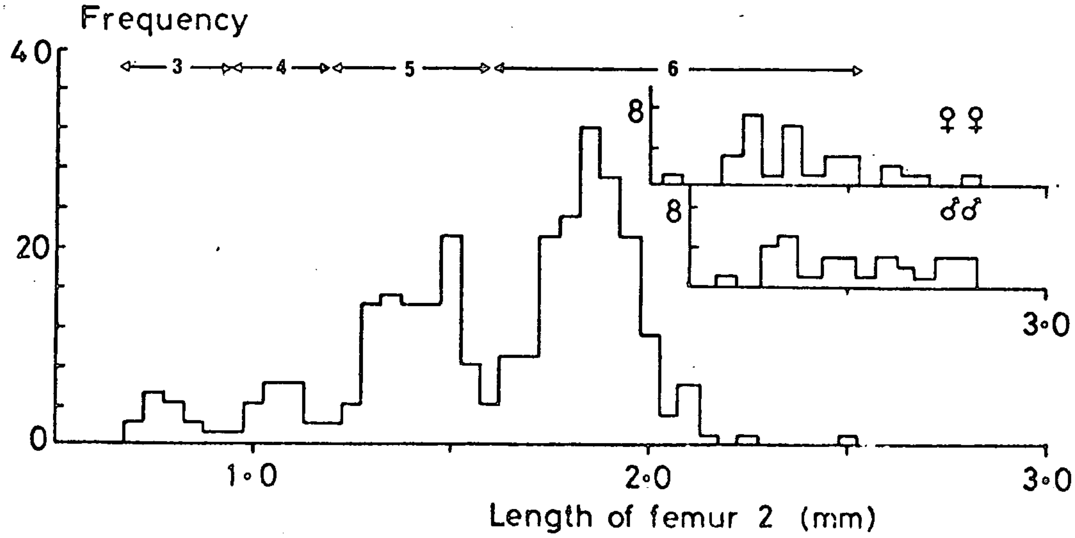
a. *M. morio* from Muggleswick 476m

b. *M. morio* from Bog End 549m

a


Frequency
60
40
20
0
2
3
4
5
6
8
♀♀
8
♂♂
3·0
1·0
2·0
3·0
Length of femur 2 (mm)

b


Frequency
40
20
0
3
4
5
6
8
♀♀
8
♂♂
3·0
1·0
2·0
3·0
Length of femur 2 (mm)

were found to be the same as the estimated ranges. Estimation is a far more rapid method; since it is just as accurate, the limits for each instar were estimated from the polymodal frequency histograms for all the other sites. Data were more extensive for 1980. Individual specimens in each pitfall catch could then be assigned to instars, knowing the femur length range for that particular instar.

A list of the symbols and abbreviations used in this thesis is given in Appendix 6.

CHAPTER THREE

THE RELATIONSHIP BETWEEN THE UPLAND AND LOWLAND FORMS OF *MITOPUS MORIO*

3.1 Introduction

A comparison of specimens of *Mitopus morio* from upland sites with those from lower altitude sites reveals distinct differences. If samples of *M. morio* from two widely separated altitude sites were to be pooled, the combined sample would be completely divisible into the two original samples of animals on a basis of their sizes and leg lengths. The small, short-legged harvestmen from the upland sites are those identified by Pickard-Cambridge (1890) as *Oligolophus cinerascens* C.L. Koch, and by Sankey and Savory (1974) as *Mitopus morio cinerascens*. The larger, longer-legged specimens of *Mitopus morio* from the lowland sites were identified as *Oligolophus morio* Simon by Pickard-Cambridge (1890), and as *Mitopus morio morio* by Sankey and Savory (1974). A form identifiable as *cinerascens* does therefore exist in upland regions of northern Britain, but its status requires examination.

In this chapter, I shall present data to show that *M. morio* is a single but highly variable species, which in northern Britain at least exhibits an altitude-linked size cline. The typical form of *cinerascens* is simply the upland extreme of this cline.

M. morio has recently been studied in Norway by Slagsvold (1976), and a similar variation with altitude has been observed. He studied *M. morio* over several years and found that femur lengths of adults from high altitude localities were, in general, smaller than those from lower-lying sites. He later showed, using multiple regression analyses, that 72-88% of femur length variation could be accounted for by a combination of three factors: latitude, altitude and aspect (Slagsvold 1979).

This study was in progress before Slagsvold's work became available. My conclusions were derived totally independently, although they are comparable.

Pitfall collections were made in three years over a wide altitude range, with four main collecting sites on upland moorland in 1979, and seven sites in 1980 and 1981 on both moorland and woodland. Site details are given in Chapter Two. The instar complement for each trapping period was analysed by the method given on page 10.

3.2 Between-year differences

The mean femur lengths for each instar from specimens of *M. morio* trapped in 1979, 1980 and 1981 (calculated by the method described in Chapter Two) are given in Tables 3.1 and 3.2. The mean femur lengths of adult males are consistently greater than those of adult females at each site. The mean femur lengths of each instar trapped in different years have been compared using Student's *t*-tests: the results are presented in Table 3.3. The significant differences in mean femur lengths are mostly due to the small sample sizes obtained. Adult males and females from 549m were significantly longer-legged in 1979 than in 1980.

3.3 Growth increments

The mean femur lengths of all instars in 1980 for both the upland *cinerascens* and the lowland form of *M. morio* have been plotted on a logarithmic scale in Figures 3.1, 3.2 and 3.3. The values of the mean femur lengths of the first and second instars, for the three sites for which they have been plotted, have been calculated from measurements taken of animals which hatched from laboratory-laid eggs. First instars are distinguishable by the possession of an egg tooth. They moult to the second instar within minutes of hatching. Values for both field-

Table 3.1 Mean lengths of the second femurs (mm) ± one standard deviation of instars of *Mitopus morio* in 1979. Sample sizes in parentheses.

Site	Instar					
Altitude (m)	3	4	5	6	7 ♀♀	7 ♂♂
76			1.95±0.18 (4)	2.65±0.23 (11)	4.13±0.42 (16)	4.73±0.63 (5)
260	0.94±0.06 (3)	1.14±0.06 (5)	1.70±0.15 (12)	2.23±0.12 (29)	3.11±0.29 (17)	3.77±0.23 (3)
411		1.18±0.05 (12)	1.58±0.11 (31)	2.13±0.13 (43)	2.80±0.19 (45)	3.05±0.26 (31)
476		1.28±0.10 (17)	1.58±0.08 (35)	1.91±0.13 (99)	2.58±0.16 (45)	2.87±0.24 (27)
549	0.91±0.09 (18)	1.16±0.07 (22)	1.52±0.10 (99)	1.87±0.13 (138)	2.46±0.15 (216)	2.65±0.16 (57)

Table 3.2 Mean lengths of the second femurs (mm) ± one standard deviation of instars of *Mitopus morio* in 1980. Sample sizes in parentheses.

Site	Instar						
Altitude (m)	2	3	4	5	6	7 ♀♀	7 ♂♂
76	* 0.565±0.033 (31)	* 0.817±0.008 (3)	† 1.433±0.093 (6)	† 1.979±0.119 (17)	2.682±0.167 (17)	3.8112±0.341 (14)	4.100±0.364 (10)
137						3.577±0.289 (26)	3.870±0.316 (10)
152						3.210±0.377 (20)	3.512±0.463 (21)
260	* 0.518±0.032 (40)	0.875±0.100 (2)	1.242±0.057 (13)	1.697±0.102 (138)	2.193±0.150 (233)	3.055±0.249 (30)	3.468±0.249 (22)
411	* 0.555±0.040 (30)	0.900 (1)	1.100±0.05 (3)	1.593±0.114 (103)	2.086±0.171 (218)	2.763±0.185 (56)	2.972±0.216 (34)
476	* 0.502±0.028 (32)	0.814±0.063 (32)	1.079±0.053 (38)	1.497±0.101 (208)	1.941±0.160 (275)	2.545±0.197 (60)	2.889±0.297 (37)
549		0.793±0.070 (15)	1.067±0.049 (18)	1.417±0.098 (96)	1.863±0.123 (165)	2.380±0.171 (30)	2.510±0.181 (30)

* Hatched in laboratory

† Data collected in 1981

Table 3.3 The results of t-tests showing the significance of the differences in mean femur lengths of instars of *M. morio* between 1979 and 1980. ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$)

Site altitude (m)	Instar					
	3	4	5	6	7 ♀♀	7 ♂♂
76			0.307	0.398	2.294 *	2.070
260	0.826	3.275 **	0.068	1.519	0.657	2.112 *
411		2.479 *	0.572	1.916	0.984	1.309
476		7.811 ***	5.450 ***	1.909	1.004	0.283
549	4.198 ***	4.928 ***	7.264 ***	0.478	2.436 *	3.566 ***

Figure 3.1 : Mean lengths of the second femurs (mm) of *Mitopus morio* plotted on a logarithmic scale against instar number for

(a) Muggleswick 260m and

(b) Muggleswick 411m.

Curves have been fitted by eye.

□ Laboratory-hatched

□ Hand-collected and pitfall-trapped samples

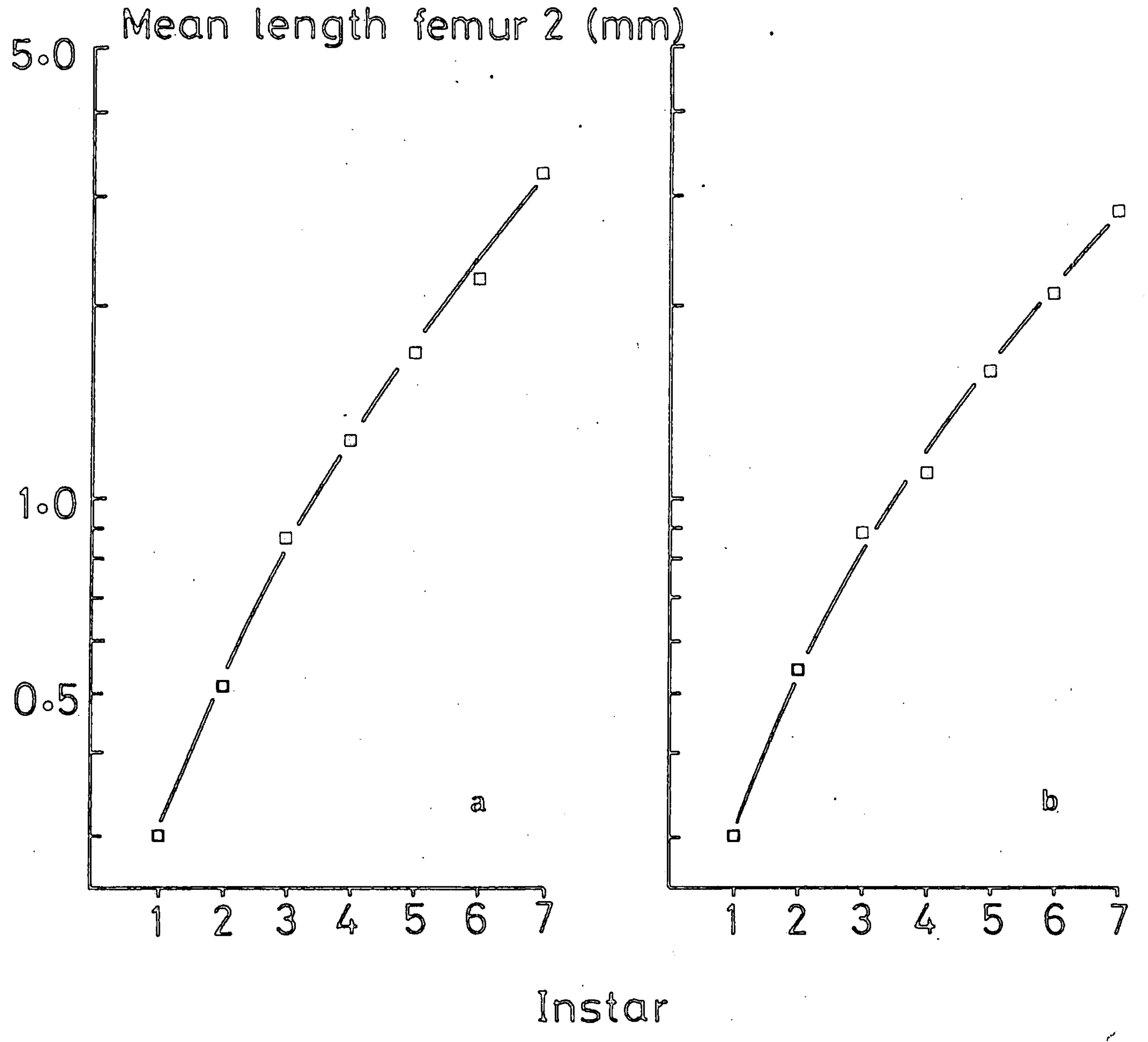

Mean length femur 2 (mm)
5·0
1·0
0·5
a
b
1
2
3
4
5
6
7
Instar

Figure 3.2 : Mean lengths of the second femurs (mm) of *Mitopus morio* plotted on a logarithmic scale against instar number for

(a) Muggleswick 476m and

(b) Bog End 549m.

Curves have been fitted by eye.

□ Laboratory-hatched

□ Hand-collected and pitfall-trapped samples

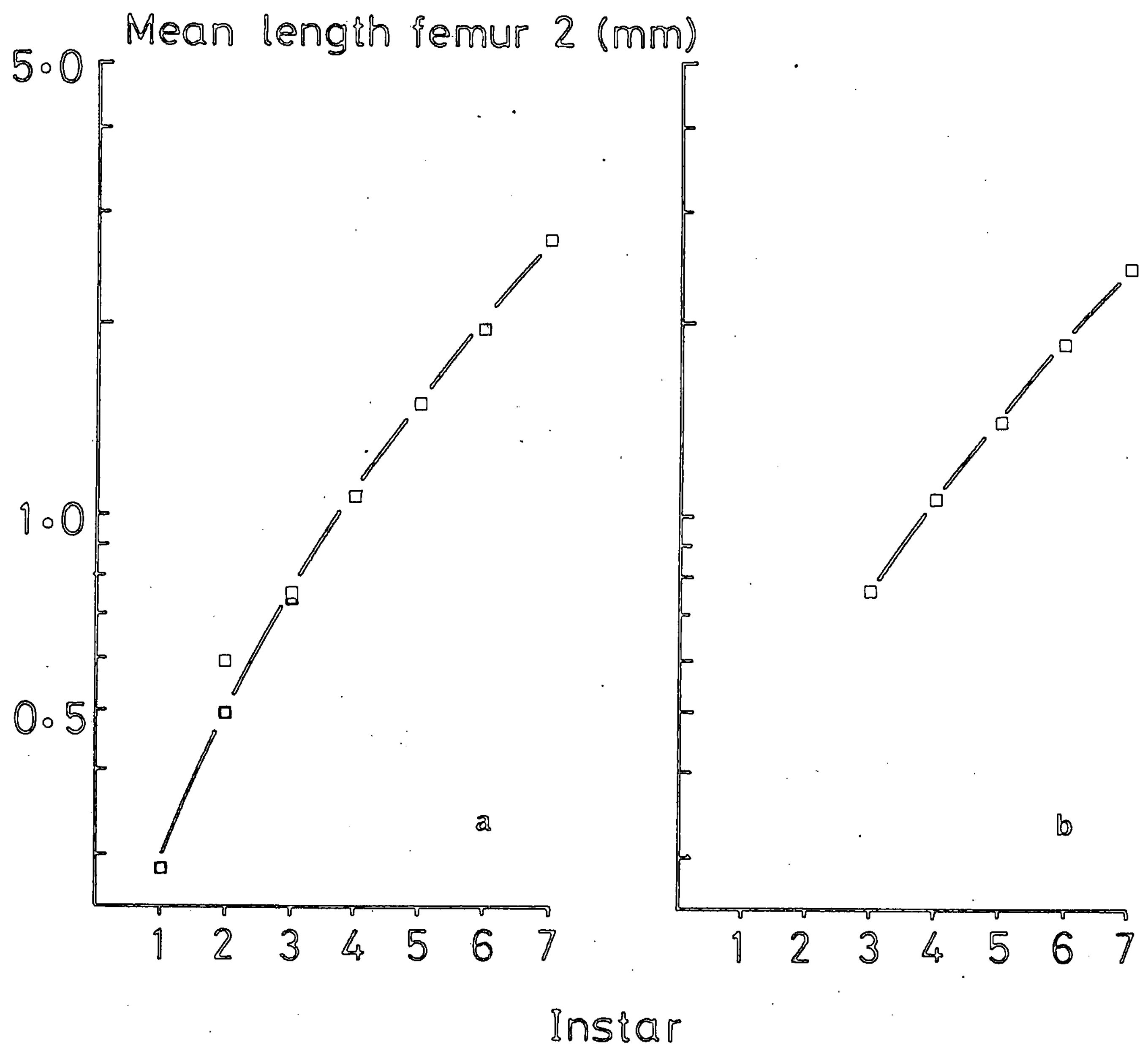

Mean length femur 2 (mm)
5·0
1·0
0·5
a
b
1 2 3 4 5 6 7
1 2 3 4 5 6 7
Instar

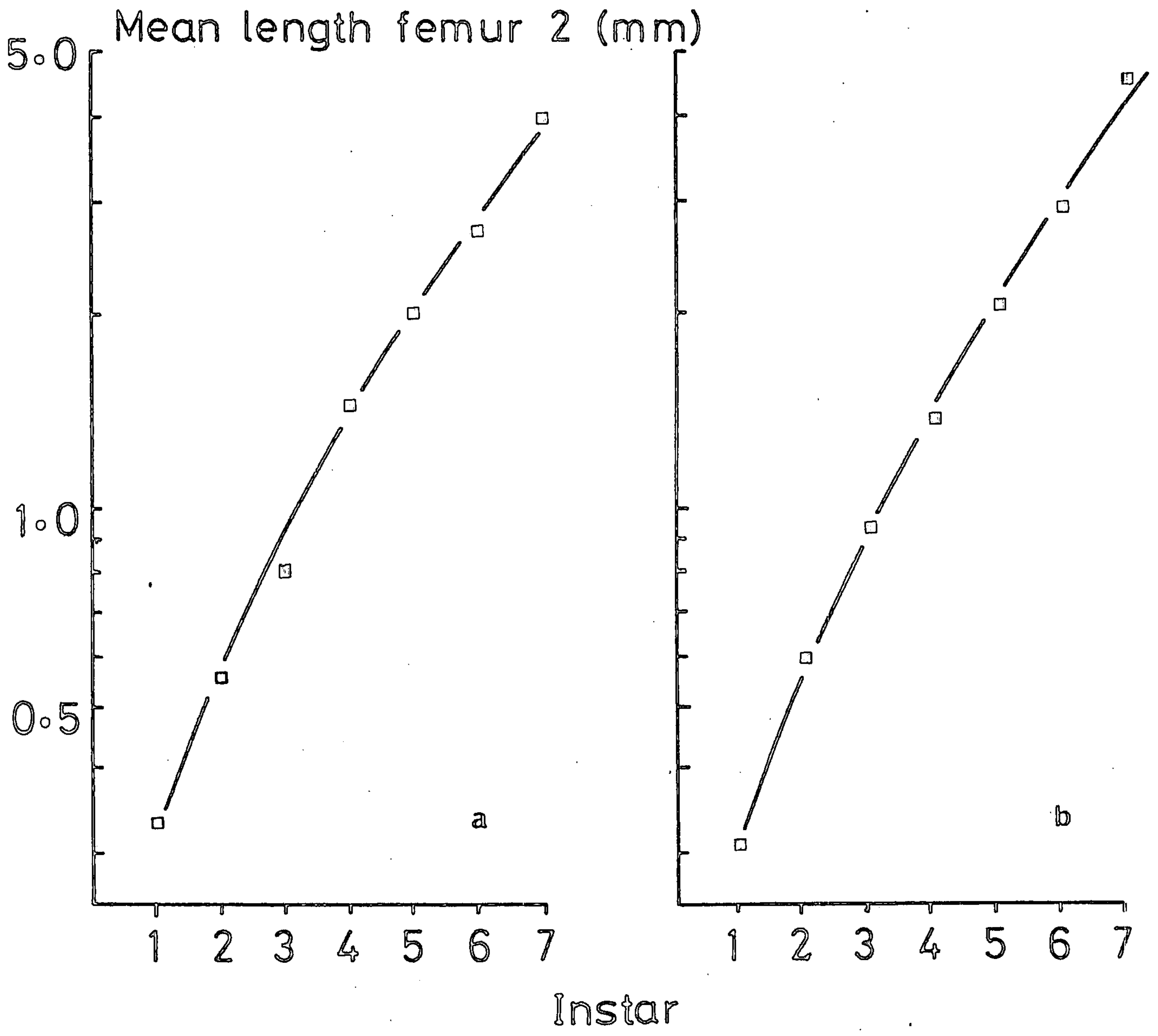
Figure 3.3 : Mean lengths of the second femurs (mm) of *Mitopus morio* plotted on a logarithmic scale against instar number for

(a) Field Station 76m site in 1980 and

(b) Field Station 76m site in 1964. Unpublished data from Heighton (1964).

□ Laboratory-hatched

▣ Hand-collected and pitfall-trapped samples


Mean length femur 2 (mm)
5·0
1·0
0·5
1
2
3
4
5
6
7
a
b
Instar

trapped and laboratory-reared second instars are available only for Muggleswick 476m. Eggs laid in the laboratory by females of *M. morio* of the form *cinerascens* produced second instars which were 16% smaller ($p < 0.05$) than those trapped in the field.

For insects, Dyar's law (Chapman 1971) states that there is a constant growth increment between moults. This produces a linear relationship between size (logarithmic scale) and instar number; the value of Dyar's factor (the ratio between consecutive instars) is often about 1.4 (Chapman *loc. cit.*). Figures 3.1, 3.2 and 3.3 show that the relationship between the logarithmic values of mean femur length and instar number is curvilinear for *M. morio* from five of the sites where it was taken. The omission of an instar would create a break in the curve. However, the fact that the curve is smooth indicates that no instars have been missed in the sampling. Unpublished data from Heighton collected from the 76m site shows the same relationship for *M. morio* in 1964 (Figure 3.3). In general, the Dyar's factors were greatest between first and second instars (approximately 1.75), and least between the sixth and seventh instars (approximately 1.41). There is also a decrease in the value of the Dyar's factor between instars six and seven with increasing altitude. It is 1.48 for 76m but 1.31 for 549m.

3.4 Size differences in relation to altitude

It is clear from Table 3.1 that in 1979 the mean lengths of the second femurs of nearly all the instars of *M. morio* of the form *cinerascens* are shorter at the higher altitudes than at the lower sites. However, each sample is composed of individuals with a range of different femur lengths. In Figure 3.4, the form *cinerascens* has been designated as being composed of adult females with a second femur length of less than 3.10mm.

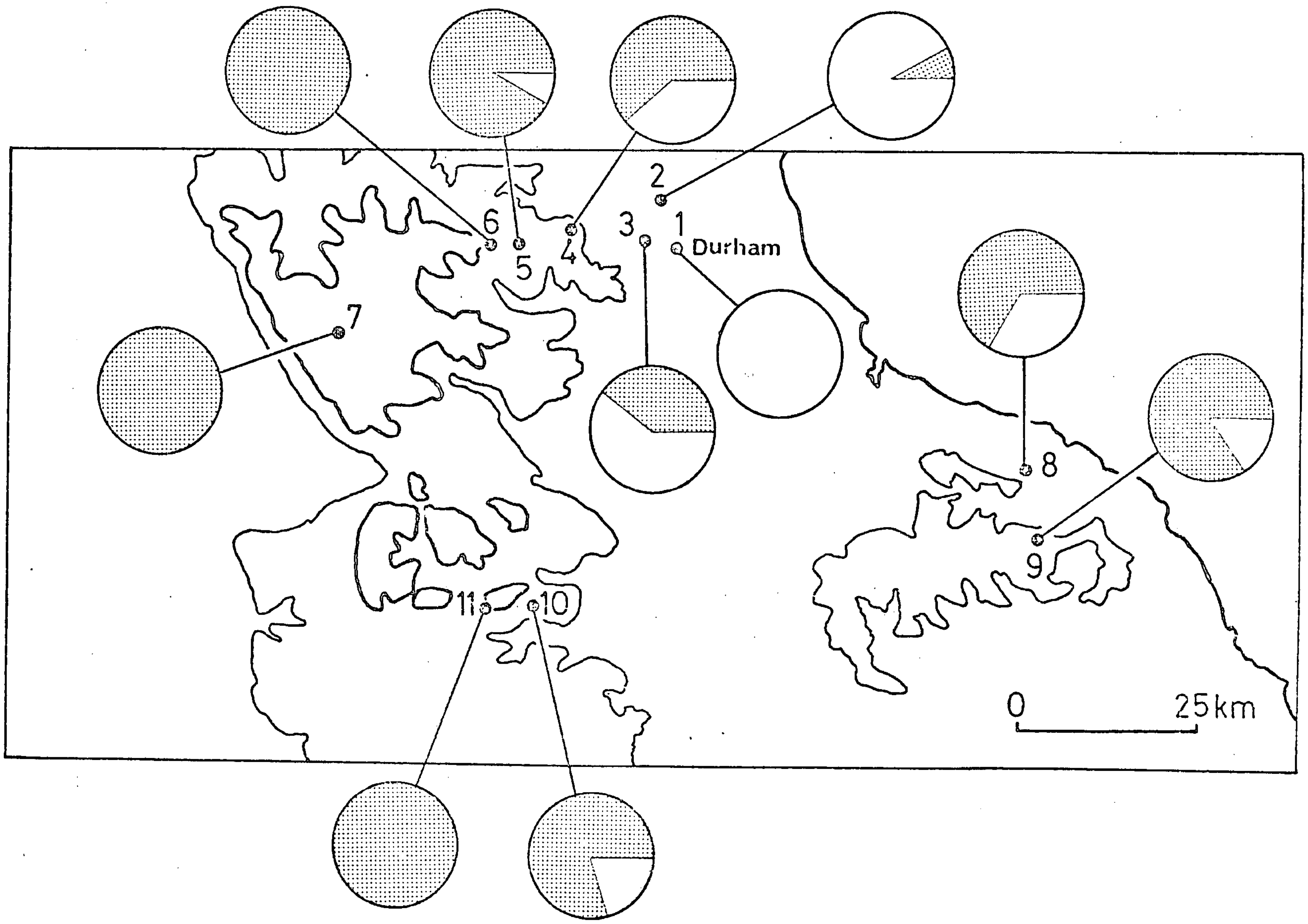
Figure 3.4 : The proportion of the total female specimens of *Mitopus morio* trapped at each of the seven main altitude sites in 1980 (subsidiary sites 1977 to 1979) which have been assigned to the form *cinerascens*; i.e. the proportion with a second femur shorter than 3.10mm.

SITE

1 76m - Field Station
2 137m - Waldridge Fell
3 152m - Esh Winning
4 260m - Muggleswick
5 411m - Muggleswick
6 476m - Muggleswick
7 549m - Muggleswick
8 213m - Tranmire - North Yorkshire Moors
9 305m - Yarlsey - North Yorkshire Moors
10 457m - Golden Groves - Yorkshire Dales
11 488m - Beldon Bottom - Yorkshire Dales

Key to symbols

⁘	proportion of *M. morio* trapped with second femur length less than 3.10mm (i.e. proportion of *cinerascens* trapped)
—	244m contour
═	488m contour


2
1
3
Durham
6
5
4
7
8
9
11
10
0
25km

Specimens from the highest sites all have second femurs of less than 3.10mm, but specimens from intermediate altitude sites may have femur lengths greater or less than this. None or very few of the samples collected at the lowest altitudes contained any specimens with second femurs as short as this. Thus, although the small form *cinerascens* from the highest sites is completely separable from the larger lowland form of *M. morio*, a gradient exists with altitude in the proportion of small short-legged specimens obtained in the particular sample.

Using the values for adults in Table 3.1, a regression line may be fitted to a plot of mean femur length (on a logarithmic scale) against altitude for specimens from 260m, 411m, 476m and 549m, indicating that the upland form of *M. morio (cinerascens)* exhibits a size gradient with altitude. It was also observed in 1979 that the lowland form of *M. morio* from 76m appeared to fit on to the upper end of this altitude cline. More extensive data were therefore collected at intermediate altitudes in 1980. The results of the calculation of mean femur lengths of *M. morio* from a range of altitudes in 1980 are given in Table 3.2. The logarithms for the values of adults in both years have been plotted against site altitude in Figures 3.5 and 3.6. These figures show that specimens of all forms of adult *M. morio* collected in 1980 fall on the same regression line, according to sex. For each sex, femur length decreases with increasing site altitude for all sites sampled. Altitude accounts for approximately 96% of log. femur length variation ($r^2 \approx 0.96$). There is approximately an 11% decrease in femur length for every 100m increase in altitude for both sexes at the main sites in 1979, and 9% in 1980. This relationship applied to both adult males and females in the two years. The value for the slope for female mean femur lengths (logarithmic scale) in 1979 is not significantly different from that in 1980, whilst that for males is greater in the first of the two years ($p < 0.05$). There are no significant differences in the values of the

Figure 3.5 : Mean lengths of the second femurs (mm) ± two standard errors of females of *Mitopus morio* in 1979 and 1980 plotted on a logarithmic scale against altitude (m).

The slopes of the regression equations are given by:

1979 $y = -0.000468x + 0.637477$

$n = 5$ $r = -0.987$ S.E. of slope $= 0.000044$ $p < 0.001$

1980 $y = -0.000399x + 0.595992$

$n = 7$ $r = -0.980$ S.E. of slope $= 0.000036$ $p < 0.001$

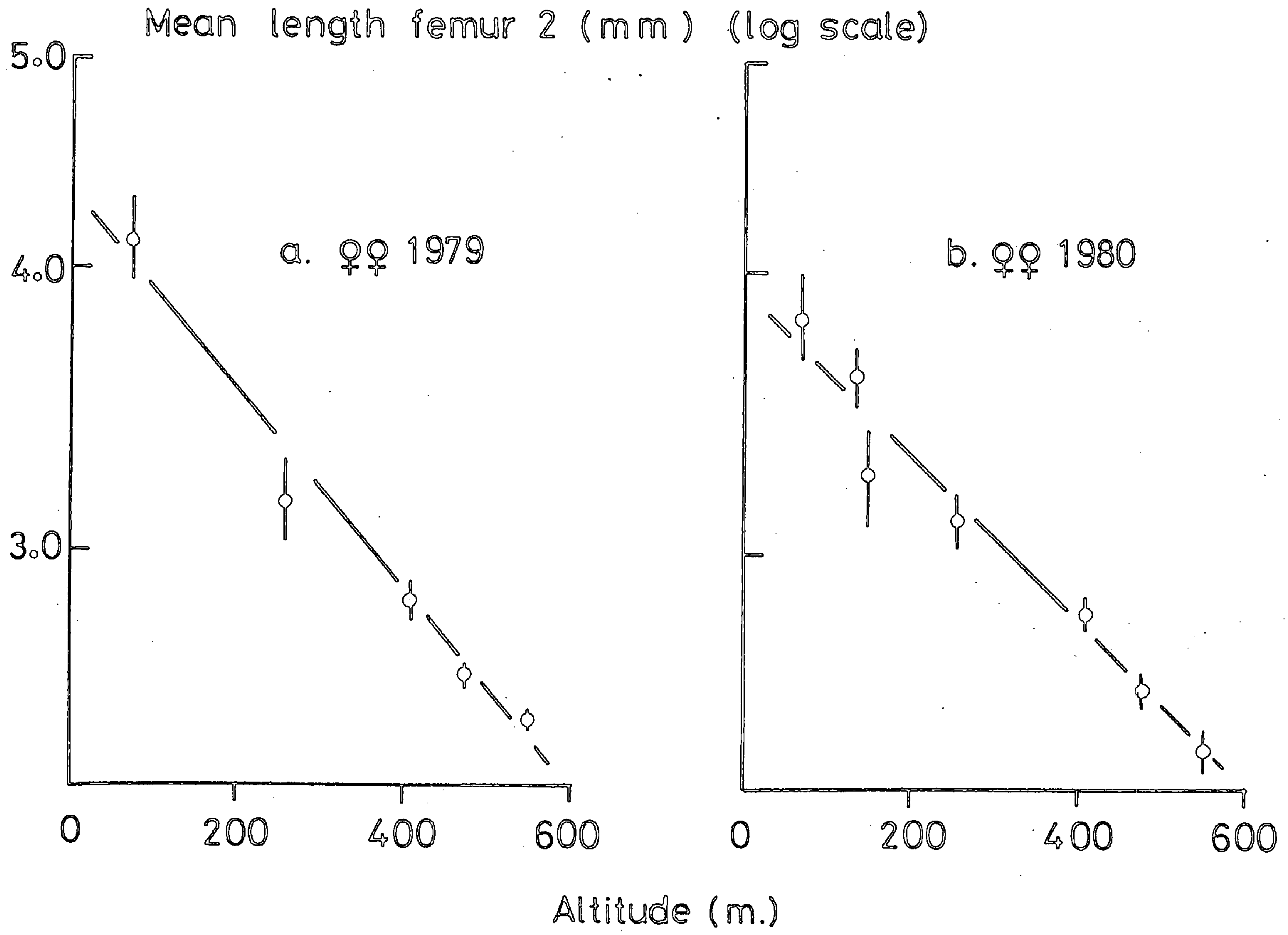

Mean length femur 2 (mm) (log scale)
5.0
4.0
3.0
a. ♀♀ 1979
b. ♀♀ 1980
0
200
400
600
0
200
400
600
Altitude (m.)

