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Species Diversity and Community Stability:
Cause or Effect?
A study using moorland spiders
and other invertebrates.

Daniel Keith Ellis

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A dissertation submitted in part fulfilment of the requirements for the degree of Master
of Science in Ecology by advanced course

Department of Biological Sciences
University of Durham
September, 1994



- 6 NOV 1995

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SUMMARY

- 1) Pitfall trapping was used to sample invertebrate communities on Monk's Moor, County Durham.
- 2) The effects of habitat and altitude upon communities of invertebrates, in particular spiders, were analysed using indices of alpha and beta diversity. The diversity indices were then compared to investigate any relationship between the diversity and stability of the communities.
- 3) Spider diversity was significantly higher in heather moorland than in pasture. This was thought to reflect greater spatial heterogeneity within the heather moorland. No relationship was found between spider diversity and altitude.
- 4) A significant relationship was established between the invertebrate community and both habitat and altitude. However, it was limitations of the statistical technique, rather than biological effects that caused the significant relationship.
- 5) The lack of a marked effect of altitude upon diversity prevented detailed analysis of the diversity - stability hypothesis.

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1.0 INTRODUCTION

The stability of communities is often assumed to vary in direct proportion to the diversity of species within them, because irregularities within a more complex system are more easily compensated for by minor adjustments elsewhere. This assumption appears to be supported by the fact that the most stable communities (tropical communities by comparison to polar ones, late successional communities by comparison to pioneer stages) tend to be those with greater species diversity. However, rather than stability being the result of increased diversity in these systems, it may be that high diversity is a consequence of inherent stability. These two conflicting views of the relationship between species diversity and community stability have yet to be resolved.

Moorland invertebrates provide a potentially useful model for an investigation of the relationship between diversity and stability because they show distinct changes with habitat and increasing altitude. Coulson and Butterfield (1986) clustered 42 peat and upland grassland sites in the north of England according to the similarities of their spider fauna. The sites divided into two major groups; i) sites where grasses or *Juncus squarrosus* were dominant and ii) sites where *Eriophorum vaginatum* and *Calluna vulgaris* were dominant. Stability of the invertebrate communities could be assessed by their response to disturbance, *i.e.* the contrast between a heather moorland fauna and rough pasture.

Diversity (complexity) of invertebrate faunas decreases with decreasing temperature. Throughout the year, the temperature is lower at higher altitudes (Coulson *et al* 1976; Grace and Unsworth 1988). In a study at Moor House (22km west of the field site) the average decrease in temperature was 0.5°C per 100m rise in altitude and the effect was evident throughout the year (Coulson 1988). The difference in the average temperature (2.4°C) between two sites at 370m and 847m but only 1km apart, was equivalent to that at sea level between Plymouth and Edinburgh, a distance of 1100km (Coulson *et al* 1976). The direct effects of temperature are probably the most important factor limiting the distribution of invertebrates in the uplands (Coulson 1988). The total number of arthropod species shows a modest decline with increasing altitude, but predatory taxa including Araneae, tend to be represented by significantly fewer species at higher altitudes (Coulson 1988).

Teesdale provides a particularly good location for investigating diversity and stability of moorland communities as diversity is known to change with altitude and disturbed and undisturbed sites can be found side by side across a range of altitudes.

1.1 Effect of taxonomic level on community diversity

Diversity and stability can be studied at a range of taxonomic levels. A comparison between taxa may then reveal a relationship between between species and order diversity. Significant positive correlations between the number of families and the number of species in a defined area have been found by Williams and Gaston (1994). If the richness distribution of higher taxa is predictive of the distribution of species richness, considerable time and costs could be saved as identification to species level would be unnecessary (Williams and Gaston 1994). Although the predictive value of this relationship is expected to decline at progressively higher taxonomic ranks (as the proportion of higher taxa becomes increasing widespread) the strength of the relationship between order and species diversity requires further investigation.

1.2 Study Aims

The objectives of this project were to conduct a pilot study to examine;

- i) the relationships among habitats, species diversity and community structure,
- ii) the relationships among altitude, species diversity and community structure,
- iii) the relationship between initial species diversity and response to disturbance.

The following sections provide the background to the stability - diversity debate and explain the techniques used to analyse the data.

1.3 Diversity - Stability hypothesis

Stability is a dynamic concept that refers to the ability of a ecosystem or community to return to its initial (assumed equilibrium) state after disturbances. A community is thought of as stable if the constituent populations show little fluctuation over a long period of time (Krebs, 1985).

Elton (1958) developed six arguments to show that increased diversity causes greater species population stability compared to a simpler community system. By the late 1960s it came to be accepted that fluctuations in numbers of individual species are greater in simpler communities than complex ones. This seemed intuitively correct as the number of interrelationships which might stabilise numbers of one species is increased in more diverse communities.

The process by which diversity may lead to stability was first proposed by MacArthur (1955). He stated that stability was a function of the number of links between species in a trophic web. The more trophic links between species (higher connectance) the more likely there are to be compensating mechanisms operating if one species became rare or abundant. If one species became rare, predators are assumed to prey on its competitors, enabling a chance for recovery. Conversely if one

species became competitively superior and therefore more abundant, predators would shift attention to this more available species and restore the balance.

However, more recent work suggests rather than stability being the result of increased diversity in these systems it appears diversity is a consequence of inherent stability. May (1976) found that as a mathematical generality "increasing complexity makes for dynamic fragility rather than robustness" May (1976) then states "...ecosystems will evolve to be as rich and complex as is compatible with the persistence of most populations. In a predictable environment the system need only cope with relatively small perturbations, and can therefore achieve this fragile complexity". Models by Pimm (1979) also describe the tendency for model communities to become less stable with increasing species number, because of a reduction in the size and stability of constituent populations of each species.

Watt (1968) explained simpler ecosystems had greater stability because their food webs had higher connectance (the number of actual interactions between pairs of species / total number of possible interactions between species) than complex communities. In a simple community, generalist feeders are most common allowing many connections between species on one trophic level and between other trophic levels. More complex communities have a higher proportion of specialist feeders and although there are more species interactions in total, connectance falls, leading to fragility.

1.4 Measurement of diversity and stability

The diversity versus stability debate is a central theme in ecology but the methods used to measure diversity and stability have also caused considerable debate. Diversity is hard to define because it combines two components, the variety and the relative abundance of species. How these two factors are incorporated into a measure of diversity is explained below. Stability also combines two components, constancy (a lack of change in some parameter of a community, such as species richness or taxonomic composition) and resilience (the ability of a community to continue functioning even though it may have changed its form). Diverse communities may thus be less able to maintain species composition or population sizes following perturbation (have lower constancy) but may be more able to continue functioning despite changes in composition (have greater resilience). However this remains largely speculative and few studies have compared the effects of habitat disturbance upon the structure of communities of differing initial diversities.

1.5 Species abundance models

Species abundance models developed from the observation that no community contained species that were all equally common. Instead, a few species are abundant, some are less common, while most are represented by only a few individuals and therefore described as rare. The degree of community organisation can be measured by studying the distribution of species abundance amongst the species present. The shape of a ranked species abundance plot indicates which model of species abundance should be applied to the data. Diversity is then compared to four main models; the geometric series, the logarithmic series, the log normal distribution and MacArthur's broken stick model. These models represent a progression ranging from the geometric series where the community is dominated by a few individuals and the majority are rare, through the log series and log normal distributions where species of intermediate abundance become more common to where all species are almost equally dominant in the broken stick model (Magurran 1988). The majority of communities studied by ecologists display a log normal pattern of species abundance. It is said to indicate a large, mature and varied natural community, which reflects the many processes at work in the communities ecology (May 1975). Although such mathematical descriptions may tell us little of the underlying biological reasons for the shape of the curve, they allow for objective comparisons between the curves of the different communities. As a species abundance distribution utilises all the information gathered in a community it is the most complete mathematical description of the data (Magurran 1988).

The log normal distribution was first applied to species abundance data by Preston (1948). Preston (1948) plotted species abundances on a logarithmic scale (base 2) and termed the resulting classes octaves. Each octave represented a doubling of the species abundance. When he converted the scale, relative abundance data took the form of a bell shaped normal distribution and because the X axis was expressed on a logarithmic scale, the distribution was called log normal (Krebs, 1989).

When a logarithmic conversion does not result in a typical symmetrical bell shaped curve of a log normal distribution it is difficult to decide whether a log normal or log series distribution is most appropriate. If the data to which the curve is fitted derived from a finite sample, the left hand side of the curve (representing the rarest and hence unsampled species) are obscured. The truncation point is known as the veil line and the smaller the sample the further the veil line moves right across the curve. For most data sets, only the right hand portion of the curve is visible as only in immense data collections covering wide biogeographic area is the full curve apparent (Magurran 1988).

1.6 Analysis of alpha diversity

Species richness is the simplest measure of alpha (within site) diversity. It is a straightforward count of the number of species in a defined sampling unit. Species richness provide an instant comprehensible expression of diversity and avoid many of the problems which may be encountered when models and indices are used (Magurran 1988). In a typical sample however, the majority of species are rare, represented by only a few individuals, with only a few species occurring abundantly. Such heterogeneity of abundance would be ignored by simple counts of species richness. To describe diversity adequately therefore it is usually considered necessary for both species richness and the relative evenness of abundance of the different species to be considered together. Five measures of alpha diversity were used in the analysis and are briefly described below, summarised from Magurran (1988).

Margalef's index (D_{Mg}) is a simple measure of diversity that combines species richness and the total number of individuals present.

$$D_{Mg} = (S-1) / \ln N$$

S - the number of species recorded.

N - the total number of individuals summed over all the species.

Margalef's index is not widely used, due mainly to its high sensitivity to sample size, but its good discriminant ability and ease of calculation make it a useful first step in the analysis of diversity data.

Shannon's Index (H') is calculated from the equation:

$$H' = - \sum p_i \ln p_i$$

p_i - proportion of individuals found in the i th species.

The Shannon index assumes that individuals are taken from an "indefinitely large" population and that all species are represented in the sample. The index was developed from information theory and is a measure of uncertainty. The higher the value of the calculated index, the greater the uncertainty involved in the predicting the species of the next individual randomly drawn from a population (Burchfield 1993). A high index indicates a high level of species diversity.

The Williams α index of diversity is derived from the equation:

$$\alpha = N(1-x) / x$$

N - total number of individuals.

x - iterative seed. In practice x is almost always > 0.9 and never > 1.0 .

Taylor (1976) came out strongly in favour of α , the log series index, because of its good discriminant ability and the fact that it is not unduly influenced by sample size (Magurran 1988). However, recent work by Downie (pers. comm.) has shown that α is more influenced by sample size than either the Shannon or Simpson index, a finding in direct contrast to that of Taylor.

The Simpson and Berger-Parker index are weighted towards the abundances of the most common species and so provide a measure of species dominance rather than species richness (Magurran 1988).

The Berger-Parker index (d) is the simplest measure of dominance, which expresses the proportional importance of the most abundant species.

$$d = N_{\max} / N$$

N_{\max} - number of individuals in the most abundant species.

N - total number of individuals.

The reciprocal form of the Berger-Parker index is usually adopted so that an increase in the value of the index accompanies an increase in diversity and a reduction in dominance.

Simpson's index (D) is based on the probability of any two individuals drawn at random from an infinitely large community belonging to the same species, and is therefore biased towards the commonest species.

$$D = (n_i(n_i-1) / N(N-1))$$

n_i - the number of individuals in the i th species.

N - the total number of individuals.

As D increases, diversity decreases and Simpson's index is therefore usually expressed as $1 - D$ or $1/D$. Simpson's index is heavily weighted towards the commonest species in the sample while being less sensitive to species richness.

1.7 Analysis of beta diversity

Beta (between site) diversity defines the degree of change in species composition and abundance between paired sites.

The easiest way to measure the beta diversity of pairs of sites is to use similarity coefficients. Sorenson's qualitative index (C_S) is one of the oldest and simplest techniques but an extensive evaluation of similarity measures found Sorenson's qualitative index as one of the best (Magurran 1988).

$$C_S = 2j / (a+b)$$

j - the number of species found in both sites.

a - number of species in site A.

b - number of species in site B.

The biggest disadvantage of Sorenson's qualitative index is that it takes no account of the relative abundance of species.

Sorenson's quantitative index (C_N) is one of the simplest measures of site similarity that takes account of the relative abundances of species. It was calculated from the following equation.

$$C_N = 2j_N / (aN+bN)$$

jN - the sum of the lower of the two abundances recorded for species found at both sites.

aN - total number of individuals in site A.

bN - total number of individuals in site B.

Both of Sorenson's indices fluctuate between 0 and 1. Complete similarity is indicated by a value of 1, whereas a value of 0 means that sites have no species in common. Beta diversity is a measure of species turnover between sites and therefore the lower the similarity between sites the higher the beta diversity.

2.0 MATERIALS AND METHODS

2.1 Site Description

The study site was situated on the eastern flank of Monk's Moor (Photograph 2.1), in the eastern Pennines, 4km north-east of Middleton in Teesdale, County Durham (National Grid Reference NY 984283-974287). Monk's Moor has mid-altitude heathland, called 'northern heaths' by Gimingham (1972) which are found extensively in the uplands of northern England. On the higher slopes (*ca.*440m and above), *Calluna vulgaris* was the dominant vegetation type with an extensive and relatively even distribution (Photograph 2.2). Fragmentation of *C.vulgaris* at higher altitudes was due to burning, a standard land management practice for a grouse moor (Photograph 2.3). At lower altitudes (*ca.*440m and below), especially in the flatter, wetter areas *C. vulgaris* became increasingly fragmented (Photograph 2.4) as *Juncus effusus* and *Eriophorum vaginatum* became locally dominant. *Agrostis tenuis*, *Poa pratensis*, *Anthoxanthum odoratum* and *Juncus squarrosus* were also common.

Due to a change in land management, rough pasture has now replaced the heathland vegetation on the Moor's north eastern slopes. *Anthoxanthum odoratum*, *Deschampsia caespitosa* and *Festuca ovina* dominated the more homogeneous grassland. *Juncus squarrosus* and *Eriophorum vaginatum* were also relatively common and in the wetter areas *Juncus effusus* became abundant.

These two distinct habitats were separated by a fence running east to west, across an altitude range of approximately 140m. The close proximity of the two habitats meant that climatic or geological effects would be negligible. The only variables to affect the invertebrates sampled were therefore assumed to be the difference in the vegetation and the changing climatic conditions associated with increasing altitude. For the altitude range covered by sampling *ca.*360m to *ca.*500m annual mean temperatures were likely to fall 1 - 1.5°C (Coulson *et al* 1976; Grace and Unsworth, 1988).

2.2 Methodology

A total of ten sites was chosen for pitfall trapping; five stations were established in each habitat at altitudes of approximately 360m, 400m, 440m, 480m and 500m a.s.l. Each station comprised six pitfall traps, two metres apart, arranged in a straight line across the slope, directly opposite its comparable site in the other habitat. The use of six traps per station rather than the eight recommended by Uetz and Unzicker (1976) represented a compromise between increasing the number of stations and increasing the number of pitfalls at each station. Traps were placed sufficiently far from the fence to exclude sampling within the ecotone between the two habitats.



Photograph 2.1: View west towards Monk's Moor. The heather moorland is to the left of the fence.



Photograph 2.2: View east from the 500m pitfall station in the heather.



Photograph 2.3: Area of recently burnt heather between pitfall stations at 440m and 480m.



Photograph 2.4: View east from the 400 m pitfall station towards the more fragmented areas of heather at lower altitudes.