Figure 3.6 : Mean lengths of the second femurs (mm) ± two standard errors of males of *Mitopus morio* in 1979 and 1980 plotted on a logarithmic scale against altitude (m).

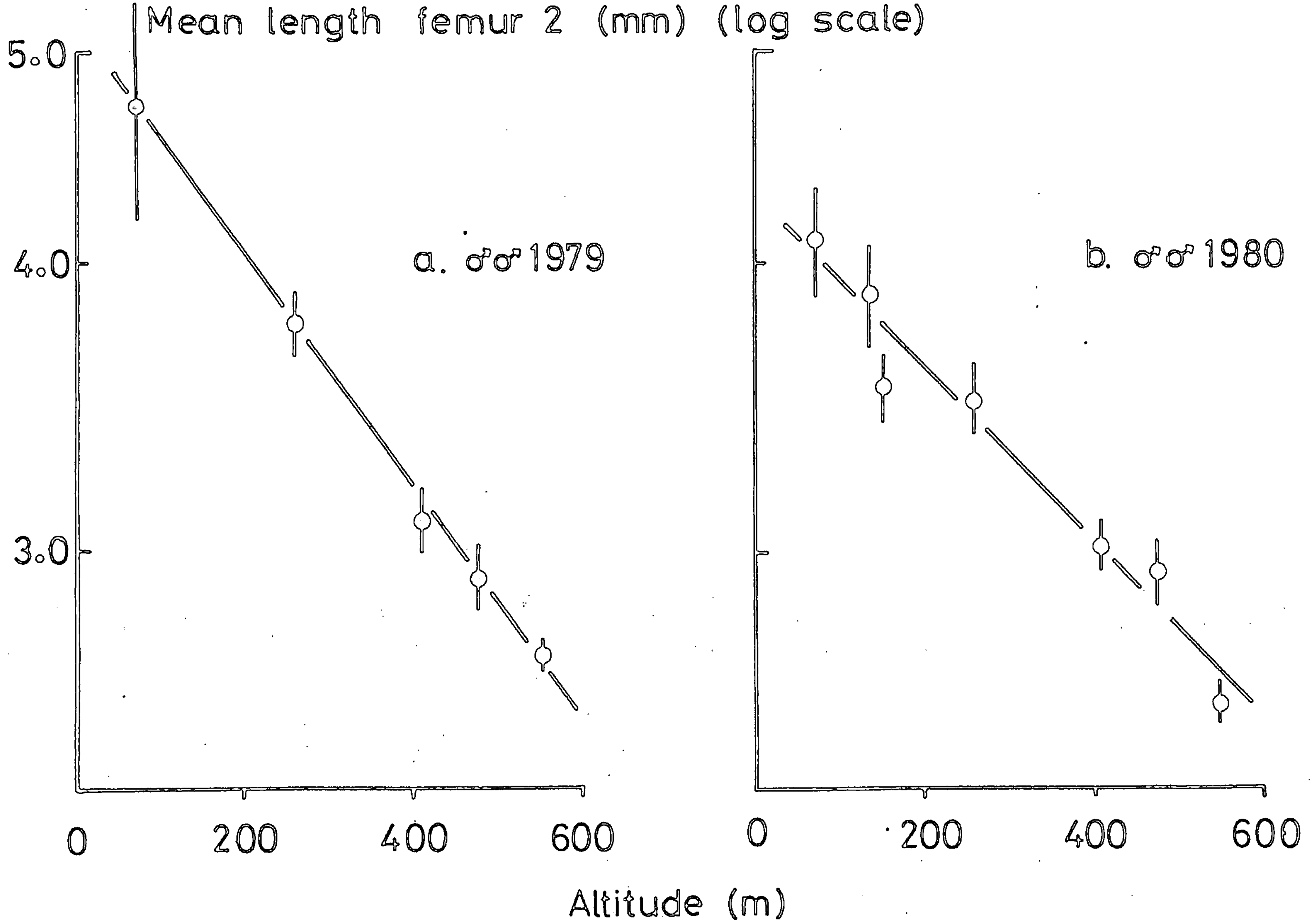
The slopes of the regression equations are given by:

1979 $y = -0.000540x + 0.714714$

$n = 5$ $r = -0.999$ S.E. of slope = 0.000016 $p < 0.001$

1980 $y = -0.000400x + 0.634841$

$n = 7$ $r = -0.977$ S.E. of slope = 0.000039 $p < 0.001$

Mean length femur 2 (mm) (log scale)
5.0
4.0
3.0
a. ♂♂ 1979
b. ♂♂ 1980
0
200
400
600
0
200
400
600
Altitude (m)

slopes for females compared with males in either year. It is likely that since the difference in the values of the slopes of female femur length with altitude is not significant, the difference between slopes for males is not a real one, in biological terms. It may simply be the result of the very small samples of males trapped at the lower altitude sites, particularly in 1979. This altitude relationship has been extended by including all samples from the additional moorland sites (listed in Appendix 1). The mean lengths of the second femurs of adults trapped at the subsidiary sites in the Yorkshire Dales and North Yorkshire Moors in the 1979 field season were calculated as well as those of female specimens obtained from the 1977 and 1978 field seasons by Coulson and Butterfield for the Nature Conservancy Council Moorland Characterisation Survey. The mean lengths of the second femurs of adult females are given in Table 3.4. The values for female specimens have been plotted on a logarithmic scale against altitude in Figure 3.7. These additional moorland sites cover a broad area of northern England and the vegetation structure at each site differs widely. However, Figure 3.7 shows that despite any differences in habitat structure, a clear relationship still exists between femur length and altitude. Altitude change accounts for approximately 84% of femur length variation over five years (1977 to 1981), there being an 8% decrease in femur length per 100m increase in altitude for females. Data for males are less extensive but the relationship is similar. The change is considerably more dramatic than that which Slagsvold (1979) found for *M. morio* in Norway. His measurements of the length of the femur of the fourth walking leg show a decrease of only 2% over a 100m altitude increase. However, his data were collected over six years from sites which were also latitudinally separated, introducing extra variables.

Table 3.4 Mean lengths of the second femurs (mm) ± one standard deviation of females of *Mitopus morio* from the additional sites (1977 to 1979)

Site		1977			1978			1979		
Altitude (m)	Region	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
213	NYM	3.22	0.22	8	3.20	0.14	6	2.64	0.20	3
240	NYM	3.10	0.27	9	3.15	0.39	4			
259	NYM							3.12	0.13	3
260	P							3.12	0.28	17
305	NYM	3.12	0.25	23	3.06	0.25	14	2.96	0.17	5
396	YD	2.84	0.20	29	2.82	0.14	30	2.95	0.08	3
400	Y							3.06	0.29	7
411	P	2.76	0.31	16				2.80	0.18	45
411	YD	2.73	0.20	13	2.75	0.19	27	2.63	0.14	5
457	YD	2.80	0.21	26	2.84	0.29	5			
476	P							2.58	0.16	45
488	YD	2.78	0.19	4	2.93	0.21	3	2.52	0.07	5
549	P	2.55	0.17	21				2.46	0.15	216
625	P	2.55	0.15	46						
627	P	2.44	0.22	24	2.46	0.16	34			

NYM	North Yorkshire Moors
YD	Yorkshire Dales
P	Pennines / Co. Durham
Y	Yorkshire (Malham Tarn)

Figure 3.7 : Mean lengths of the second femurs (mm) of females of *Mitopus morio* collected from all the altitude sites in northern Britain, 1977 to 1981, plotted on a logarithmic scale against altitude (m).

The regression equation is given by:

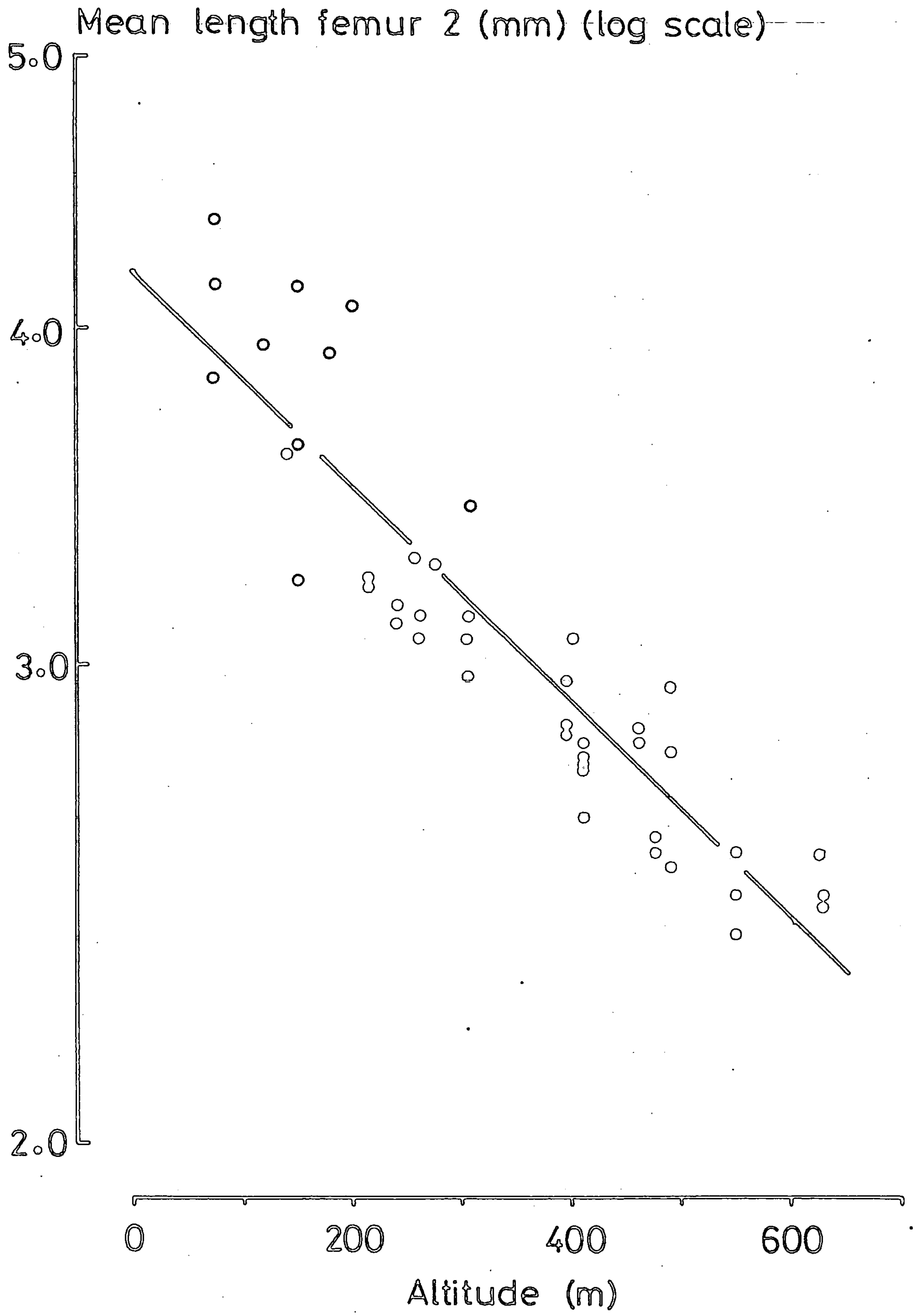
$$y = -0.000403x + 0.6195$$

$n = 44$ $r = -0.912$ S.E. of slope = 0.00028 $p < 0.001$

Key to symbols:

○ Woodland sites

○ Open/moorland sites


Mean length femur 2 (mm) (log scale)
5.0
4.0
3.0
2.0
0
200
400
600
Altitude (m)

3.4.1 Further evidence for altitudinal size clines in *M. morio*

Further evidence for the presence of an altitudinal size cline exhibited by *M. morio* as a more widespread phenomenon has been obtained as a result of pitfall collections made along two additional transects: one on the north west aspect of Cairn Gorm, Inverness-shire, and a second on Great Dun Fell, Cumbria (sites listed in Chapter Two and Appendix 1).

Pitfall trap collections from Cairn Gorm were composed largely of pre-adult sixth instars, and adult males and females. The mean lengths of the second femurs of adult males and females of *M. morio* at the eight Cairn Gorm sites from which this species was collected are presented in Table 3.5. The data for Great Dun Fell are given in Table 3.6.

Table 3.5 The mean lengths of second femurs (mm) ± one standard deviation of adults of *Mitopus morio* from the Cairn Gorm sites

Site Altitude (m)	Females			Males		
	Mean	S.D.	n	Mean	S.D.	n
213	4.23	0.39	2	4.17	0.29	3
305	3.61	0.30	19	3.99	0.35	8
454	3.18	0.35	30	3.31	0.30	30
576	2.88	0.21	30	3.06	0.25	30
665	2.84	0.18	30	3.06	0.25	30
768	2.53	0.18	30	2.81	0.25	30
972	2.31	0.27	30	2.62	0.30	30
1137	2.36	0.29	9	2.18	-	1

Table 3.6 The mean lengths of second femurs (mm) ± one standard deviation of adults of *Mitopus morio* from the Dun Fell sites

Site Altitude (m)	Females			Males		
	Mean	S.D.	n	Mean	S.D.	n
427	3.24	0.21	19	3.57	0.25	4
518	2.64	0.22	31	2.95	0.21	17
579	2.53	0.16	30	2.78	0.21	31
823	2.21	0.06	10	2.50	0.14	12
853	2.27	0.17	4	2.53	0.20	8

The mean values have been plotted (solid line) on logarithmic scales against altitude in Figures 3.8 and 3.9. On both graphs, the broken lines are the slopes fitted to the corresponding data for mean femur lengths of *M. morio* (log. scale) collected from the seven main altitude sites in northern England in 1980 and plotted in Figures 3.5 and 3.6. The relationship between femur length and altitude at these supplementary transects is similar to that exhibited by *M. morio* at the main study sites in northern England, with femur length decreasing with increasing altitude. Altitude accounted for approximately 93% of the femur length variation in 1980 (both sexes combined) for *M. morio* collected on Cairn Gorm, and 84% for Dun Fell. However, although the slopes are nearly parallel, they are displaced to the right of those from the main sites, since specimens of both sexes collected on Dun Fell and Cairn Gorm are, on average, longer-legged than those at similar altitudes at the main English sites. The relationships are probably not exactly linear, but a logarithmic plot approximates to a straight line. There is a 6% decrease in femur length of adults for every 100m increase in altitude for both sexes of *M. morio*

Figure 3.8 : Mean lengths of the second femurs (mm) ± two standard errors of adults of *Mitopus morio* from Cairn Gorm plotted on a logarithmic scale against altitude (m).

The equation for the regression line (solid line) for females is given by:

$y = -0.000274x + 0.641873$

$n = 8$ $r = -0.952$ S.E. of slope = 0.000036 $p < 0.001$

That for males is given by:

$y = -0.000286x + 0.671905$

$n = 8$ $r = -0.983$ S.E. of slope = 0.000022 $p < 0.001$

The broken lines represent the slopes fitted to the corresponding data collected from the seven main altitude sites in 1980.

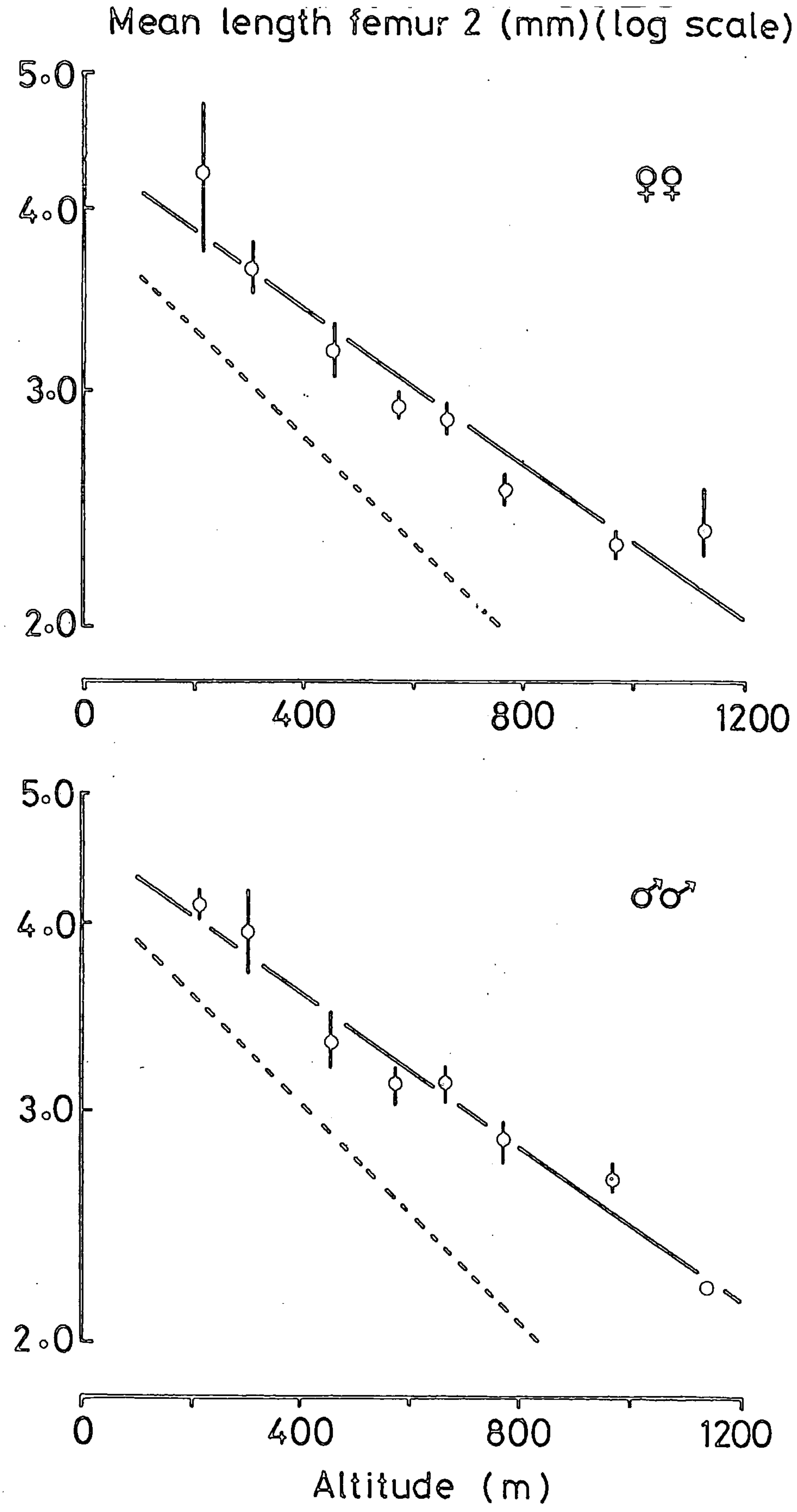

Mean length femur 2 (mm)(log scale)
5.0
4.0
3.0
2.0
♀♀
0
400
800
1200
5.0
4.0
3.0
2.0
♂♂
0
400
800
1200
Altitude (m)

Figure 3.9 : Mean lengths of the second femurs (mm) ± two standard errors of adults of *Mitopus morio* from Dun Fell plotted on a logarithmic scale against altitude (m).

The equation for the regression line (solid line) for females is given by:

$y = -0.000323x + 0.612872$

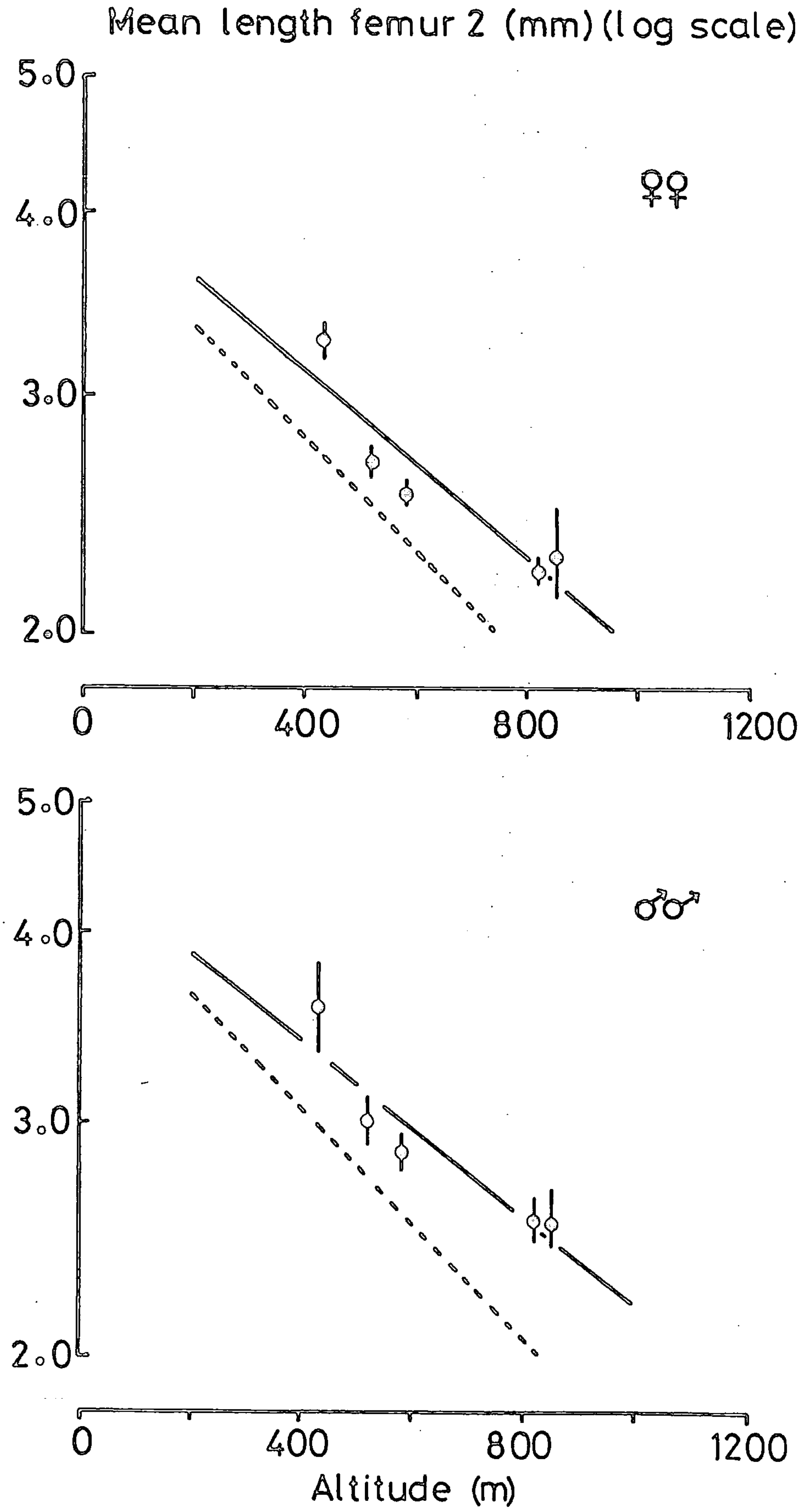
$n = 5$ $r = -0.919$ S.E. of slope = 0.000080 $p < 0.01$

That for males is given by:

$y = -0.000304x + 0.648145$

$n = 5$ $r = -0.914$ S.E. of slope = 0.000078 $p < 0.05$

The broken lines represent the slopes fitted to the corresponding data collected from the seven main altitude sites in 1980.


Mean length femur 2 (mm) (log scale)
5.0
4.0
3.0
2.0
♀♀
0
400
800
1200
5.0
4.0
3.0
2.0
♂♂
0
400
800
1200
Altitude (m)

from Cairn Gorm. This is 4% less than the cline exhibited in northern England. The differences in the slopes are significant for both sexes ($p < 0.05$). For adult males and females taken on Dun Fell, the mean femur length decreases by 7% with an increase of 100m altitude, although the results do not differ significantly from the main site data.

3.5 Variability of mean femur lengths

The standard deviation associated with each mean femur length of both adult males and females from the seven main study sites in northern England in 1980 (given in Table 3.2) appear to increase with decreasing sample site altitude. This might suggest that populations of *M. morio* from lower altitudes have more variable femur lengths than those from higher altitudes. However, the magnitude of the standard deviation as a measure of variability is related to the size of the mean, given the same scale of measurement. The coefficient of variation examines the variation within samples with respect to the magnitude of their means, and is an independent value.

$$\begin{array}{c}\text{coefficient of}\\ \text{variation} \pm \text{standard}\\ \text{error of c.v.}\end{array} = \frac{\text{standard deviation}}{\text{mean}} \times 100 \pm \frac{\text{c.v.}}{\sqrt{2n}}$$

When the coefficients are calculated for the mean femur lengths of females from the seven main altitude sites, no significant differences in variability of sample means are found, except between females from 152m and 549m ($p < 0.05$), and between males from 411m and 476m ($p < 0.05$). The decrease in standard deviation with increase in altitude is simply a function of the corresponding decrease in the value of the mean femur length.

3.6 Chromosome studies

In order to examine whether or not there were any chromosome differences between the upland and lowland forms of *M. morio,* testes squashes were prepared from adult males of *M. morio* from the lowland 76m site and the upland 476m site.

3.6.1 Method

The use of fresh material was necessary. Male specimens were killed in ethyl acetate vapour. Each testis (a 'U' shaped white loop lying in the ventral abdomenal region) was dissected out under water, and placed on a glass coverslip with a drop of propionic orcein. Each testis was stained for about twenty minutes. It was then mounted by pressing firmly with the thumbnail on to a glass slide. Slides were placed on dry ice until the preparations froze and the coverslips could be flipped off with the testes attached. These were dehydrated in two changes of absolute alcohol and then cleared in two changes of xylene. Each squash was mounted in D.P.X. on to a glass slide.

3.6.2 Results

No differences were observed between the chromosome complement of adult male specimens of the upland form of *M. morio (cinerascens)* and the lowland form; each had sixteen pairs of chromosomes. The preparations were not suitable for a more detailed examination of the structure of each chromosome.

3.7 The relationship between dry weight and altitude

There is a lack of parameters to measure with respect to the body of a harvestman because there are so few rigid, hard parts. It would be expected, however, that other features apart from femur length are affected by altitude. In order to study the effect of altitude on body size, the dry weights of samples of animals from the seven main altitude sites were determined.

3.7.1 Method

Animals were used which had been stored in 10% formalin solution as a preservative.

Specimens were adult seventh instar males.

Adult females were not used since their body weights are influenced by the state of their egg development. The legs were removed at the coxal joint and the specimens were dried to a constant weight at 60°C. Dry weights (in milligrams) were obtained using a balance accurate to a hundreth of a milligram.

3.7.2 Results

The mean dry weights of adult males from seven altitude sites are given in Table 3.7: male weights have been

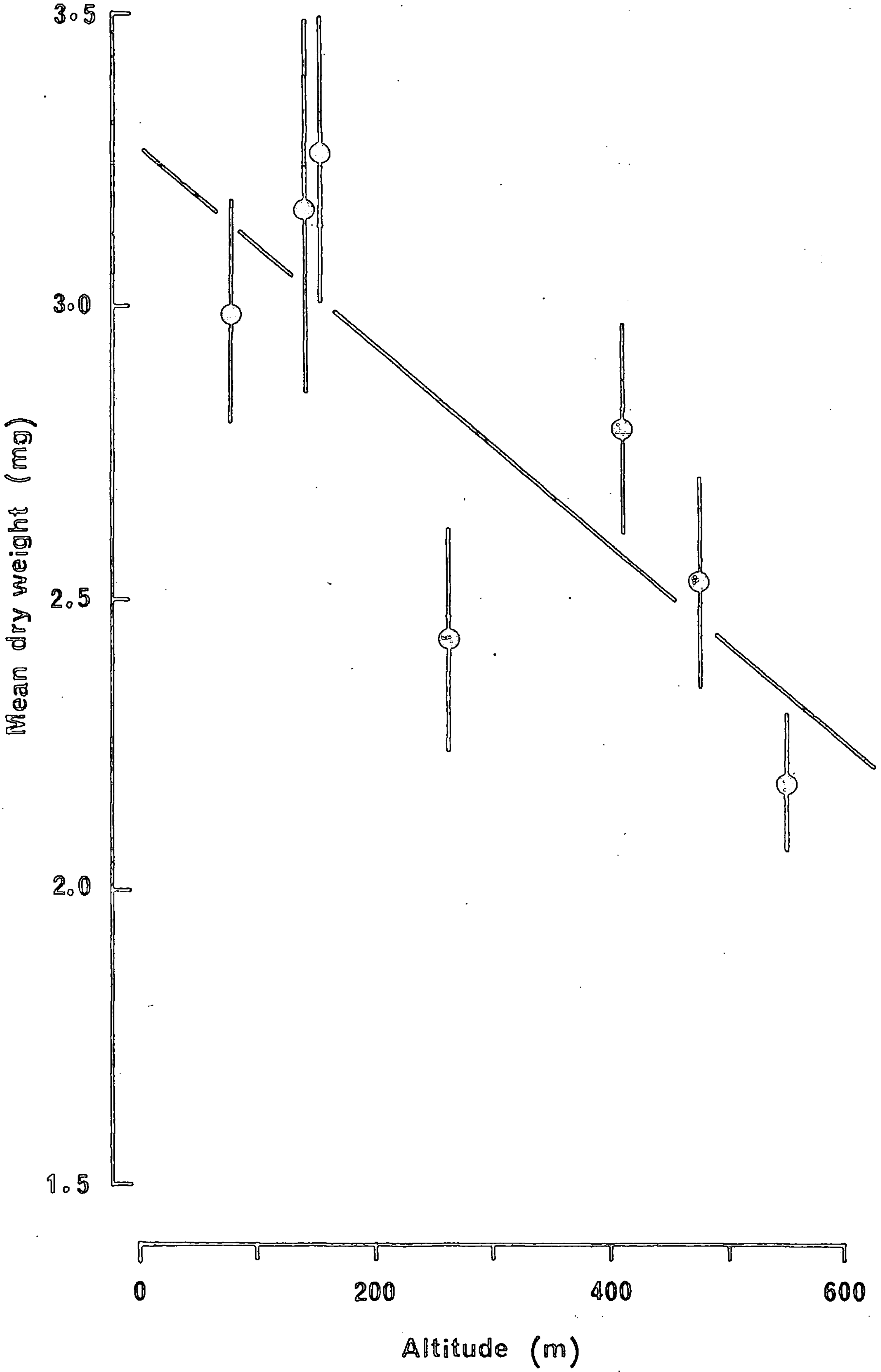
Table 3.7 Mean dry weights (mg) ± one standard deviation of males of *Mitopus morio* from seven different altitude sites

Site Altitude (m)	Mean dry weight (mg)	Standard deviation	n
76	2.99	0.23	6
137	3.17	0.51	10
152	3.26	0.54	19
260	2.43	0.44	21
411	2.79	0.54	30
476	2.53	0.48	30
549	2.19	0.33	29

Figure 3.10 : Mean dry weights (mg) ± two standard errors of males of *Mitopus morio* plotted against site altitude (m). The equation for the regression line is given by:

$$y = -0.001812x + 3.318453$$

$n = 144$ $r = -0.484$ S.E. of slope = 0.00028 $p < 0.001$


3.5
3.0
2.5
2.0
1.5
Mean dry weight (mg)
0
200
400
600
Altitude (m)

plotted with two standard errors in Figure 3.10. The regression line has been fitted to the individual dry weights obtained for each site (n = 144) rather than the mean for the altitude, since the sample sizes available for each mean were very variable.

There is a significant linear relationship ($p < 0.001$) of decreasing body weight with increasing altitude for male specimens of *M. morio*, similar to that for femur length and altitude. There is a decrease of 0.18mg per 100m increase in altitude. However, the magnitude of change in body weight is slightly less than that for femur length: approximately a 6% decrease in body weight for every 100m increase in altitude.

3.8 General morphology

The overall body patterning, colouration and arrangement of spines of *M. morio* is similar for specimens collected throughout the altitudinal range over which this study was made. Apart from the size differences, specimens from uplands are very similar to those from lowland sites. There is as much variation in depth of pigmentation and clarity of the abdomenal "hourglass" markings of the dorsal saddle within any one site as there is between sites. The dorsal pattern may be sharply delineated or more uniformly brownish. The ventral abdomen is a paler colour than the dorsal surface, often yellowish to pinkish. Males are usually more darkly pigmented than females. Males frequently possess a simple, black "figure of eight" dorsal pattern instead of the "hourglass" markings. The degree of spininess and the number of spines are variable characters among Opiliones in general (Goodnight and Goodnight 1953). There is sexual dimorphism: adult males are more spiny than females both on the legs and on the ocularium. There does not appear to be any altitudinal variation in the number and arrangement of the spines or in the colouration of *M. morio*.

3.8.1 Genital morphology

Penis morphology has been used to differentiate between species of harvestmen (Sankey 1949a) since this is considered to be subject to less variation than other features of Opiliones (Martens 1978). The penis is also one of the few rigid parts of a harvestman.

Various measurements have been made of penes dissected from adult male specimens of *M. morio* from different altitude sites. The mean lengths of the corpora penes of males from four of the main sites are given in Table 3.8. The length of the corpus penis is related to altitude, since absolute penis size is related to overall body size. However, there is no difference in penis shape between males from the lowland and upland sites; the change is one of length and not of proportion.

Table 3.8 Mean length of the corpus penis (mm) ± one standard deviation of adult males of *Mitopus morio* taken at different altitude sites

Site (m)	Mean length of corpus penis	S.D.	Sample size
76	2.225	0.169	11
260	1.964	0.131	11
411	1.910	0.080	11
476	1.853	0.084	10

3.9 Phenology and the effect of altitude

Manley (1943) demonstrated that between Durham (102m) and Moor House (558m) there was a temperature lapse rate of approximately 0.7°C per 100m altitude change. His estimates were based on data collected over ten years. Data for these two sites averaged over 29 and 24 years respectively are now available (Daily Meterological Observations 1979, Durham University Observatory; Moor House 19th Annual Report), and have been used to calculate the average lapse rate between the two sites for this period. A plot of monthly temperature averages for the two recording stations results in a linear relationship (Appendix 2), and the annual lapse rate may be estimated from the intercept of the y axis and the altitude difference between the two sites (456m):

$$\text{Lapse rate per 100m} = \frac{3.54}{456} \times 100$$

$$= 0.78^{\circ}\text{C}$$

This rate estimate is slightly higher than that found by Manley (1943). Coulson *et al.* (1976) showed that the lapse rate in soil temperatures on Dun Fell was not constant throughout the year but was highest in the autumn and lowest in the spring. The air temperature lapse rate between Durham and Moor House does not vary significantly throughout the year. Thus, at any one time, the temperature at the 76m Field Station site is likely to be 3.7°C warmer than at Bog End 549m. This is a fairly large difference when considering the onset of growth and development in a poikilothermic animal such as *M. morio*. The temperature above which plant growth occurs has been suggested as being 5°C (Manley 1942, Taylor 1967), and eggs of *M. morio* which have been through a winter diapause at 5°C in the laboratory rapidly hatch at temperatures above this (Chapter Six). Such temperatures, which are experienced during late March and early April in Durham, are not reached until mid-May at Bog End. This results in a retardation in hatching and subsequent development. In Figures 3.11 and 3.12 the mean instar present on the mid-trap date between pitfall collections has been plotted for four different altitude sites in 1980.

Figure 3.11 : Mean instar composition of pitfall catches of *Mitopus morio* plotted against mid-trap date ± two standard errors, for Muggleswick 260m and 411m in 1980. Curves have been fitted by eye.

▤ Hand-collected

◍ Pitfall-trapped

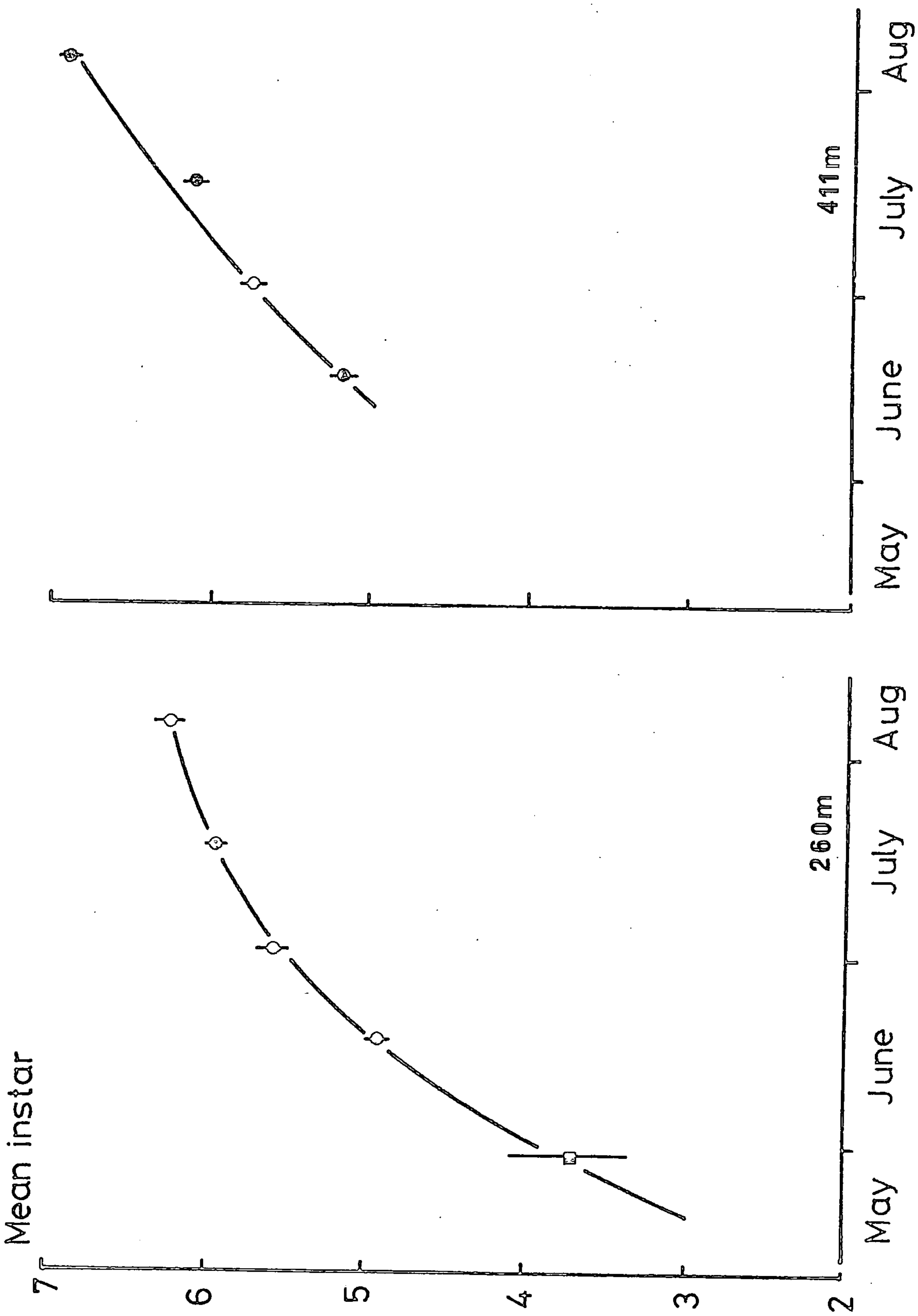
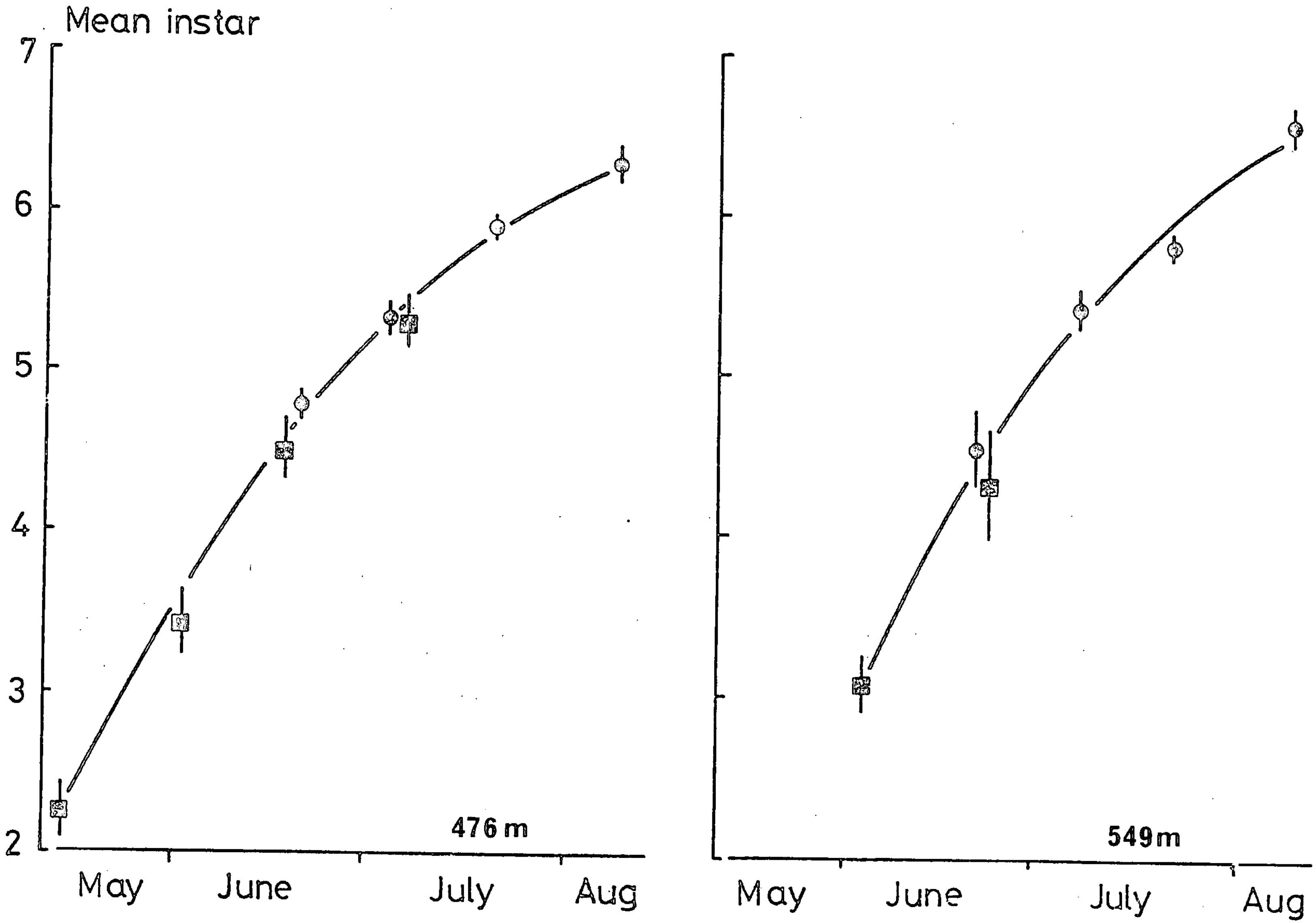

Mean instar
7
6
5
4
3
2
May
June
July
Aug
260m
May
June
July
Aug
411m

Figure 3.12 : Mean instar composition of pitfall catches of *Mitopus morio* plotted against mid-trap date ± two standard errors, for Muggleswick 476m and Bog End 549m in 1980. Curves have been fitted by eye.

☐ Hand-collected

○ Pitfall-trapped


Mean instar
7
6
5
4
3
2
May
June
July
Aug
476 m
May
June
July
Aug
549m

3.9.1 Between site differences in phenology

The date on which a particular mean instar is reached at each site may be estimated from these development curves; the values for 1979 and 1980 are given in Table 3.9 and 3.10. *M. morio* at Bog

Table 3.9 Dates of mean instars of *Mitopus morio* in 1979 estimated from the mean instar/date curves presented in Appendix 4

Site Altitude (m)	Mean Instar 3	4	5	6
260	6 June	15 June	28 June	17 July
411		13 June	26 June	13 July
476		18 June	2 July	21 July
549	11 June	22 June	6 July	24 July

Table 3.10 Dates of mean instars of *Mitopus morio* in 1980 estimated from the mean instar/date curves presented in Figures 3.11 and 3.12

Site Altitude (m)	Mean Instar 3	4	5	6
260	24 May	6 June	21 June	22 July
411			16 June	11 July
476	24 May	8 June	25 June	25 July
549	3 June	15 June	29 June	20 July

End 549m did not reach the third instar in 1980 until ten days after this instar was entered at Muggleswick 260m. This corresponds to the predicted delay in the mean temperature received at these two sites (Appendix 3). The mean temperatures experienced during May at

Muggleswick 260m are not experienced at Bog End 549m until the beginning of June. There was a similar delay (nine days) in the dates on which the mean instar of the nymphs was four at these two sites in 1980. The intermediate altitude sites have intermediate mean instar dates. The results were similar in 1979, with a delay of five to seven days between 260m and 549m. The difference in the dates of the mean instars between these two sites decreased with increasing mean instar in 1980.

Growth rates at all the main sites apparently decrease towards the end of the season, but this is simply because the value of the mean instar can never exceed seven: i.e. when there are no nymphs present in the samples. Hence the mean date of occurrence of adults cannot be estimated from these curves. The median date for the occurrence of adults (seventh instar) in pitfall traps may be calculated instead. The value for Muggleswick 260m and Bog End 549m are given in Table 3.11. The median date is not the same as the estimated date of occurrence of a mean instar: it is the date by which 50% of the total adult *Mitopus morio* trapped during a particular season had been caught. The median date is therefore partially dependent on the longevity of the adults (and also on the length of the trapping period). There is a difference

Table 3.11 Median dates of the adult (seventh) instar (days) ± one standard error of *Mitopus morio* at Muggleswick 260m and Bog End 549m in 1979

Site	Date	No. of adults trapped
Muggleswick 260m	17 August ± 8.7	19
Bog End 549m	15 September ± 1.6	504

of 29 days in the median dates of the seventh instar at the two sites; this is considerably greater than the difference in the estimated dates of mean instars. Adults were trapped for the same time interval. Adults at Muggleswick 260m seem to be shorter-lived than those at Bog End 549m. Adult longevity has been estimated from the interval between the median dates of the sixth and seventh instars. It is about 35 days for Muggleswick 260m adults and 55 days for adults from Bog End.

3.9.2 Between year differences in phenology

The growth rate curves of harvestmen from the four main sites in 1979 are similar in shape to those fitted to the 1980 data, but consistently displaced to the right of the 1980 curves (Appendix 4). *M. morio* in 1979 were in an earlier instar on the same date than in 1980. This results in the delay in the estimated dates of mean instars between years presented in Tables 3.9 and 3.10. The winter of 1978/79 was severe, and the following spring temperatures were low. At Bog End 549m, the mean temperatures were below average until late May (Moor House 21st Annual Report). This resulted in the dates of particular mean instars occurring later in 1979 than in 1980. Temperatures at the start of the 1980 field season were, in general, above the mean monthly averages (M. Rawes, pers. comm.), allowing the onset of growth and development to occur earlier in the season.

3.10 Geographical variation in size

In the preceding sections, altitude has been shown to have a considerable impact on the development and final size of *M. morio*. Several factors vary along an altitude gradient, including temperature, precipitation, windspeed and exposure. Biologically, temperature is probably the most important factor for poikilotherms, since it affects their growth rate. Temperature regimes also vary between the localities of the different study transects within the British Isles, and *M. morio* from these transects would be expected to show corresponding temperature-mediated size variations.

Temperature records are available for the summits of Dun Fell 834m (Manley 1942) and Cairn Gorm 1344m (Dr J S Barton, pers. comm.). Manley (1942) found the average temperature lapse rate between the summit of Dun Fell and the lowland recording station to the west at Newton Rigg (171m) was 0.73°C per 100m. This is similar to the lapse rate between Durham and Moor House (0.78°C). It is thus possible to calculate the predicted mean monthly temperatures at 558m on Dun Fell from the summit recordings, and compare them with the observed temperature recordings at Moor House 558m. Assuming that a similar lapse rate occurs on Cairn Gorm, mean monthly temperatures may also be predicted for an altitude of 558m on this mountain. The values for the predicted temperatures for Dun Fell and Cairn Gorm have been plotted with the observed Moor House temperatures in Figure 3.13.

The most important months in terms of the development of *M. morio* are probably between late March and June. During this time the eggs hatch and the nymphs grow towards maturity. Figure 3.13 shows that during these months the temperature is consistently lower at Moor House 558m and highest at Cairn Gorm 558m. The observed temperatures for Moor House and the predicted temperatures on Dun Fell and Cairn Gorm (558m) for March until June are given in Table 3.12. The differences in temperature between Moor House and Cairn Gorm 558m have been expressed as a percentage of the temperature at Moor House in Table 3.12. The estimated temperatures at Cairn Gorm 558m are on average 52% warmer than at Moor House 558m during March, April and May, although only 8% warmer in June;

Figure 3.13 : Observed mean monthly temperatures at Moor House 558m (averaged over 24 years) and the predicted values for Dun Fell and Cairn Gorm

Key to Symbols:

—△—	predicted temperature at 558m on Cairn Gorm
- - -□- - -	predicted temperature at 558m on Dun Fell
—□—	observed mean monthly temperature at 558m at Moor House

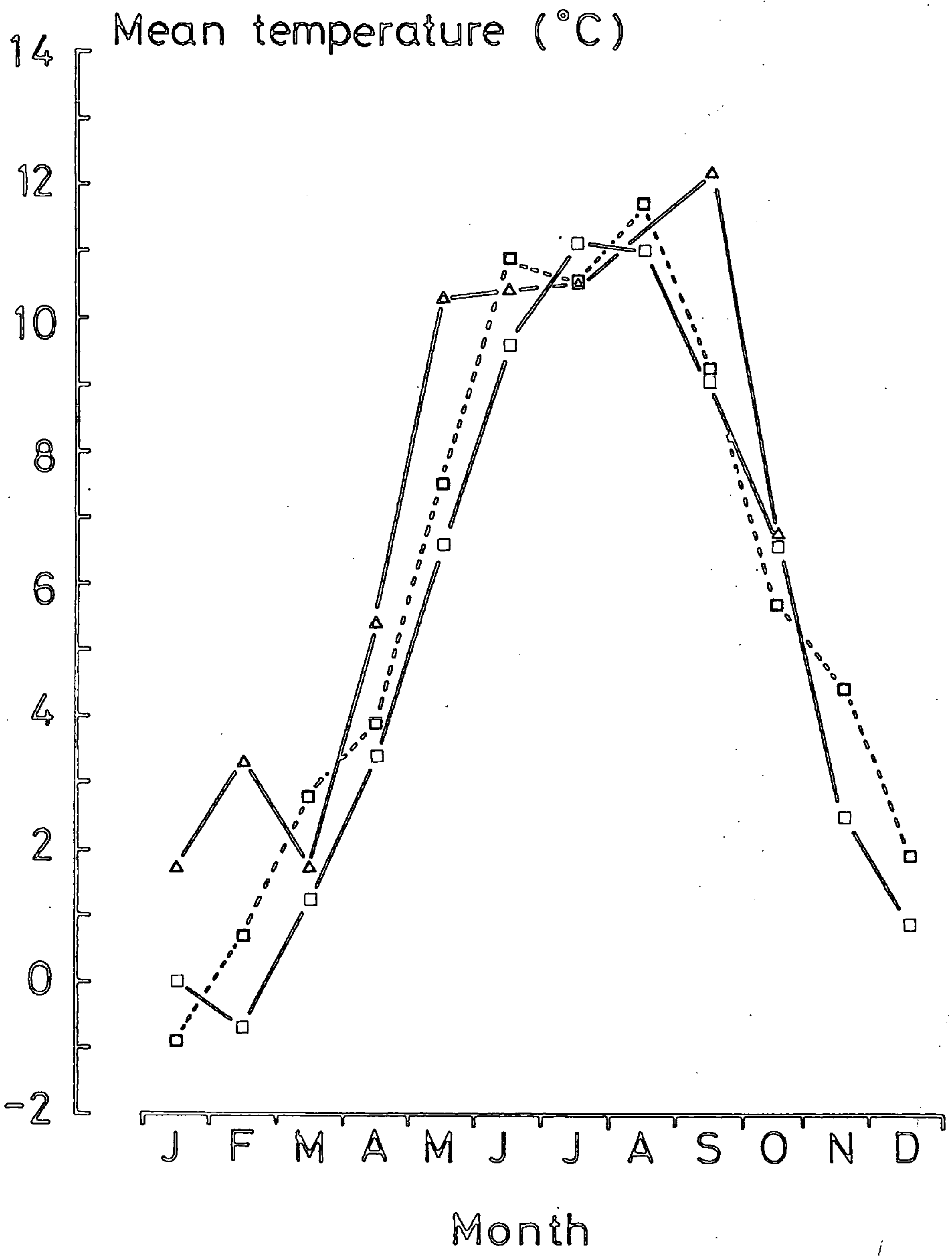

Mean temperature (°C)
14
12
10
8
6
4
2
0
-2
J
F
M
A
M
J
J
A
S
O
N
D
Month

Table 3.12 The mean monthly temperatures (°C) from March until June at Moor House 558m and the predicted values for Dun Fell and Cairn Gorm at the same altitude; the number of degrees by which Cairn Gorm is warmer than Moor House has been expressed as a percentage of the Moor House temperature for each month

Locality	March	April	May	June
Moor House	1.2	3.4	6.6	9.6
Dun Fell	2.8	3.9	7.5	10.9
Cairn Gorm	1.7	5.4	10.3	10.4
Percentage temperature difference between Moor House and Cairn Gorm	41.7	58.8	56.1	8.3

that is 41% warmer over the four month period. The femur lengths of adult males and females of *M. morio* for 558m at Moor House, Dun Fell and Cairn Gorm estimated from the regression equations are presented in Table 3.13, together with the real femur lengths of specimens taken from

Table 3.13 Estimated femur lengths (mm) of adults of *Mitopus morio* at 558m in the three localities, and the actual femur lengths at the sites closest to this altitude

Locality	Estimated femur length at 558m (mm)		Actual femur length (mm)		Site Altitude (m)
	Female	Male	Female	Male	
Moor House	2.36	2.58	2.38	2.51	549
Dun Fell	2.71	3.01	2.53	2.78	579
Cairn Gorm	3.08	3.25	2.88	3.06	576

the altitude sites closest to 558m. The estimated femur lengths of females from Cairn Gorm are 31% longer than those of females from Moor House at the same altitude, whilst males are 26% longer-legged. The differences between Moor House and Dun Fell are not so great. An examination of the true mean femur lengths of *M. morio* taken at altitudes closest to 558m in the three areas shows that these differences are still present: both sexes are significantly ($p < 0.001$) longer-legged at Cairn Gorm 576m and Dun Fell 579m when compared with specimens from Moor House 549m. The consistently warmer temperatures on Cairn Gorm and Dun Fell, altitude for altitude, may explain why specimens of *M. morio* are longer-legged at these sites than at the corresponding altitude at Moor House.

It is possible that aspect may also cause *M. morio* from Cairn Gorm and Dun Fell to have longer legs than specimens from the main Pennine sites. Both Cairm Gorm and Dun Fell are under a predominantly westerly influence, which presumably has some ameliorating effect on their climates. Muggleswick 260m and Bog End 549m have north east aspects, whilst Muggleswick 411m and 476m are flatter. Slagsvold (1979) showed that site aspect was significantly correlated with femur lengths of *M. morio* in Norway: animals trapped on south-facing slopes had longer legs than those trapped on north-facing slopes. He also showed that latitude accounted for 1-67% of the femur length variation in adults and juveniles of *M. morio*. His specimens from higher latitude sites were shorter-legged than those from lower latitudes. Between the main Pennine sites and Cairn Gorm there is a latitude difference of three degrees, but the Dun Fell sites are at a similar latitude to the other Pennine sites. Latitude does not seem to have a significant influence in this instance.

Temperature is most likely to be the over-riding factor determining femur length in *M. morio*. These additional sampling areas indicate that clinal variation occurs not just over an isolated region but that it is a widespread phenomenon exhibited by *M. morio*. A model is proposed from which the mean femur length of specimens of *M. morio* from a particular locality may be predicted, knowing the altitude, latitude and temperature regime of that locality. This model will be developed further in Chapter Five, in which the geographical variation displayed by *M. morio* is examined in specimens from other sites in Britain and abroad.

3.11 The effect of temperature on instar duration and growth increment of *Mitopus morio* in the laboratory

Temperature has been suggested as the major factor controlling size of *M. morio* in the field; since *M. morio* is poikilothermic, it would be expected to have an influence on all instars. Laughlin (1963) demonstrated for the garden chafer *Phyllopertha horticola* (L.) that the duration of the third instar feeding period was unaffected by temperature (within the range 12^{o} - 20^{o}C), but the rate of growth did increase with temperature. The result was that at higher temperatures bigger larvae were produced at the given instar interval. If the interval between moults is a fixed value for a given instar of *M. morio*, then animals feeding and growing under a warmer temperature regime will become larger than those receiving lower temperatures.

The experiment described below was performed in order to examine the effect of different constant temperature regimes on final size and on instar duration of specimens of *M. morio*. Batches of individual animals were maintained at one of three different constant temperatures, 7^{o}C, 10^{o}C and 15^{o}C. Animals were third and fourth instars collected in the field. Between 30 and 45 specimens were maintained at each constant temperature.

Measurements were made of the lengths of the second femurs both of animals which died in culture and of cast skins from animals which moulted in the laboratory. Time intervals between moults were recorded.

3.11.1 Results

Harvestmen are notoriously difficult to maintain in the laboratory (Sankey 1949b, Klee and Butcher 1968). Both eggs and early instars are susceptible to humidity changes, and the nymphs are frequently cannibalistic. Maintaining the animals through several moults at any one temperature proved to be almost impossible. Even in constant temperature rooms, the humidity fluctuations in the culture jars resulted in death, either by desiccation or too high a humidity. This happened despite daily attendance to each culture jar.

There were no significant differences in mean femur lengths of dead animals and cast skins from the same instar and temperature regime. Results have therefore been combined and are presented in Table 3.14, together with the values for the mean growth increment between each moult at the three temperatures. The values for third instar femur lengths are from cast skins only. It appears from these results that animals kept at 15°C attained a larger size in terms of femur length than those at 7°C, for all instars measured. However, there are no significant differences between the femur lengths at different treatments or between the values for the mean Dyar's factors.

The duration of the fourth, fifth and sixth instars of *M. morio* at the three different temperatures are given in Table 3.15. The duration of the fourth instar at 15°C is significantly shorter ($p < 0.001$) than at 10°C or 7°C. The length of the fifth instar of *M. morio* reared at

Table 3.14 The mean lengths of the second femurs (mm) ± one standard deviation of instars of *Mitopus morio* maintained at one of three different constant temperatures (7°C, 10°C, 15°C); and the mean growth increment (Dyar's factor) ± one standard deviation at each temperature. Sample sizes are given in parentheses.

Temperature	Instar 3	Instar 4	Instar 5	Instar 6	Dyar's factor
7°C	0.783 ±0.038 (30)	1.052 ±0.058 (42)	1.402 ±0.061 (22)	1.867 ±0.062 (3)	1.355 ±0.068 (27)
10°C	0.793 ±0.044 (30)	1.059 ±0.053 (23)	1.409 ±0.076 (11)	1.800 ±0.071 (2)	1.331 ±0.056 (16)
15°C	0.795 ±0.031 (15)	1.071 ±0.061 (7)	1.471 ±0.109 (11)	1.983 ±0.189 (9)	1.403 ±0.124 (15)

Table 3.15 Instar duration (days) ± one standard error of instars of *Mitopus morio* at three different temperatures (7°C, 10°C, 15°C). Sample sizes are given in parentheses.

Temperature	Instar 4	Instar 5	Instar 6
7°C	27.2 ±1.0 (20)	26.9 ±1.1 (7)	-
10°C	26.9 ±1.4 (13)	18.6 ±2.3 (5)	-
15°C	15.3 ±1.3 (6)	15.2 ±1.2 (5)	14.7 ±1.7 (3)

15°C is no different from that of fifth instars at 10°C, but shorter than those kept at 7°C ($p < 0.01$). The duration of all instars (four, five and six) was about 15 days at 15°C. Instars four and five both lasted for about 27 days at 7°C. Instar four is longer than instar five at 10°C ($p < 0.01$).

3.11.2 Discussion

The small sample sizes obtained in this experiment, resulting from the high mortality of animals in culture, do not allow firm conclusions to be drawn as to the effect of temperature on growth increments and instar duration in *M. morio*. However, there seems to be a greater increase in the femur lengths of animals kept under warmer temperature regimes: with more data it may be possible to obtain significant results.

The duration of different instars in the field has been estimated from the data presented in Tables 3.9 and 3.10 for four different altitude sites in 1979 and 1980 and are given in Table 3.16. They are similar to

Table 3.16 Estimated instar duration (days) of instars of *Mitopus morio* at four altitude sites in 1979 and 1980. Values have been estimated from Tables 3.9 and 3.10

	Site	Instar		
	Altitude (m)	3	4	5
1979	260	9	13	19
	411		13	17
	476		14	19
	549	11	14	18
1980	260	13	15	31
	411			25
	476	15	17	30
	549	12	14	21

to the laboratory results for 10°C and 15°C: field temperatures during June and July fluctuate between 10°C and 15°C at these sites.

The long time intervals between moults at 7°C may not be due entirely to temperature dependency effects. Nymphs may not have been feeding and growing satisfactorily on their laboratory diet at this temperature. Poor nutrition would result in even slower growth.

3.12 Adult sex ratio

There is some evidence to suggest that the ratio of adult males to adult females caught in pitfall traps changes throughout the season, with proportionately fewer males than females trapped at the beginning. A Chi-squared test (Table 3.17) shows that the ratio of males to females trapped during the first four weeks after adults had begun to

Table 3.17 A 2 x 2 contingency table to test the Null Hypothesis that there is no difference in the sex ratio of *Mitopus morio* caught during the first four weeks after the first appearance of adults in pitfall traps, compared with the following five weeks

	Females	Males	
No. trapped in first four weeks	64	23	87
No. trapped in next five weeks	32	32	64
	96	55	151

$\chi^2 = 8.84$ $p < 0.01$ Null Hypothesis rejected appear in the traps in 1979 at the three Muggleswick sites (pooled data) was significantly less than the sex ratio during the subsequent five weeks. Males may mature later than females, so that they appear in pitfall traps at a later date. Alternatively, female longevity may be less than that of males. The first hypothesis may be tested in two ways: by examining the change in mean femur length of catches of sixth instar pre-adults, and by examining the numbers of each sex caught in hand collections. If pre-adult females mature before pre-adult males, the mean femur lengths of the pitfall catches of sixth instar *M. morio* would gradually increase with time, as the proportion of longer-legged pre-adult males in the sample also increased. This assumes both that pre-adult males are longer-legged than pre-adult females (as adult males are longer-legged than adult females) and that each sex has an equal probability of being caught in pitfall traps. When the mean lengths of the second femurs were calculated for sixth instars trapped on four different dates (mid-trap dates) at Muggleswick 476m in 1980, there was no significant difference in the mean femur lengths on successive dates, despite the large sample size (n = 201). Thus the ratio of pre-adult males to pre-adult females is a constant one throughout the period. It has not been possible to test between-sex differences in longevity.

Despite the differences in adult sex ratios during the season, overall, there were significantly more females trapped in pitfalls than males ($\chi^2 = 11.13$; $p < 0.001$) (Table 3.18). The ratio of adult males to females caught in pitfall traps may be compared with the ratio in hand collections. In all hand collections made at several sites over two years, proportionately more males than females were caught ($\chi^2 = 20.8$; $p < 0.001$). Thus the difference in the sex ratios may be a behavioural one:

Table 3.18 Numbers of adult males and females in hand and pitfall collections, 1979 and 1980

	Females	Males
No. in pitfalls (1979)	96	55
No. in hand collections (1979-1980)	69	134

since oviposition seems to occur in the substrate, females may be relatively more active at ground level throughout the season. Males may be more active in the upper vegetation layer and so encounter sunken pitfall traps much less frequently than females. When hand collecting in the field, it has often been observed that males are more readily found crawling in and on the vegetation, whilst females are frequently to be caught at the stem bases.