The pitfall traps were round plastic cups of 7cm diameter, set 8cm deep so their tops were flush with the ground. The traps were filled to a depth of 1-2 cm with a preservative-killing solution of 2% formalin and teepol®, a detergent to reduce surface tension. Curtis (1980) considered this to be the most efficient design of trap.

Within each habitat the pitfall sites were chosen to be as representative of the dominant vegetation type as possible so that variation of habitat between sites was kept to a minimum. Pitfall sites on the moorland therefore, were restricted to areas with a relatively continuous, even distribution of *Calluna vulgaris*. To avoid edge effects due to the fragmented distribution of *C. vulgaris* pitfalls were placed at least 10m away from any obvious changes in the vegetation type or structure. One consequence of periodic heather burning was irregular variation of age of heather across the hillside. Pitfall sites were chosen from the mature or degenerative stages of heather growth. These represented the more stable areas of the habitat as the age of heather in the latter growth stages usually exceeds 18-20 years (Gimingham 1960). Once suitable sites were identified in the heather, comparable sites (at the same altitude) were set in the pasture. The more homogeneous structure of the pasture vegetation meant the siting of pitfalls there was not a problem.

The traps were in position from late April until mid July and samples were collected at fortnightly intervals. Upon collection, the six pitfalls at each of the ten sites were combined into one container.

All the invertebrates were identified to order level using Tilling (1987). Spiders were then chosen for further analysis as they represented an abundant order and their cursorial nature made pitfall traps the most effective method of sampling. All spiders were identified to species level using Locket and Millidge (1951, 1953), Locket, Millidge and Merrett (1974) and Roberts (1987a,b,c), with nomenclature and classification corresponding to the check list given in Roberts (1987b). Juvenile Linyphiidae could not be identified to species level so they were excluded from diversity analysis. Juvenile non-Linyphiidae could be identified with confidence so were incorporated into all measures of diversity.

2.3 Data Analysis

The diversity of the Araneae and total invertebrate fauna were analysed using statistical techniques described by Magurran (1988) and explained in further detail in the Introduction (Sections 1.5 - 1.7). The data were initially investigated to assess how continued sampling may have effected the diversity values calculated.

The seasonal distribution of the more common spiders was analysed. The restricted sampling period may have caused differences between the relative proportions of species, and this effect could be appraised.

Data for each habitat were then fitted to log series and log normal models of species abundance (May 1975; Magurran 1988).

Alpha diversity at each site was measured using six diversity indices. The number of species present (species richness) gave the first indication of species variety, but five other indices of alpha diversity that incorporated species abundance were also used. The Margalef, Shannon, Williams α , Berger-Parker and Simpson index measured the diversity of species in relation to total number of individuals collected at each site.

Beta diversity (species turnover between sites) was calculated using Sorenson's Qualitative and Quantitative indices.

The effect of habitat and altitude upon all these indices was then analysed using Analysis of Variance (Anova). Kolmogorov-Smirnov one sample tests showed the data to be normally distributed and f-tests showed all data to be homoscedastic.

3.0 RESULTS

The results are presented in two parts. The spider species data were analysed first. Analysis of the total invertebrate data followed the same procedure except when certain techniques were considered inappropriate.

3.1 Araneae

During the survey 6371 spiders (adults and juveniles) were collected representing 88 species from 10 different families. Although occasional captures were made of spiders from the families Dictynae, Clubionidae, Gnaphosidae, Thomisidae, Agelenidae and Hahniidae they contributed less than 2.0% of the total, which can be regarded as made up of the Linyphiidae, Lycosidae, Tetragnathidae and the Theridiidae. Of these families the Linyphiidae contributed the greatest number of species and individuals, 68 (77%) and 3879 (61%) respectively. Of the remaining families, Lycosidae represented 34% of total abundance although only seven species were collected. Together the Linyphiidae and Lycosidae represented 85% of all species and 95% of the total abundance. The abundance and distribution of the 88 species of spider recorded in this study are given in Appendix 1.

3.2 Sample size

Diversity analysis requires equal sample sizes large enough to be representative of the species within the area (Magurran 1988). The initial sampling design ensured all stations reflected equal trapping effort. The sample size was, however, restricted by the relatively short period of time available for sampling; the early summer months.

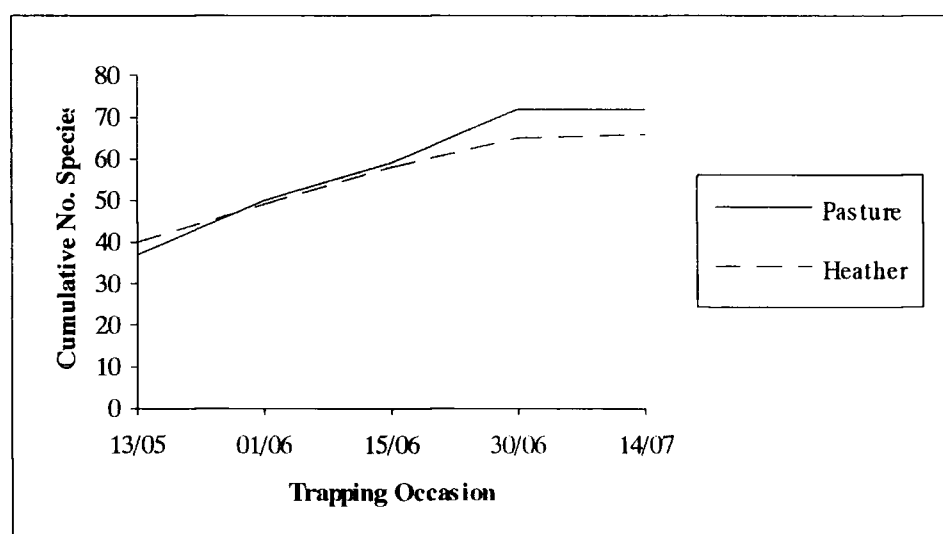


Figure 3.1: Cumulative increase in species richness over the trapping period.

Figure 3.1 shows the accumulation of species (the number of new species recorded for the first time) for both habitats over the trapping period. Each habitat shows a similar trend. The first four trapping occasions record a steady rate of accumulation, with five or six new species being added at each collection. By the final collection only one new species was added to the sample.

3.3 Effect of sample size on measures of diversity

Figures 3.2 and 3.3 plot the diversity indices for each habitat against the cumulative increase in sample size. Most show a similar response to increased sample size.

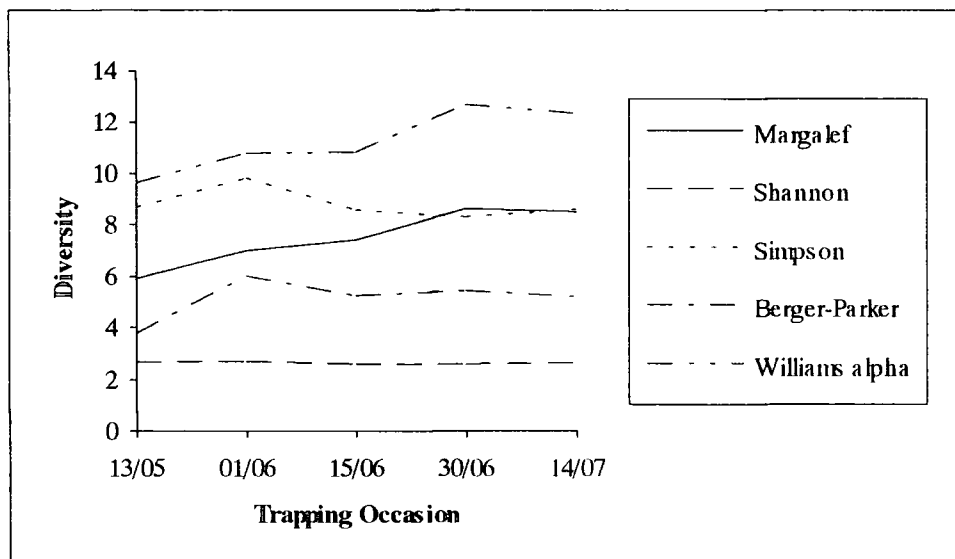


Figure 3.2: Diversity values for each pasture pitfall station, plotted against the cumulative increase in species richness and abundance.

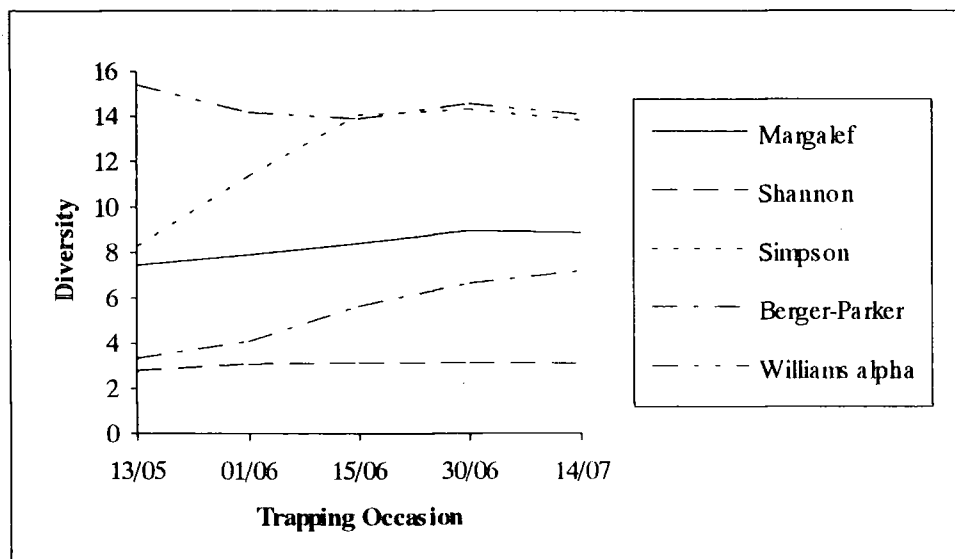


Figure 3.3: Diversity values for each heather pitfall station, plotted against the cumulative increase in species richness and abundance.

As species richness (the number of species sampled) increased, the indices measured higher diversity. By the last trapping date the increase in species richness was negligible and the indices stabilised. Maximum diversity was not necessarily recorded after the last collection (Figures 3.2 and 3.3). Williams α recorded maximum diversity in the heather after the first collection whereas maximum diversity in the pasture was reached after the fourth collection. Other indices show similar variation across dates and habitats. When maximum diversity was associated with a small sample size, it was clear this was not a true measure of the habitat's diversity. As a representative sample was collected, extremes of diversity were avoided.

Figures 3.4 and 3.5 plot the proportional change of each diversity index between each collection date. They reflect the same stabilisation of diversity as figures 3.2 and 3.3 but now the response of each index to increased sample size can be compared. The dominance indices (Berger-Parker and Simpson index) showed the greatest fluctuation initially but all indices reflected a rather similar pattern overall. By the last trapping date, all the diversity values appeared to have stabilised.

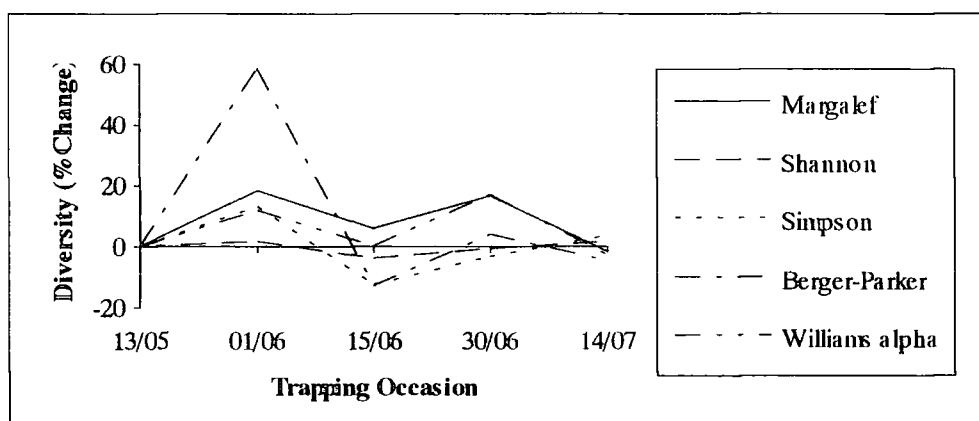


Figure 3.4: Percentage change of each diversity index between each trapping occasion in the pasture as a result of the cumulative increase in species abundance and richness.

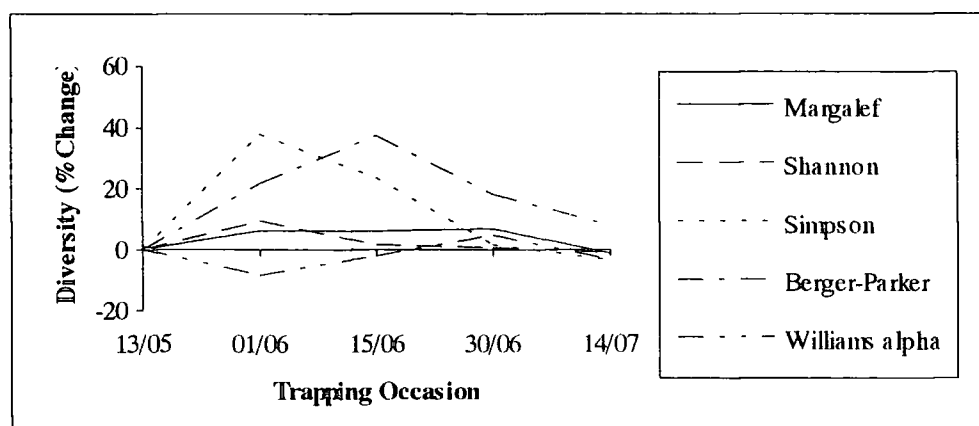


Figure 3.5: Percentage change of each diversity index between each trapping occasion in the heather as a result of the cumulative increase in species abundance and richness.

3.4 Seasonality

The seasonal distribution of spider abundance in both habitats is compared graphically in Figures 3.6 and 3.7. Spider abundance in both habitats peaked in early-June and then decreased during July.