3.13 Discussion

It is evident from the sampling over a wide altitudinal range that *M. morio* does not have two geographically distinct subspecies populations in northern Britain. The trinomial forms *M. morio cinerascens* and *M. morio morio* mentioned by Sankey and Savory (1974) are simply the two extremes of an altitude-linked cline of size variation, affecting both femur length and, to a lesser extent, overall body size. Lowland populations are larger and longer-legged than upland populations, and although the two extremes are statistically distinct and easily separable, the whole range of intermediate-sized animals exists. *M. morio* has the greatest range of all harvestmen (Roewer 1923). It is hardly surprising, therefore, that a species with such a large geographical distribution should be so variable. Roewer (1912) was correct in synonymising many of the described species of *Mitopus* under *M. morio*; he stated, "the great variability of this species is the reason why its representatives were described by earlier authors under the most varied names...". Martens (1978) also commented on the great heterogeneity of *M. morio* with regard to its colour, body patterns, body size and absolute and relative leg lengths, stating that individuals from mountain populations often had markedly short legs compared with lowland specimens. He suggested that genital morphology was a more constant feature. Upland and lowland populations of *M. morio* do not differ in the basic shape of the penis, although the length varies with body size and hence altitude. The model proposed below, and summarised in Figure 3.14, attempts to account for the way in which clinal variation in size occurs in *M. morio*. The combined effects of the factors outlined in this model are exemplified when a comparison is made between the mean sizes of the instars of *M. morio* and their dates of occurrence from two sites which are widely separated in altitude (by 279m): the data for Muggleswick 260m and Bog End 549m are presented in Figure 3.15. Presumably, it is the climatic change along the altitude gradient which influences the phenotype in some way, to bring about the cline of variation. *M. morio*, being poikilothermic, is dependent on environmental temperature for its growth and development. Phenology is the appearance of the life history in consideration of the season and weather. *M. morio* develops under different temperature regimes at the different altitudes at which it occurs, but still maintains a univoltine life cycle at each site. Coulson *et al.* (1976), in considering larval development in the tipulid *Molophilus ater* Meigen suggested three possible ways in which larvae developing under different temperature regimes could reach the same developmental stage by the end of the year. Two of these mechanisms seem to be applicable to *Mitopus morio*. For *Molophilus ater*, they suggested that the larvae

Figure 3.14 : A model to account for between-site differences in size of *Mitopus morio* taken at different altitudes

A model to account for between-site differences in size of *Mitopus morio* taken at different altitudes

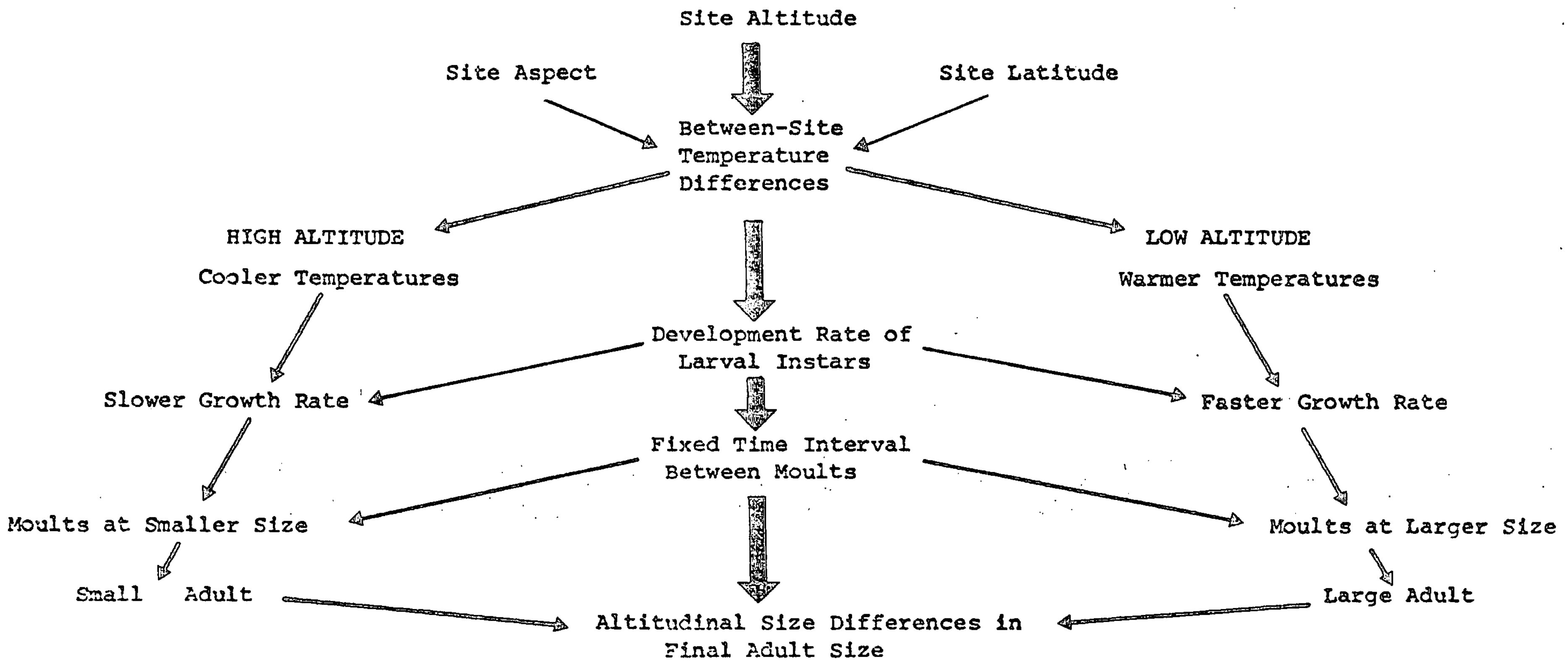
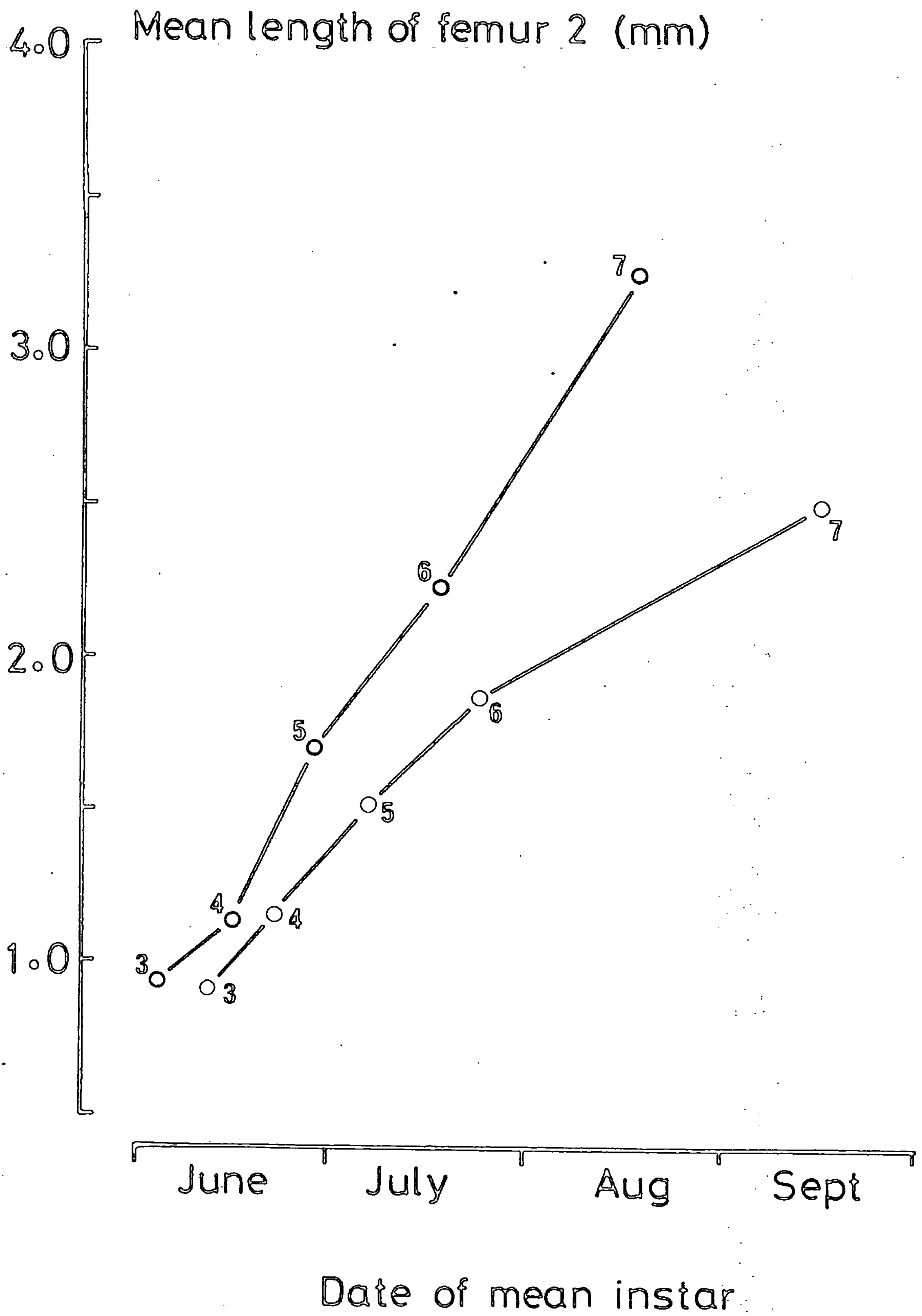


Figure 3.15 : The relationship between mean length of the second femur of instars of *Mitopus morio* and the date of occurrence of each mean instar in 1980 at 260m (○) and 549m (●). The instar numbers are indicated.


Mean length of femur 2 (mm)
4.0
3.0
2.0
1.0
3
4
5
6
7
3
4
5
6
7
June
July
Aug
Sept
Date of mean instar

at the higher and colder sites might pupate at a smaller size than those at the warmer and lower sites. Also, larvae may, after completion of a temperature-dependent growth phase, enter a diapause. It has been shown that the garden chafer, *Phyllopertha horticola* (L.) pupates at a smaller size in cooler temperatures (Laughlin 1963). Mani (1962) states that a decrease in body size is a typical high altitude specialisation, giving examples for Carabidae. Laughlin (1963) also demonstrated that the duration of the third instar feeding period of the garden chafer was unaffected by temperature. Animals feeding and growing under a warmer temperature regime became larger than those receiving lower temperatures for the same time interval. If the duration of an instar was fixed for *M. morio* (within certain temperature limits), then a similar mechanism would apply. Estimates of the duration of different instars in the field have been obtained from the dates of occurrence of the different mean instars at the four altitude sites given in Table 3.16. Although the values must be treated with some caution since they have no confidence limits, the duration of the third, fourth and fifth instars seems to be similar between altitude sites. However, the laboratory evidence for instar duration under constant temperature may be conflicting, since the interval between moults was significantly longer at 7°C than at 15°C. It may be that instar duration is only fixed over a narrow temperature regime; temperatures below this (e.g. 7°C) extend the instar interval. Thus it is possible that nymphs moult after a constant time interval regardless of the growth achieved, provided that temperatures are above a certain threshold. Most growth in the field is achieved during June and July, when temperatures are between 10°C and 15°C. Harvestmen at Muggleswick 260m experience temperatures which are, on average, higher than those at Bog End 549m and at the other higher altitude sites.

Muggleswick 260m nymphs may be expected to feed and grow more rapidly during the same instar interval, and consequently produce larger and longer-legged individuals at the next moult.

The difference in the median dates of the seventh instar between Muggleswick 260m and Bog End 549m indicates that *M. morio* adults mature earlier at the lower altitudes. Female *M. morio* at the lower sites are gravid earlier and lay eggs sooner than those at higher altitudes. If eggs did not then undergo a developmental arrest, early, untimely hatching would result in the event of a mild autumn, and nymphs would probably fail to survive the winter. This is prevented since eggs laid relatively early at the lower altitudes are firmly in diapause, and remain so until the following spring. Diapause in *M. morio* is more fully examined in Chapter Six.

M. morio, by possessing a flexibility in its phenotype, is able to live over a broad range of altitudes. It is adapted to complete its life cycle over the widely differing temperature regimes, by the apparent possession of a temperature-independent instar duration, with the ability to moult after a given time interval regardless of size and temperature; and an egg diapause to bring about seasonal synchrony.

CHAPTER FOUR

THE RELATIONSHIP BETWEEN *MITOPUS MORIO* AND THE FORM *ALPINUS*

4.1 Introduction

In this chapter, a new species of *Mitopus* is described for Britain. The species now described as *Mitopus ericaeus* sp. n. has been incorrectly assigned in the past to another taxon, *M. alpinus* (Herbst 1799). The history of the nomenclature of this species is confused: descriptions have been made in several languages, and incorrect translations may well have helped to maintain the taxonomic disarray. The generic names of current members of the genus *Mitopus* have also been altered several times in the past. The genera have included *Phalangium* Linnê, *Opilio* Herbst and *Oligolophus* C. L. Koch. In order to avoid confusion in this chapter, the species referred to below have all been placed in the genus *Mitopus* Thorell (irrespective of the genus used in the original description), as they are in more recent taxonomic works (Roewer 1923) and keys (Sankey and Savory 1974). (Koch (1839) placed the species in the genus *Opilio* and Simon (1879) and Pickard-Cambridge (1890) in the genus *Oligolophus*.)

In his monograph of the British species of harvestmen, Pickard-Cambridge (1890) referred to three closely related species: *Mitopus morio* (Fabricus), *M. cinerascens* (C.L. Koch 1839) and *M. alpinus* (Herbst). He mentioned *M. morio* as being a long-legged lowland species: *M. cinerascens* was readily distinguishable from *M. morio* since it was smaller, shorter-legged and belonged to northern or "alpine" regions. With regard to *M. alpinus*, he remained somewhat vague. He stated that it too belonged to mountainous or alpine districts, but that it resembled *M. morio* in size, colour and markings: it was "so nearly allied to... *M. morio*, that it seems questionable ... whether it be really distinct or not." He suspected that a long series collected from lowland localities through to upland regions would reveal that *M. alpinus* was simply the upland form of *M. morio*, with intermediate specimens at intermediate altitudes. It is now clear that this is not the case. In an attempt to distinguish the two species, Pickard-Cambridge sent material to Simon, who had written an extensive work on harvestmen in France (Simon 1879). Simon was the source of the misidentification of Pickard-Cambridge's *M. alpinus* (Simon *loc.cit.)* Herbst (1799) recorded *M. alpinus* from Mt Brevent in the Chamonix Valley (then in Switzerland, now in France). He described and illustrated this species as having short thick legs. Subsequent literature confirms this (Koch 1848); Thorell (1876) in his original description stated very clearly that in *M. alpinus* the legs are shorter than in *M. morio*; likewise Simon (1879), despite the fact that he later identified the relatively long-legged specimens, sent to him from Britain by Pickard-Cambridge, as *M. alpinus*. I have examined specimens of *M. morio* from Germany, Austria and Norway, and I believe that it is likely that the confusion and misidentification by Simon arose partly because all European specimens are considerably longer-legged than their British counterparts (particularly collection-site altitude for altitude). Simon apparently had no previous experience of specimens from Britain.

Another European, Roewer (1912, 1923), collected all these species together as synonyms of *M. morio* (Fabr.), where they have remained until the present day. It is thought (Goodnight and Goodnight 1976) that in many cases Roewer redescribed species from past publications, without seeing examples of all of them. He appears to have assumed that the *M. alpinus* of Pickard-Cambridge was the same as the European specimens of that name, and made *M. alpinus* another synonym of *M. morio*.

Further confusion has arisen since Sankey and Savory (1974) included in their key three British forms of *M. morio* to which they give trinomial status: *M. morio alpinus* and *M. m. cinerascens* (both from upland regions of Britain), which they believed to be allopatric with the lowland *M. m. morio*. They based their evidence on observations made by both Girling and Stallybrass (unpublished M.Sc. dissertations) who identified the existence of harvestmen possessing the characteristics of *M. cinerascens* and *M. alpinus* as outlined by Pickard-Cambridge (1890): that is, a small short-legged member of the genus *Mitopus* (about which Pickard-Cambridge agrees with the description of Koch (1839) for *M. cinerascens*); and larger, longer-legged specimens, which Pickard-Cambridge incorrectly referred to as *M. alpinus*. Both types of harvestmen were collected in the uplands of northern Britain, the region referred to by Pickard-Cambridge.

Chapter Three has provided the evidence that the harvestmen referred to as *M. cinerascens* (C.L. Koch) by Pickard-Cambridge is not a distinct British species, but the upland extreme of an altitude-linked size cline of *M. morio*.

M. ericaeus sp. n. (incorrectly identified as *M. alpinus* by Pickard-Cambridge) differs from *M. morio* in morphology, biometrics and phenology. *M. ericaeus* is restricted to upland regions in northern Britain, and throughout its known range is sympatric with *M. morio*. The distribution of *M. morio* thus overlaps that of *M. ericaeus* in the upper parts of its altitudinal range, but *M. morio* is the only lowland *Mitopus* in Britain.

4.2 Systematics

Mitopus ericaeus sp. n.

HOLOTYPE

Adult female collected from Muggleswick Common, Co. Durham, England, 476 metres (Grid ref. NZ 004449), 18 August 1980, (A.L. Jennings). (B.M.(N.H.) 1981.6.5.1).

PARATYPES

Four males from Moor House National Nature Reserve, Cumbria, 549 metres (Grid ref. NY 264329), (B.M.(N.H.) 1981.6.5.2-6); four females and five juveniles from Muggleswick Common, Co. Durham, 476 metres, (B.M.(N.H.) 1981.6.5.7-11).

DERIVATIO NOMINIS

ericaeus is the adjective derived from the Latin '*erice*' and means 'collected from the heath flower'. This was thought to be appropriate since *M. ericaeus* is typically found on heather moorland.

HOLOTYPE DESCRIPTION

Body length 6.7mm. Frontal margin of carapace with small black-tipped tubercles, trident obscure. Ocularium set towards the hind end of the carapace, about one and a half times its width from the frontal edge. Ocularium with two rows of prominent tubercles.

Abdominal tergites with transverse rows of small granulations, well separated. Coxae each with a small distal tubercle. Sternites with fine granulations (as tergites).

Chelicerae of usual form, with characteristic ventral spur on proximal segment. Proximal segment with dorsal setae, unarmed ventrally. Distal segment similar.

Pedipalps 4.8mm (Fe 1.5 : Pt 0.8 : Ti 0.9 : Ta 1.8mm). Femorae with a few dorsal setae, the ventral surface with longer setae, more densely arranged. Distal tips of femorae slightly swollen, each with a tuft of setae on the inner surface. Tibiae densely setose above and below, with smooth median area dorsally. Tarsi with setae and lanugo.

Legs relatively long. Second leg 18.9mm (Fe 4.1 : Pt 1.5 : Ti 3.7 : Mt 0.4 : Ta 9.2mm). Sharply angulated: femora strongly toothed with longitudinal rows of black denticulae interspersed with small setae.

COLOUR Carapace brown, continuous with strong hour-glass saddle markings dorsally. Median stripe greyish brown. Saddle pattern edged with white. Lateral areas of the dorsal surface of the abdomen grading from dark brown to pinkish brown. Sternites dark brown marbled with pinkish brown. Chelicerae yellowish brown, the basal segment with small dark brown patches dorsally. Pedipalps with yellowish brown femora, patellae and tibiae with longitudinal patches of dark brown. Legs yellowish brown; patellae, tibiae and distal ends of femora darker brown.

4.3 Distribution

In this study, *M. ericaeus* was found at several localities in northern Britain. All sites were above 250m, namely: Muggleswick Common, Co. Durham, three sites: 260m, 411m and 476m; Bog End 549m on the Moor House National Nature Reserve, Cumbria, and numerous other sites in Cumbria and Co. Durham; various sites in the North York Moors and Yorkshire Dales; and along an altitude transect on the north-west aspect of Cairn Gorm, Inverness-shire. Details of these sites are given in Chapter Two and Appendix 1.

M. ericaeus was not recorded from pitfall traps from Preseli Mountain, 335m, Pembrokeshire (Grid Reference SN 084325).

4.4 Abundance

M. ericaeus was taken in pitfall traps from 42 out of 48 upland sites at altitudes above 250 metres. At all the sites where it was taken, *M. ericaeus* was found co-existing with *M. morio*. It was absent from only six of the 48 upland sites where *M. morio* was taken.

The two species differ in their relative abundance at each site, but the number of *M. ericaeus* trapped was always less than that of *M. morio*, whatever the method of trapping. The percentages of *M. ericaeus* caught in pitfalls in 1979 and by hand in 1980 are given in Table 4.1.

The ratio of *M. ericaeus* : *M. morio* was never greater than 1 : 3, except at Muggleswick 260m in 1980. This exception may well be the result of a sampling error: this percentage is based on only 19 specimens hand-collected on one day, early in the field season (2 June 1980). At this time of year, *M. morio* individuals are tiny (third instar), relatively inactive and so more difficult to find in the litter, compared with the larger and more active *M. ericaeus*.

4.5 Morphological diagnosis

M. ericaeus may be distinguished from *M. morio* using various anatomical characteristics.

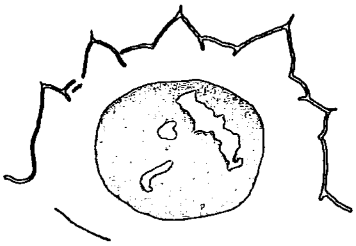
4.5.1 Colour and spination

Although pigmentation is a very variable character among Opiliones (Goodnight and Goodnight 1953), *M. ericaeus* specimens are more darkly pigmented than *M. morio*, both in body and legs. The differences are most prominent in the zone of overlap. Sexual dimorphism is pronounced: males of both species are more darkly pigmented than females. Figure 4.1 illustrates the contrast in abdominal pigmentation between the

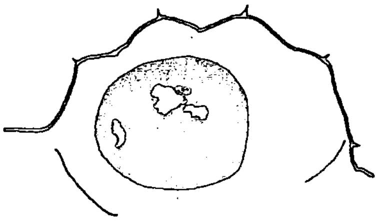
Table 4.1 The numbers of *Mitopus ericaeus* expressed as percentages of the total numbers of *Mitopus* trapped in pitfalls (1979) or by hand (1980) at four altitude sites

Site (m)	1979 Pitfall trapped		1980 Hand collected	
	Percentage of *M. ericaeus* in sample	Total no. of *Mitopus* trapped	Percentage of *M. ericaeus* in sample	Total no. of *Mitopus* trapped
260	22%	88	63%	19
411	10%	202	-	-
476	33%	351	10%	155
549	2%	800	15%	77

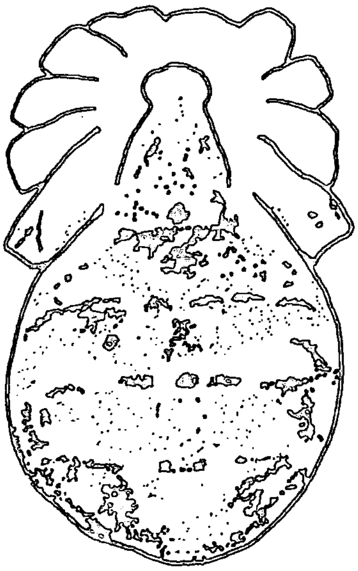
Figure 4.1 : Ocularia and ventral abdomenal pigmentation of females of *Mitopus ericaeus* (A) and *M. morio* (B)



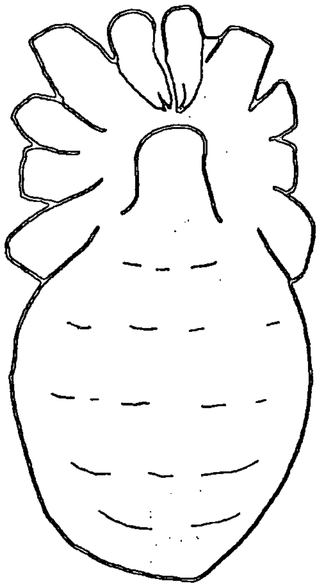
A



B



A



B

females of the two species. Male pigmentation is similar. The ventral surface of the abdomen of *M. morio* is lighter than its dorsal surface, and it is of a uniform colour in both sexes: it may vary from yellowish to pinkish. The ventral surface of the abdomen of *M. ericaeus* is strongly pigmented, being dark brown with pinkish marbled patches. There is less contrast between the dorsal and ventral surfaces in *M. ericaeus* than in *M. morio*. This degree of pigmentation also enables younger instars of *M. ericaeus* to be distinguished from those of *M. morio*, where the two species occur at the same site. These features are present in alcohol-preserved and in formalin-preserved specimens as well as in live material.

Figure 4.1 also illustrates the difference between *M. ericaeus* and *M. morio* in the degree of spination of the ocularium. The ocularium of *M. ericaeus* possesses five pairs of pronounced tubercles, at least four of which support a black-tipped spine. These features are much less developed in *M. morio*: the tubercles are represented by smaller mounds, tipped with small spines which are rather obscure. There is sexual dimorphism in both species: males possess more pronounced tubercles than females. However, the between-species differences may still be used to separate specimens of either sex.

Spines and general armature are more pronounced in *M. ericaeus* than in *M. morio*. *M. ericaeus* has a harder and less flexible cuticle which is apparent when specimens are handled with forceps in a dissecting dish. The palp femur of *M. ericaeus* is very setose and tends to be dark on the ventral surface. That of *M. morio* is paler and less setose. In male specimens of *M. ericaeus*, the dorsal surface of the proximal chelicera segment is studded with short black granular denticulae, which are not present in *M. morio*.

4.5.2 Body size

M. ericaeus is appreciably larger and heavier than *M. morio*. Table 4.2 shows that males of *M. ericaeus* are 44% heavier by weight than *M. morio* ($p < 0.001$) where the two species are taken at the same altitude site.

Table 4.2 Mean dry weights (mg) of *Mitopus ericaeus* and *M. morio* males ± one standard deviation

Species and altitude site (m)	Dry weight (m)	± standard deviation	sample size
M. ericaeus (476m + 411m)	3.64	0.38	10
M. morio (476m)	2.53	0.48	30
M. morio (76m)	2.99	0.23	6

Males of *M. morio* from the lowland sites, where *M. ericaeus* does not occur, are also significantly smaller ($p < 0.001$) than males of *M. ericaeus*.

4.5.3 Biometrics

A series of measurements were made of the lengths of the second femurs of adults and earlier instars of *M. ericaeus*, the length of each glans penis and corpus penis dissected from adult males of *M. ericaeus* and *M. morio*, and the diameter of eggs of both species laid by females in the laboratory.

Mean egg diameters are given in Table 4.3. Although eggs were laid under laboratory conditions, the females of both species were mated in the field and collected, when gravid, from the same altitude site, Muggleswick 476m.

Table 4.3 Mean egg diameters (mm) ± one standard deviation, and mean egg volumes (mm^3) of *Mitopus ericaeus* and *M. morio* from 476m

	Mean egg diameter ± S.D.		Mean egg volume	No. of eggs
M. ericaeus	1.080	0.048	0.660	20
M. morio	0.953	0.313	0.453	131

The eggs of *M. ericaeus* were found to be 13% larger in diameter ($p < 0.001$) than those of *M. morio*. The eggs are approximately spherical in shape, enabling the calculation of mean egg volumes using the formula for the volume of a sphere ($^4/_3 \pi r^3$). The values are given in Table 4.3. First instar nymphs of *M. ericaeus* hatch from eggs which are 46% greater in volume than those of *M. morio*.

Early instars of *M. ericaeus* were not readily found in the field, either by hand or in pitfall traps. The lengths of the second femurs of those specimens available, from four altitude sites in 1980, are given in Table 4.4. Second and third instars were reared in the laboratory from eggs laid by female *M. ericaeus* in the autumn of 1979. The data for 476m have been plotted on a logarithmic scale against instar number in Figure 4.2. The value for first instar *M. ericaeus* was obtained from eggs which were laid by a female collected from 396m in the Yorkshire Dales, and which hatched in the laboratory. The smooth curvilinear relationship indicates that no instars were missed during the sampling. Like *M. morio, M. ericaeus* has seven instars from hatching to mature adult.

There appears to be no altitude-linked size cline in femur lengths of adult *M. ericaeus* as there is for *M. morio* at these sites, although fifth and sixth instars (pre-adults) from 260m were significantly longer-legged than those from 476m ($p < 0.01$; $p < 0.001$, respectively.)

Table 4.4 Mean lengths of the second femurs (mm) ± one standard deviation of instars of *Mitopus ericaeus* from four altitude sites in 1980. Sample sizes are given in parentheses. Data for second and third instars are from laboratory-hatched eggs

Site	Instar						
(m)	2	3	4	5	6	7	7
260			1.842±	2.722±	3.647±	4.655±	-
			0.066	0.161	0.110	0.623	-
			(5)	(9)	(14)	(2)	
411					3.636	4.655	5.586
					0.294	0.375	0.260
					(21)	(12)	(3)
476	0.655±	1.040±	1.796±	2.499±	3.312±	4.293±	5.149±
	0.035	0.030	0.089	0.103	0.252	0.665	0.346
	(35)	(9)	(12)	(6)	(132)	(42)	(11)
549						4.917±	5.488±
						0.180	0.138
						(6)	(2)

Figure 4.2 : Mean lengths of the second femurs (mm) of instars of *Mitopus ericaeus* from Muggleswick 476m plotted on a logarithmic scale against instar number. Data are from 1980.

The value for the first instar has been obtained from laboratory-hatched eggs laid by a female collected from 396m in the Yorkshire Dales.

Curve has been fitted by eye.

☐ Laboratory-reared specimens

☐ Pitfall trapped and hand-samples

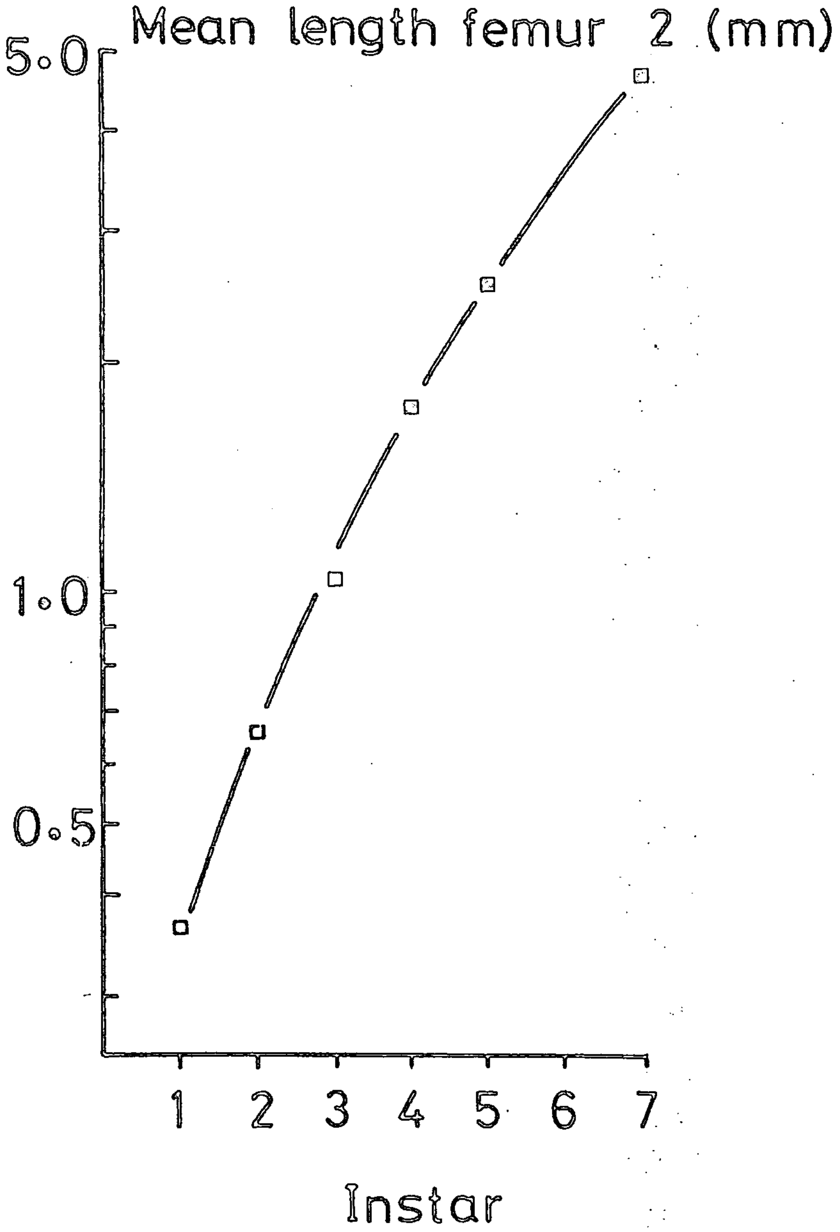

Mean length femur 2 (mm)
5·0
1·0
0·5
1
2
3
4
5
6
7
Instar

Table 4.5 Mean lengths of the second femurs (mm) ± one standard deviation of instars of *Mitopus ericaeus* and *M. morio* from 476m. The lengths of the second femurs of *M. morio* have been expressed as a proportion of those of *M. ericaeus* at corresponding instars

	Instar						
	2	3	4	5	6	7	7
M. ericaeus	0.655± 0.035 (35)	1.040± 0.030 (9)	1.796± 0.089 (12)	2.499± 0.103 (6)	3.312± 0.252 (132)	4.293± 0.665 (42)	5.149± 0.346 (11)
M. morio	0.597± 0.034 (32)	0.814± 0.063 (32)	1.079± 0.053 (38)	1.497± 0.101 (208)	1.941± 0.160 (275)	2.545± 0.197 (60)	2.889± 0.297 (37
Ratio *morio : ericaeus*	1.1	1.3	1.7	1.7	1.7	1.7	1.8

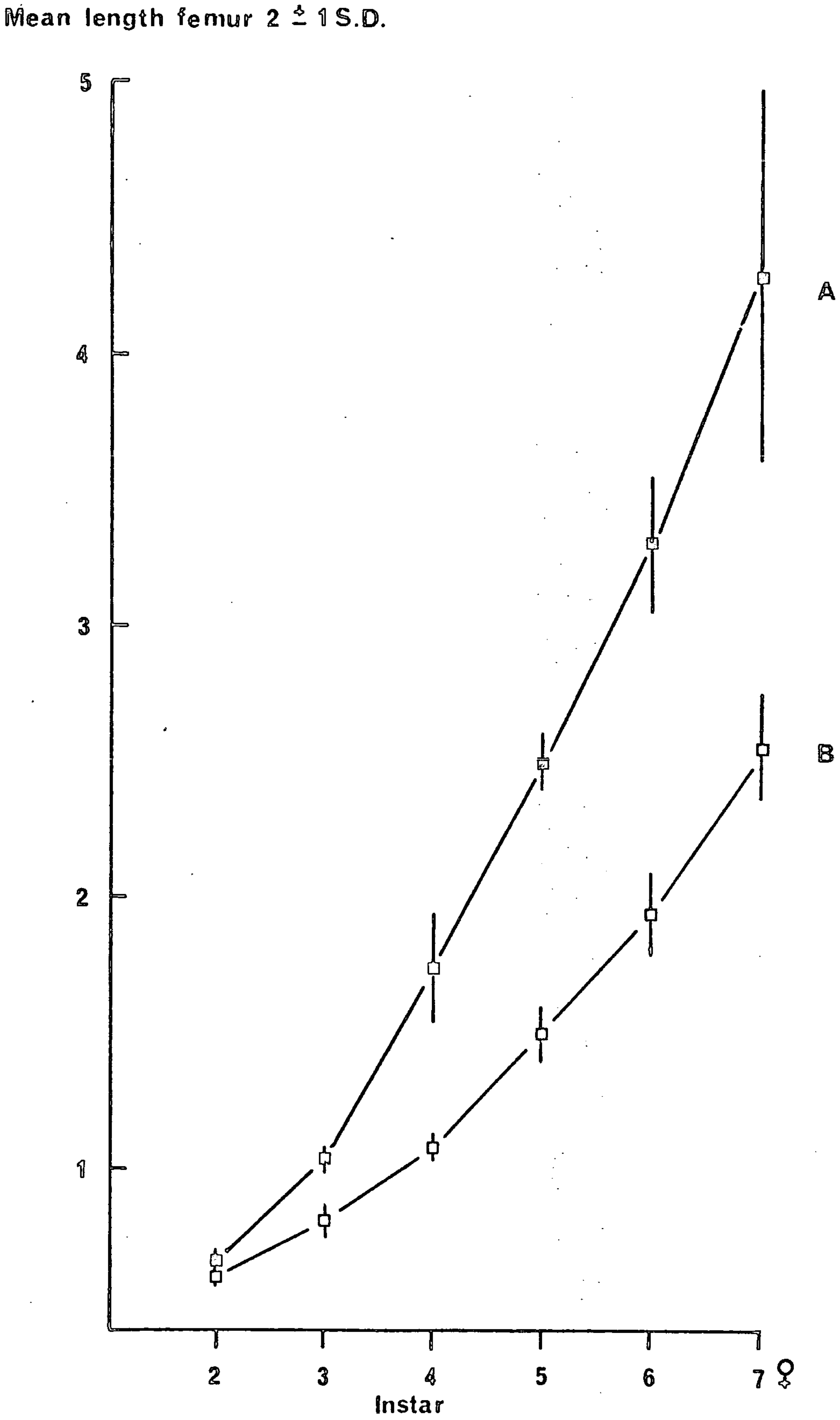
The lengths of the second femurs of adults and earlier instars of *M.* *ericaeus* and *M.* *morio* from the 476m site have been re-presented in Table 4.5. They indicate that the two species are readily distinguishable as separate size classes from hatching and throughout their development. The lengths of the second femurs of *M.* *ericaeus* are significantly longer ($p < 0.001$) than those of *M.* *morio* for all instars. The values of the ratios of the lengths of the second femurs of *M.* *morio* : *M.* *ericaeus* from 476m are also given in Table 4.5. The ratio becomes proportionately greater through successive instars, such that adult females of *M.* *ericaeus* possess femurs which are 69% longer than those of *M.* *morio* females from the same altitude site. These differences have been expressed graphically in Figure 4.3. The amounts by which the second femurs of adults of *M.* *ericaeus* (from 476m) are longer than those of *M.* *morio* adults (from seven different altitude sites) have been expressed as percentages of *morio* femur lengths in Table 4.6. Females of *M.* *ericaeus* range from

Table 4.6 The amount by which the second femurs of adult *Mitopus ericaeus* from 476m are longer than those of *M.* *morio* from seven different altitude sites (in 1980), expressed as percentages of *morio* femur lengths

	Percentage longer	
Site (m)	Female	Male
76	13	26
137	20	33
152	34	47
260	41	49
411	55	73
476	69	78
549	80	105

Figure 4.3 : Mean lengths of the second femurs (mm) ± one standard deviation of instars of *Mitopus ericaeus* (A) and *M. morio* (B) from 476m, plotted against instar number.