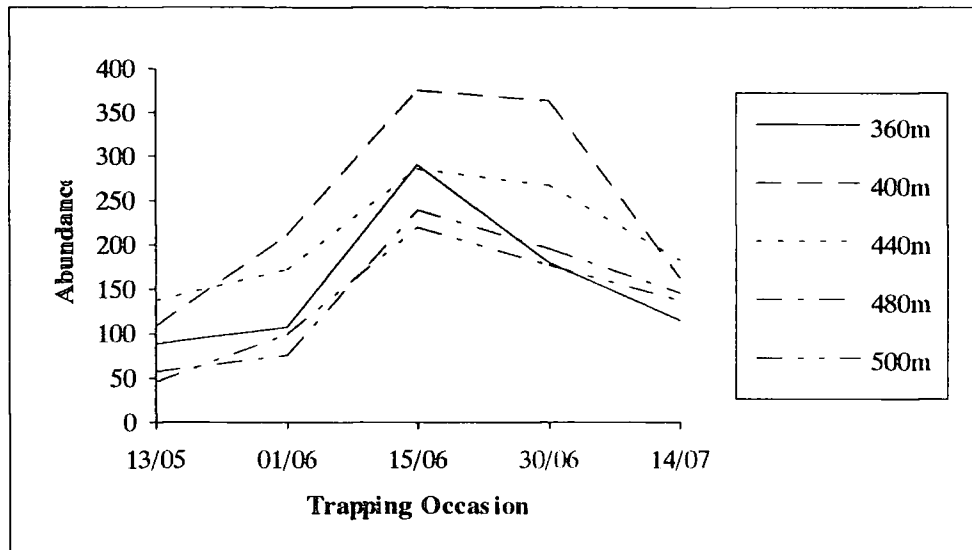


Figure 3.6: Seasonal distribution of abundance for all spiders caught in the pasture

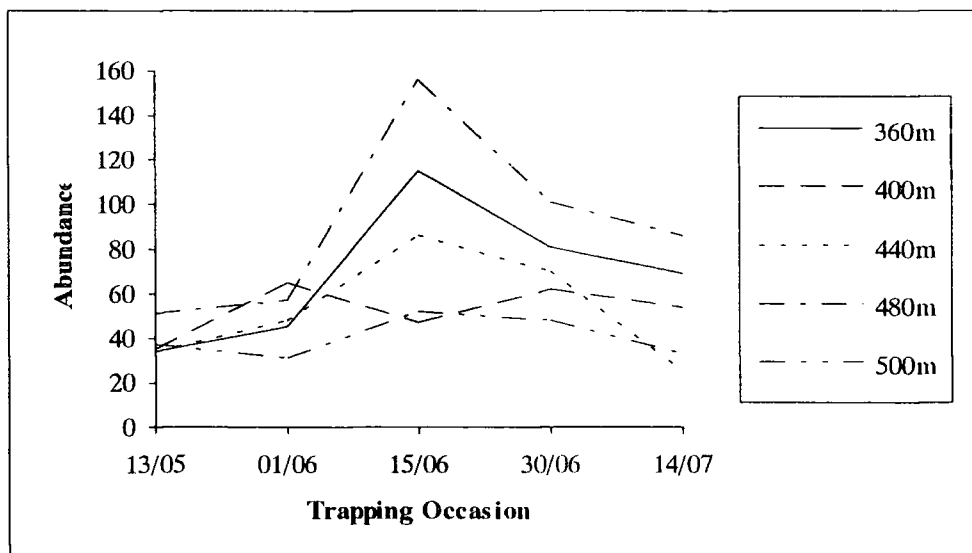


Figure 3.7: Seasonal distribution of abundance for all spiders caught in the heather

Figure 3.8 shows the seasonal abundance of the most frequently trapped Lycosidae. *A. pulverulenta*, *P. pullata* and *P. nigriceps* were caught in greatest numbers in early June. *T. terricola* abundance, however, remained relatively constant throughout May and early June.

The seasonal distribution of Linyphiidae abundance appeared to differ markedly between habitats (Figure 3.9). The distribution of abundance on pasture rose sharply in early June to a maximum in late June before decreasing rapidly in July. The distribution

in the heather however, remained relatively constant across the sampling period.

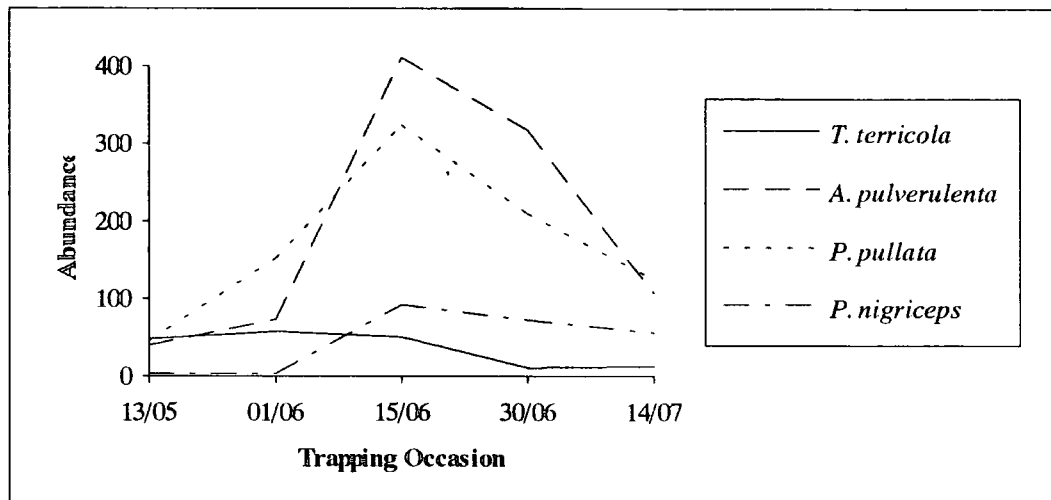


Figure 3.8: Seasonal distribution of abundance of the commonest Lycosidae.

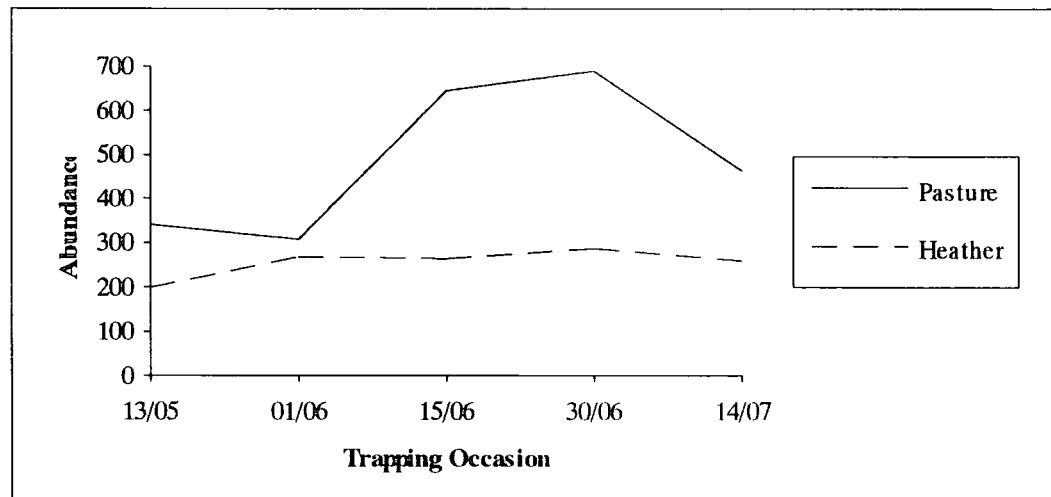


Figure 3.9: Seasonal distribution of abundance of Linyphiidae.

3.5 Species abundance models

Whittaker plots of ranked species abundance were constructed for each habitat to provide a first indication of the distribution of species abundance data as recommended by Magurran (1988) and Krebs (1989). The sigmoid curve seen in Figures 3.10 and 3.11 most closely resembles a log normal distribution. However, a simple comparison of the dominance diversity curve may not necessarily represent the closest mathematical fit.

A logarithmic conversion was applied to the spider data (Figure 3.12). From these data it was difficult to decide which model of species abundance was most appropriate as the conversion had not resulted in a symmetrical bell shaped curve, typical of a log normal distribution. To distinguish between a truncated log normal or a

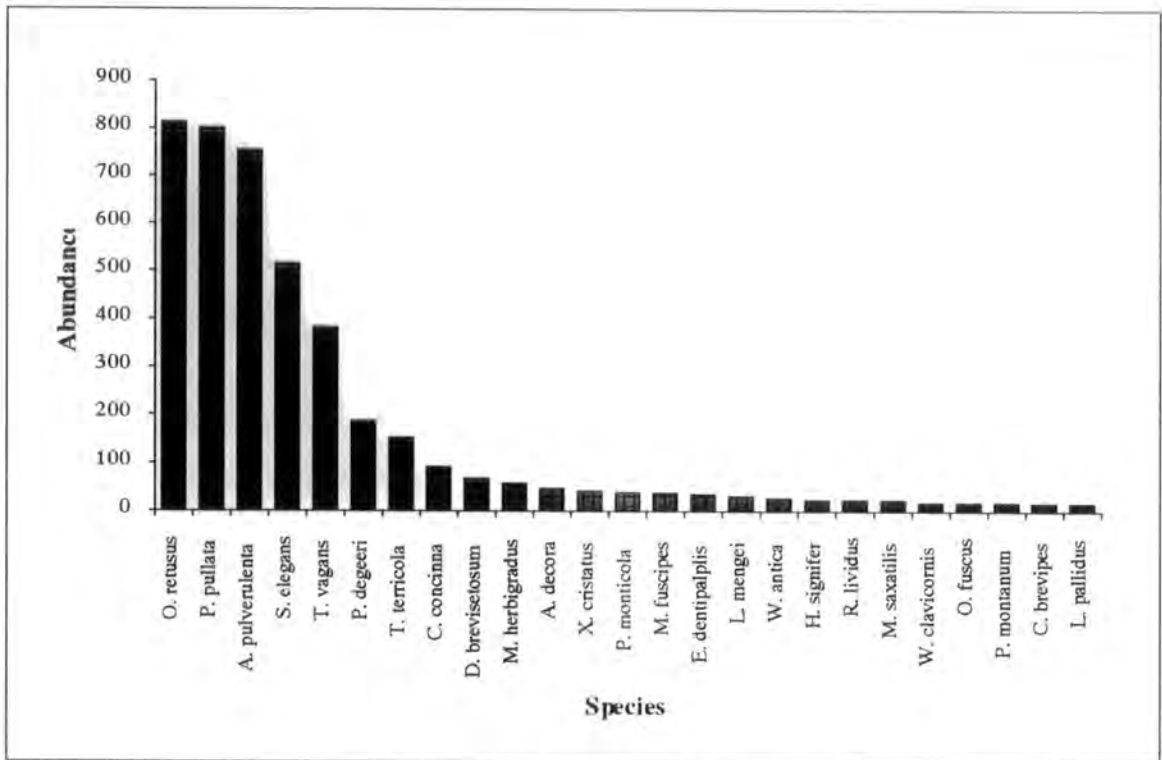


Figure 3.10: Whittaker plot of species abundance on species rank. The 25 most common species in the pasture are shown.

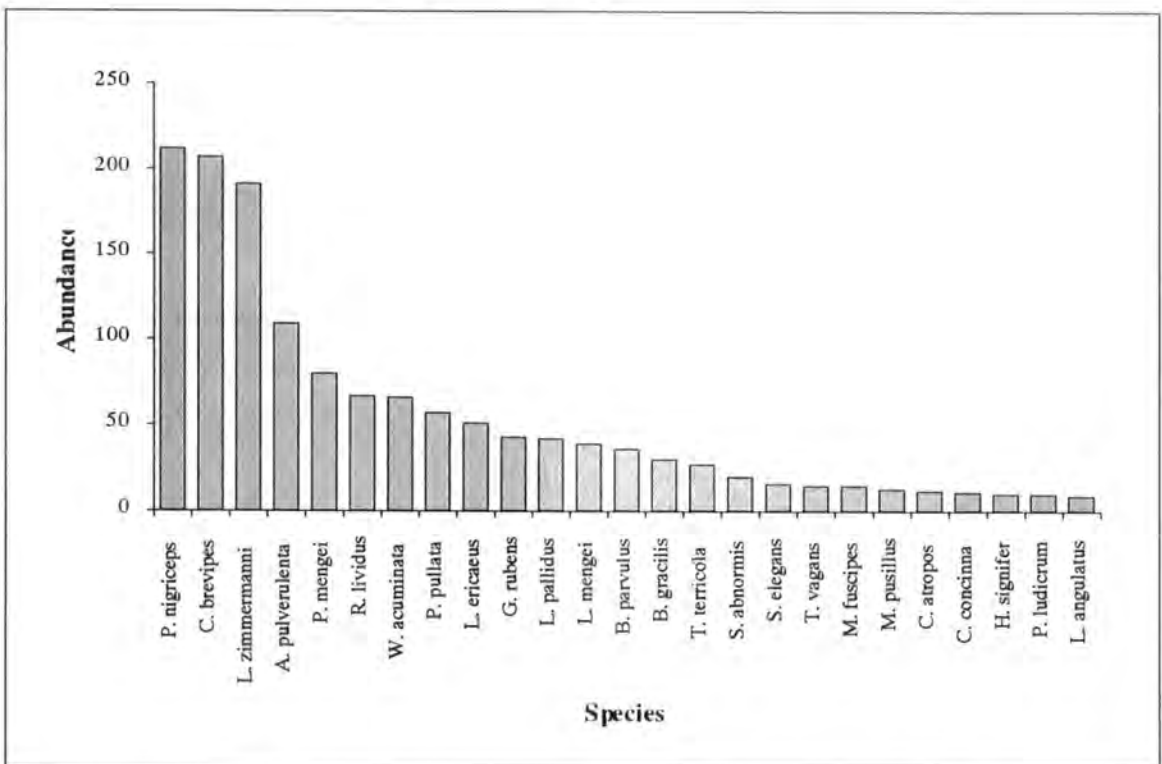


Figure 3.11: Whittaker plot of species abundance on species rank. The 25 most common species in the heather are shown.

log series distribution is almost impossible (Krebs 1989). Krebs (1989) believed that a sample should not be described as having a truncated log normal distribution, unless there was evidence that the mode or maximum in the species - abundance curve had been reached. The distribution of species abundance in Figure 3.12 did not meet this requirement. Nonetheless, so that the species abundance curves for each habitat could be compared a Kolmogorov-Smirnov one sample test was used to estimate the significance of deviation away from a log normal distribution. Neither habitat differed significantly ($P > 0.05$).

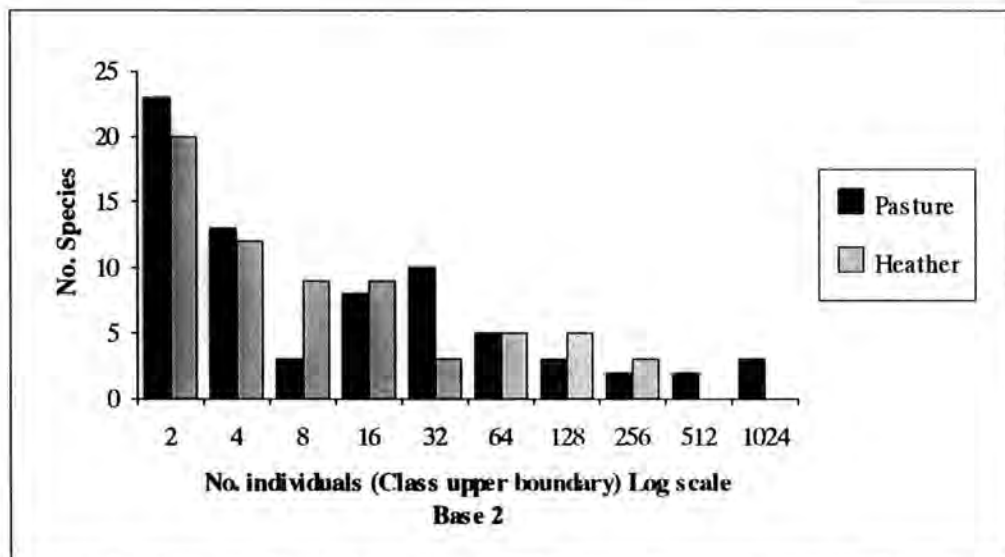


Figure 3.12: Number of species plotted against species abundance on a logarithmic scale (base 2). Each octave represents a doubling of species abundance.

3.6 Analysis of alpha diversity.

For each site on every trapping occasion species richness, species abundance and the Margalef, Shannon, Williams α , Simpson and Berger-Parker diversity indices were calculated. These values were then analysed using two way Analysis of Variance (Anova) to determine whether there was a significant relationship between altitude or habitat and species diversity. The mean number of species, abundance and the mean value for each diversity index are presented in Table 3.1.

3.7 Effect of habitat

The difference in species abundance between habitats was found to be highly significant ($F_{40,1} = 43.0$, $P < 0.001$). The mean number of spiders collected from each site in the pasture was over 500 more than those in the moorland (Table 3.2). This large difference was due mainly to the relative dominance of a few species like *Oedothorax retusus*, *Pardosa pullata* and *Alopecosa pulverulenta* in the pasture. Their combined abundance accounted for 2368 individuals, 53% of the total abundance for

the pasture. There was no difference in species abundance associated with changes in altitude ($F_{40,4} = 1.3$, $P = 0.30$).

Table 3.1: Mean species richness, species abundance and diversity for each pitfall station.

	Pasture				
Altitude (m)	360	400	440	480	500
No. Species	20	23	21	21	20
Abundance	156	244	209	209	136
Margalef Index	3.66	3.95	3.75	3.78	3.91
Shannons Index	2.19	2.18	2.27	2.23	2.13
Williams Alpha α	6.22	6.19	5.86	6.59	6.99
Berger Parker Index 1/d	3.82	3.78	4.36	3.95	3.29
Simpsons Index 1/D	6.41	6.08	6.99	6.80	5.63
	Heather				
Altitude (m)	360	400	440	480	500
No. Species	19	16	20	19	14
Abundance	68	52	52	90	40
Margalef Index	4.48	3.91	4.90	4.18	3.60
Shannons Index	2.50	2.34	2.61	2.30	2.28
Williams Alpha α	10.69	8.60	13.28	8.15	8.14
Berger Parker Index 1/d	5.38	4.44	4.81	3.04	4.01
Simpsons Index 1/D	9.49	8.37	10.25	6.19	7.30

Table 3.2: Number of adult spiders caught at each pitfall station.

Altitude (m)	Rough Pasture	Heather Moorland
360	780	344
400	1221	263
440	1045	263
480	713	451
500	679	201
Mean	887	304

The Shannon, Williams α and Simpson indices of alpha diversity differed significantly between habitats ($F_{40,1} = 8.4, P < 0.01, F_{40,1} = 25.3, P < 0.001$ and $F_{40,1} = 8.6, P < 0.01$ respectively). The heather moorland spider fauna was the significantly more diverse habitat because of the greater evenness of abundance. The proportional abundances of the 25 commonest species for each habitat are plotted together in Figure 3.13. The lower dominance and higher evenness of the heather spider community is clear.

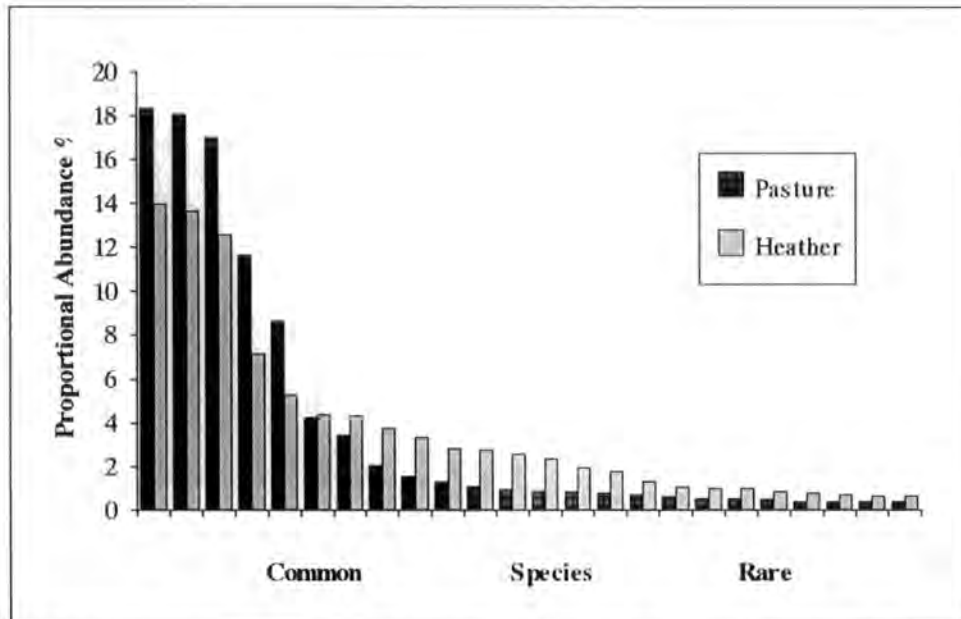


Figure 3.13: Ranked abundance of the 25 commonest spider species expressed as a percentage of the total abundance for each habitat

Table 3.3 lists the ten commonest species in each habitat and their proportional abundance. The five commonest species of spider caught in the pasture, *Oedothorax retusus*, *Pardosa pullata*, *Alopecosa pulverulenta*, *Silometopus elegans* and *Tiso vagans* accounted for 74% of the total. The most abundant species in the heather, *Pardosa nigriceps*, *Ceratinella brevipes*, *Lepthyphantes zimmermanni*, *Alopecosa pulverulenta* and *Pelecopsis mengei* represented just 52% of the total. For an equivalent 74% of the total moorland fauna to be represented, the commonest 11 species totals needed to be combined. The distribution of abundance in the heather was far more homogeneous, with lower abundance for their common species and higher abundance for their rarer species (Table 3.3 and Figure 3.13).

Table 3.3: Total abundance and proportional abundance of the ten commonest species of spider in each habitat.

Pasture	Abundance	% of total	Heather	Abundance	% of total
<i>O. retusus</i>	813	18.32	<i>P. nigriceps</i>	212	13.94
<i>P. pullata</i>	801	18.05	<i>C. brevipes</i>	207	13.61
<i>A. pulverulenta</i>	754	16.99	<i>L. zimmermanni</i>	191	12.56
<i>S. elegans</i>	516	11.63	<i>A. pulverulenta</i>	109	7.17
<i>T. vagans</i>	383	8.63	<i>P. mengei</i>	80	5.26
<i>P. degeeri</i>	188	4.24	<i>R. lividus</i>	67	4.40
<i>T. terricola</i>	153	3.45	<i>W. acuminata</i>	66	4.34
<i>C. concinna</i>	91	2.05	<i>P. pullata</i>	57	3.75
<i>D. brevisetosum</i>	69	1.56	<i>L. ericaeus</i>	51	3.35
<i>M. herbigradus</i>	58	1.31	<i>G. rubens</i>	43	2.83

3.8 Effect of altitude

There was no significant relationship between altitude and the Shannon index ($F_{40,4} = 1.3$, $P = 0.27$), Williams α index ($F_{40,4} = 1.6$, $P = 0.2$) or the Simpson index ($F_{40,4} = 1.6$, $P = 0.19$).

The data were then analysed at the family level. Coulson and Butterfield (1986) recorded that the proportion of Linyphiidae to non-Linyphiidae showed a significant increase with increased altitude. They found the proportion of the two groups changed according to the relationship: % Linyphiidae = $57.2 + 0.042 \times \text{altitude (m)}$, ($r = +0.824$, $P < 0.001$). The proportion of Linyphiidae to non-Linyphiidae on Monk's Moor were compared to the above equation (Table 3.4).

Table 3.4: Proportion of Linyphiidae (%) at each pitfall station, with expected values from Coulson and Butterfield (1986).

Altitude(m)	Pasture	Heather	Expected
360	70.8	82.5	72.3
400	90.6	76.3	74.0
440	61.1	72.9	75.7
480	59.1	72.2	77.4
500	90.7	75.7	78.2

Chi-square analysis was used to see if the proportion of Linyphiidae observed in this study differed significantly from those predicted by Coulson and Butterfield (1986). The proportional values were converted back to original values for Chi-square analysis. The χ^2 values for the pasture ($\chi^2 = 0.075$ df = 4) and the heather ($\chi^2 = 0.211$ df = 4) proved the proportion of Linyphiidae was not significantly different ($P > 0.05$) from the proportions calculated by Coulson and Butterfield (1986). However, regression analysis of the observed proportions failed to find the same significant relationship with altitude ($P > 0.05$) as recorded by the predicted values.

The relationship between the abundance of the ten commonest species in each habitat (Table 3.3) with increased altitude was investigated using a Spearman's Rank Correlation. In the pasture the abundance (the number of individuals) of *A. pulverulenta* and *P. degeeri* decreased significantly with increased altitude ($P < 0.001$ and $P = 0.037$ respectively). The abundance of *P. pullata* increased significantly with increased altitude ($P = 0.037$) in the pasture. In the heather only *W. acuminata* abundance increased significantly ($P < 0.05$) with increased altitude.

Although *A. pulverulenta* and *P. pullata* were relatively common in the heather there was no comparable trend with altitude in this habitat ($P = 0.747$ and $P = 0.873$ respectively).

No significant relationship was found between species richness ($F_{40,5} = 1.56$, $P = 0.19$), Margalef's diversity index ($F_{40,5} = 1.5$, $P = 0.21$) or the Berger-Parker index ($F_{40,5} = 1.4$, $P = 0.26$) and habitat or altitude. There were no significant interactions between habitat and altitude.

3.9 Analysis of beta diversity

Sorenson's quantitative and qualitative indices were used to calculate the similarity between adjacent sites in the same habitat and between sites at the same altitude in different habitats. Sorenson's qualitative index was also used to compare Monk's Moor spider fauna to the Moor House fauna collected by Cherrett (1964). The quantitative index was not used as only presence - absence data were available in the latter study.

3.10 Effect of habitat

Anova found beta diversity between successive pitfall stations in the pasture was significantly lower (higher similarity) than between comparable sites in the heather, $F_{32,1} = 22.7$, $P < 0.001$ (Table 3.5). The lower beta diversity between sites in the pasture was probably a consequence of its lower alpha diversity and higher species dominance.

Table 3.5: Mean similarity between pitfall stations calculated from Sorenson's Quantitative index.

Altitude (m)	Pasture		Moorland	
	Mean	St. Dev	Mean	St. Dev
360-400	0.66	0.12	0.61	0.09
400-440	0.83	0.04	0.52	0.16
440-480	0.60	0.19	0.53	0.10
480-500	0.83	0.09	0.54	0.09
Mean	0.73		0.55	

The mean Sorenson's Quantitative Index between habitats at each corresponding altitudes was 0.2, indicating these two habitats have very different spider faunas. Unsurprisingly the similarity within habitats (Table 3.5) was consistently higher. Figure 3.14 shows the combined abundances from both habitats in a rank abundance plot. It clearly shows that no species were common in both types of habitat.

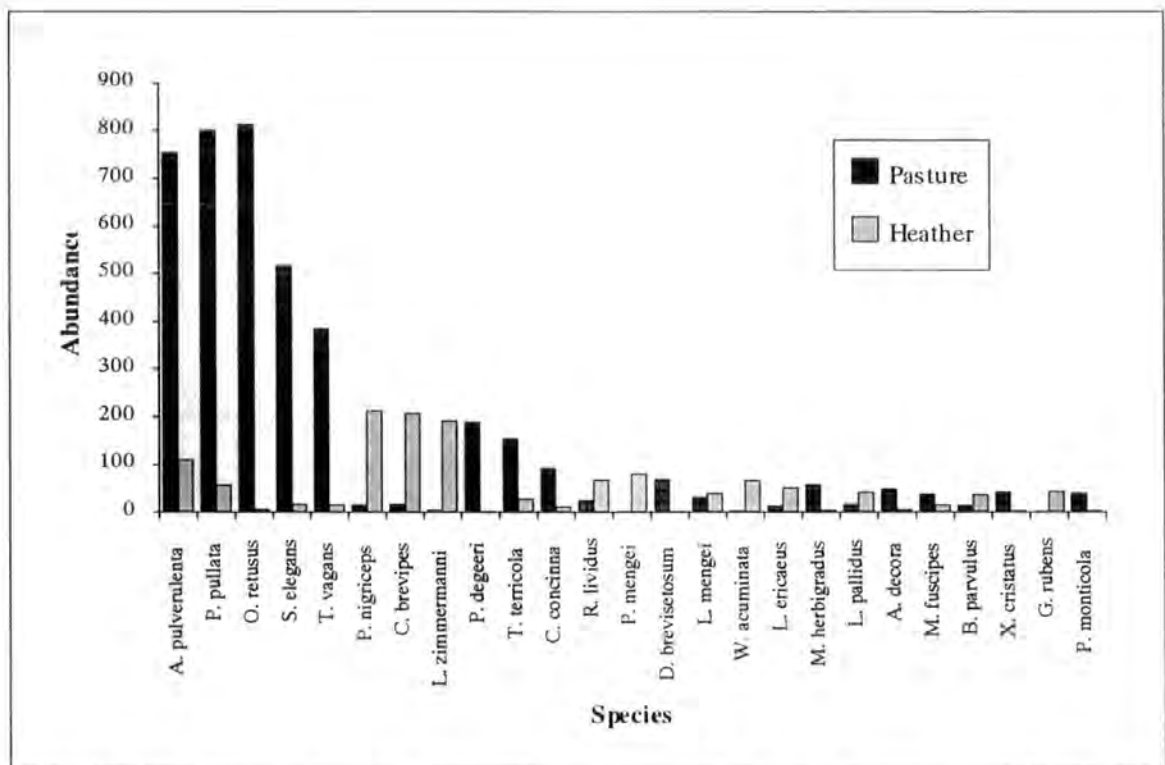


Figure 3.14: Plot of species abundance on species rank. Total abundance combined across habitats.

The family composition of the Monk's Moor spider fauna was very similar to that of Moor House National Nature Reserve as presented by Cherrett (1964).

Sorenson's Qualitative index (Table 3.6) showed the similarity between the two localities (0.67) to be almost identical to the similarity between pitfall stations in each habitat (0.68 and 0.70).

Table 3.6: Mean similarity between pitfall stations calculated from Sorenson's Qualitative index.

Mean similarity between:	Beta value
habitats (pasture vs heather)	0.62
pasture sites	0.70
heather sites	0.68
Monk's Moor and Moor House	0.67

3.11 Effect of altitude

Beta diversity was not significantly related to increased altitude in either habitat ($F_{32,3} = 2.24$, $P = 0.10$).

Beta diversity between habitats showed marginal significance with increasing altitude ($F_{20,4} = 2.86$, $P = 0.05$). A Tukeys range test narrowed the significance to sites at 480m and 500m (Table 3.7).

Table 3.7: Mean similarity between habitats with increasing altitude, calculated from Sorenson's Quantitative Index

Altitude (m)	Mean	St. Dev
360	0.24	0.13
400	0.16	0.09
440	0.20	0.07
480	0.31*	0.11
500	0.11*	0.08

* indicates the difference in mean beta diversity between the two altitudes is significant.

3.12 Invertebrates

During the survey 33, 818 invertebrates were sampled from 18 different orders. Over 23, 000 invertebrates were caught from the pasture with Collembola, Araneae, Diptera and Coleoptera dominating this habitat's fauna (Figure. 3.15). These four orders represented 89% of all individuals caught at the 400m pasture pitfall station.