The figure illustrates the proportionately greater divergence in size through successive instars between the two species.


Mean length femur 2 ± 1 S.D.
5
4
3
2
1
A
B
2
3
4
5
6
7 ♀
Instar

being 41% to 80% longer-legged than females of *M. morio* where they occur sympatrically at sites between 260m and 549m. *M. ericaeus* males are 49% to 105% longer-legged than males of *M. morio* over the same altitude range. This difference is due to the altitudinal size cline exhibited by *M. morio* but absent in *M. ericaeus*. Females of *M. ericaeus* from 476m are 13% longer-legged than the longest-legged female specimens of *M. morio* from 76m ($p < 0.001$) where *M. morio* occurs alone. *M. ericaeus* males from 476m are 26% longer-legged than *M. morio* males from 76m.

4.5.4 Genital morphology

Genital morphology has been used to separate adult specimens of different species of opilionids (Bristowe 1949, Sankey 1949a, McGhee 1977, Martens 1978). The ovipositors of females are not very variable in character, and so they are not as frequently examined for taxonomic differences as are the penes of male specimens. Penis dimensions for *M. ericaeus* and *M. morio* are given in Table 4.7.

Table 4.7 Penis dimensions (mm) ± one standard deviation of *Mitopus ericaeus* and *M. morio* from 476m. Sample size in parentheses.

	mean length corpus ± S.D.	mean length glans ± S.D.
M. ericaeus	2.468 ± 0.079 (10)	0.375 ± 0.025 (9)
M. morio	1.853 ± 0.084 (10)	0.270 ± 0.020 (10)

M. ericaeus has a much longer corpus penis and glans penis than *M. morio* ($p < 0.001$) from the same site. This could simply be a function of overall size. Figure 4.4 illustrates the relationship between femur length and corpus penis length. Where the two species are sympatric, a penis length/femur length plot results in two clusters of points. *M. morio* from 76m are longer-legged and possess a longer corpus penis than those from uplands. However, specimens of *M. morio* as large as those at the 76m site are never found in sympatry with *M. ericaeus*, but only at the lowland sites, and penis length alone may be used to separate the two species where they occur sympatrically.

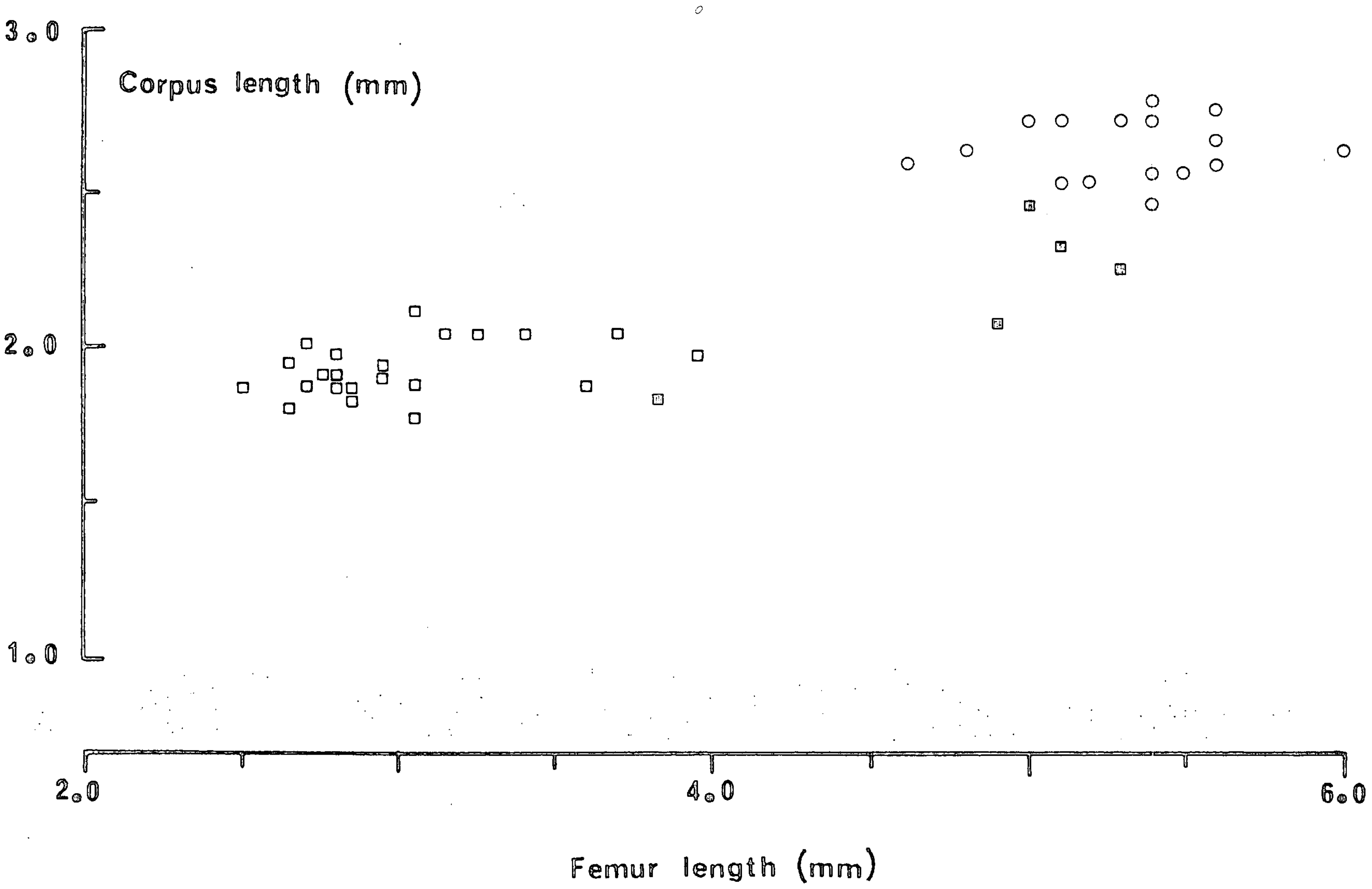
Apart from the differences in length, the shape and proportions of the corpus penis differs between the two species. Figure 4.5 illustrates this. The corpus penis tapers from a wide base to the narrow distal end: in *M. ericaeus* the length of the narrow distal region of the corpus is proportionately longer than the wider proximal section; there is a distinct junction between the two sections. The corpus of *M. morio* tapers more gradually; the narrow section is proportionately shorter. This is a difficult feature to quantify but the following method demonstrates the differences. A series of photographs were taken from slides of penes dissected from both species. Penes were mounted in lactophenol and flamed to clear. Measurements were made from the photographs of the widest part of the corpus, a, (Figure 4.6 inset), and the distance, b, between this widest part and the region where the width of the corpus was one third that of the widest part of the corpus ($^1/_3\ a$). A third measurement, c, was taken from the distal end of the corpus penis to the point where the width of the narrow portion of the corpus was one third a. The ratio $c : b$ has been plotted against the total length of the corpus penis for each individual in Figure 4.6.

Figure 4.4 : Corpus penis length (mm) plotted against second femur length (mm) of males of *Mitopus ericaeus* and *M. morio*.

○ *M. ericaeus* from 260m, 411m and 476m

□ *M. morio* from 260m, 411m and 476m

□ *M. morio* from 76m where *M. ericaeus* is absent



3.0
Corpus length (mm)
2.0
1.0
2.0
4.0
6.0
Femur length (mm)

Figure 4.5 : Penis morphology of *Mitopus morio* (A) and *M. ericaeus* (B). Side and ventral views are shown

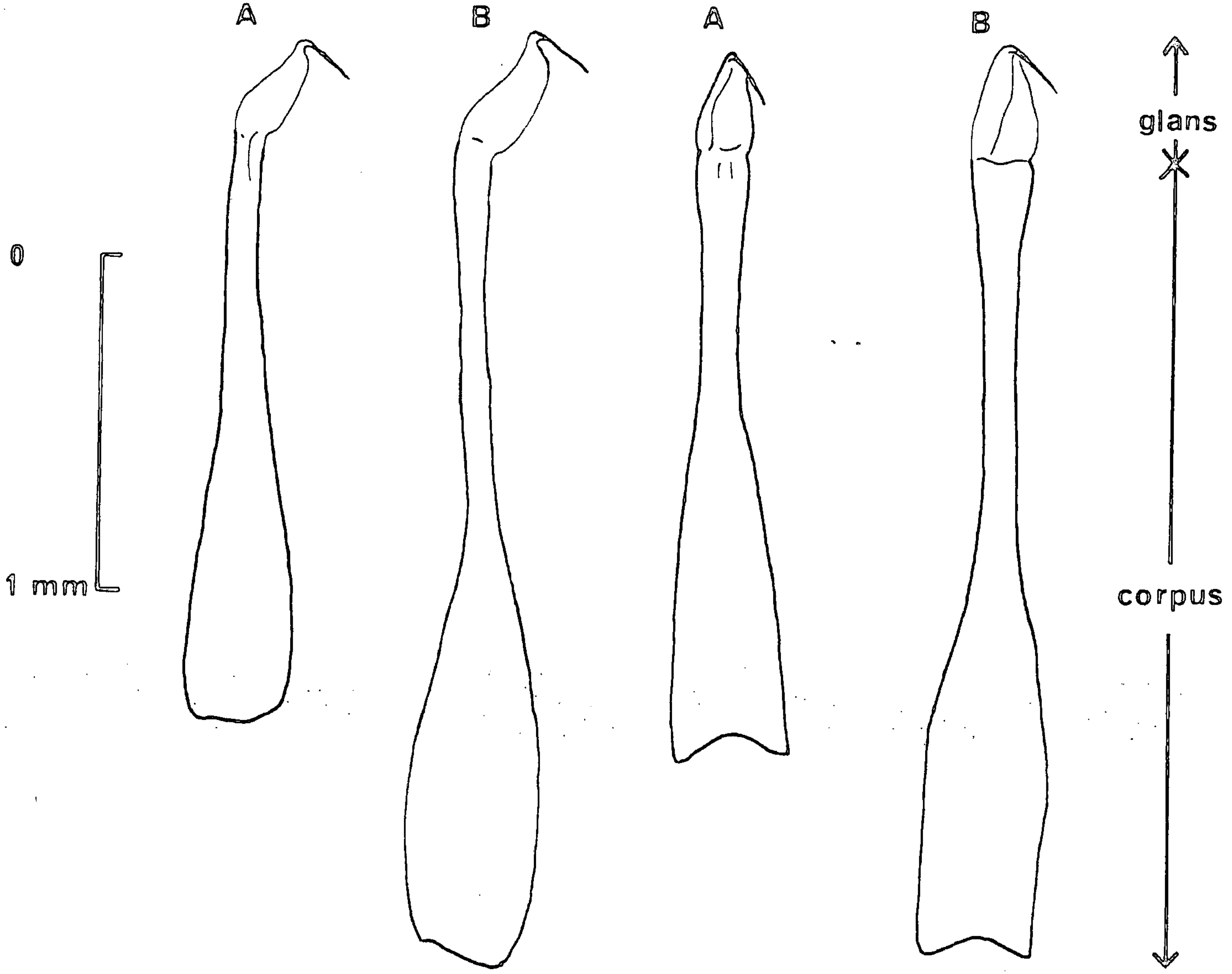
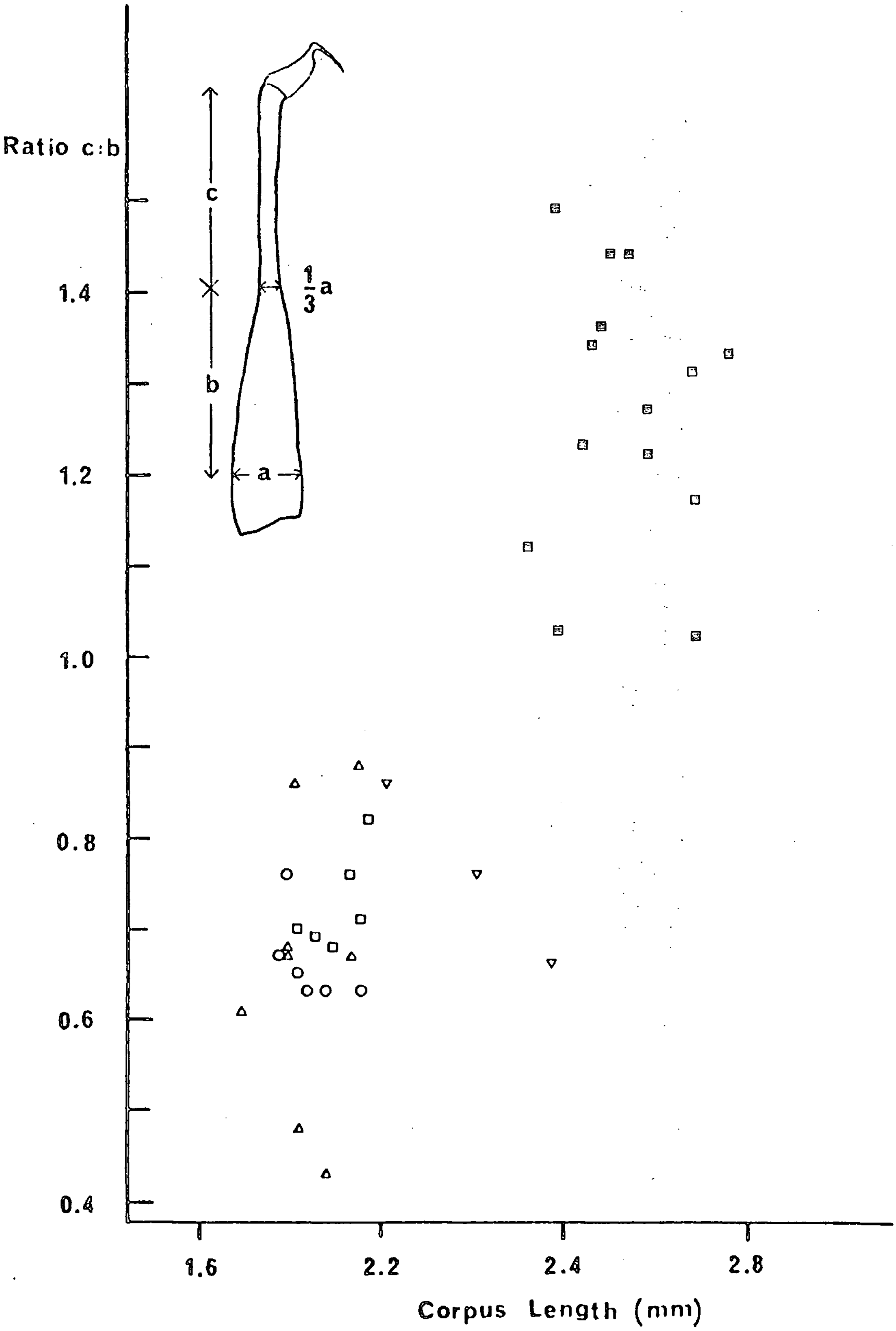

A
B
A
B
glans
corpus
0
1 mm

Figure 4.6 : Ratio c:b plotted against corpus penis length (mm) for *Mitopus ericaeus* and *M. morio*

☐	*M. ericaeus*	(from 411m and 476m)
▽	*M. morio*	(from 76m)
□	*M. morio*	(from 260m)
○	*M. morio*	(from 411m)
△	*M. morio*	(from 476m)


Ratio c:b
1.4
1.2
1.0
0.8
0.6
0.4
c
$\frac{1}{3}$a
b
a
1.6
2.2
2.4
2.8
Corpus Length (mm)

The two species cluster out into two groups: *M. ericaeus* specimens having a *c : b* ratio averaging 1.3 (n=14), and always greater than one: and *M. morio* individuals having a mean ratio of 0.7 (n=23), always less than one.

The seminal receptacles were examined by dissecting out the ovipositors from six females of each species, dehydrating them in alcohol and clearing in lactic acid (P. Hillyard, pers. comm.). The between-species differences are illustrated in Figure 4.7. The seminal receptacles of *M. morio* are short, stout and straight, whilst those of *M. ericaeus* are relatively longer, with a right-angled central section.

4.5.4 Chromosome studies

A series of testis squashes were prepared from males of *M. ericaeus* and *M. morio* to elucidate whether or not there were chromosome differences between the two species. The method is described in Chapter Three.

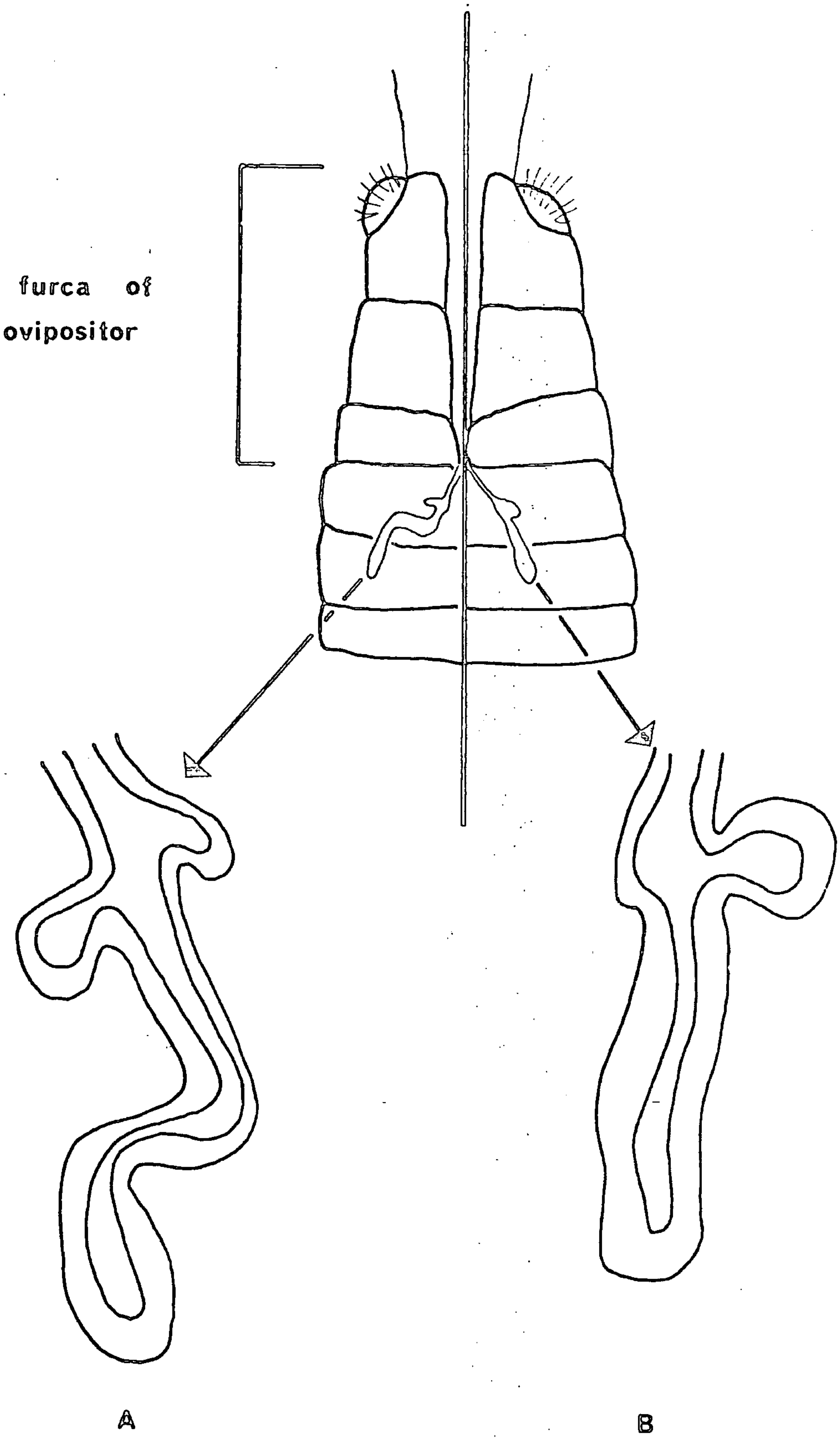
M. ericaeus and *M. morio* were both found to possess 16 pairs of chromosomes each. No structural differences in the chromosomes were observed between the two species.

4.6 Egg surface structure

Eggs laid by females of *M. ericaeus* and *M. morio* were examined for surface differences using a scanning electron microscope. Eggs were coated prior to examination to prevent them splitting under vacuum.

Observations were made over a range of different magnifications, but no differences were found in the surfaces of the eggs between the two species. For both, the surface structure is similar to that described by Balbiani (1872) for *Phalangium*. There is an outer envelope (chorion) which is irregularly bumpy; and an inner, smoother membrane.

Figure 4.7 : Seminal receptacles of *Mitopus ericaeus* (A) and *M. morio* (B)


furca of
oviposítor
A
B

4.7 Phenology of *Mitopus ericaeus*

Specimens of *M. ericaeus* were removed from pitfall trap collections, and together with those trapped by hand were assigned to instars on a basis of femur length measurements in a similar way to that described in Chapter Two for *M. morio*. These data were used to calculate the mean instar of *M. ericaeus* present on the mid-trap date. The values for Muggleswick 476m for 1979 and 1980 have been plotted in Figure 4.8 and may be compared with the values of the mean instars of *M. morio* on equivalent mid-trap dates. The corresponding data for *M. morio* presented in Appendix 4 and Figure 3.12 have been re-plotted on Figure 4.8 for ease of comparison with *M. ericaeus*.

On any particular date, *M. ericaeus* was always in a later instar than *M. morio* at the same site. The mean dates of occurrence of instars three to six given in Tables 4.8 and 4.9 have been interpolated from these graphs; they are estimates and have no confidence limits. The mean date of occurrence of the seventh (adult) instar cannot be graphically estimated, since this is an asymptote. The first dates of the occurrence of adults in pitfall traps are also given in Table 4.8 and 4.9. It is possible to calculate the true mean dates for the occurrence of the fifth, sixth and seventh instars of both species assuming a normal distribution; these are given with one standard error in Table 4.10. They are similar to the estimated dates, except that for fifth instar *ericaeus*. The calculated date is 8 days later than the graphical estimate. This is probably because only a few (n=19) fifth instar *M. ericaeus* were trapped.

It is not possible to calculate the true mean dates with confidence limits for the third and fourth instars. This is because these younger instars are not very active and do not fall into pitfall

Figure 4.8 a. Mean instar composition of pitfall catches of *Mitopus ericaeus* (□) in 1979 at Muggleswick 476m ± two standard errors plotted against mid-trap date. The corresponding data for *M. morio* (□) have been re-plotted from Appendix 4.

b. Mean instar composition of pitfall catches and hand collections of *Mitopus ericaeus* (□) in 1980 at Muggleswick 476m ± two standard errors plotted against mid-trap date. The corresponding data for *M. morio* (□) have been re-plotted from Figure 3.12.

Curves have been fitted by eye.

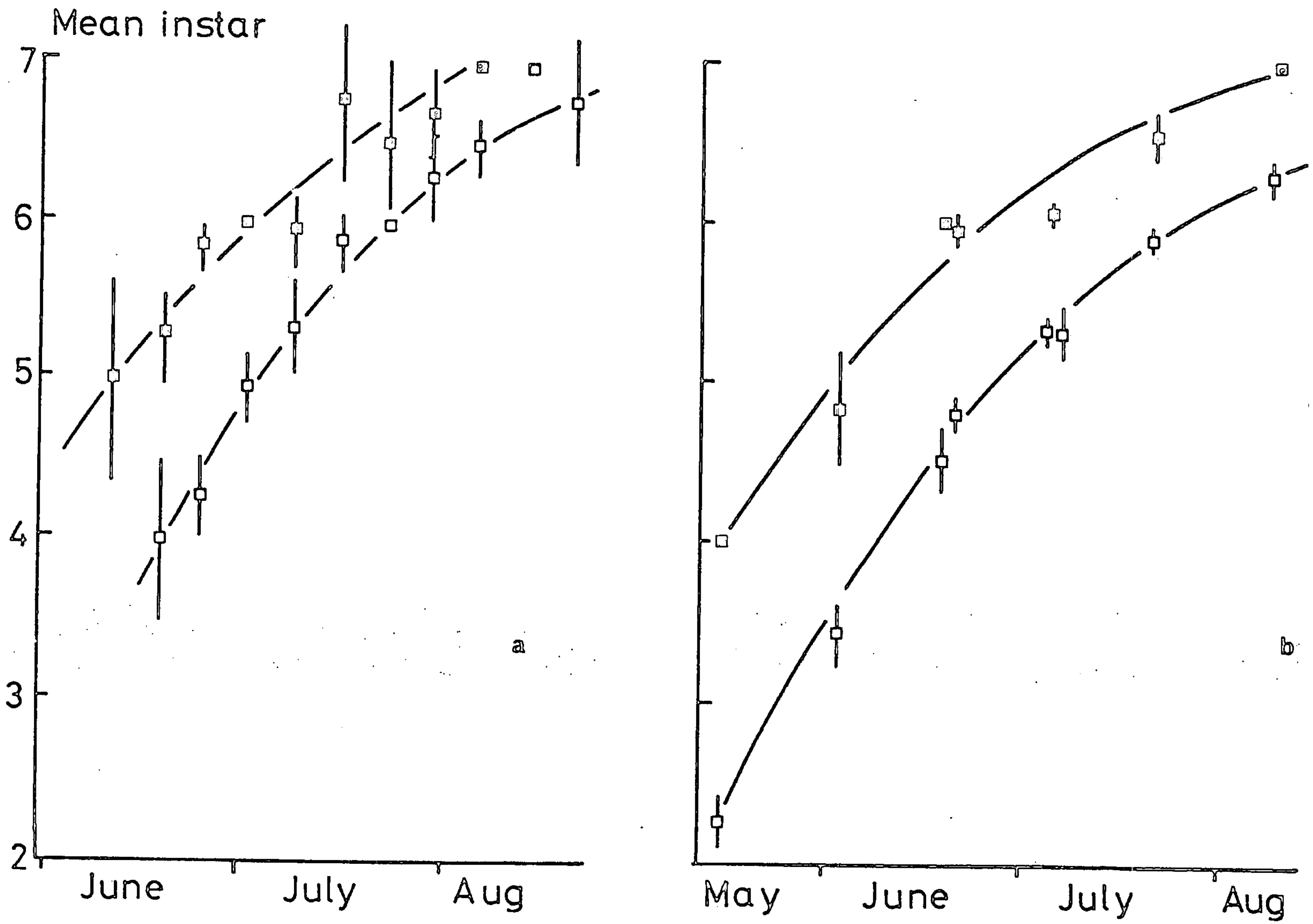

Mean instar
7
6
5
4
3
2
June
July
Aug
a
May
June
July
Aug
b

Table 4.8 Dates of mean instars of *Mitopus ericaeus* and *M. morio* in 1979 at Muggleswick 476m. The values have been estimated from the mean instar/date curves in Figure 4.8 and Appendix 4

	Instar				
	3	4	5	6	Date when first adult trapped
M. ericaeus		26 May	10 June	2 July	14 July
M. morio	4 June	18 June	2 July	21 July	28 July
Days difference		23	22	19	14

Table 4.9 Dates of mean instars of *Mitopus ericaeus* and *M. morio* in 1980 at Muggleswick 476m. The values have been estimated from the mean instar/date curves in Figures 3.12 and 4.8.

	Instar				
	3	4	5	6	Date when first adult trapped
M. ericaeus		15 May	2 June	25 June	4 July
M. morio	24 May	8 June	25 June	25 July	31 July
Days difference		24	23	30	27

Table 4.10 Calculated dates of mean instars ± one standard error of *Mitopus ericaeus* and *M. morio* in 1979 at Muggleswick 476m. (Data from pitfall trap collections.) Sample sizes are given in parentheses

	Instar		
	5	6	7
M. ericaeus	18 June ± 1.7 (19)	2 July ± 1.0 (77).	27 July ± 1.7 (16)
M. morio	4 July ± 1.8 (40)	23 July ± 1.1 (96)	24 Aug ± 3.0 (74)
Days difference	16	21	28

traps readily. The mean instar/date plots for these instars are based on individual days' hand collections. However, since the other estimated mean dates in Table 4.8 differ little from the true means given in Table 4.10, it is probably reasonable to suggest that the estimated dates for third and fourth instars are fairly reliable.

Despite these limitations, it is clear that *M. ericaeus* reaches a particular instar in advance of *M. morio*. In both 1979 and 1980, *M. ericaeus* entered both the fourth and fifth instars over three weeks before *M. morio*. Throughout their pre-adult development, the two species are always at least one instar apart.