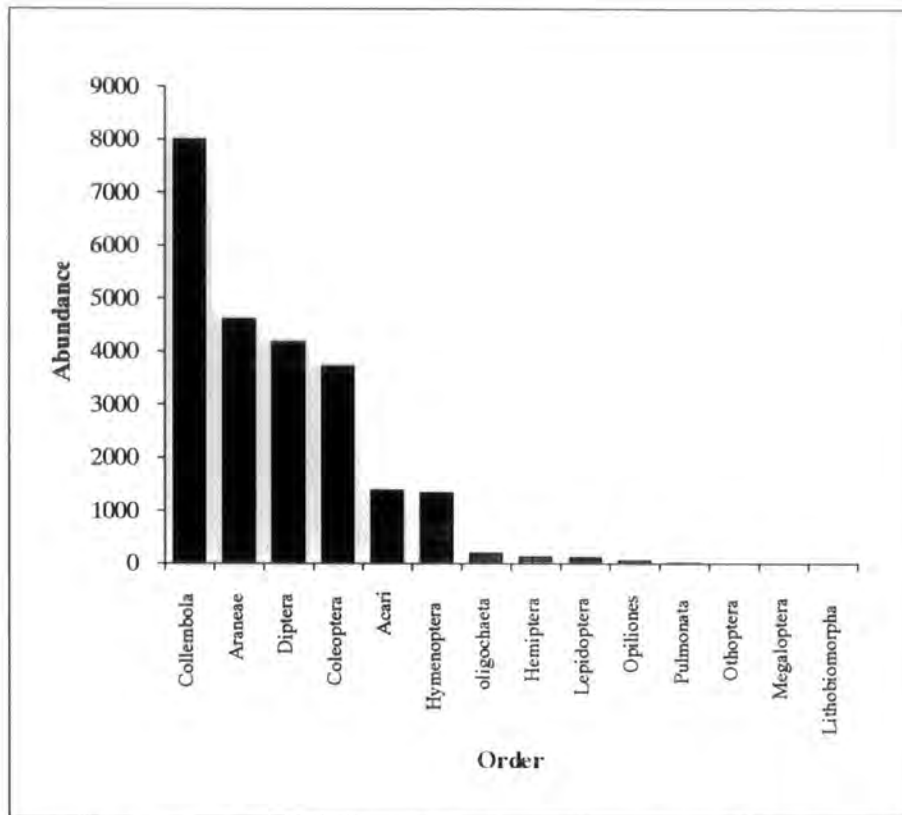


Figure 3.15: Rank abundance plot of invertebrate orders in the pasture.

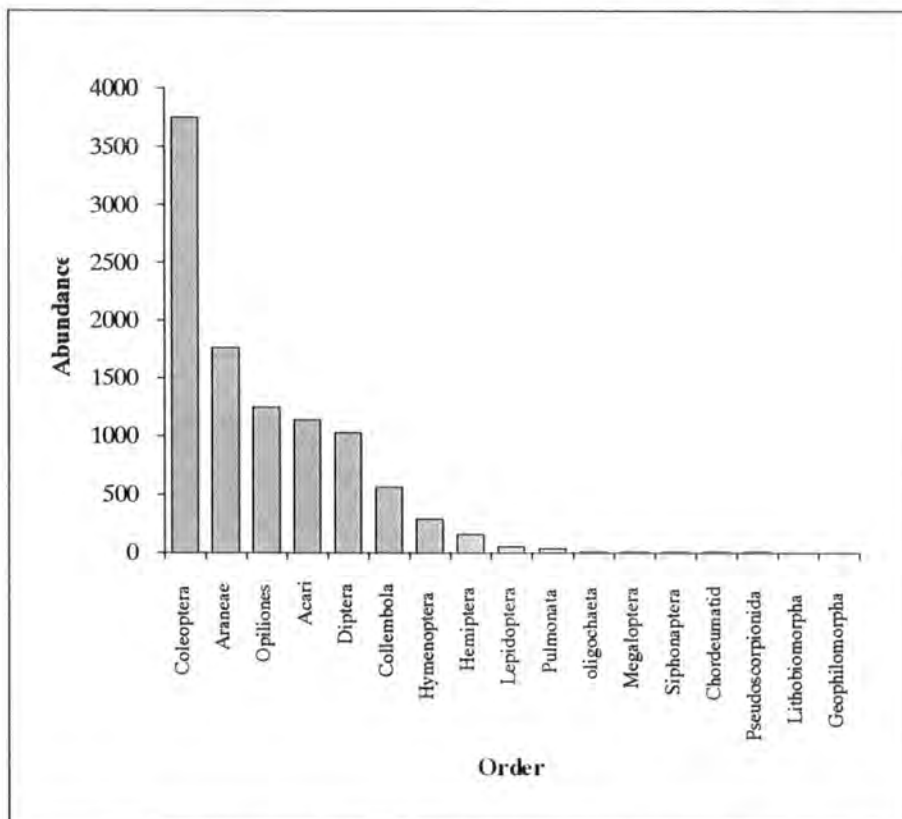


Figure 3.16: Rank abundance plot of invertebrate orders in the heather.

The moorland invertebrate fauna was dominated by Coleoptera, but Araneae, Opiliones, Acari and Diptera were also abundant (Figure 3.16). The abundance and distribution of the invertebrates recorded in this study are given in Appendix 2.

3.13 Sample size

The accumulation of new invertebrate orders over time for each habitat is presented in Figure 3.17. The trend reflected by the accumulation of spider species was repeated by the order data. After four collections that increased the number of orders only one new order was added at the last collection.

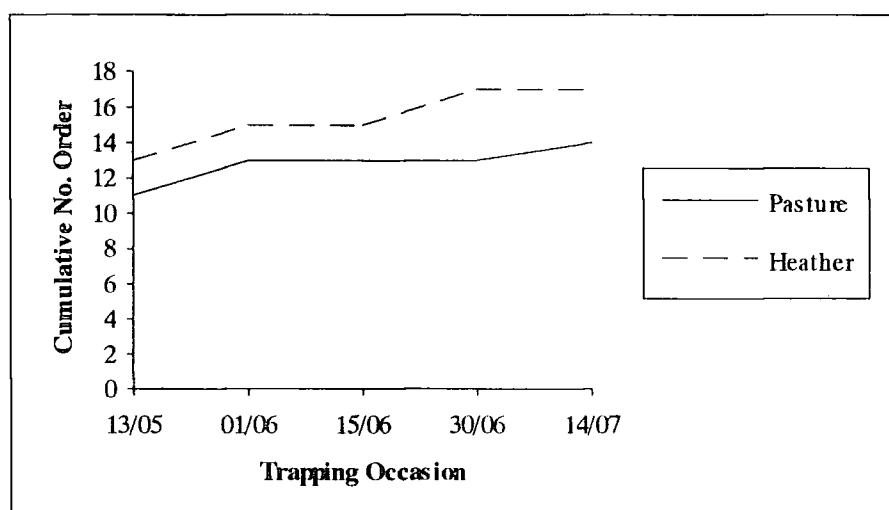


Figure 3.17: Cumulative increase in order richness over the trapping period.

3.14 Analysis of alpha diversity: effect of habitat

Margalef's index found the diversity in the heather was significantly higher than in the pasture (2-way Anova; $F_{40,1} = 20.6$, $P < 0.001$). The mean diversity for the pasture was 1.33, whereas the heather diversity was 1.55 (Table 3.8).

Table 3.8: Mean Margalef diversity index at each pitfall station.

Altitude (m)	Pasture		Heather	
	Mean	St. Dev	Mean	St. Dev
360	1.40	0.21	1.64	0.13
400	1.35	0.09	1.74	0.27
440	1.39	0.18	1.53	0.18
480	1.19	0.14	1.35	0.19
500	1.32	1.17	1.52	0.09
Mean	1.33		1.55	

This result was due to the presence of 17 of the 18 invertebrate orders present (Orthoptera absent) on the heather sites while the pasture had only 14 invertebrate orders present (Siphonaptera, Chordeumatid, Pseudoscorpionida and Geophilomorpha were absent).

3.15 Effect of altitude

Margalef's index was the only measure of diversity to find a significant relationship between diversity and altitude ($F_{40,4} = 3.8$, $P = 0.01$). Table 3.8 shows the higher diversity values are at the lower sites and the diversity decreases with increased altitude. Decreased diversity with increased altitude is a commonly recognised ecological pattern, although it was not apparent in the spider data.

Only Margalef's index showed no significant interaction between habitat and altitude. Accurate interpretation of diversity indices that show interactions between variables is difficult, as the cause of significance cannot be reliably defined.

4.0 DISCUSSION

4.1 Sample Size

Diversity analysis required sample sizes large enough to be representative of the species within each habitat. The accumulation of species (Figure 3.1) suggested the sample size for both habitats could be considered large enough to have caught the majority of trapable spiders. Sampling intensity has, however, been shown to affect the number of species caught. Taylor (1986) used light traps in an insect survey and new species were added to the species total in each successive year of sampling. Continued pitfall sampling would undoubtedly have recorded new species. For this study it was more important to assess how diversity would have been affected by further sampling. Figures 3.2 - 3.5 show that fluctuations in diversity were smallest by the last sampling date. It appears therefore, that sampling for a longer period of time would not have affected greatly the diversity values obtained. Moreover, although the data presented in this study do not represent total diversity of invertebrates at Monk's Moor, they are valid for comparison between habitats and altitudes.

Indices that incorporate species abundance into their measure of diversity may be affected by sample size. The last pitfall collection added one new species (1.2%) and 1011 more individual spiders (16%) to the sample. If further sampling had recorded no increase in the number of species, diversity indices sensitive to sample size would measure a progressively lower diversity as the distribution of species abundance became increasingly heterogeneous. This lowering of diversity was not noticeable in the present study.

4.2 Pitfall Trap Efficiency

Studies of the effectiveness of pitfall traps often relate specifically to Carabidae (Coleoptera) but the findings may also be applied to cursorial spiders. The efficiency of various pitfall trap designs has been looked at in depth by Luff (1975) and Curtis (1980). Luff (1975) compared pitfall traps of different sizes and different materials and concluded that glass pitfalls were the best as they had the highest catches in proportion to their size. All traps caught about 75% of beetles that contacted its perimeter but it was the lower rate of escape from glass traps that made them most efficient. However, all traps were dry to prevent any preservative or killing agent attracting or deterring invertebrates from entering the traps. Greensdale (1964) found that neither baiting or camouflaging the traps effected the numbers of Carabidae caught. Although Curtis (1980) found some exceptions to this, most species were caught in the same proportions to the relative efficiency of the traps. Dry traps, however, allowed winged invertebrates to escape and predation of trapped animals to continue until traps were

collected. As pitfalls were collected only once a fortnight in this study, a preservative-killing solution was used to prevent such predation. Experiments by Curtis (1980) using both dry traps and ones with a preservative-killing solution found that traps containing a 4% formalin solution and detergent consistently caught the largest numbers of invertebrates. These also gave the best representation of species richness of the community and had the extra benefit of keeping specimens in better condition.

The present study relied on pitfall catches for the quantitative assessment of invertebrates and specifically Aranean faunas. Pitfall traps have been used extensively in the study of cursorial invertebrates especially Araneae and Coleoptera, but their effectiveness in collecting a representative sample of the community is often questioned. This has led to considerable discussion on the validity of pitfall traps being used for any type of quantitative assessment of invertebrate faunas.

Early studies showed that pitfall catches were influenced by numerous variables unrelated to species abundance. These included changes in activity due to prevailing weather conditions and the physiological state of the animal (Grüm 1959), food supply and temperature, (Briggs 1961), the habitat surrounding the trap and soil moisture, (Mitchell 1963). Briggs (1961) concluded "it is evident that the size of the population plays at most a minor role in determining the numbers trapped". Greenslade (1964) stated "...catches are determined primarily by the size of the population at risk and the level of locomotor activity but species may show differential susceptibility to trapping according to size, behaviour and the strata in which they are active in the ground vegetation" and that "catches of a single species may vary in different types of ground cover depending on the resistance they present to horizontal movement". Greenslade (1964) also noted how capture efficiency varied between species as those active during the day seemed able to avoid the trap. Greenslade (1964) concluded; "pitfall trapping cannot properly be used for the quantitative assessment of the Carabidae fauna of any habitat, nor should it be employed to compare the numbers of one species in different habitats". Southwood (1966) after reviewing the work by Briggs (1961) and Greenslade (1964) concluded that pitfalls "...are of little value for the direct estimation of populations or for the comparison of communities" and pitfall data are to be "used with caution".

In contrast, more recent work by Uetz and Unzicker (1976) Baars (1979) and Coulson and Butterfield (1985) have shown pitfall traps to be the most effective and reliable measure of invertebrate sampling. Uetz and Unzicker (1976) found that in a comparison between pitfall and quadrat sampling methods, pitfalls consistently gave a closer estimate of the total number of species in a community and were therefore more useful in studies of species diversity. Uetz and Unzicker (1976) concluded that pitfalls were the preferred method for cursorial species and overall were the best available

technique. Quadrat sampling was suitable only for non-motile species and web-builders. Baars (1979) showed that for several species of Carabidae, continuous pitfall sampling provided a reliable measure of the sizes of Carabidae populations in different habitats; "the influence on numbers trapped of the high mobility of beetles in unfavourable habitats is probably not significant". Baars (1979) based his conclusions on year-samples and suggested that the much shorter duration of the studies by Grüm (1959), Briggs (1961) and Mitchell (1963) may explain why they came to a different conclusion. Briggs (1961) and Mitchell (1963) also sampled a relatively small area where it was possible to show exchange with surrounding areas, where vegetation structure and densities may have been quite different (Baars 1979). Baars (1979) also found that Carabidae perform "a certain and hardly variable total amount of locomotive activity in a reproductive season and weather affects only the distribution of that amount". In continued good weather, activity (and consequently catches) increases more rapidly than if there is a long spell of colder weather, when the same number are caught but over a longer time span.

Coulson and Butterfield (1985) considered four invertebrate sampling methods for upland areas of moorland and grassland; sweep netting, vacuuming, extraction of soil samples and pitfall trapping. Sweep nets and vacuum methods were impractical as the frequency of rainfall and the high rainfall totals in these areas meant the vegetation was rarely dry enough for good, consistent results to be obtained. Sweeping and vacuuming methods only sample periodically when convenient for the investigator, so provide a very incomplete assessment of the invertebrate fauna. Nocturnal species for example would always be missed. Soil samples gave absolute densities but often only larvae were present which could not be identified to species level. Pitfalls caught the largest number of species, and mainly adults that could be identified to species level. Most importantly, unlike previous methods pitfall traps sampled continuously so nocturnal species were fully represented.

The latter studies give support for using pitfalls for quantitative analysis of cursorial spiders. They recognise that abundance values are a reflection of species population size (density) and species activity. Although pitfall traps do produce a biased sample of the invertebrate fauna, due to over representation of cursorial species, many of the fears that lead earlier workers to dismiss the method, have been over emphasised as their effect can not always be found significant. Pitfalls are cheap, require little labour or maintenance and they offer a valuable means of monitoring invertebrate populations: there is no better single alternative.

None of the studies above mention the effectiveness of pitfall traps for sampling other types of invertebrates, such as Diptera, Acari and Hymenoptera which were also commonly found in this study. Previous studies have used pitfall traps to study a

variety of invertebrates; Oligochaeta (Standen 1979), Diptera (Coulson 1988), Coleoptera (Butterfield and Coulson 1983) and Opiliones (Williams 1962). Although there may be more effective ways of catching some of these orders (formalin extraction, high temperature gradients, wet funnels, sticky traps, vegetation sweeping *etc.*) time constraints meant that pitfalls were the sole sampling method employed. However, the important consideration is that each site represents equal trapping effort and for the purposes of this study it is not the total diversity but the comparative diversity between sites that is important.