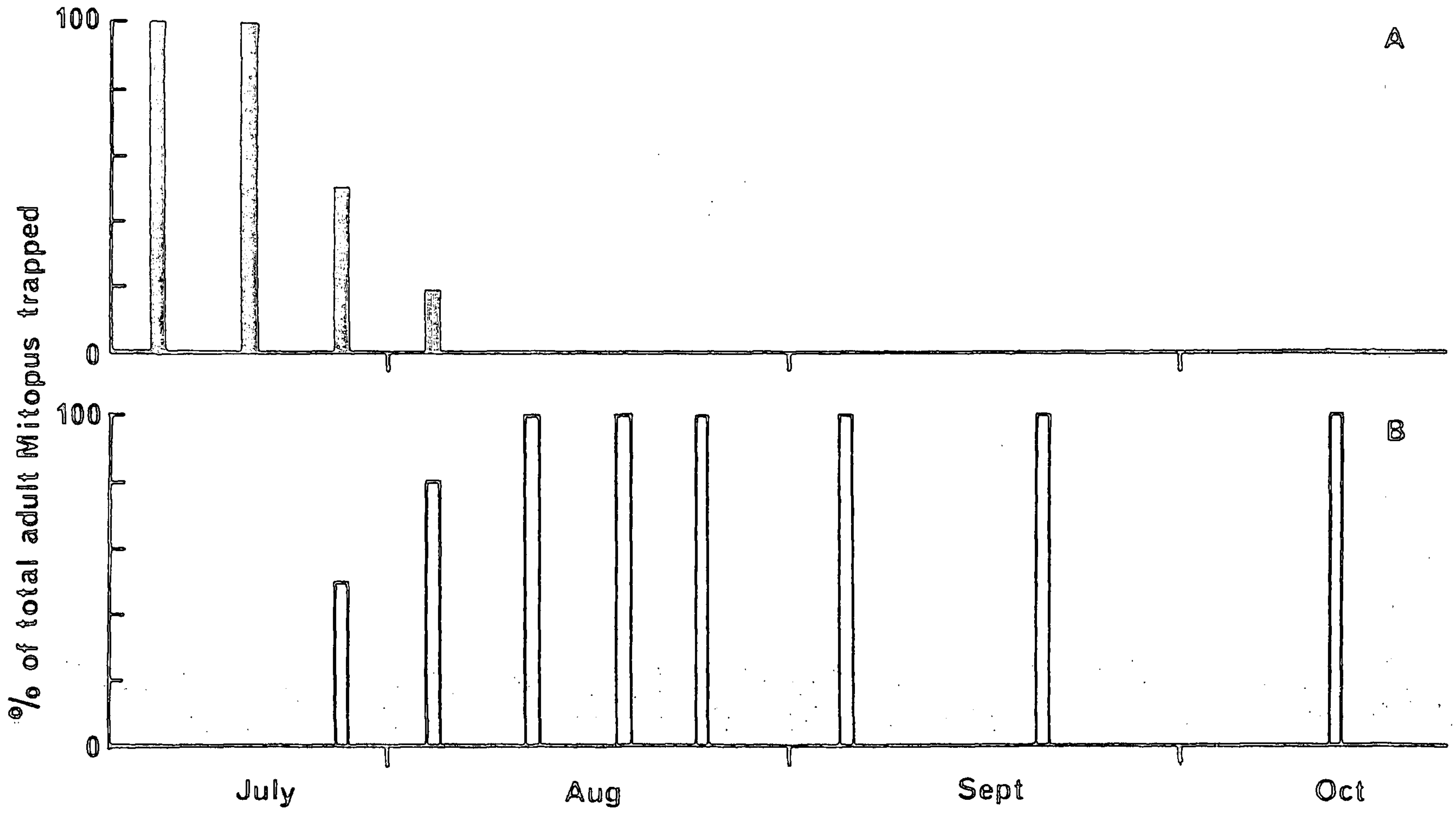
The median date for the occurrence of an instar is the date by which 50% of the total number of that instar trapped during the season have been caught. The median dates of occurrence of the fifth, sixth and seventh instars for 1979 of both *M. ericaeus* and *M. morio* have been interpolated from cumulative percentage/date plots for each instar; the values are given in Table 4.11. The standard errors of the median dates have been calculated from 1.5 times the standard errors of the corresponding mean dates given in Table 4.10.

Table 4.11 Median dates of instars of *Mitopus ericaeus* and *M. morio* ± one standard error (days) at Muggleswick 476m in 1979

	Instar		
	5	6	7
M. ericaeus	16 June ± 2.5	26 June ± 1.5	25 July ± 2.6
M. morio	29 June ± 2.7	17 July ± 1.6	13 Aug ± 4.4
Days difference	13	21	19

These median dates differ slightly, but not significantly from the mean dates (estimated and calculated). In 1979, the median date for the occurrence of sixth instar *M. ericaeus* was three weeks earlier than for *M. morio*. The median date for the occurrence of adults of *M. ericaeus* was 19 days earlier than that for *M. morio* at the same site. Thus *M. ericaeus* matures earlier than *M. morio*, reducing the overlap in sexually mature adults of the two species. This is emphasised by the fact that *M. ericaeus* adults appear to have a much narrower temporal spread than *M. morio* adults. The latter occur in traps over a period of twelve weeks compared with three weeks for *M. ericaeus*. This is illustrated in Figure 4.9.

Figure 4.9 : The numbers of adult *Mitopus ericaeus* (A) and *M. morio* (B) expressed as percentages of the total number of adult *Mitopus* trapped in pitfalls at Muggleswick 476m in 1979. The values have been plotted against mid-trap date.


A
B
100
0
100
0
% of total adult Mitopus trapped
July
Aug
Sept
Oct

However, the estimated duration of the adult instar (i.e. the difference between the median dates of the sixth and seventh instars) is the same for both species.

The genital plate remains closed until the seventh (adult) instar; most female *M. ericaeus* are probably fertilised before *M. morio* males have reached the adult instar. This reduces any possible opportunities for interbreeding to occur in the field.

Under laboratory conditions the two species did not interbreed, although successful matings and egg-layings ensued when *M. morio* males and females were placed together, and likewise for *M. ericaeus* pairs. (*M. morio* has never been found to lay parthenogenetic eggs.) Animals chosen for cross-breeding experiments were pre-adults (sixth instar) taken from the field, thus ensuring that they had not been mated previously. *M. morio* males were always eaten by *M. ericaeus* females when they were paired, although food was provided in the breeding tanks. Gravid *M. morio* females occasionally ate *M. morio* males inhabiting the same tank. *M. morio* females did not eat *M. ericaeus* males or vice-versa.

4.8 Discussion

Mitopus ericaeus sp. n. corresponds in characteristics to the upland harvestmen mentioned by Pickard-Cambridge (1890) but incorrectly referred to by him as *M. alpinus*. The original description of *M. alpinus* (Herbst 1799) is clearly that of a harvestman with short, thick legs. *M. ericaeus* has very long legs and has not been previously described. Another high altitude species found alone and only above the tree-line (*M. glacialis* Heer) occurs throughout the Alps (Martens 1978). I have examined specimens of *M. glacialis*. *M. ericaeus* differs from this species, and does not conform to the description given by Martens (*loc. cit.*) in morphological features; it has considerably shorter legs than *M. glacialis* and a different penis morphology.

M. ericaeus is sympatric with *M. morio* in the upper altitudinal regions of the latter's range. *M. ericaeus* differs from *M. morio* in all instars by being more darkly pigmented, more spiny, larger and longer-legged. The two species may be distinguished by their different penis morphologies. *M. ericaeus* has a different phenology to *M. morio*.

M. morio is smaller when it occurs in sympatry with *M. ericaeus* than when it occurs alone. *M. ericaeus* does not apparently display an altitude-linked size gradient comparable with that of *M. morio*, and it has not been found in allopatry. Two closely related species with overlapping ranges, which are more divergent in the zone of overlap are said to exhibit character displacement (Brown and Wilson 1956). However, *M. morio* has been shown to exhibit a character gradient which is continuous throughout its range, whether in allopatry or in sympatry with *M. ericaeus*. Grant (1972) has already stated that many examples of divergent character displacement simply represent a gradual clinal variation associated with various environmental gradients.

Co-existing congeneric species are often postulated as being at some time in competition (Gause 1934, Lack 1945). Hutchinson (1959) stated that in species which co-exist on a basis of a size difference, the largest form often reproduces before the smaller one. He based these observations on annual insects (corixids). *M. ericaeus* reaches the final (adult) instar several weeks earlier than *M. morio*, reducing the overlap in mature adults of the two species. Interbreeding is unlikely to occur. The separation between mature adults of the two species is exaggerated by the fact that the adult longevity of *M. ericaeus* is much less than that of *M. morio*. The differences in penis length as well as the regular predatory nature of the females of *M. ericaeus* on males of *M. morio* may be a physical barrier to cross mating.

On any particular date, *M. ericaeus* is more advanced in its development than *M. morio* throughout the life cycle; it is at least one instar ahead until the pre-adult stage. For example, the majority of specimens of *M. morio* collected at the end of June are in the fifth instar, whilst specimens of *M. ericaeus* are in the sixth instar. The size difference between individuals of each species collected on the same date is thus even more pronounced. At the end of June, *M. ericaeus* nymphs are more than twice the size of *M. morio* nymphs; the second femur length ratio of sixth instar *ericaeus* : fifth instar *morio* is 2.2 : 1.0. Should the two species occur in the same part of the habitat, food competition is unlikely because of this size difference between them. It has been suggested (Wilson 1975) that larger animals take a larger prey size, which is unavailable to smaller competitors. It is obvious that *M. ericaeus*, twice the size of *M. morio*, is able to handle larger prey. Hutchinson (1959) showed that for co-existing, congeneric species of insects, birds and mammals, ratios of mouthpart sizes ranging from 1.2 to 1.4 were characteristic. Lack (1976) produced body weight ratios varying from 1.6 to 3.3 for congenerics, and Fenchel (1975) found species of Hydrobiiae (Mollusca) in stable co-existence with body size ratios of 1.3 to 1.5. This size difference was sufficient to segregate the species on food size selectivity. The second femur length ratio for adult *M. morio* and *M. ericaeus* males is 1.8 for specimens collected at the same site. The body weight ratio for males is 1.4. Both of these ratios are in excess of the values suggested as being necessary for avoiding major interspecific competition.

It is not possible to perform feeding experiments on prey-size selection with species which are not selective predators: *M. ericaeus* and *M. morio* feed both as predators and scavengers, hence prey selection has not been tested for these two species. Phillipson (1960) suggested that opilionids remain stationary to feed, their legs functioning in a similar way to a spider's web. However, this is contrary to my own and other observations (Roters 1944, Sankey 1949b, Adams pers. comm.). I believe that opilionids, under natural conditions, are active foragers and scavengers. Phillipson (1960) showed that *M. morio* did not respond to the presence of prey until physical contact was made with it: because of the lack of chemosensory and visual ability, harvestmen cannot actively select particular prey items; they grapple with whatever they meet in their wanderings, rejecting or accepting it on a basis of its manageability and palatability thereafter. The larger *M. ericaeus* is able to deal with larger prey items than *M. morio,* and for most of their life-cycles the two species are separated by one instar, which magnifies the size-ratio between them considerably, decreasing any overlap in the prey size available to each species.

It has been suggested that habitat structure is more important than prey availability for arachnids (Pearson and White 1964, Duffey 1966, Uetz 1979). Adams (pers. comm.) has found field layer opilionids to be extreme generalist feeders, taking most prey species offered to them; this confirms my own observations. Niche separation is more likely to be the result of a morphological type rather than prey selection. *M. ericaeus* may well be excluded from the denser lower vegetation layers due to its inability to utilise them, because of its size and leg length; these parts of the habitat and their concomitant food resources will be more accessible to the smaller, shorter-legged *M. morio*. Field observations confirm this: *M. ericaeus,* with its extremely long legs, is rarely found in the dense vegetation and litter at the base of the heather. It is more often found in the upper layers. Pianka (1976) observed that for potential competitors it was necessary to look at the multidimensional resource utilisation, and niche separation along more than a single niche dimension. When all the factors which may be involved in bringing about niche separation of the two species are examined, it seems unlikely that any kind of competition occurs between *M. morio* and *M. ericaeus*.

CHAPTER FIVE

MITOPUS MORIO AT OTHER SITES IN THE BRITISH ISLES AND ABROAD

5.1 Introduction

Specimens of *Mitopus morio* have been examined from sites altitudinally and latitudinally separated from the sites already described in England and Scotland. The samples were from widely differing habitats in Britain (Pembrokeshire, St Kilda), Europe (central and northern Norway, Austria), and Iceland. Site details are presented in Table 5.1 below. The varying locations from which samples were obtained are a further indication of the great extent of the range of *M. morio*. It was taken in very large numbers at some of the sites. The sources of material are given in Appendix 6.

M. ericaeus was not recorded from any of the samples from the localities described below.

5.2 Method

All specimens of *M. morio* examined were adults. Observations were made on the general size, pigmentation and armature, and measurements were made of the lengths of the femurs of the second walking legs of both sexes, as for the British specimens described in the preceding chapters. Penes were dissected from adult males, and measurements of the lengths and ratios of the distal and proximal portions of the corpora penes were made, as described for *M. ericaeus* and *M. morio* in Chapter Four.

Climatological data were obtained from the World Meterological Organisation (1971).

5.3 Results

Data for all the sites are summarised in Table 5.1. The localities of the six Iceland sites are marked on Figure 5.1.

Femur lengths of *M. morio* from the different sites were extremely variable, the Austrian specimens being twice as long-legged as those from Iceland.

A plot of mean femur lengths of adult males against mean femur lengths of adult females from the additional sites in Britain and abroad (Figure 5.2) shows that there is a linear relationship regardless of the sample locality. The slope of the fitted regression line is not significantly different from one, indicating that the male femur length to female femur length ratio is 1 : 1, and constant for all sites examined. The two Austrian sites have not been included in this regression; site details are not known, and specimens from here had very variable femur lengths; the small samples have mean femur lengths with large standard deviations associated with them (Table 5.1).

Figure 5.3 shows the relationship between corpus penis length and femur length of males of *M. morio* from all the sites in Britain and abroad, except the Austrian sites. These values have been excluded from the fitted regression line for the same reasons given above. The slope of this regression line is significantly different from unity ($p < 0.05$), indicating that for a unit increase in penis length, femur length is almost doubled. Although they are directly correlated ($p < 0.02$), penis length is considerably less variable a character than femur length.

The shapes and proportions of the corpora penes were similar to those of the British specimens of *M. morio* described in Chapter Four: the ratio of the distal tapered section to the proximal basal region having a value less than one. For many of the penes, the width of the

Table 5.1 Summary of the site details (altitude and latitude), mean lengths of the second femurs (mm) ± one standard deviation of adult females and males, the mean lengths of the corpora penes of males (mm) ± one standard deviation, and the c : b ratio of the penis proportions of *Mitopus morio* from the additional sites in the British Isles and abroad. Sample sizes are given in parenthese.

Site and Altitude (m)	Latitude	Mean length of second femur ± 1 S.D.		Mean length of corpus penis ± 1 S.D.	Mean Ratio (c : b) ± 1 S.D.
		Adult ♀♀	Adult ♂♂		
St Kilda	57° 49'N				
36	"	3.22 ± 0.22 (10)	3.79 ± 0.35 (8)	2.45 ± 0.17 (6)	0.71 ± 0.14 (5)
100	"	3.43 ± 0.24 (15)	3.86 ± 0.33 (10)	2.45 ± 0.10 (9)	0.73 ± 0.14 (8)
340	"	3.17 ± 0.17 (10)	3.47 ± 0.39 (10)	2.37 ± 0.05 (6)	0.65 ± 0.13 (6)
Pembrokeshire	51° 55'N				
152	"	3.57 ± 0.19 (16)	4.19 ± 0.40 (4)		
335	"	3.01 ± 0.29 (30)	3.27 ± 0.32 (30)		

/continued..........

Table 5.1 continued......

Site and Altitude (m)	Latitude	Mean length of second femur ± 1 S.D.		Mean length of corpus penis ± 1 S.D.	Mean Ratio (c : b) ± 1 S.D.
		Adult ♀♀	Adult ♂♂		
Norway Finse	60° 36'N	3.95 ± 0.57 (100)	4.71 ± 0.67 (30)	2.39 ± 0.16 (19)	0.65 ± 0.04 (19)
Norway Andoya	69° 05'N	3.82 ± 0.24 (9)	4.15 ± 0.40 (6)		
Austria 380	48° 15'N		7.47 ± 0.47 (11)	2.76 ± 0.22 (10)	0.67 ± 0.13 (10)
1400	"	4.07 0.51 (6)	5.38 0.71 (17)		
1900	"	3.39 ± 0.42 (9)	5.65 ± 1.32 (21)	2.76 ± 0.10 (8)	0.67 ± 0.13 (8)

/continued.........

Table 5.1 continued ....

Site and Altitude (m)	Latitude	Mean length of second femur ± 1 S.D.		Mean length of corpus penis ± 1 S.D.	Mean ratio (c : b) ± 1 S.D.
		Adult ♀♀	Adult ♂♂		
Iceland	64° 05'N				
R1 (61m)		3.19 ± 0.29 (30)	3.37 ± 0.26 (15)	2.31 ± 0.12 (15)	0.65 ± 0.12 (15)
R5 (61m)	64° 30'N	3.52 ± 0.31 (19)			
R6 (152m)	65° 00'N	3.62 ± 0.34 (16)			
R9 (152m)	65° 36'N	3.03 ± 0.36 (30)	3.64 ± 0.35 (15)	2.33 ± 0.09 (8)	0.54 ± 0.13 (8)
R10 (152m)	"	3.43 ± 0.36 (23)			
R11 (610m)	65° 50'N	3.61 ± 0.39 (7)	4.10 (1)		

Figure 5.1 : Location of the sample sites in Iceland

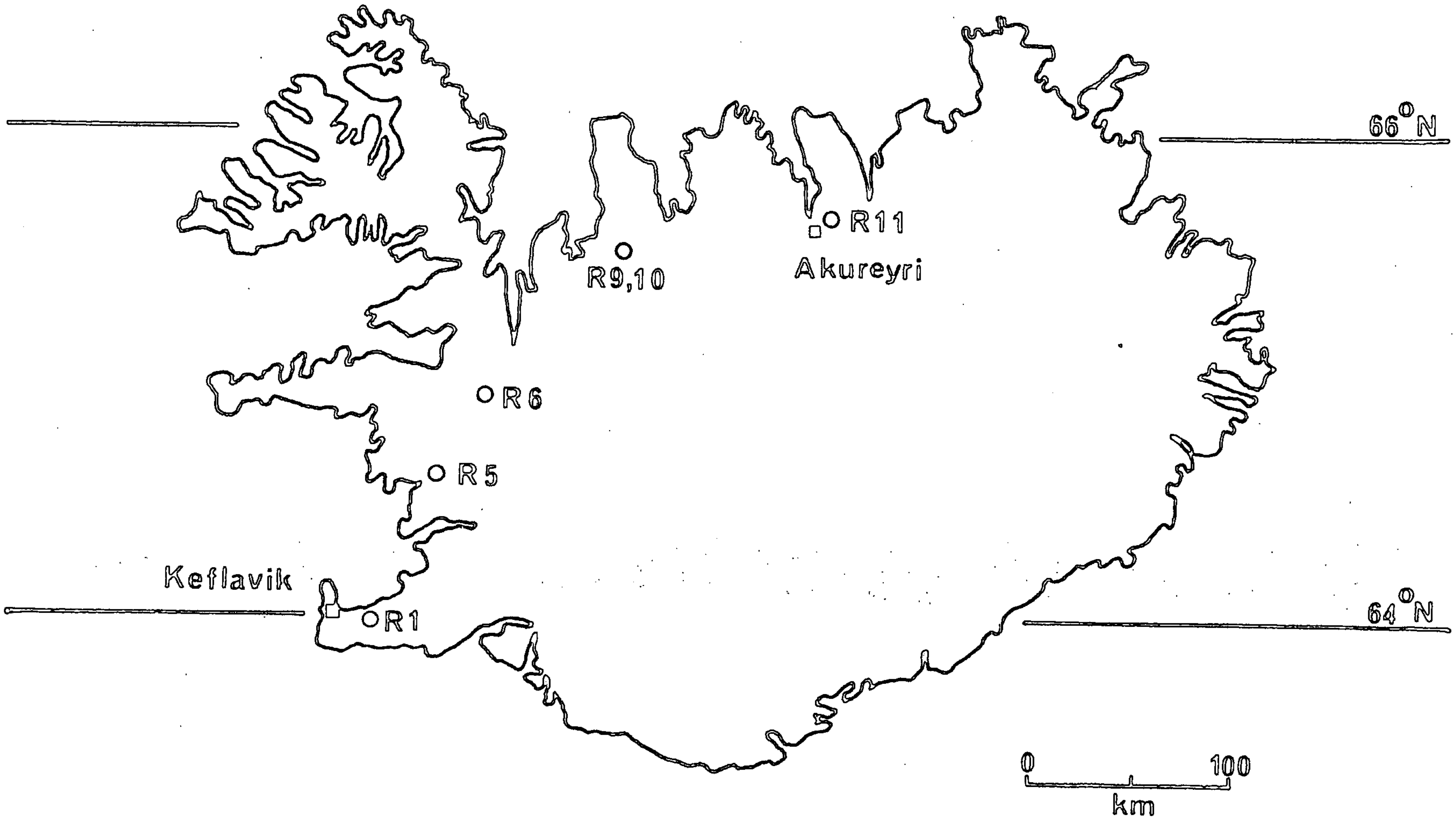

66° N
R11
Akureyri
R9,10
R6
R5
Keflavik
R1
64° N
0
100
km

Figure 5.2 : Mean length of the second femurs (mm) of males of *Mitopus morio* plotted against mean femur lengths of females (mm) from the additional sites in Britain and abroad.

The regression equation is given by:

$$y = 1.249x - 0.390$$

$n = 10$ $r = 0.926$ S.E. of slope = 0.180 $p < 0.001$

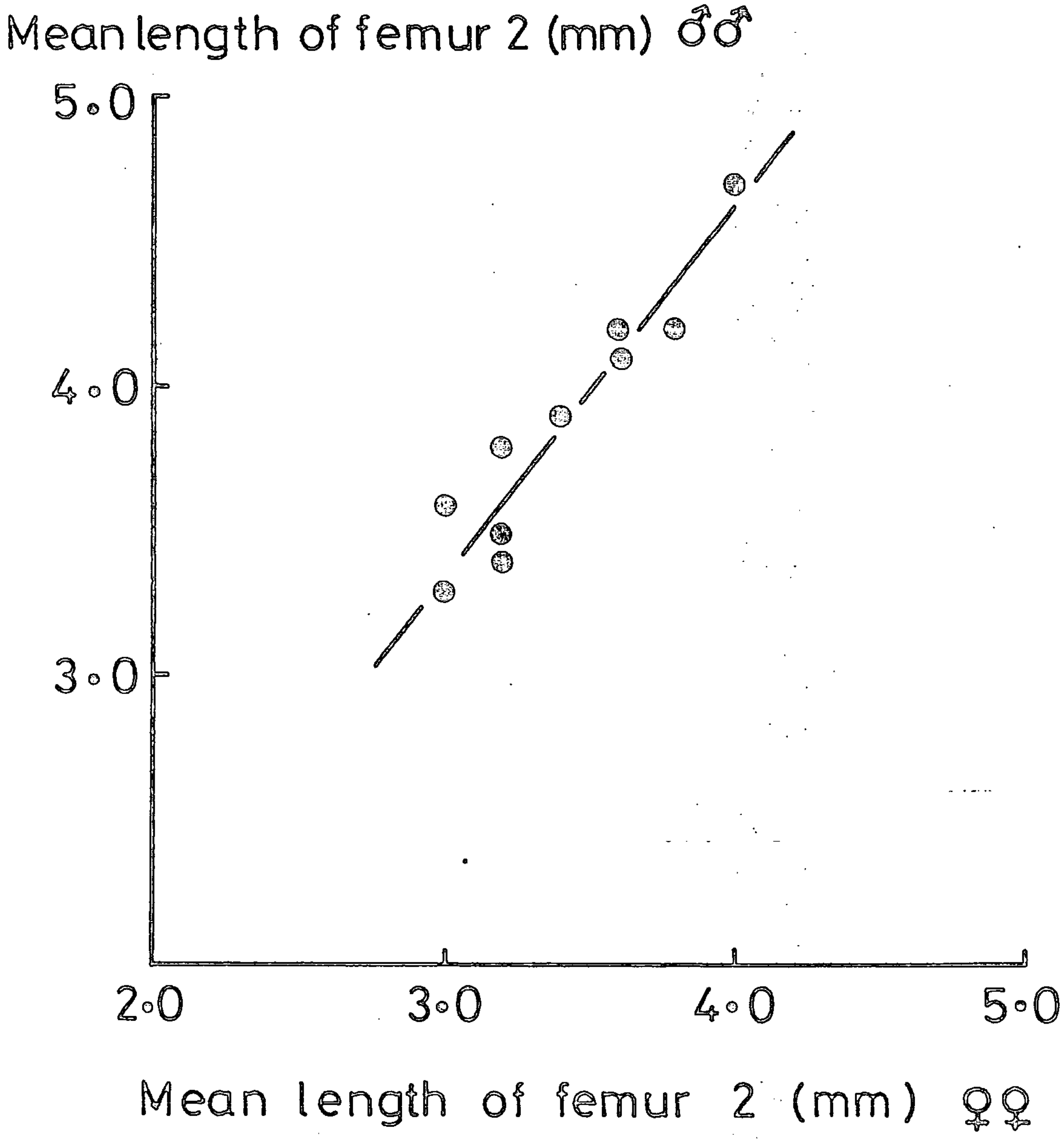
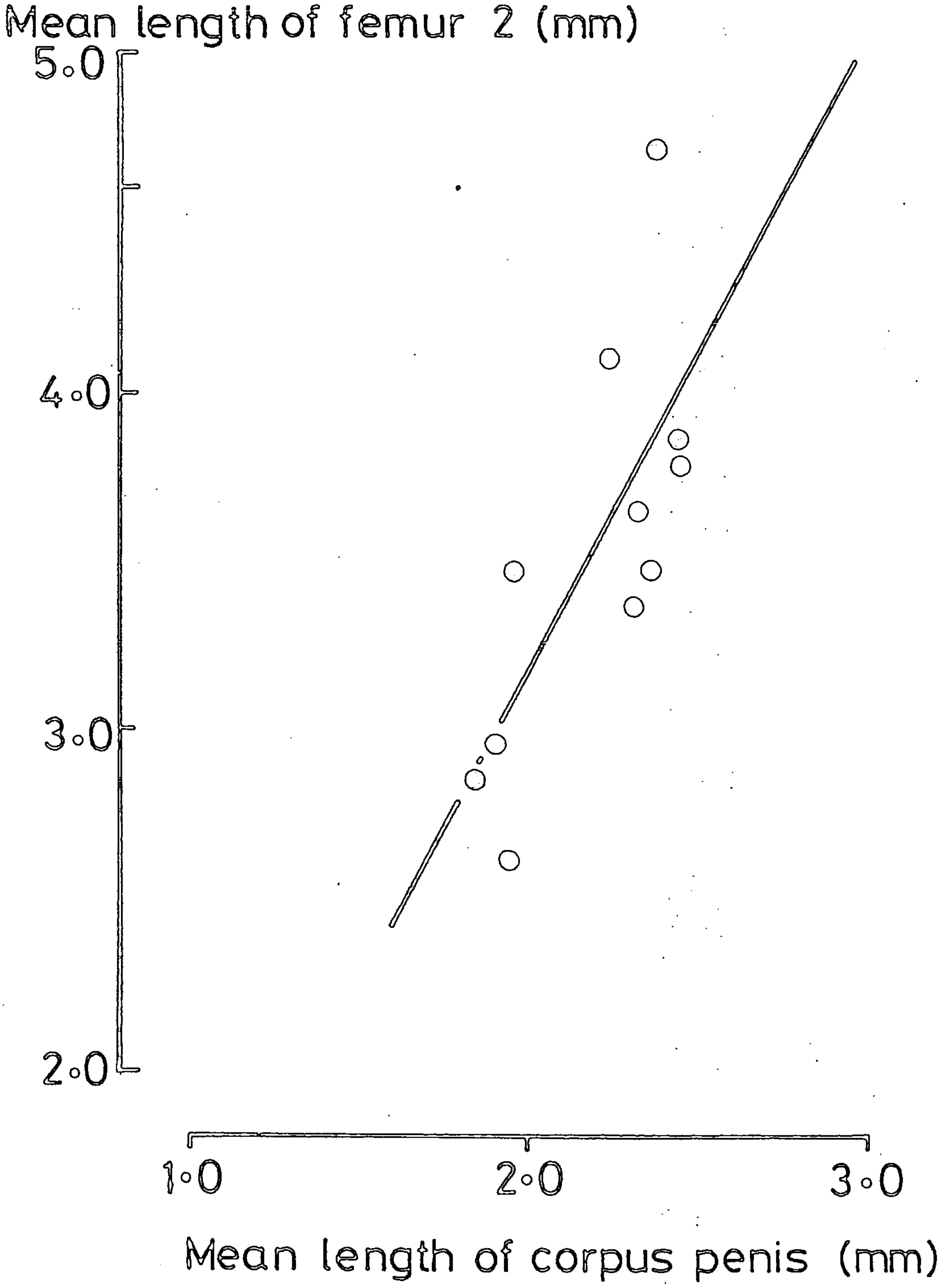

Mean length of femur 2 (mm) ♂♂
5·0
4·0
3·0
2·0
3·0
4·0
5·0
Mean length of femur 2 (mm) ♀♀

Figure 5.3 Mean lengths of the second femurs (mm) plotted against mean lengths of the corpora penes (mm) of males of *Mitopus morio* from all the sites in Britain and abroad.

The regression equation is given by:

$$y = 1.865x - 0.570$$

$n = 11$ $r = 0.733$ S.E. of slope = 0.353 $p < 0.02$


Mean length of femur 2 (mm)
5.0
4.0
3.0
2.0
1.0
2.0
3.0
Mean length of corpus penis (mm)

narrowest region of the corpus was never as narrow as one third of the widest portion. The relatively narrow distal part of the corpus was thus very short, giving the penis a rather squat appearance. This shape applied to those penes which were as long as those of the British *M. ericaeus*, so that the two species could readily be distinguished on their penis proportions, despite their femur length similarities. Details of the appearance of the specimens of *M. morio* from the different localities are listed individually below.

Sankey and Savory (1974) have suggested that *M. morio borealis*, an Arctic form of *M. morio* (referred to in Chapter One) may occur in the extreme north and on coastal islands in Scotland, although they give no evidence for this. Presumably they reasoned that relict populations are more often found on isolated islands. Thorell (1876) described the species *M. alpinus* var. *borealis* (*sic*) as possessing very spiny legs; his specimens had been taken in northern Norway and Sweden (68° north to 70° north in latitude). Spininess is a difficult feature to quantify, and is very variable in Opiliones (Goodnight and Goodnight 1953); also Thorell's description was vague. Specimens from north-east Scotland (Cairn Gorm) referred to in Chapter Three were not of the form *borealis*. The island of St Kilda, lying off the north-west coast of Scotland may, on the basis of the assumptions of Sankey and Savory (1974) support populations of *borealis*. Samples were available from this island, and were closely examined.

5.3.1 St Kilda

St Kilda specimens of *M. morio* were large pale animals, with pale yellowish legs, not very spiny. For example, the fourth femur was well clothed with denticles, but the second femur possessed very few. Specimens were very similar to the lowland examples of *M. morio* from the mainland (Co. Durham), and there is no evidence that a spiny form "*borealis*" does exist on St Kilda.

There is no significant difference in the mean lengths of the femurs of specimens from the different altitudes, for either sex. This lack of altitudinal variation probably reflects the marked maritime influence on the island. St Kilda covers a small area, and the whole island is likely to possess a uniform climate. Climatic uniformity results in a relative uniformity of femur lengths of specimens of *M. morio*, and a lack of clinal variation in size with altitude.

5.3.2 Pembrokeshire

The vegetation at both of the Welsh sites was dominated by *Calluna vulgaris* (L.) Hull. Specimens of *M. morio* were obtained from pitfall traps laid in 1977 (see Appendix 6).

Specimens of *M. morio* of both sexes from Plumstone Mountain (Grid reference SM 917234) at 152m were longer-legged than those from the higher altitude site at Preseli, 335m (SN 084325): females at 152m were 19% longer-legged than those at 335m ($p < 0.001$) and males 28% longer-legged at 152m ($p < 0.001$). When the altitude values are substituted into the regression equation given in Figure 3.7, the predicted mean femur lengths (log scale) for the Pembrokeshire females are only slightly greater than the observed values (3.62 at 152m, and 3.05mm at 335m). These results are additional evidence for the widespread nature of clinal variation on *M. morio*.

5.3.3 Iceland

M. morio was the only species of harvestman taken on Iceland. Specimens of both sexes from all the sites were more strongly pigmented than those from St Kilda, the legs being a brownish-yellow and very spiny;

even the second femurs were well-denticulated, in both sexes. These specimens may correspond to the harvestman *borealis* referred to by Thorell (1876), since they can be distinguished as a spiny form of *M. morio*, but not as a separate species; they do not differ in penis proportions from those of other specimens of *M. morio*.

The dorsal saddle patterning of the Iceland specimens varied from a well-marked "hour-glass" pattern, to very weak markings. Femur lengths of both sexes were extremely variable. There appears to be no size relationship with altitude. Sites R6, R9 and R10 were all at an altitude of 152m. However, female specimens of *M. morio* from R9 were significantly shorter-legged than those from the other two sites ($p < 0.001$). Females from R1 (61m) were significantly shorter-legged than those from R11 (610m) ($p < 0.02$). This may be a consequence of the small sample size or the climate: sites R1, R5 and R11 were coastal; the highest site (R11) lay on a ridge at the mouth of a valley. The maritime influence may be sufficiently ameliorating to negate any effect of increasing altitude on femur length. The highest and lowest sites are also separated by 1° 43' latitude. However, the climatic differences between them are less marked than might be expected for this combined latitude and altitude difference, especially during the mid-summer months; temperatures are similar at Keflavik in the south (near the 61m site) and Akureyri in the north (near the 610m site), but Akureyri has a lower precipitation. A high precipitation frequently has the effect of lowering the ambient temperature, and this may be the case at Keflavik. This would result in specimens of *M. morio* being shorter-legged than expected at this site.

5.3.4 Norway

Specimens of *M. morio* were caught in pitfall traps at Finse, in the north-west region of the Hardangervidda mountain plateau in central Norway, over an altitude range of 1220m to 1350m; and on the Norwegian island of Andoya, nine degrees latitude to the north of Finse.