4.3 Seasonal distribution of spider abundance and activity

Upper Teesdale in the Northern Pennines has an environment described as subarctic (Manley 1936) and several Arctic / alpine species are found in the flora. The area is subject to wet windy Autumns, stormy winters with long spells of snow and the mean April air temperature rises little above freezing. The mean maximum daily temperature does not exceed 5.6°C until early May. There is a rapid transition in climate associated with altitude as a slight increase in elevation is accompanied by a remarkably large decrease in the length of the growing season (a shortening of ten days for every 80m) (Manley 1936). Although Middleton in Teesdale close to Monk's Moor does not experience the worst of the weather it receives 1270-1400mm of rainfall a year (Piggot 1956). Beneath stands of *Calluna vulgaris* however, the climate is more equitable. Maximum ground surface temperatures are lowered, humidity is higher and less variable. An atmospheric humidity of 45% may be associated with 87% humidity below *C. vulgaris* (Gimingham 1960). There is also restricted light penetration (as little as 0.5% of that in the open). The moorland provides a more varied habitat structurally and a more stable microclimate. Uetz (1991) suggested the shade, cooler temperatures and refuges provided by the heather architecture may "dampen interactions between spiders and decrease the impact of natural enemies".

Apparent fluctuations in abundance have been proved to be influenced by the prevalent conditions during the period of sampling. Pitfall traps depend upon movement for capture of invertebrates and so the probability of capture increases not only with an increasing population but also with favourable weather conditions. Changes in seasonal abundance (Figures 3.6-3.9) therefore in part represent changes in the activity of individual species. "The dependence of activity of Lycosidae on incident sunlight is immediately apparent on casual examination of any piece of open ground for, when the sun is shining, large numbers can be seen running over the ground only to disappear completely under duller conditions" (Williams 1962). Lycosidae provide the most reliable estimates of abundance as the animals move with sufficient momentum to fall readily into a trap and a fairly representative catch is possible

(Williams 1962). Peaks of activity are assumed to indicate the period of copulation as mates are actively sought (Vlijm, Annette & Kessler-Geschiere 1967). *T. terricola* showed no peak in abundance similar to that of the other Lycosidae as they are active earlier in the year, with their catch increasing from March onwards with their peak in activity in late April (Williams 1962). The restricted sampling period of this study has probably under-estimated the relative abundance of *T. terricola* within this family. Ideally sampling should extend throughout the year as species that have a life cycle in which peak abundance / activity does not coincide with the study period will be proportionally under represented by this study.

The seasonal distribution of Linyphiid abundance differed markedly between habitats (Figure 3.9). The heather community showed no pronounced peak in abundance (activity) over the trapping period. In contrast, the Linyphiidae caught on the pasture show a marked increase in abundance throughout June. Two reasons may explain the different distributions. The heather canopy may buffer climatic extremes creating a more equitable microclimate which may extend the reproductive period available to spiders. Alternatively the difference may simply reflect the lower species dominance in the heather. The activity periods of species in the heather are less dominated by a few species that contribute to the majority of abundance. The peak in abundance seen in the heather is largely due to the spring activity of *Oedothorax retusus* and *Silometopus elegans*.

4.4 Habitat preferences

In terms of geographical distribution and relative abundance, most species caught in this study were described by Roberts (1987a,b) as widespread, common or both. Lycosid species such as *Alopecosa pulverulenta*, *Pardosa pullata* and *Trochosa terricola* are commonly found over most of the British Isles in a wide variety of terrestrial habitats. Although abundances were highest in the pasture, *A. pulverulenta* and *P. pullata* were also relatively common in the heather vegetation. None of the other spider species were found in such high proportion in both habitats. *Pardosa nigriceps* is associated with low vegetation such as gorse and heather, and was the commonest species caught on the moorland. *Lepthyphantes ericaeus*, *Gonatium rubens*, *Bathyphantes parvulus* and *Bathyphantes gracilis* are other species associated with bushes and undergrowth that were only commonly found in the heather. *Oedothorax retusus*, *Silometopus elegans* and *Tiso vagans* were found almost entirely associated with the moss, grass and detritus at ground level associated with the pasture, although undergrowth may be another important habitat for them (Roberts 1987b). *S. elegans*, *Centromerita concinna*, *Agyneta decora* and *Pelecopsis mengei* are only typical of more northern upland areas.

The main contrast in the spider fauna between the two habitats was not a result of distinct and separate spider communities but in the difference in relative abundance between the two. This is demonstrated most clearly by the difference in the beta diversity calculated from Sorenson's Qualitative index (0.62) and Sorenson's Quantitative Index (0.2). By taking relative abundance into consideration the two faunas are reflected as being almost separate, rather than sharing the majority of species as assessed by a present / absent technique. The heather habitat was found to be the more diverse due not to higher species richness but to the more even distribution of abundance (Table 3.3).

Duffey (1978) found a positive correlation between the complexity of habitat structure and spider diversity. Heather has a more varied vertical structure that may be the cause of the higher diversity. The grazed pasture provided a more two-dimensional habitat with restricted vertical structure. In the relatively two-dimensional pasture, pitfalls sample the only habitat structure available to spiders; the ground surface. The heather vegetation provides spiders with other microhabitats in which to live, and they may rarely descend to the ground level. The dense straggly nature of mature heather vegetation may impede movement and reduce catches of certain cursorial spiders (e.g. Lycosidae). If *A. pulverulenta* and *P. pullata* are impeded in their search for food by the vegetation it means the habitat is less suitable and their abundances are likely to be lower. In the pasture, movement and vision are less obstructed and the spiders may forage more efficiently. In a more optimal habitat abundances will be higher. Another Lycosid, *P.nigriceps* is typically associated with gorse and heather vegetation (Roberts 1987a) and was the most frequently caught species in the moorland. Pitfall traps reflected this preference even though *P.nigriceps* may spend much of its time in the vegetation. Baars (1979) concluded that restriction of movement due to vegetation was not a major influence on Carabid catches. Observation of the invertebrate data shows that Coleoptera abundances were slightly greater in the moorland, which may support Baars' work. Although spiders may be affected differently than Coleoptera by vegetation the difference in relative abundance in this study (Table 3.3) are so large that it is felt to be a reflection of the true situation not a distortion caused by sampling inadequacies.

The dominance of Lycosidae have often been associated with disturbed habitats as the former can rapidly colonise new areas. Uetz (1976) found that Lycosids dominated a forest floodplain but were less abundant in more diverse stable habitats. Flooding affected the spider communities by destroying egg sacks and forcing spiders to disperse away from the habitat. Lycosids carry their egg sacks with them and their rapid movement allows them to rapidly colonise an area when the disturbance has receded. As the depth and complexity of leaf litter built up the dominance of Lycosids

decreased and other families (Clubionidae, Gnaphosidae, Thomisidae, Hahnidae and Agelenidae) increased in importance. The pasture, although more seasonally stable than a flood plain can still be considered a perturbation from the more natural moorland and the abundance of *A. pulverulenta* and *P. pullata* suggest that the habitat is a disturbed one. The heather is less dominated by these species and has representatives of two families not found in the pasture, Dictynidae and Hahniidae - two web builders. The heather provides more refuges from predators, amelioration of physical environment, crevices for egg attachment and web construction.

The importance of vegetation structure on spider diversity was first observed by Lowrie (1948). He noticed successional changes in the spider community associated with the stages of plant successional on sand dunes along Lake Michigan. The strongest correlation with spider diversity was vegetation structure, not the increase in the diversity of available prey. Greenstone (1984) also found clear trends between web spinner diversity and vegetation structure diversity. This was attributed to more attachment sites in habitats with greater spatial heterogeneity. No correlation was found with increased prey abundance. Uetz (1991) stated "the physical structure of environments has an important influence on the habitat preferences of spider species and ultimately on the composition of spider communities". Vegetation may influence the spiders habitat selection not only through vegetation architecture but through other associated variables, such as problems of desiccation, exposure of the web to wind and exposure to insolation.

4.5 Problems in detecting an altitudinal influence.

The change in structure of spider communities along altitudinal gradients has been observed by Coulson and Butterfield (1986), and Otto and Svesson (1982). "Diversity declines with increase in altitude, as does the number of species caught. The decline in the number of species caught is the effect of a decrease in non-Linyphiidae species with increasing altitude" Coulson and Butterfield (1986). These studies involved pitfall trapping across a wide altitude range (at least 800m) and sampling continued for over a year.

The statistically significant correlations of *A. pulverulenta*, *P. pullata*, *P. degeeri* and *W. acuminata* with changes in altitude in this study may not however, be biologically significant. The absence of comparable trends in each habitat undermines confidence in any biological explanation. The marginal significance of beta diversity recorded between pitfall stations at 480m and 500m also appears fortuitous. The lack of significant differences between stations with a greater range in altitude cast doubt on there being any biological reason for the correlation.

There are several reasons why the present study failed to detect significant

changes in spider diversity with altitude. The altitude range covered by sampling may have been too small, the sampling period may have been too short or more pitfall traps or other sampling methods may have been required. The altitude range of the present study was only *ca.*140m but it was hoped the high sampling intensity (pitfalls every 40m or less) would be sufficient to detect changes in diversity. Coulson and Butterfield (1986) showed that Williams α diversity showed a progressive decline with increasing altitude due mainly to the marked reduction in the numbers of non-Linyphiidae species. Approximately one non-Linyphiidae species disappeared for every 43m rise in altitude, representing a loss of 21% of the species in a 100m (413 - 513m) range (Coulson and Butterfield 1986). This altitude range is comparable to the present study and so a significant change may have been expected. However, a 21% loss of non-Linyphiidae species was a finding based on the entire altitude range. Within just the 413-513m range Coulson and Butterfield (1986) recorded considerable scatter which this study fails to define sufficiently to recognise the same trend.

Changes to the methodology involving a longer sampling period, more pitfall traps, more pitfall station, or using other sampling methods were prohibitive due solely to the limitations of time.

4.6 Affinities of the Monk's Moor spider fauna

Cherrett (1964) compared the family composition of spiders at Moor House to those of Brazil, France, Britain and Iceland and noticed the family structure followed a general Sub-Arctic pattern, more akin to Iceland than the rest of Britain. The family composition of Monk's Moor fauna, especially the increased importance of the Linyphiidae (77%), shows the same affinity to more northern regions. Cherrett (1964) recorded 71 species of spider at Moor House and although slightly more were collected at Monk's Moor they both reflect an impoverished spider fauna, both in the number of species and in the number of families represented. Duffey (1962) for example, collected 141 species from a lowland limestone grassland near Oxford.

4.7 Invertebrate data

Margalef's index recorded a significant relationship between diversity and both habitat and altitude. The diversity values also showed that the higher the initial diversity in the heather the larger the fall in diversity to the pasture. The larger fall in diversity from initially the more diverse sites may be a reflection of how the more complex (diverse) communities can be the least stable. This supports the models of Pimm (1979) and May (1976) who argue against the more traditional view that complexity causes stability. However, due to the small number of orders involved in the diversity calculation these data cannot be used to confidently support these models.

Margalef's index is based solely on richness (*i.e.* number of orders present) and total abundance so the distribution of abundance is ignored. As the number of orders was so low Margalef's index was very sensitive to change in the number of orders. For example, a typical pasture site had an average of 10 orders and 1000 individuals. A decrease by only one order has the same effect on the index as that of doubling abundance. The disappearance of one order (five individual Pulmonata) at pitfall station 480m in the pasture was sufficient to establish a significant relationship with altitude. The statistical significance of these results can be attributed to limitations in the analysis and not to underlying biological causes. The order level of invertebrate identification was probably too high a taxonomic level to be sensitive to subtle changes in diversity.

5.0 SPECIES CHECK LIST

Classification and nomenclature corresponds to the check list given in volume II of The Spiders of Great Britain and Ireland (Roberts 1987b).

DICTYNIDAE	<i>Dictyna arundinacea</i>	(Linnaeus, 1758)
GNAPHOSIDAE	<i>Drassodes cupreus</i>	(Blackwall, 1834)
	<i>Haplodrassus signifer</i>	(C. L. Koch, 1839)
	<i>Gnaphosa leporina</i>	(L. Koch, 1866)
CLUBIONIDAE	<i>Clubiona trivialis</i>	(C. L. Koch, 1841)
	<i>Clubiona diversa</i>	(O. P. -Cambridge, 1862)
THOMISIDAE	<i>Xysticus cristatus</i>	(Clerck, 1757)
	<i>Oxyptila trux</i>	(Blackwall, 1846)
LYCOSIDAE	<i>Pardosa monticola</i>	(Clerck, 1757)
	<i>Pardosa pullata</i>	(Clerck, 1757)
	<i>Pardosa amentata</i>	(Clerck, 1757)
	<i>Pardosa nigriceps</i>	(Thorell, 1856)
	<i>Alopecosa pulverulenta</i>	(Clerck, 1757)
	<i>Trochosa terricola</i>	(Thorell, 1856)
	<i>Pirata piraticus</i>	(Clerck, 1757)
AGELENIDAE	<i>Coelotes atropos</i>	(Walckenaer, 1825)
HAHNIIDAE	<i>Antistea elegans</i>	(Blackwall, 1841)
THERIDIIDAE	<i>Robertus lividus</i>	(Blackwall, 1836)
	<i>Pholcomma gibbum</i>	(Westring, 1851)
TETRAGNATHIDAE	<i>Pachygnatha degeeri</i>	(Sundevall, 1830)
LINYPHIIDAE	<i>Ceratinella brevipes</i>	(Westring, 1851)
	<i>Walckenaeria nudipalpis</i>	(Westring, 1851)
	<i>Walckenaeria vigilax</i>	(Blackwall, 1853)
	<i>Walckenaeria antica</i>	(Wider, 1834)
	<i>Walckenaeria cucullata</i>	(C. L. Koch, 1836)
	<i>Walckenaeria nodosa</i>	(O. P. -Cambridge, 1873)
	<i>Walckenaeria clavicornis</i>	(Emerton, 1882)
	<i>Walckenaeria acuminata</i>	(Blackwall, 1833)
	<i>Dicymbium nigrum</i> f. <i>brevisetosum</i>	(Locket, 1962)
	<i>Dicymbium tibiale</i>	(Blackwall, 1836)
	<i>Hypomma bituberculatum</i>	(Wider, 1834)
	<i>Gonatium rubens</i>	(Blackwall, 1833)
	<i>Peponocranium ludicrum</i>	(O. P. -Cambridge, 1861)