M. morio is relatively long-legged in Norway (at both sites), and often darkly pigmented dorsally and on the legs. The ventral abdomen is characteristically pale in contrast to the dorsal abdomen in most cases, like all other specimens of *M. morio*. The penis proportions distinguish the specimens very well from similar sized examples of *M. ericaeus* from Britain: the distal portion of the corpus penis is relatively short and thick, resulting in a c : b ratio of less than one.

5.3.5 Austria

Examples of *M. morio* from Austria were the longest-legged of all specimens of *M. morio* examined. In appearance, lowland males from the Vienna forest (380m) were very like lowland specimens of *M. morio* collected from the 76m site in Britain, except for the femur length differences; the dorsal saddle pattern often being a simple "figure of eight" shape. The legs were yellowish-brown and not strongly denticulated. Frequently, lowland females were also rather faintly patterned, like their British counterparts. Males from Styria (1900m) were both more darkly pigmented and more strongly denticulated than British examples. Femur lengths were very variable, some specimens possessing very long femurs, others very short. The mean femur lengths were shorter at the higher altitudes ($p < 0.001$).

Males from both altitudes had penis proportion ratios corresponding to those of *M. morio* at all the other sites, despite the greater lengths of the corpora penes.

5.4 Discussion

Mitopus morio is a harvestman which is extremely variable in its phenotype. The femur lengths, pigmentation and general armature may be very different between specimens from sites which are geographically widely separated. In the preceding chapters, femur length variation has been shown to be related to altitude through the climatic changes associated with an altitude gradient. The physiological processes of poikilotherms depend largely upon the temperature regime of the external environment. Eurythermal poikilotherms often exhibit plasticity in their morphological adaptations (Soulé and Kerfoot 1972). There has been considerable discussion concerning the application of Bergmann's rule on body size and Allen's rule on protruding body parts to poikilotherms, but they do possess validity for some poikilotherm species (Ray 1960, Kauri 1966). Kauri (*loc. cit.*) showed that *Leiobunum paessleri* Roewer from the Aleutian Islands was larger-bodied and longer-legged from islands with a warmer climate, than specimens from cooler islands. Slagsvold (1979) found that the mean long-term summer maximum temperature during June to September, together with latitude, accounted for a significant proportion of femur length variation of *Mitopus morio* in Norway.

Since specimens of *M. morio* from geographically widely separated regions are variable in their external morphology in a way which is consistent from year to year, it is therefore suggested that the differences are determined by the prevailing climatic conditions. These in turn depend upon latitude locality as well as altitude; the specimens from more northerly latitudes experience a cooler, and in some instances, a maritime climate with a resultant shorter growing season. These specimens are smaller and shorter-legged than their central European counterparts at lower latitudes where the climate is continental and the growing season longer, and on average warmer; hence this explanation would account for the fact that specimens from the most southerly latitudes (Austria) were the largest and longest-legged of all examples of *M. morio* examined.

It is possible to construct a model from which to make predictions concerning the femur lengths of specimens of *M. morio* knowing the altitude, latitude and prevailing temperatures experienced at the locality from which the specimens were taken. For some of the sites discussed above, data for all three of these variables are available. Multiple regression analyses were implemented for thirteen of these sites using the following variables: log. femur length of adult females, site altitude, mean temperature at that site (April to June), and site latitude. The correlation coefficients for the individual regressions are given in Table 5.2. Latitude and temperature were found to be highly correlated with one another ($p < 0.01$) and were combined into a fifth variable "latitemp", by multiplying their corresponding values together.

Table 5.2 Correlation coefficients for the variables log. femur length of female *Mitopus morio*, altitude, latitude, temperature and "latitemp" (latitude x temperature)

	Log. Femur	Altitude	Latitude	Temperature	Latitemp
Log. Femur	1.0000	-0.5995	0.3792	0.3353	0.5295
Altitude		1.0000	0.0083	-0.5149	-0.6311
Latitude			1.0000	-0.7239	-0.5475
Temperature				1.0000	0.9715
Latitemp					1.0000

Of the four variables, only altitude was significantly correlated with femur length ($p = 0.023$), explaining 36% of the variation in femur length ($r^2 = 0.36$). In a stepwise multiple regression of altitude, latitude and temperature with log. femur length, altitude was entered first and temperature last. A very high percentage of variation (93%) was apparently accounted for by this combination of variables. However, this was probably a spurious result, arising from the high degree of correlation between temperature and latitude. Although latitude did not account for a significant proportion of the variation in femur length alone, when it followed altitude into the regression equation, these two variables together accounted for 51% of the variation ($p = 0.0201$); the slope of the altitude regression remained virtually unchanged when latitude was included in the regression. On the small amount of data available, latitude appears to be positively correlated with femur length, such that for a given altitude, specimens of *M. morio* are longer-legged at higher latitudes. As a consequence of this, although altitude and latitude are both negatively correlated with temperature, it is not possible to explain femur length variation entirely in terms of temperature over a very large geographical area. Further investigation is therefore necessary before this problem can be elucidated.

However, the following regression equation may be used to predict (with a limited degree of accuracy), the femur length (y) of any female specimen of *M. morio*, given the altitude and latitude coordinates of the locality from which it was collected:

$$\log_{10} y = -0.0001894 \text{ altitude} + 0.005285 \text{ latitude} + 0.2517$$

This simple regression accounts for half of the variation ($r^2 = 0.51$) in femur length. For greater accuracy of estimation, the model requires considerable refinement. Further independent variables on which femur length is dependent and more analyses are needed, before a greater amount of variation can be explained, and the effect of latitude fully accounted for.

CHAPTER SIX

OVERWINTERING STUDIES ON *MITOPUS MORIO*

6.1 Introduction

Mitopus morio overwinters in the egg stage (Todd 1949). Eggs are laid during the autumn (September and October) after which the adults die, the eggs remaining in diapause through the winter months and hatching during the following spring. The diapause mechanism prevents untimely hatching of the earliest-laid eggs in the event of a mild autumn; thus nymphs, which may be unable to survive the winter, do not emerge too early.

Diapause is a widespread form of dormancy amongst arthropods, allowing synchrony of the life cycle with favourable environmental conditions, and enhancing survival during unfavourable circumstances by preserving the species in a resistant stage (Andrewartha 1952, Lees 1955). It is a state of developmental arrest which may occur at any stage in the life cycle; it is largely a physiological rather than morphological condition. During diapause, development does not respond immediately to any ordinary amelioration of the external environment; unlike quiescence which is a response to currently unfavourable conditions, resuming as soon as these conditions improve. There is a wealth of literature concerning insect diapause, and the following generalisations have been made (Tauber and Tauber 1976): for most insects, photoperiod and temperature are the major diapause-maintaining environmental factors. Photoperiod changes in the environment are invariable and predictable (season to season) and allow the state of diapause to be entered before unfavourable conditions arise. Frequently, as in *Wyeomyia smithii* (Coq.), short daylength induces diapause (Tauber and

Tauber 1976); this also occurs in the fruit tree red spider mite *Metatetranychus ulmi* (Koch) (Lees 1953a). More rarely, diapause is induced by long daylength, as in *Bombyx mori* L. (Kogure, in Lees 1955). In most arthropods, temperature is influential in controlling the onset of diapause; for example, in *Metatetranychus ulmi* high temperatures avert diapause, whilst low temperatures induce it.

Diapause is a dynamic state; as the season progresses, diapause depth or intensity decreases and the insect's response to diapause-maintaining factors diminishes. Few species have been known to require a specific stimulus to end diapause, although diapause has often, in the past, been regarded as a state of inhibited development which must be "broken" by the stimulus of cold. In most species with an "overwintering diapause", diapause has ended by mid-winter rather than by spring (Tauber and Tauber 1976). Andrewartha (1952) suggests that the events preceding the resumption of growth can be looked upon as a gradual process which is induced (for example) by temperature in a similar way to morphogenesis. Different temperatures may be optimal for different stages of diapause development. For example, in some species the final stages can be completed at higher temperatures than the first.

Diapause in arthropods other than insects has been much less studied, apart from the acarine *Metatetranychus ulmi* (Lees 1953a and b). It was shown for the harvestman *Opilio parietinus* Deg. that a period of chilling (-6°C for one week) was required before eggs would continue their development (Holm 1947). *Phalangium opilio* L. has also been mentioned as a harvestman which lays eggs that possess an egg diapause (Todd 1949, Bennett, unpublished Ph.D. thesis, University of Leicester). It seems likely that most harvestmen which lay eggs in late summer and early autumn, and which overwinter as eggs, will possess an egg diapause mechanism to prevent premature hatching of nymphs in autumn.

6.2 Preliminary investigations

Preliminary investigations into egg development and hatching, of a qualitative nature, were made in the autumn of 1979 and spring of 1980. Adult pairs of *M. morio* were placed in breeding tanks kept on a long day photoperiod (16 hours light) at a constant temperature of 15°C during August, September and October 1979 until eggs had been laid.

Guental (1944a) found that female *Phalangium opilio* would lay eggs into moist soil lining their containers; but it was then necessary to sift through the soil to find the eggs. Later, Klee and Butcher (1968) found that female *Phalangium opilio* would lay eggs into holes punched into damp blocks of styrofoam. During the present investigation, small blocks of florist's "Oasis" (approximately 18 x 2 x 2cm) with punched holes of 0.2cm diameter and 3cm long, were put into the breeding tanks. The blocks were kept moist and were readily accepted as oviposition sites by the female *M. morio*. The eggs were left in the moist blocks at 15°C until 5 December 1979, when they were transferred to a 5°C constant temperature room.

Eggs may be examined under a dissecting microscope by dropping them into immersion oil (Holm 1947). This renders the external membrane transparent, and makes examination of the egg easier. Eggs kept in oil tend to shrink unless they are replaced on a damp substrate fairly quickly after examination. Eggs examined on 27 January 1980 were all well advanced in their development, with the pigmented ocularia and legs clearly visible. This is illustrated in Figure 6.1. However, in the field, eggs do not hatch until the following spring (Phillipson 1959).

Different egg batches were brought to laboratory temperatures (16° - 20°C) at intervals between January and April 1980, in an attempt to hasten their hatching. Details of ten batches are presented in Table 6.1. Results are summarised in Figure 6.2.

Figure 6.1 : The appearance of eggs of *Mitopus morio* just prior to hatching

a. Anterior oblique view

b. Anterior view

c. Dorsal view

d. Ventral view

Key to symbols:

CH	chelicera
CL	claw
E	eye
ET	egg tooth
OC	ocularium
OP	opisthomal segments
PR	prosomal segments
WL	walking leg

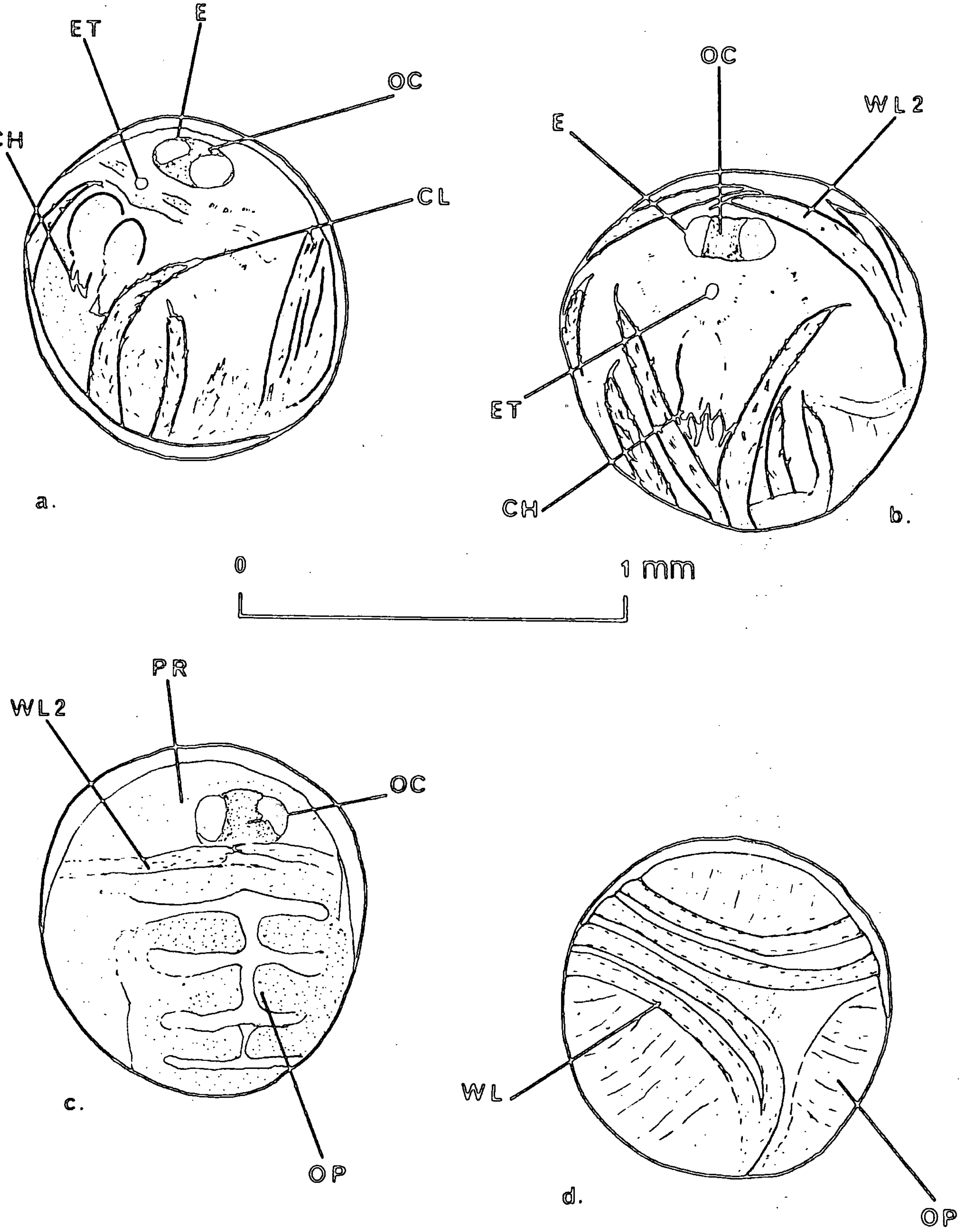

ET
E
OC
CH
CL
a.
OC
E
WL 2
ET
CH
b.
0
1 mm
PR
WL 2
OC
OP
c.
WL
OP
d.

Table 6.1 Dates of transference of eggs of *Mitopus morio* from constant temperature rooms to laboratory temperatures (16°C - 20°C); and hatching dates of different egg batches in 1979/1980. Preliminary results were of a qualitative nature; quantitative data are not available. Results have been summarised in Figure 6.2.

Date	Batch 1	Batch 2	Batch 3	Batch 4
Dec 5	All egg batches from 15°C to 5°C			
Jan 14	From 5°C to 1°C	From 5°C to 1°C	From 5°C to 1°C	
Jan 22	From 1°C to 8°C			
Jan 27	All egg batches examined (1°C, 5°C, 8°C). Dark pigmented ocularia visible			
Jan 30	From 8°C to lab.*	From 1°C to lab.**		
Feb 5	First eggs hatch; hatching commencing after 6 days at lab. temperature	First eggs hatch; hatching commencing after 6 days at lab. temperature		
Mar 4			From 1°C to lab. +	From 5°C to lab. ++
Mar 10			80% eggs hatch. Hatching commencing after 6 days at lab. temperature	80% eggs hatch. Hatching commencing after 6 days at lab. temperature

* Batch 1 had been at 5°C for 33 days, 1°C for 8 days and 8°C for 9 days.

** Batch 2 had been at 5°C for 33 days and 1°C for 17 days

\+ Batch 3 had been at 1°C for 50 days

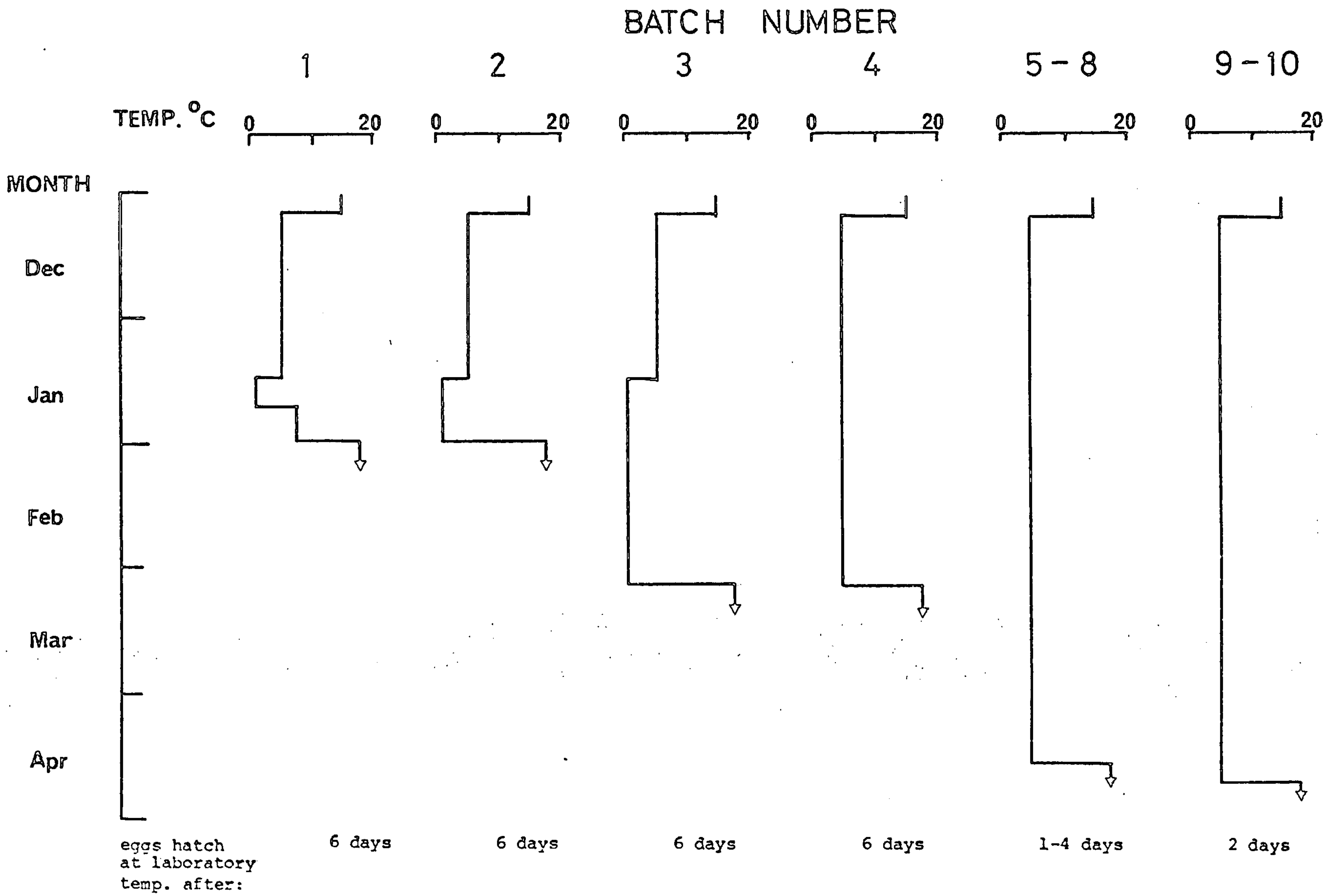
++ Batch 4 had been at 5°C for 50 days.

/continued.........

Table 6.1 continued..........

Date	Batches 5 - 8	Batches 9 - 10
Dec 5	All batches from 15°C to 5°C	
Jan 27	All egg batches examined.	Dark pigmented ocularia visible
Apr 16	From 5°C to lab. temperature	
Apr 17	First hatchings from batch 5	
Apr 19	First hatchings from batches 6 and 7	
Apr 20	First hatchings from batch 8; hatching commencing after 1 - 4 days at lab. temperature	From 5°C to lab. temperatures
Apr 21	Last eggs to hatch from batches 5 - 8	
Apr 22		First eggs to hatch from batches 9 and 10; hatching commencing after 2 days at lab. temperature
Apr 27		Last eggs to hatch from batches 9 and 10.

Figure 6.2 : A summary of dates of transference of eggs of *Mitopus morio* from constant temperature rooms to laboratory temperatures (16°C - 20°C) in 1979. Data have been taken from Table 6.1.


BATCH NUMBER
1
2
3
4
5 - 8
9 - 10
TEMP. °C
0
20
MONTH
Dec
Jan
Feb
Mar
Apr
eggs hatch at laboratory temp. after:
6 days
6 days
6 days
6 days
1-4 days
2 days

Eggs were removed from their "Oasis" blocks and initially placed on a double layer of damp filter paper over water (Guental 1944b). This method led to rapid growth of mould on the eggs and an improved method was used thereafter, placing the eggs in petri dishes filled with dampened Plaster of Paris.

The results obtained from egg batches 1 to 10 presented in Table 6.1 and summarised in Figure 6.2 indicate that eggs in batches 1 to 4 were no longer in diapause at the end of January, since, after a short incubation period at laboratory temperatures (six days), post-diapause development was completed and the eggs hatched. It is also apparent from these results that the small temperature changes experienced by batches 1 to 3 prior to transference to laboratory temperatures had no effect on the duration of the time lapse before eggs hatched. For batches 1 to 4, this lapse was of six days. Eggs only developed to hatching after receiving a large temperature increase. Hatching within an egg batch was synchronous, most eggs hatching within 48 hours (of each other). Presumably, in the field, post-diapause development is prevented until spring by the low ambient temperatures. The results in Table 6.1 also indicate that batches of eggs left at 5°C until April (batches 5 to 10) and then brought to laboratory temperatures hatched synchronously after a shorter period (one to four days) than those brought into the laboratory three months earlier. This indicates that some post-diapause development must have occurred in these eggs at 5°C between the beginning of March and April.

6.3 Experiment to examine the egg diapause of *Mitopus morio* and *M. ericaeus*

6.3.1 Introduction

As a result of the preliminary investigations in the autumn and winter of 1979/1980, the following experiment was designed to examine the diapause mechanism in *M. morio* and *M. ericaeus* during the autumn and winter of 1980/1981. The 1979 results indicated that eggs of *M. morio* respond to chilling by coming out of diapause and hatching synchronously after experiencing the large temperature increase on being returned to laboratory temperatures; this happened at about two months earlier than hatching occurs in the field. The following experiment, set up in the autumn of 1980, was designed to examine the optimum chilling temperature and length of the chilling period required for diapause to be completed in eggs of *M. morio* and *M. ericaeus*.

6.3.2 Method

Eggs were laid in the laboratory during September and October 1980 by females of *M. morio* collected from the 76m, 411m and 476m sites and by *M. ericaeus* from 411m, 476m and 549m. The eggs were maintained on a constant longday photoperiod (16 hours light) at 15°C in blocks of damp "Oasis" until the beginning of November. Samples of eggs examined at this time showed no visible sign of development (ocularia or legs). Each egg batch (comprising of a variable number of eggs) was subdivided, and each sub-batch was placed in a different treatment. The larger egg batches could be divided into ten sub-batches and exposed to all ten regimes, whilst smaller batches were subjected to fewer regimes. Treatments thus had differing numbers of replicates. There were nine different treatments: eggs were placed at one of three different temperatures (1°C, 5°C and 10°C), for one of three different time intervals (one day, one week or one month). They were then returned to 15°C and examined for further development up to hatching. Control batches were maintained at 15°C throughout the experiment.

6.3.3 Results

No data are available for the treatments of 5°C for one day since these egg batches became infected by fungus.

Egg batches were found to develop slowly under all regimes, including the controls at a constant temperature of 15°C. Hatching within all these 1980 egg batches was asynchronous, unlike hatching in the previous year. The time interval between the first and last egg hatching in a batch at any particular treatment was often in the order of several (12 to 15) weeks.

The data presented in Table 6.2 are for *M. morio* and show the mean dates on which the first egg hatched from batches at eight different treatments and one control; and the dates by which 50% of the total hatchings (median date) had occurred for each regime. Table 6.3 gives the hatching success of the *M. morio* egg batches at different treatments over the total period of the study (until the final egg had hatched). The corresponding data for *M. ericaeus* are given in Table 6.4. Hatching success has been expressed as the percentage number of eggs in each treatment which hatched of the total number of eggs subjected to that treatment.

The mean dates on which the first *M. morio* eggs hatched are not significantly different between treatments, or from the control at 15°C. For eggs of *M. ericaeus*, the mean date on which the first egg hatched from the batches at 5°C for one month was significantly earlier ($p < 0.005$)

Table 6.2 Hatching dates of eggs of *Mitopus morio* in 1980. The mean dates ± one standard deviation (in days) on which the first egg hatched at one of eight treatments (three different temperatures for one of three different time intervals) and one control at 15°C are given. The median date, or date by which 50% of the total number of eggs which hatched during the experiment had hatched is also given. (n) = number of batches.

	Treatment								Control at
	One Day		One Week			One Month			
	1°C	10°C	1°C	5°C	10°C	1°C	5°C	10°C	15°C
Total no. of eggs	86	76	192	182	88	183	192	86	389
Date of first egg hatching (mean of (n) replicates)	14 Feb ±19 (7)	19 Feb ±18 (6)	27 Feb ±18 (14)	10 Feb ±20 (15)	23 Feb ±22 (8)	26 Feb ±20 (15)	11 Feb ±13 (15)	5 Feb ±19 (8)	7 Feb ±25 (11)
Median date of hatching	15 Mar	11 Mar	17 Mar	7 Mar	11 Mar	7 Mar	5 Mar	19 Feb	11 Mar

Table 6.3 Hatching success of eggs of *Mitopus morio* subjected to one of three different temperature regimes (1°C, 5°C, 10°C) for one of three different time intervals (one day, one week, one month), after which they were returned to 15°C. Control egg batches were maintained at 15°C throughout the experiment. Hatching success has been expressed as the percentage number of eggs in each treatment which hatched of the total number of eggs subjected to that treatment, ± one standard error.

	Treatment								Control at
	One Day		One Week			One Month			
	1°C	10°C	1°C	5°C	10°C	1°C	5°C	10°C	15°C
Total no. of eggs	86	76	192	182	88	183	192	86	389
Percentage hatched	45	49	29	41	43	45	59	50	12
	± 5	± 6	± 3	± 7	± 5	± 4	± 4	± 5	± 2

Table 6.4 Hatching success of eggs of *Mitopus ericaeus* subjected to one of two different temperature regimes (1°C, 5°C) for one of two different time intervals (one week, one month), after which they were returned to 15°C. Control egg batches were maintained at 15°C throughout the experiment. The mean dates ± one standard deviation (days) on which the first egg hatched at each treatment and the control are given. The date by which 50% of the total number of eggs at each regime which hatched during the experiment had hatched (median date) is also given. Hatching success has been expressed as the percentage number of eggs in each treatment which hatched of the total number of eggs subjected to that treatment, ± one standard error. (n) = number of batches.

	Treatment				Control at
	One Week		One Month		
	1°C	5°C	1°C	5°C	15°C
Total no. of eggs	42	42	42	42	22
Date of first egg hatching	28 Feb	27 Feb	13 Feb	30 Jan	25 Feb
(Mean of (n) replicates)	± 10	± 10	± 11	± 10	
	(3)	(3)	(3)	(3)	(1)
Median date of hatching	11 Mar	25 Mar	3 Mar	9 Mar	11 Mar
Percentage hatched	17	67	55	60	19
	± 6	± 7	± 8	± 8	± 8

than for those hatching from both the treatments at 1°C and 5°C for one week. It is of no value to calculate the mean date on which eggs in any given treatment hatched, because of the broad time span over which hatching occurred; there was no modal peak of hatching at any treatment. The median dates of hatching seem to be earlier in the treatments where the temperature was lowered for one month, for eggs of both *M. morio* and *M. ericaeus*. This is not a significant difference, however, since the standard errors associated with each median date are very large, due to the asynchrony of hatching. Further investigations may show that eggs which have had their ambient temperature lowered for a longer period may hatch significantly earlier than eggs which have been exposed to lowered temperatures for only a short duration.

The percentage of eggs hatching from individual batches at different treatments has been tested to examine the variation of hatching success within and between treatments. The data set for *M. morio* were transformed using the arcsine transformation and tested by a two-way analysis of variance on the proportion of eggs hatching from each treatment. Two anovars were performed: the first on the batches from the eight treatments and the control batches; and the second on the treatment batches alone. The anovar tables have been constructed in Tables 6.5 and 6.6.

Table 6.5 The results of an analysis of variance test on the proportion of eggs of *Mitopus morio* hatching from the eight different experimental treatments and one control regime given in Table 6.2.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Squares	Variance	p
Batch	2.621	14	0.187	2.53	N.S.
Treatment (after batch)	2.646	8	0.331	4.47	< 0.01
Residual	5.923	80	0.074		
Total	11.190	102			

Table 6.6 The results of an analysis of variance test on the proportion of eggs of *Mitopus morio* hatching from the eight different experimental treatments given in Table 6.2 (Control batches excluded.)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Squares	Variance Ratio	p
Batch	2.997	14	0.214	1.466	N.S.
Treatment (after batch)	1.022	7	0.146	2.281	<0.05
Residual	4.335	68	0.064		
Total	8.354	89			

The values given for the treatment sum of squares are those calculated after the batch effect has been accounted for. The results show that there was no significant variation between batches. However, there was a significant variation between treatments in an analysis of variance both including ($p< 0.01$), and excluding ($p < 0.05$) the control egg batches. From this, it may be postulated that those treatments at which the highest percentage of eggs hatched had most effect; that is, eggs left at a lowered temperature for one month had the greatest hatching success.

6.4 Discussion

The entire life cycles of *M. morio* and *M. ericaeus* from first nymphs to adults may be completed in four months in the field. It may thus be assumed that eggs of *M. morio* and *M. ericaeus* were in diapause after being laid, since they did not hatch for at least four months even at laboratory temperatures (15°C).

Whilst in the preliminary investigation in 1979 eggs hatched synchronously after cold treatment for two months (5 December to 30 January), hatching was asynchronous in the following year. These results indicate that none of the time periods used in the 1980 experiments were of sufficient duration to allow completion of diapause development in all the eggs; or that the chilling period was given at a time when the eggs were not susceptible to cold treatment. Eggs were chilled for two months in 1979, whereas the maximum duration of any cold treatment was one month in 1980, and eggs were chilled one month earlier than in the previous year. The results of the diapause experiment described indicate that eggs left at low temperatures (1°C and 5°C) for a month had a greater hatching success and perhaps hatched earlier than those left at the same temperature for less time, or at higher temperatures. Further experiments are required before more conclusive statements can be made. It may be that diapausing eggs of *M. morio* and *M. ericaeus* are similar to diapausing eggs of *Bombyx mori* which are only responsive to the effects of temperature and photoperiod quite late on in embryogenesis (Lees 1955).

It is generally stated that development stops when diapause begins. Later, certain environmental factors cause this inhibition of development to be inactivated, thereby ending diapause. However, this course of events is not always strictly followed. In some eggs which enter diapause at an early stage of embryogenesis, the arrest of growth is not absolute: for example, eggs of *Austroicetes cruciata* Sauss. when exposed to moderate temperatures continue to develop slowly, reaching anatrepsis in about two months (Andrewartha 1943).

The mechanism of diapause in eggs of *M. morio* appears to be similar. Egg batches in the laboratory which are left at 15°C continue their development at a slow rate, and the eggs eventually hatch asynchronously, the time span over which hatching occurs being the result of the variation of individual eggs in the time taken for the completion of embryonic development. If eggs are put to 5°C for a certain length of time, they will all eventually reach the same stage of development, but initially, unless the temperature is raised, they will remain in quiescence. If they are now brought back to 15°C, the large temperature change triggers synchronous hatching. However, if left for sufficiently long at 5°C (four months) hatching will eventually occur, regardless of the temperature. The duration of the time interval at 5°C must be sufficiently long for all the eggs to reach the same stage of development for hatching to be synchronous when the temperature is raised again. From the synchrony of hatching in 1979, it may be concluded that the duration at 5°C must be a minimum of two months. Less than this results in asynchronous hatching. There may also be a stage which is more sensitive to cold treatment, since eggs were brought to 5°C one month earlier in 1980 when hatching was asynchronous, than in 1979 when hatching was synchronous.

In the field, eggs would continue to develop slowly during the autumn at all temperatures at or above 5°C. At a certain stage in their development, cooler temperatures (5°C or less) bring about a "traffic light" effect in the egg batches: the low ambient temperatures of winter allow eggs to develop up to a certain stage, but prevent completion to hatching. Eggs are held in quiescence. Although eggs are capable of eventually hatching at low temperatures of about 5°C, in the field, the temperature rises in the spring and results in synchronous hatching of eggs. This usually happens before low temperature hatching would have occurred.

The same mechanisms seem to apply to diapausing eggs of *M. ericaeus*.

CHAPTER SEVEN

GENERAL DISCUSSION

> 'The geographic variation of the species is the inevitable consequence of the geographic variation of the environment.'
>
> (Mayr 1963)

A species is defined as a group of actually or potentially interbreeding populations which are reproductively isolated from other such groups (Mayr *loc. cit.*). Current taxonomic theory is flexible in its recognition of a multidimensional concept of a species, which allows for character variation over large geographical areas and the change in these characters as populations adapt to their environments. Practical taxonomy, on the other hand, has tended to remain at a more typological level (International Code of Zoological Nomenclature 1964), at which variations are sometimes still regarded as 'imperfections' deviating from the ideal 'type'. Even modern numerical taxonomy is a fundamentally typological scheme (Sokal 1962), although it has the advantage of employing a large number of characters in an attempt at an objective assessment of affinities between taxa.

Huxley (1939) pointed out the lack of a recognised terminology for geographical or ecological gradients in species characteristics, and introduced the concept of clines; he believed that where inter-group gradation existed, simply naming and describing the separate groups did nothing to bring out the gradation in their characters. Yet since this time, practical taxonomy has not evolved a term of classification to deal with polytypic species such as *Mitopus morio* which display their wide geographic variation in a graded way, and clines have no formal nomenclatural recognition. Hence there still remains a proliferation of references to subspecies and varieties of species, where frequently the species in question varies in a continuous rather than a discreet way. Another example occurs in the harvestman *Leiobunum politum* Weed. The type specimen of this species was described from Illinois (Weed 1889). Later, Weed (1893) described a subspecies *L. politum magnum* Weed from Mississippi, which differed from *L. politum politum* chiefly in its leg length. Recently, McGhee (1977) showed that the two subspecies could be identified along different parts of a cline in leg length, although other body parts did not follow the same variation and clinal characteristics displayed by leg length. Stanley *et al.* (1981) mention the problem of the taxonomy of the herring gull, *Larus argentatus* Pont., which exhibits a north - south cline through Scandinavia in its wing length, bill size, body weight and mantle colour. Gulls from northern Norway are the largest and darkest mantled, but all Norwegian herring gulls are classified as *L. argentatus argentatus*, although there are large differences between northern and southern specimens (Barth 1968). Barth (1966, 1968) also showed that the cline in mantle colour extends through Norway, Sweden and Denmark to the Netherlands. However, the smaller and paler Dutch herring gulls at the southern end of the cline are similar to gulls from Britain, which are classified as *L. argentatus argenteus* (Barth 1968). The two cline extremes are described as separate subspecies. Mayr *et al.* (1953) deal with the naming of subspecies even when they are known to be clinal: 'if a new species is composed of populations which, together with populations of another subspecies form a cline, the type locality should be placed as near as possible to that end of the character gradient which is most distant from the other subspecies.' Problems then arise when attempting to classify specimens from intermediate localities, such as herring gulls from Denmark in the preceding example. There is a need for a general revision of accepted taxonomic principles. Clines apply to characters and not to populations. A population can belong to only one subspecies, but to several clines. Sibley (1954) suggested that in order to develop clinal terminology it was not necessary to eliminate the trinomial from taxonomic usage. The description of a cline should be an addition to the present system, rather than a substitute. To describe *Mitopus morio* as a single species might obscure the nature of its great variability; even the two extremes of a relatively short altitudinal cline are statistically distinct and easily separable in terms of size. A new approach is required, but population analysis below the species level (infraspecific variation) is perhaps too complex to be bound by formal taxonomic and nomenclatural rules. Each species is unique in its requirements and should be treated by whatever methods seem best suited to it.

Although the adaptive significance of a cline may not be obvious, and not all phenotypic expressions of geographic variation are necessarily adaptive, ecotypic adaptation, by selection of the most suited phenotype must surely be a central evolutionary force, assuming that the phenotype is the manifestation of genotypic variation and not a product of its environment. Non-genetic variation can adapt the individual, but it is genetic variation on which natural selection may act and which adapts a population. The phenotype is a compromise of a multitude of selection pressures to which an organism is exposed (Mayr *et al*. 1953).

Similar adaptations shown by widespread species which live in similar conditions are often expressed in terms of "ecological rules". An example is Bergmann's Rule, which states that 'the smaller-sized geographic races of a homiothermic species are found in the warmer parts of the range, the larger-sized races in the cooler districts.'

Ray (1960) showed that parallel adaptations existed amongst some species of poikilotherms. He emphasized that his examples were simple observations made intraspecifically, correlating size and form with temperature. However, such generalisations cannot be universally applied, because temperature is only one of several factors influencing size in animal species. Martof and Humphries (1959) showed, for *Rana sylvatica* Le Conte, that there seems to be a selective value in maturing in a shorter time in the shorter available growing season. *R. sylvatica* achieves this by maturing at a smaller size in more northerly regions. The same response has been demonstrated in the field cricket *Teleogryllus emma* (Ohmachi et Matsuura) in Japan (Masaki 1967). This is a univoltine species, with an obligatory egg diapause. It shows an apparently adaptive response to the reduced growing season experienced at more northerly latitudes: the duration of the nymphal developmental stages is proportional to the duration of the growing season in each locality. Individuals that mature faster become smaller adults, which are less fecund (Masaki *loc. cit.*); but these individuals are selected for, since crickets which mature too late perish by frost, leaving no eggs to overwinter. *Mitopus morio* also appears to be univoltine throughout its range, and matures at a smaller size at higher altitudes. It has been postulated in this thesis that this is the result of animals moulting after a fixed duration of time, regardless of the growth they have achieved (measurable in terms of femur length), in order to complete the life cycle in a single season. Only the final seventh instars (adults) are sexually mature, so that this development stage must be reached by the end of the growing season in order that progeny (as overwintering eggs) may be left for the next generation. Natural selection will act against those animals not reaching sexual maturity in one season, since they can leave no progeny.

The apparently temperature-related response reflected in the negative altitude relationship with femur length is not expressed in the variation shown by *M. morio* at high latitudes. At these latitudes, *M. morio* is longer-legged than expected, assuming that temperatures are generally cooler at higher latitudes. However, microenvironmental effects tend to obscure clines related to latitude (Ray 1960), since the long hours of summer insolation experienced at high latitudes result in high temperatures for the duration of a few weeks. This warm spring/summer period is the most relevant to a univoltine species, such as *M. morio* which develops and is active for only these four to five months of the year. The same explanation of high summer insolation may also account for the extremely long-legged specimens of *M. morio* (described in Chapter Five) from very high altitudes in Austria; these experience a continental climate.

Isolation, followed by the acquisition of isolating mechanisms, is necessary for speciation. Isolating mechanisms are biological properties of individuals that prevent interbreeding of populations which are actually or potentially sympatric (Mayr 1963). Thus, the widely separated ecogeographical variants manifested by some species may themselves become incipient species. For *M. morio*, the isolated island populations, such as those found on Iceland, have the greater opportunities for becoming an incipient species; rather than the two extremes of an altitude-linked cline, since by definition the cline represents a gradual and nearly continuous change of a character in a series of contiguous populations. The theory of geographic speciation (Mayr 1942) states that a new species develops when:

> 'a population which is geographically isolated from its parental species, acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers break down.'

Although most geographical isolates do not produce new species, most new species are produced by peripheral isolates (Mayr 1963).

The descriptions of new species of invertebrates are frequently still founded on the old systematic practice of describing general morphology, with the addition of some measurements (e.g. Luff 1972, Silhavy 1976). This method is based on a typological concept and has been shown for two species of chironomids to be inadequate (Heimbach 1978). Until 1978, the Baltic and Atlantic populations of the chironomid *Clunio balticus* Heimbach and *Cl. marinus* Hal. had both been classified as *Cl. marinus*, because no striking morphological differences could be found between them. Heimbach (*loc. cit.*) showed, however, that the two species were reproductively isolated in the field by their diel emergence time. Interbreeding between the two species could be induced in the laboratory when the cultures had been phase-shifted, resulting in intermediates. In the field, interbreeding does not occur because of the separation in daily emergence time, and intermediates are not found. An appraisal of the morphological differences between species is, of course, an inherent part of taxonomic description, but they are not always definitive. Some species are easier to separate than others on a morphological basis. A greater credibility and assurance that any morphological variation observed is not, for example, simply a function of geographic variation, can be achieved by a parallel detailed analysis of distributional and ecological differences between the species in question. This practice has been recently used in vertebrate taxonomy (Macdonald 1981, Nilson and Andrén 1981), and in most cases has only served to emphasize the differences between species. This *ad hoc* approach to taxonomy for which there are no formal nomenclatural rules, should perhaps become more widespread. This technique has been used in this thesis to describe a new species of harvestman, *Mitopus ericaeus*, which shows striking morphological differences from *M. morio*, and also displays large differences in its ecology, particularly its phenology. The niche separation in size and development is necessary for the coexistence of these two species. Lack (1971) stated that many congeneric species of birds separated by feeding differed markedly from each other in the size of body or beak. Femur length and body weight ratios for *M. morio* and *M. ericaeus* were found to 1.8 and 1.4 respectively. However, for birds, the difference in beak length ratios of 1.2 to 1.4 suggested by Hutchinson (1959) as necessary to prevent competition are not always representative since beak adaptation is not the sole adaptation to a difference in feeding. For example, for birds this may involve a difference in the feeding position in the tree strata. Sympatric species of spiders (Robinson 1981) and gerrids (Heteroptera) (Spence 1981) have also been shown to avoid overlap by their differing preferences in the habitat architecture. Some habitat separation may occur between *M. ericaeus* and *M. morio*; it has been suggested that the larger, longer-legged *M. ericaeus* is unable to inhabit the denser, low vegetation strata accessible to *M. morio*, since for most of its life cycle, it is twice the size of *M. morio*. It may also be assumed that the size difference would enable different-sized prey to be exploited by the two species, *M. ericaeus* taking items too large to be handled by *M. morio*. Prey selection does not occur in *Mitopus*: harvestmen have been shown to be extreme generalist feeders. It has therefore not been possible in this study to carry out feeding experiments with *M. ericaeus* and *M. morio* to test for prey differences (size or species). However, it may be possible to develop immunological techniques for the preparation of sera from prey species for the analysis of gut contents. This has already been done to examine the predator species of some invertebrates (Dempster 1960, Davies 1969, Sunderland and Sutton 1980).

An analysis of the prey species of generalist feeders such as harvestmen would however involve the preparation of a very wide range of sera.

The habitat and food differences between *M. morio* and *M. ericaeus* are an adequate means of ecological isolation where the two are sympatric. A similar pattern of coexistence has been found for a spider guild (Turner and Polis 1979). Niche overlap values were calculated for the five species of spiders (three of which were congeneric) in the guild, using four resource dimensions (season, microhabitat, prey species, prey size). Where there was high overlap along one resource dimension, low overlap occurred along a complementary dimension. The phenologies of the members of the spider guild differed, and temporal separation of guild members was shown to be important in reducing niche overlap. There are future possibilities for a parallel study to be carried out to analyse more closely the resource partitioning between *M. ericaeus* and *M. morio*.

There are now many new techniques available to taxonomists, apart from the traditional formal rules of nomenclature. Recent advances have been made in the use of immunological techniques, and electrophoresis is available to systematists (Post and Uzzell 1981). There is scope for similar methods to be applied to *M. ericaeus* and to *M. morio* in different parts of its range, as well as to many other invertebrate species. The individual worker now has a wide choice of less formal procedures available for supplementing and augmenting taxonomic descriptions.

SUMMARY

1. Previous workers have suggested that the harvestman *Mitopus morio* has three forms in Britain, two from upland areas *(cinerascens* and *alpinus)*, and one from lowland regions *(morio)*.

2. *M. morio* has been studied over a large geographical area; specimens were collected from a wide range of altitude sites in northern Britain during 1979 to 1981 and samples from other parts of Europe have been examined.

3. The instars of *M. morio* have been separated by measurements of the second femur lengths. Polymodal frequency histograms of the lengths of the second femurs indicated that *M. morio* had seven instars from hatching until the final adult instar, in all parts of its range.

4. In many cases there were no significant between-year differences (1979/1980) in the lengths of the second femurs of instars of *M. morio* at individual sites.

5. The relationship between log. mean femur length and instar number is curvilinear for *M. morio*. Dyar's factors were greatest between instars one and two (1.75), and least between instars six and seven (1.41). The Dyar's factors between instars six and seven decreased from 1.48 to 1.31 with increasing altitude, over the range 76m to 549m.

6. The mean lengths of the second femurs of all instars of *M. morio* decreased progressively with increasing altitude; the upland *cinerascens* lying at the opposite extreme to the lowland *morio*. Altitude accounted for 96% of the variation in femur length. There was approximately a 10% decrease in the femur lengths of adults of both sexes with every 100m increase in altitude, over the range 76m to 549m in northern England in 1979 and 1980.

7. This altitude relationship was extended to include all additional specimens collected in northern England from 1977 to 1981. Altitude accounted for 84% of the femur length variation over the five year period. There was an 8% decrease in femur length of female *M. morio* per 100m increase in altitude.

8. The altitudinal cline exhibited by *M. morio* in northern England was also shown by specimens collected on Cairn Gorm, Inverness-shire

and Great Dun Fell, Cumbria. Femur length decreased by 6% on Cairn Gorm and 7% on Dun Fell for a corresponding increase of 100m altitude. Specimens of both sexes were longer-legged in these two regions than those at similar altitudes at the main sites.

9. *M. morio* has sixteen pairs of chromosomes. No differences were observed in the chromosome complement of the upland and lowland forms.

10. Dry weights of male *M. morio* decreased by 6% per 100m increase in altitude, over the range 76m to 549m.

11. Pigmentation and spininess were very variable characters between specimens of *M. morio*. This variation was not related to altitude.

12. Corpus penis length decreased with increasing altitude, as a function of total body size. Penis shape did not vary with altitude.

13. Climatic data for Durham (102m) and Moor House (558m) averaged over 29 and 24 years respectively, showed that there was a lapse rate of 0.78°C per 100m altitude between these two sites.

14. The date on which a particular mean instar was reached was delayed at the higher altitudes. In 1980, the mean date of occurrence of the third instar in pitfall traps was 10 days later at 549m than at 260m. The difference in the dates of the mean instars between these sites decreased with increasing mean instar number.

15. The growth rate curves for 1979 were similar but later than those for 1980. Temperatures were lower, on average, in 1979 than in 1980.

16. The longer-legged specimens of *M. morio* from similar altitude sites on Cairn Gorm and Dun Fell compared with those from Moor House have been explained in terms of temperature. Altitude for altitude, Cairn Gorm and Dun Fell experience consistently warmer temperatures than Moor House.

17. Instars of *M. morio* kept at different temperatures in the laboratory may moult to longer-legged individuals at warmer temperatures than those at cooler temperatures.

18. Results of the duration of instars of *M. morio* at different temperatures in the laboratory are inconclusive but suggest that instar duration is less dependent on temperature than might be expected. It may be fixed for a given instar.

19. More females than males were trapped in pitfall traps at the beginning of the season; overall, a greater number of females were trapped in pitfalls, whilst more males were caught by hand. Females seem to be more active at ground level than males.

20. The upland form of *M. morio* previously referred to as *alpinus* has been shown to be a distinct British species. *Mitopus ericaeus* sp.n. is described.

21. *M. ericaeus* was only taken from upland sites above 250m in northern Britain. At all the sites where it was taken, it was found co-existing with *M. morio*, but was less abundant.

22. *M. ericaeus* was 44% larger by weight, more spiny and more darkly pigmented than *M. morio*. It hatched from eggs which were 46% larger by volume than those of *M. morio*, and was longer-legged at all instars. Adult female *M. ericaeus* were 69% longer-legged than *M. morio* females from the same site.

23. *M. ericaeus* did not display an altitude-linked size cline comparable to that shown by *M. morio*.

24. *M. ericaeus* and *M. morio* differed in their penis morphologies, both in the shape and the size of the penis.

25. *M. ericaeus* has 16 pairs of chromosomes.

26. On any particular date, *M. ericaeus* was always in a later instar than *M. morio* at the same site. Throughout their pre-adult development the two species were separated by one instar. The overlap in adults of the two species is decreased by the earlier maturation of *M. ericaeus* and shorter duration of the adult instar. Interbreeding does not occur.

27. Samples of *M. morio* from Pembrokeshire, St Kilda, central and northern Norway, Austria and Iceland have also been examined; *M. ericaeus* was not recorded from any of these samples.

28. The lengths of the second femurs of *M. morio* from these additional sites were very variable, but the ratio of female femur length to male femur length was constant regardless of locality; it was 1:1.

29. The lengths of the corpora penes of all the specimens of *M. morio* examined were correlated with the corresponding femur lengths, although penis length was less variable than femur length.

30. The shapes and proportions of the penes of males of *M. morio* from the additional sites were similar to those described for *M. morio* from the main northern England sites.

31. Multiple regression analyses have been implemented for specimens of *M. morio* from 13 localities using the variables: log. femur length of females, site altitude, mean temperature at that site (April to June), and site latitude. A regression equation has been calculated which explains 51% of log. femur length variation in terms of site altitude and latitude.

32. The egg diapause of *M. morio* and *M. ericaeus* has been studied. Preliminary investigations showed that batches of eggs laid in the autumn responded to chilling by coming out of diapause, and developed to hatching on being brought to laboratory temperatures, two to three months before hatching occurred in the field. Hatching within these egg batches was synchronous.

33. Later experiments were not conclusive, since both chilled egg batches and constant temperature control batches all developed to hatching, but asynchronously. The results suggest that the duration of the chilling periods in the later experiments were insufficient for eggs to have reached the same stage of development. It may also have been given at a time when the eggs were not responsive to cold treatment.

34. The results of this study have been discussed in relation to current taxonomic principles, with regard to clinal variation and sympatric species. A less formal approach to taxonomic classification is suggested.

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APPENDIX 1 : Additional sites sampled 1977 to 1979 (hand collections and pitfall traps)

	Altitude (m)	Site	Grid Reference
1.	274	*North Plantation	NZ 083455
2.	411	Waskerley	NZ 016447
3.	411	Waskerley	NZ 014446
4.	627	Kilhope	NY 800432
5.	625	Langdon Common	NY 863349
6.	674	Grass Common	NY 827357
7.	674	Grass Common	NY 825357
8.	533	Moor House	NY 755332
9.	561	Moor House	NY 756328
10.	549	Moor House	NY 764332
11.	551	Moor House	NY 765333
12.	427	Dun Fell	NY 697295
13.	518	Dun Fell	NY 702298
14.	579	Dun Fell	NY 708302
15.	625	*Dun Fell	NY 713307
16.	823	Dun Fell	NY 711319
17.	500	*Cow Green	NY 814302
18.	500	Cow Green	NY 814303
19.	518	Tailbridge	NY 810042
20.	518	Tailbridge	NY 811043
21.	335	Sunbiggin	NY 687090
22.	274	Sunbiggin	NY 680083
23.	336	Scar Close	SD 755779
24.	336	*Scar Close	SD 754780
25.	457	Golden Groves	SE 044945
26.	388	Apedale	SE 022943
27.	396	Apedale	SE 023944
28.	411	Rowantree Scar	SE 032932
29.	411	Rowantree Scar	SE 032932
30.	488	Beldon Bottom	SD 967940
31.	213	Tranmire	NZ 762117
32.	274	Kildale	NZ 620111
33.	240	Murk Mire	NZ 797025
34.	305	Yarlsey	NZ 750007
35.	259	Job Cross	NZ 692110
36.	427	Botton Cross	NZ 701017

* Sites at which *Mitopus morio* was trapped, but not *M. ericaeus*.

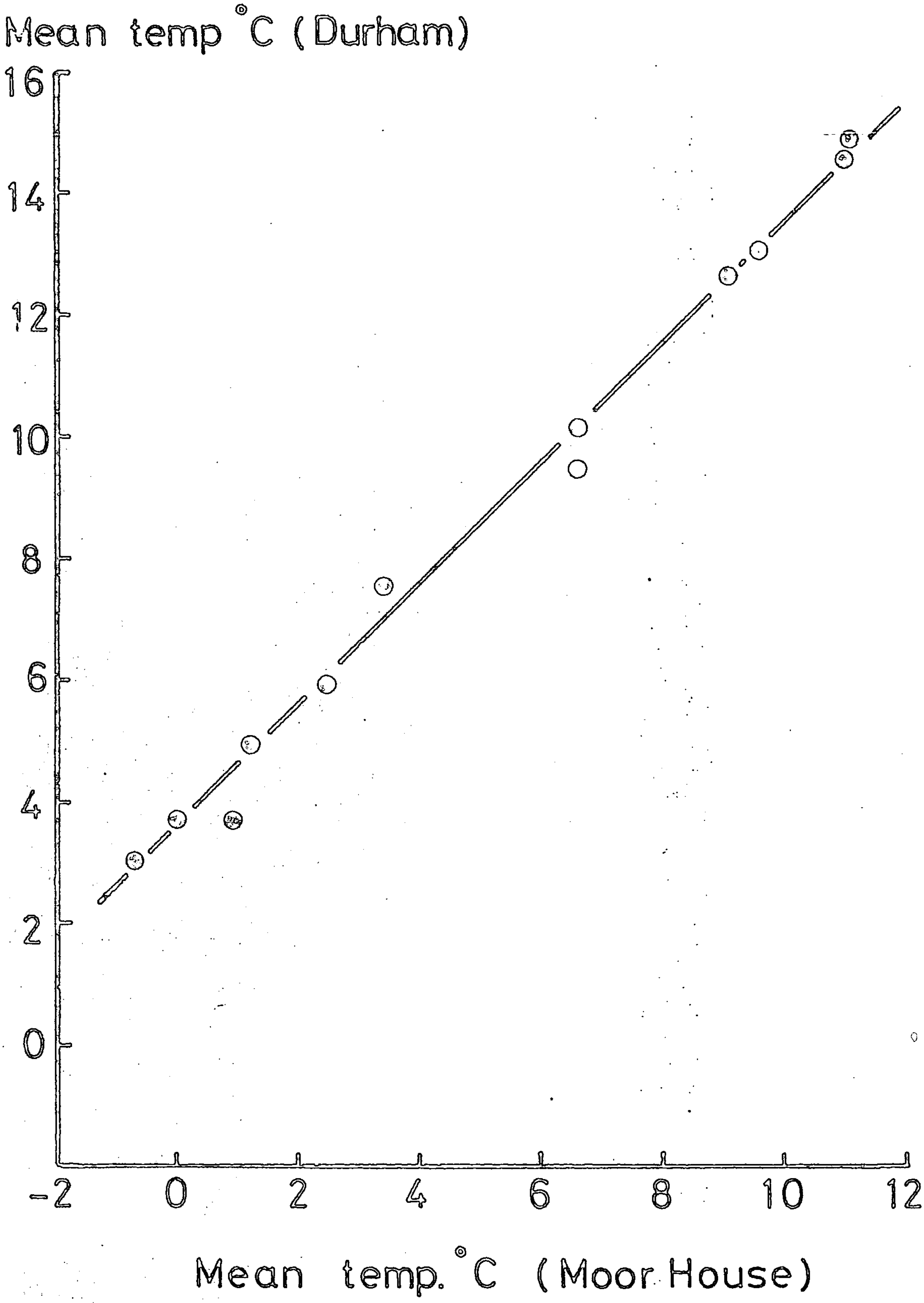
APPENDIX 2 : Mean monthly air temperatures (^{o}C) at Durham 102m plotted against mean monthly temperatures at Moor House 558m.

Durham temperatures have been averaged over 29 years (1936 - 1965); those for Moor House over 24 years (1953 - 1977).

The regression equation is given by:

$$y = 1.0032x + 3.542$$

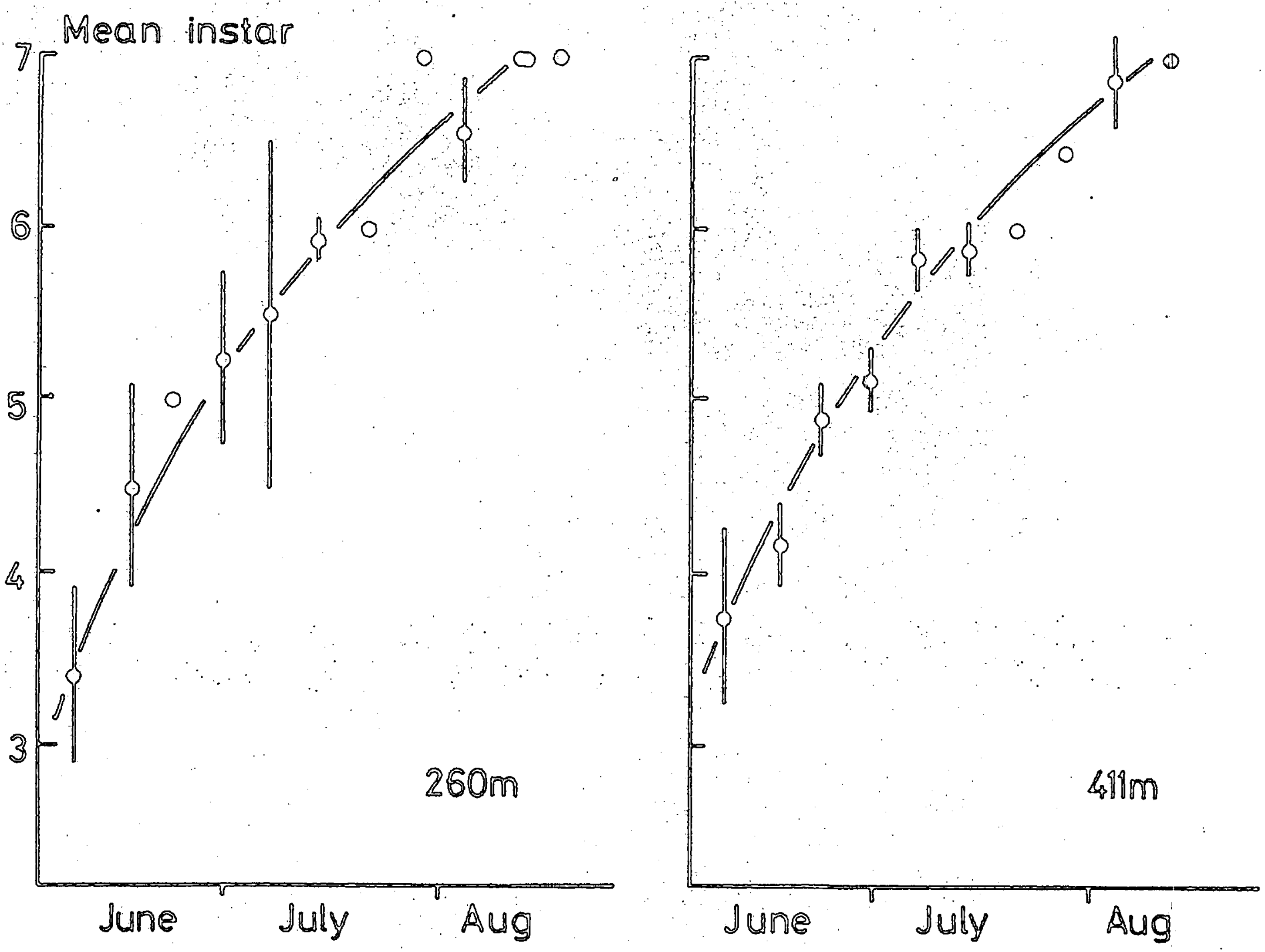
$n = 12$ $r = 0.996$ S.E. of slope = 0.0269 $p < 0.001$

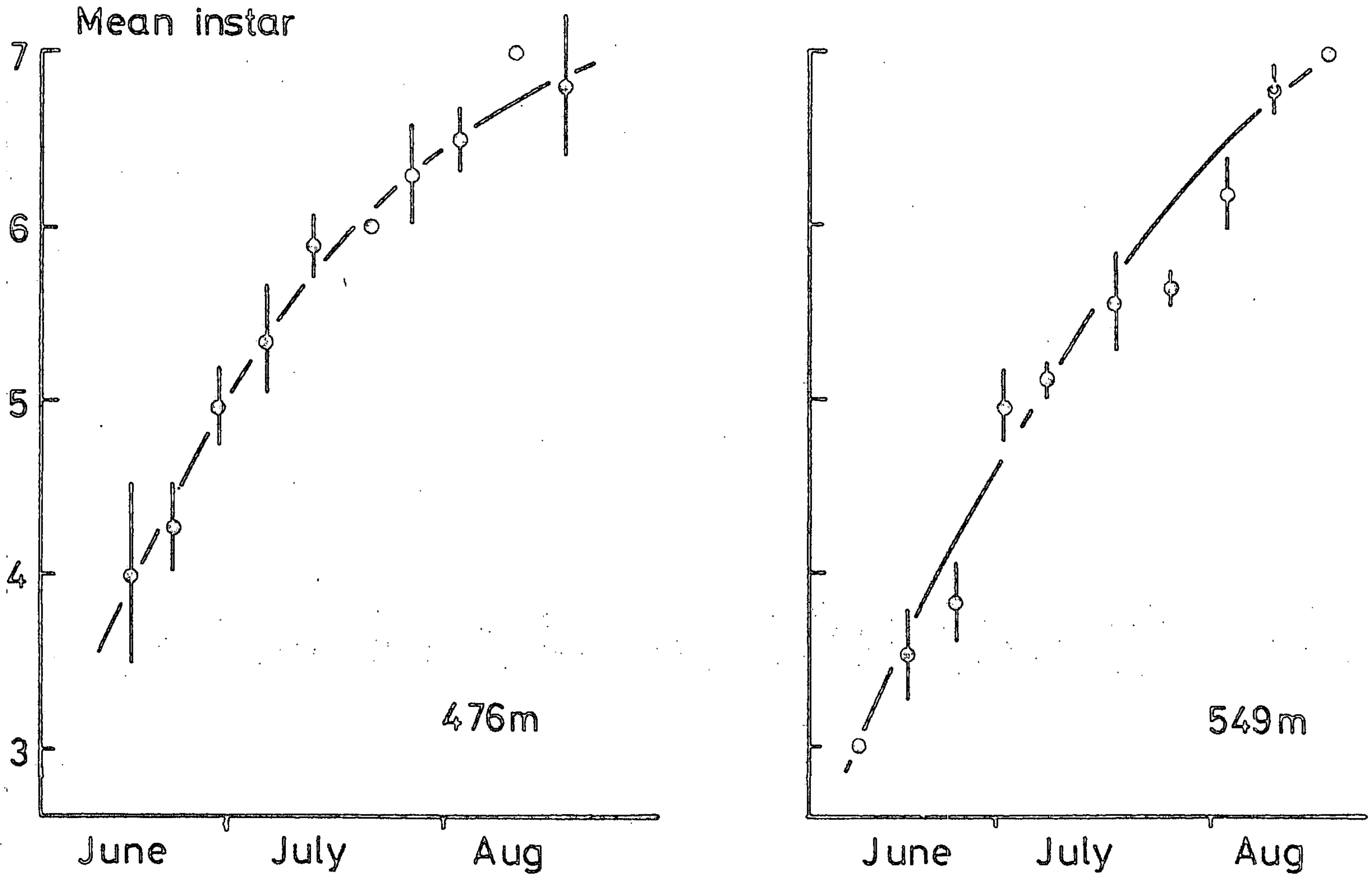

Mean temp °C (Durham)
16
14
12
10
8
6
4
2
0
-2
0
2
4
6
8
10
12
Mean temp. °C (Moor House)

APPENDIX 3 : Predicted mean monthly air temperatures (°C) at the seven main altitude sites, estimated from 29 and 24 year averages from Durham 102m and Moor House 558m respectively, and a temperature lapse rate of 0.78°C per 100m

Site (m)	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
76	3.95	3.25	5.15	7.75	10.35	13.40	15.10	14.80	12.90	9.70	6.15	3.90
137	3.48	2.78	4.68	7.28	9.88	12.93	14.63	14.33	12.43	9.23	5.68	3.43
152	3.36	2.66	4.56	7.16	9.76	12.81	14.51	14.21	12.31	9.11	5.56	3.31
260	2.52	1.82	3.72	6.32	8.92	11.97	13.67	13.37	11.47	8.27	4.72	2.47
411	1.34	0.64	2.54	5.14	7.74	10.79	12.49	12.19	10.29	7.09	3.54	1.29
476	0.83	0.13	2.03	4.63	7.23	10.28	11.98	11.68	9.78	6.58	3.03	0.78
549	0.26	-0.44	1.46	4.06	6.66	9.71	11.41	11.11	9.21	6.01	2.46	0.21

APPENDIX 4 : Mean instar composition of pitfall catches of *Mitopus morio* in 1979 plotted against mid-trap date ± two standard errors for Muggleswick 260m, 411m, 476m and Bog End 549m. Curves have been fitted by eye.


Mean instar
7
6
5
4
3
June
July
Aug
260m
June
July
Aug
411m


Mean instar
7
6
5
4
3
476m
June
July
Aug
549m
June
July
Aug

APPENDIX 5 : Sources of additional specimens of *Mitopus morio*: the following collectors are gratefully acknowledged:

Collector	Locality
Dr J.E.L. Butterfield and Dr J.C. Coulson	Iceland
Dr J. Gruber (Naturhistorisches Wien)	Austria
Dr P. Knights (via Dr J.E.L. Butterfield)	Pembrokeshire
Dr E. Østbye and Dr S. Hagvar (University of Oslo)	Norway (Finse)
Mr J. Richardson and Dr L. Davies	St Kilda
Dr S. Wanless and Dr N. Duncan	Norway (Andoya)

APPENDIX 6 : A list of the statistical symbols and abbreviations used in the text

χ^2	Chi-squared
c.v.	Coefficient of variation
n	Sample size
N.S.	Not significant
p	Probability
r	Correlation coefficient
t	Student's 't' statistic
S.D.	Standard deviation
S.E.	Standard error