<i>Pocadicnemis pumila</i>	(Blackwall, 1841)
<i>Pocadicnemis juncea</i>	(Locket & Millidge, 1953)
<i>Hypselistes jacksoni</i>	(O. P. -Cambridge, 1902)
<i>Oedothorax gibbosus</i>	(Blackwall, 1841)
<i>Oedothorax fuscus</i>	(Westring, 1851)
<i>Oedothorax retusus</i>	(Westring, 1851)
<i>Pelecopsis mengei</i>	(Simon, 1884)
<i>Silometopus elegans</i>	(O. P. -Cambridge, 1872)
<i>Cnephalocotes obscurus</i>	(Blackwall, 1834)
<i>Tiso vagans</i>	(Blackwall, 1834)
<i>Minyriolus pusillus</i>	(Wider, 1834)
<i>Tapinocyba praecox</i>	(O. P. -Cambridge, 1873)
<i>Tapinocyba pallens</i>	(O. P. -Cambridge, 1872)
<i>Monocephalus fuscipes</i>	(Blackwall, 1836)
<i>Lophomma punctatum</i>	(Blackwall, 1841)
<i>Gongylidiellum vivum</i>	(O. P. -Cambridge, 1875)
<i>Micrargus herbigradus</i>	(Blackwall, 1854)
<i>Erigonella hiemalis</i>	(Blackwall, 1841)
<i>Savignya frontata</i>	(Blackwall, 1833)
<i>Diplocephalus permixtus</i>	(O. P. -Cambridge, 1871)
<i>Diplocephalus latifrons</i>	(O. P. -Cambridge, 1863)
<i>Araeoncus crassiceps</i>	(Westring, 1861)
<i>Scotinotylus evansi</i>	(O. P. -Cambridge, 1894)
<i>Erigone dentipalpis</i>	(Wider, 1834)
<i>Erigone atra</i>	(Blackwall, 1841)
<i>Latithorax faustus</i>	(O. P. -Cambridge, 1900)
<i>Leptothrix hardyi</i>	(Blackwall, 1850)
<i>Hilaira excisa</i>	(O. P. -Cambridge, 1870)
<i>Porhomma campbelli</i>	(F. O. P. Cambridge, 1894)
<i>Porhomma montanum</i>	(Jackson, 1913)
<i>Agyneta decora</i>	(O. P. -Cambridge, 1870)
<i>Agyneta conigera</i>	(O. P. -Cambridge, 1863)
<i>Meioneta saxatilis</i>	(Blackwall, 1844)
<i>Centromerus sylvaticus</i>	(Blackwall, 1841)
<i>Centromerus prudens</i>	(O. P. -Cambridge, 1873)
<i>Centromerus dilutus</i>	(O. P. -Cambridge, 1875)
<i>Tallusia experta</i>	(O. P. -Cambridge, 1871)
<i>Centromerita bicolor</i>	(Blackwall, 1833)

<i>Centromerita concinna</i>	(Thorell, 1875)
<i>Oreonetides vaginatus</i>	(Thorell, 1872)
<i>Saaristoa abnormis</i>	(Blackwall, 1841)
<i>Bathyphantes gracilis</i>	(Blackwall, 1841)
<i>Bathyphantes parvulus</i>	(Westring, 1851)
<i>Diplostyla concolor</i>	(Wider, 1834)
<i>Poeciloneta globosa</i>	(Wider, 1834)
<i>Stemonyphantes lineatus</i>	(Linnaeus, 1758)
<i>Bolyphantes luteolus</i>	(Blackwall, 1833)
<i>Lepthyphantes alacris</i>	(Blackwall, 1853)
<i>Lepthyphantes obscurus</i>	(Blackwall, 1841)
<i>Lepthyphantes tenuis</i>	(Blackwall, 1852)
<i>Lepthyphantes zimmermanni</i>	(Bertkau, 1890)
<i>Lepthyphantes mengei</i>	(Kulczynski, 1887)
<i>Lepthyphantes ericaeus</i>	(Blackwall, 1853)
<i>Lepthyphantes pallidus</i>	(Simon, 1884)
<i>Lepthyphantes angulatus</i>	(O. P. -Cambridge, 1881)

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7.0 APPENDIX 1

	13/05/94	Pasture					Heather					
		Altitude (m)	360	400	440	480	500	360	400	440	480	500
Dictynidae	<i>Dictyna arundinacea</i>											
Gnaphosidae	<i>Drassodes cupreus</i>								1			
	<i>Haplodrassus signifer</i>		3		2							
	<i>Gnaphosa leporina</i>											
Clubionidae	<i>Clubiona diversa</i>				3	1					1	
	<i>Clubiona trivialis</i>											
Thomisidae	<i>Xysticus cristatus</i>					1						
	<i>Oxyptila trux</i>						1					
Lycosidae	<i>Pardosa pullata</i>	4	13	3	12	12						
	<i>Pardosa monticola</i>						3				1	
	<i>Pardosa nigriceps</i>											
	<i>Pardosa amentata</i>										3	
	<i>Alopecosa pulverulenta</i>	8	5	8	7	9			3			
	<i>Trochosa terricola</i>	22	4	19								
	<i>Pirata piraticus</i>								1	1		
Agelenidae	<i>Coelotes atropos</i>				2	1						
Hahniidae	<i>Antistea elegans</i>										2	1
Theridiidae	<i>Robertus lividus</i>											
	<i>Pholcomma gibbum</i>											
Tetragnathidae	<i>Pachygnatha degeeri</i>	12	1									
Linyphiidae	<i>Ceratinella brevipes</i>		1	1	2	1	3	19	6	22	7	
	<i>Walckenaeria nudipalpis</i>								1			
	<i>Walckenaeria vigilax</i>			1		2						
	<i>Walckenaeria antica</i>			2	1				2	1		
	<i>Walckenaeria cucullata</i>											
	<i>Walckenaeria nodosa</i>											
	<i>Walckenaeria clavicornis</i>				4							
	<i>Walckenaeria acuminata</i>		1					2	3	5	9	
	<i>Dicymbium f. brevisetosum</i>	3		13	1							1
	<i>Dicymbium tibiale</i>						1					
	<i>Hypomma bituberculatum</i>											
	<i>Gonatium rubens</i>					1	1	1	2	1	3	
	<i>Peponocranium ludicrum</i>											
	<i>Pocadicnemis pumila</i>											
	<i>Pocadicnemis juncea</i>											
	<i>Hypselistes jacksoni</i>											
	<i>Oedothorax gibbosus</i>								1			
	<i>Oedothorax fuscus</i>	12										
	<i>Oedothorax retusus</i>	14	8	11	2	4						
	<i>Pelecopsis mengei</i>						4	6		5	1	
	<i>Silometopus elegans</i>		2		1							
	<i>Cnephalocotes obscurus</i>											
	<i>Tiso vagans</i>		41	63	7	4			1	1		
	<i>Minyriolus pusillus</i>											
	<i>Tapinocyba praecox</i>		2	1	1							
	<i>Tapinocyba pallens</i>											
	<i>Monocephalus fuscipes</i>	1	19	2		1		2	1			
	<i>Lophomma punctatum</i>	1										

	<i>Gongylidiellum vivum</i>												
	<i>Micrargus herbigradus</i>	4	3	1									
	<i>Erigonella hiemalis</i>		1	1	1		5	1					
	<i>Savignya frontata</i>					1							
	<i>Diplocephalus permixtus</i>	1		1									
	<i>Diplocephalus latifrons</i>			1									
	<i>Araeoncus crassiceps</i>												
	<i>Scotinotylus evansi</i>												
	<i>Erigone dentipalpis</i>			4	1								
	<i>Erigone atra</i>	2	1										
	<i>Latithorax faustus</i>						2		1				
	<i>Leptothrix hardyi</i>								1				
	<i>Hilaira excisa</i>												
	<i>Porrhomma pygmaeum</i>												
	<i>Porrhomma campbelli</i>							1					
	<i>Porrhomma montanum</i>					1			1				
	<i>Agyneta decora</i>												
	<i>Agyneta conigera</i>												
	<i>Meioneta saxatilis</i>												
	<i>Centromerus sylvaticus</i>												
	<i>Centromerus prudens</i>												1
	<i>Centromerus dilutus</i>						1						
	<i>Tallusia experta</i>												
	<i>Centromerita bicolor</i>			1									
	<i>Centromerita concinna</i>	1	3	4	9	4	1						
	<i>Oreonetides vaginatus</i>											1	
	<i>Saaristoa abnormis</i>						1						
	<i>Bathyphantes gracilis</i>	2									2	1	
	<i>Bathyphantes parvulus</i>					1			1				
	<i>Diplostyla concolor</i>												
	<i>Poeciloneta globosa</i>												
	<i>Stemonyphantes lineatus</i>												1
	<i>Bolyphantes luteolus</i>						2				1	1	
	<i>Lepthyphantes alacris</i>												1
	<i>Lepthyphantes obscurus</i>												
	<i>Lepthyphantes tenuis</i>						1						
	<i>Lepthyphantes zimmermanni</i>	1				1	1	1	2	3		8	
	<i>Lepthyphantes mengei</i>						1		2				
	<i>Lepthyphantes ericaeus</i>					1	4	2	2	1			
	<i>Lepthyphantes pallidus</i>				1				2				
	<i>Lepthyphantes angulatus</i>						2						2
	juveniles	2	17	18	8	11	0	12	5	2		7	

	01/06/94	Pasture					Heather				
	Altitude (m)	360	400	440	480	500	360	400	440	480	500
Dictynidae	<i>Dictyna arundinacea</i>										
Gnaphosidae	<i>Drassodes cupreus</i>										
	<i>Haplodrassus signifer</i>			3							
	<i>Gnaphosa leporina</i>										
Clubionidae	<i>Clubiona diversa</i>				2						
	<i>Clubiona trivialis</i>									1	
Thomisidae	<i>Xysticus cristatus</i>	4	3	1		1					
	<i>Oxyptila trux</i>										
Lycosidae	<i>Pardosa pullata</i>	14	62	23	15	25	3		10	1	
	<i>Pardosa monticola</i>				1						
	<i>Pardosa nigriceps</i>	1					1			2	
	<i>Pardosa amentata</i>										
	<i>Alopecosa pulverulenta</i>	23	24	17	2	3	1		3		
	<i>Trochosa terricola</i>	15	13	19			2	5	4		
	<i>Pirata piraticus</i>										
Agelenidae	<i>Coelotes atropos</i>								2	3	
Hahniidae	<i>Antistea elegans</i>										
Theridiidae	<i>Robertus lividus</i>		2	1			2			7	
	<i>Pholcomma gibbum</i>										
Tetragnathidae	<i>Pachygnatha degeeri</i>	20	2	3							
Linyphiidae	<i>Ceratinella brevipes</i>				3	1	5	12	5	22	6
	<i>Walckenaeria nudipalpis</i>										
	<i>Walckenaeria vigilax</i>										
	<i>Walckenaeria antica</i>		1			1				1	
	<i>Walckenaeria cucullata</i>		1								
	<i>Walckenaeria nodosa</i>										
	<i>Walckenaeria clavicornis</i>			1	7	4					
	<i>Walckenaeria acuminata</i>							4	3		3
	<i>Dicymbium f. brevisetosum</i>	4		9	1	2			1		
	<i>Dicymbium tibiale</i>						1	2			
	<i>Hypomma bituberculatum</i>						1				
	<i>Gonatium rubens</i>							3	1	3	1
	<i>Peponocranium ludicrum</i>						2	1	2		
	<i>Pocadicnemis pumila</i>										
	<i>Pocadicnemis juncea</i>						1				
	<i>Hypselistes jacksoni</i>										1
	<i>Oedothis gibbosus</i>	2	1								
	<i>Oedothis fuscus</i>	2			1						
	<i>Oedothis retusus</i>	13	46	31	16	26					
<i>Pelecopsis mengei</i>		1				5	10			2	
<i>Silometopus elegans</i>		21	16	5	9	1		1			
<i>Cnephalocotes obscurus</i>	1										
<i>Tiso vagans</i>		16	33	6	5		1	3	1		
<i>Minyriolus pusillus</i>						1	3	1			
<i>Tapinocyba praecox</i>											
<i>Tapinocyba pallens</i>		1									
<i>Monocephalus fuscipes</i>		6					5			2	
<i>Lophomma punctatum</i>											
<i>Gongylidiellum vivum</i>											

<i>Micrargus herbigradus</i>	1	3	3		1					1
<i>Erigonella hiemalis</i>										
<i>Savignya frontata</i>	1									
<i>Diplocephalus permixtus</i>				1				1		
<i>Diplocephalus latifrons</i>										
<i>Araeoncus crassiceps</i>				1						
<i>Scotinotylus evansi</i>					2					
<i>Erigone dentipalpis</i>	2			2						
<i>Erigone atra</i>										
<i>Latithorax faustus</i>						1	1			
<i>Leptothrix hardyi</i>										
<i>Hilaira excisa</i>										
<i>Porrhomma pygmaeum</i>										
<i>Porrhomma campbelli</i>										
<i>Porrhomma montanum</i>					5					
<i>Agyneta decora</i>		4	1							
<i>Agyneta conigera</i>										
<i>Meioneta saxatilis</i>										
<i>Centromerus sylvaticus</i>										
<i>Centromerus prudens</i>							2			
<i>Centromerus dilutus</i>										
<i>Tallusia experta</i>										1
<i>Centromerita bicolor</i>		1	2							
<i>Centromerita concinna</i>	2	3	3	8	14	2	1		3	
<i>Oreonetides vaginatus</i>									1	
<i>Saaristoa abnormis</i>							1			
<i>Bathyphantes gracilis</i>						1	2		3	2
<i>Bathyphantes parvulus</i>				1				1		
<i>Diplostyla concolor</i>										
<i>Poecilometes globosa</i>										
<i>Stemonyphantes lineatus</i>				1				1	1	1
<i>Bolyphantes luteolus</i>						1			1	1
<i>Lepthyphantes alacris</i>										
<i>Lepthyphantes obscurus</i>										
<i>Lepthyphantes tenuis</i>						1				
<i>Lepthyphantes zimmermanni</i>						4	3	3	3	5
<i>Lepthyphantes mengei</i>	1					4	2	2		
<i>Lepthyphantes ericaeus</i>	1					5	5		1	2
<i>Lepthyphantes pallidus</i>			2	2			2	6	1	1
<i>Lepthyphantes angulatus</i>									2	
juveniles	1	12	16	6	6	29	13	6	12	9

	15/06/94	Pasture					Heather				
	Altitude (m)	360	400	440	480	500	360	400	440	480	500
Dictynidae	<i>Dictyna arundinacea</i>										
Gnaphosidae	<i>Drassodes cupreus</i>										
	<i>Haplodrassus signifer</i>	1	3	1	1			1		5	
	<i>Gnaphosa leporina</i>										
Clubionidae	<i>Clubiona diversa</i>				1	1					
	<i>Clubiona trivialis</i>										
Thomisidae	<i>Xysticus cristatus</i>	5	4		7	4					1
	<i>Oxyptila trux</i>										
Lycosidae	<i>Pardosa pullata</i>	37	59	39	77	84	3	1	12	8	4
	<i>Pardosa monticola</i>	3	4		1	2			1	1	
	<i>Pardosa nigriceps</i>	3	1				51		1	36	
	<i>Pardosa amentata</i>			1							2
	<i>Alopecosa pulverulenta</i>	143	78	66	44	21	2	4	27	24	1
	<i>Trochosa terricola</i>	17	15	8	1			1	5	3	
	<i>Pirata piraticus</i>								1		
Agelenidae	<i>Coelotes atropos</i>								1	1	1
Hahniidae	<i>Antistea elegans</i>						1				
Theridiidae	<i>Robertus lividus</i>	3	2		5	2	6	3	3	13	2
	<i>Pholcomma gibbum</i>										
Tetragnathidae	<i>Pachygnatha degeeri</i>	40	6	9	2	1			1		
Linyphiidae	<i>Ceratinella brevipes</i>	1			5	1	4	14	2	22	10
	<i>Walckenaeria nudipalpis</i>				1						
	<i>Walckenaeria vigilax</i>										
	<i>Walckenaeria antica</i>		3	2					1		
	<i>Walckenaeria cucullata</i>										
	<i>Walckenaeria nodosa</i>	1									
	<i>Walckenaeria clavicornis</i>			1	1						
	<i>Walckenaeria acuminata</i>					1	3	1	4	5	
	<i>Dicymbium f. brevisetosum</i>			12		1					
	<i>Dicymbium tibiale</i>		1								
	<i>Hypomma bituberculatum</i>										3
	<i>Gonatium rubens</i>						2	1		8	1
	<i>Peponocranium ludicrum</i>						1			1	
	<i>Pocadicnemis pumila</i>						3				
	<i>Pocadicnemis juncea</i>										
	<i>Hypselistes jacksoni</i>			1				2		1	
	<i>Oedothorax gibbosus</i>	2	1	1							
	<i>Oedothorax fuscus</i>	1									
	<i>Oedothorax retusus</i>	16	68	47	36	42					1
	<i>Pelecopsis mengei</i>						3	5		2	3
	<i>Silometopus elegans</i>	8	88	41	33	22	2	2	1		
	<i>Cnephalocotes obscurus</i>				1						
	<i>Tiso vagans</i>		14	23	1	8			1	1	
	<i>Minyriolus pusillus</i>							1			
	<i>Tapinocyba praecox</i>		1	1							
	<i>Tapinocyba pallens</i>										
	<i>Monocephalus fuscipes</i>		5					2	1		1
	<i>Lophomma punctatum</i>										
	<i>Gongylidiellum vivum</i>			2							

<i>Micrargus herbigradus</i>	1	5	8		2			1		
<i>Erigonella hiemalis</i>									1	
<i>Savignya frontata</i>										
<i>Diplocephalus permixtus</i>		2		6	1			1		
<i>Diplocephalus latifrons</i>										
<i>Araeoncus crassiceps</i>										
<i>Scotino tylus evansi</i>					1					
<i>Erigone dentipalpis</i>		1	2	1	4					
<i>Erigone atra</i>					1					
<i>Latithorax faustus</i>		1								
<i>Leptothrix hardyi</i>										
<i>Hilaira excisa</i>										
<i>Porrhomma pygmaeum</i>										
<i>Porrhomma campbelli</i>										
<i>Porrhomma montanum</i>			4	1	4					
<i>Agynera decora</i>	1	5	12	2	1	1		1		
<i>Agynera conigera</i>										
<i>Meioneta saxatilis</i>	4			2	1					
<i>Centromerus sylvaticus</i>										
<i>Centromerus prudens</i>										
<i>Centromerus dilutus</i>										
<i>Tallusia experta</i>										
<i>Centromerita bicolor</i>										
<i>Centromerita concinna</i>			2	8	9				1	
<i>Oreonetides vaginatus</i>										
<i>Saaristoa abnormis</i>										
<i>Bathyphantes gracilis</i>	2	1	1					1	2	1
<i>Bathyphantes parvulus</i>			1		4		1	4	5	8
<i>Diplostyla concolor</i>										
<i>Poecilonea globosa</i>										
<i>Stemonyphantes lineatus</i>				2				1	1	
<i>Bolyphantes luteolus</i>		1							1	
<i>Lepthyphantes alacris</i>							3			
<i>Lepthyphantes obscurus</i>										
<i>Lepthyphantes tenuis</i>						1				
<i>Lepthyphantes zimmermanni</i>						23	3	6	3	8
<i>Lepthyphantes mengei</i>	1	3			1	2		8	3	1
<i>Lepthyphantes ericaeus</i>		2	1			4	1	1	3	5
<i>Lepthyphantes pallidus</i>		1			1	3	1		1	
<i>Lepthyphantes angulatus</i>									3	
juveniles		9	15	8	5	19	20	8	23	15

	30/6/94	Pasture					Heather					
		Altitude (m)	360	400	440	480	500	360	400	440	480	500
Dictynidae	<i>Dictyna arundinacea</i>							1				
Gnaphosidae	<i>Drassodes cupreus</i>	1										
	<i>Haplodrassus signifer</i>		6	1	1							1
	<i>Gnaphosa leporina</i>					1						
Clubionidae	<i>Clubiona diversa</i>				1	1						
	<i>Clubiona trivialis</i>											
Thomisidae	<i>Xysticus cristatus</i>	1	2		2	1				1		
	<i>Oxyptila trux</i>						1			1		
Lycosidae	<i>Pardosa pullata</i>	17	32	41	54	55	1			2	5	3
	<i>Pardosa monticola</i>	5	1	1	2	3				1		
	<i>Pardosa nigriceps</i>	3	3				19	8	6	30		2
	<i>Pardosa amentata</i>											
	<i>Alopecosa pulverulenta</i>	68	57	33	31	16	4	1	13	13		1
	<i>Trochosa terricola</i>		5	5						1		
	<i>Pirata piraticus</i>			1						1		
Agelenidae	<i>Coelotes atropos</i>		1		1							
Hahniidae	<i>Antistea elegans</i>											
Theridiidae	<i>Robertus lividus</i>	4	1	1	1	1	10	1	2	7		
	<i>Pholcomma gibbum</i>							1				
Tetragnathidae	<i>Pachygnatha degeeri</i>	19	12	16	3					1		
Linyphiidae	<i>Ceratinella brevipes</i>		1				3	7	2	12		6
	<i>Walckenaeria nudipalpis</i>											
	<i>Walckenaeria vigilax</i>		1	2			1					
	<i>Walckenaeria antica</i>		5	5	1							
	<i>Walckenaeria cucullata</i>											
	<i>Walckenaeria nodosa</i>											
	<i>Walckenaeria clavicornis</i>											
	<i>Walckenaeria acuminata</i>								4	4	4	4
	<i>Dicymbium f. brevisetosum</i>	1	1	14								
	<i>Dicymbium tibiale</i>											
	<i>Hypomma bituberculatum</i>	2										
	<i>Gonatium rubens</i>							2	1	4		2
	<i>Peponocranium ludicrum</i>				1							3
	<i>Pocadicnemis pumila</i>											
	<i>Pocadicnemis juncea</i>		2									1
	<i>Hypselistes jacksoni</i>	1			1							
	<i>Oedothorax gibbosus</i>	1		1	1			3		3		
<i>Oedothorax fuscus</i>	1											
<i>Oedothorax retusus</i>	24	82	61	43	49	1			1			
<i>Pelecopsis mengei</i>						3	4			2	4	
<i>Silometopus elegans</i>	9	81	11	29	25	2	1				1	
<i>Cnephalocotes obscurus</i>						1						
<i>Tiso vagans</i>		46	51	8	4		1	2				
<i>Minyriolus pusillus</i>							2	2	1			
<i>Tapinocyba praecox</i>		1										
<i>Tapinocyba pallens</i>												
<i>Monocephalus fuscipes</i>		1										
<i>Lophomma punctatum</i>												
<i>Gongylidiellum vivum</i>		1	1							1		

	<i>Micrargus herbigradus</i>	3	4	7					1		
	<i>Erigonella hiemalis</i>										
	<i>Savignya frontata</i>										
	<i>Diplocephalus permixtus</i>	1				1					1
	<i>Diplocephalus latifrons</i>										
	<i>Araeoncus crassiceps</i>										
	<i>Scotinotylus evansi</i>										
	<i>Erigone dentipalpis</i>		3	2	1	1					
	<i>Erigone atra</i>	1				2					
	<i>Latithorax faustus</i>						1				
	<i>Leptothrix hardyi</i>										
	<i>Hilaira excisa</i>	1									
	<i>Porrhomma pygmaeum</i>										
	<i>Porrhomma campbelli</i>										
	<i>Porrhomma montanum</i>			1		2	1	1			
	<i>Agyneta decora</i>	2	3	4	5	2	1	1		1	
	<i>Agyneta conigera</i>		2								
	<i>Meioneta saxatilis</i>	6				1					
	<i>Centromerus sylvaticus</i>							1			
	<i>Centromerus prudens</i>		1		2		1	1		1	
	<i>Centromerus dilutus</i>						1				
	<i>Tallusia experta</i>										
	<i>Centromerita bicolor</i>										
	<i>Centromerita concinna</i>	2	2		7	4			2	1	
	<i>Oreonetides vaginatus</i>										
	<i>Saaristoa abnormis</i>		1				5				
	<i>Bathyphantes gracilis</i>							2	4	4	2
	<i>Bathyphantes parvulus</i>	3	2	1		1	2	4	2		
	<i>Diplostyla concolor</i>			1							
	<i>Poeciloneta globosa</i>										
	<i>Stemonyphantes lineatus</i>									1	
	<i>Bolyphantes luteolus</i>			1		1					
	<i>Lepthyphantes alacris</i>										
	<i>Lepthyphantes obscurus</i>							1	1		
	<i>Lepthyphantes tenuis</i>	1							1		
	<i>Lepthyphantes zimmermanni</i>		1				15	8	10	5	17
	<i>Lepthyphantes mengei</i>	2	2	4	1	1		5	3	3	
	<i>Lepthyphantes ericaeus</i>		1	1		1	2	1	1		2
	<i>Lepthyphantes pallidus</i>	1				3	2	4	1	4	2
	<i>Lepthyphantes angulatus</i>										
	juveniles		3	5	2	7	19	8	12	19	15

	14/7/94	Pasture					Heather				
	Altitude (m)	360	400	440	480	500	360	400	440	480	500
Dictynidae	<i>Dictyna arundinacea</i>										
Gnaphosidae	<i>Drassodes cupreus</i>								1	1	
	<i>Haplodrassus signifer</i>				1	1					
	<i>Gnaphosa leporina</i>										
Clubionidae	<i>Clubiona diversa</i>										
	<i>Clubiona trivialis</i>									1	
Thomisidae	<i>Xysticus cristatus</i>	1	2	1	1	1					
	<i>Oxyptila trux</i>								1	1	
Lycosidae	<i>Pardosa pullata</i>	14	25	30	27	27	1				
	<i>Pardosa monticola</i>	1	4	3	5	3		2	5	33	1
	<i>Pardosa nigriceps</i>		3		1		11				
	<i>Pardosa amentata</i>								5	6	1
	<i>Alopecosa pulverulenta</i>	20	19	27	15	10				1	1
	<i>Trochosa terricola</i>	5	2	2		1	1				
	<i>Pirata piraticus</i>					2		1		1	
Agelenidae	<i>Coelotes atropos</i>		1								
Hahniidae	<i>Antistea elegans</i>							1	1		
Theridiidae	<i>Robertus lividus</i>	1					6				
	<i>Pholcomma gibbum</i>			1							
Tetragnathidae	<i>Pachygnatha degeeri</i>	17	6	17	2			8		7	1
	<i>Ceratinella brevipes</i>						2				
	<i>Walckenaeria nudipalpis</i>				1			2			
	<i>Walckenaeria vigilax</i>		2	3					1		
	<i>Walckenaeria antica</i>			6							
	<i>Walckenaeria cucullata</i>										
	<i>Walckenaeria nodosa</i>										
	<i>Walckenaeria clavicornis</i>								2	2	4
	<i>Walckenaeria acuminata</i>			1							
	<i>Dicymbium f. brevisetosum</i>	2		4		1					
	<i>Dicymbium tibiale</i>										
	<i>Hypomma bituberculatum</i>									4	1
	<i>Gonatium rubens</i>						1				
	<i>Peponocranium ludicrum</i>										
	<i>Pocadicnemis pumila</i>										
	<i>Pocadicnemis juncea</i>										
	<i>Hypselistes jacksoni</i>										
	<i>Oedothorax gibbosus</i>	2		2			1				
	<i>Oedothorax fuscus</i>	1								2	
	<i>Oedothorax retusus</i>	19	36	32	41	46		9	1	1	2
	<i>Pelecopsis mengei</i>						8		1	2	1
	<i>Silometopus elegans</i>	12	39	10	29	25	1				
	<i>Cnephalocotes obscurus</i>							3			
	<i>Tiso vagans</i>		9	32	8	4					
	<i>Minyriolus pusillus</i>						2				
	<i>Tapinocyba praecox</i>										
	<i>Tapinocyba pallens</i>							1			
	<i>Monocephalus fuscipes</i>		3								
	<i>Lophomma punctatum</i>										
	<i>Gongylidiellum vivum</i>										

	<i>Micrargus herbigradus</i>	4	2	3	3		1					
	<i>Erigonella hiemalis</i>											
	<i>Savignya frontata</i>	1										
	<i>Diplocephalus permixtus</i>											
	<i>Diplocephalus latifrons</i>											
	<i>Araeoncus crassiceps</i>											
	<i>Scotinotylus evansi</i>											
	<i>Erigone dentipalpis</i>	2			4	1						
	<i>Erigone atra</i>		1									
	<i>Latithorax faustus</i>											
	<i>Leptothrix hardyi</i>											
	<i>Hilaira excisa</i>	1										
	<i>Porrhomma pygmaeum</i>											
	<i>Porrhomma campbelli</i>							1				
	<i>Porrhomma montanum</i>											
	<i>Agynera decora</i>		1	1	2	2	1					
	<i>Agynera conigera</i>											
	<i>Meioneta saxatilis</i>	5			2	2						
	<i>Centromerus sylvaticus</i>											
	<i>Centromerus prudens</i>											
	<i>Centromerus dilutus</i>											
	<i>Tallusia experta</i>											
	<i>Centromerita bicolor</i>											
	<i>Centromerita concinna</i>		1		3	2						
	<i>Oreonetides vaginatus</i>							7				1
	<i>Saaristoa abnormis</i>					1	5	2				
	<i>Bathyphantes gracilis</i>	1				4	1	2	2	1		2
	<i>Bathyphantes parvulus</i>						1					
	<i>Diplostyla concolor</i>									1		1
	<i>Poeciloneta globosa</i>											
	<i>Stemonyphantes lineatus</i>						1					
	<i>Bolyphantes luteolus</i>											
	<i>Lepthyphantes alacris</i>											
	<i>Lepthyphantes obscurus</i>											
	<i>Lepthyphantes tenuis</i>							14	2	17		12
	<i>Lepthyphantes zimmermanni</i>					1	15		1	2		
	<i>Lepthyphantes mengei</i>	5	5	3		2						3
	<i>Lepthyphantes ericaeus</i>	1		2	1		6	1	2	3		2
	<i>Lepthyphantes pallidus</i>		2	3		1	4					
	<i>Lepthyphantes angulatus</i>							13	4	11		12
	juveniles	3	1	5	4	4	34					

8.0 APPENDIX 2

	13/05/94	Pasture					Heather				
	Altitude (m)	360	400	440	480	500	360	400	440	480	500
Oligochaeta		18	5	4	1	1		1			
Arachnida	Pseudoscorpionida										
	Araneae	90	125	155	65	57	34	47	39	53	44
	Opiliones					2	2	3	8	14	9
	Acari	92	31	116	44	28	19	21	10	8	14
Diplopoda	Chordeumatid						1	1			
Chilopoda	Geophilomorpha										
	Lithobiomorpha										1
Insecta	Collembola	111	471	310	127	117	34	23	18	16	14
	Othoptera										
	Hemiptera		3				5	12	21	12	
	Megaloptera			1							
	Lepidoptera	4	3	3		1	2		1	4	5
	Diptera	128	95	50	62	42	40	16	19	38	24
	Siphonaptera										
	Hymenoptera	45	1	14	15	10	4	1	5	6	2
	Coleoptera	121	94	115	172	161	128	57	196	294	220
Gastropoda	Pulmonata						5		1	1	

	01/06/94	Pasture					Heather				
	Altitude (m)	360	400	440	480	500	360	400	440	480	500
Oligochaeta		23	13	7	3	1		1			
Arachnida	Pseudoscorpionida								1		
	Araneae	108	223	188	81	105	74	78	54	69	40
	Opiliones	1	1	6		2	8	4	20	101	47
	Acari	88	44	57	17	21	22	21	43	19	53
Diplopoda	Chordeumatid										
Chilopoda	Geophilomorpha										
	Lithobiomorpha							1			
Insecta	Collembola	110	435	257	97	151	61	67	7	34	24
	Othoptera		1	1							
	Hemiptera	1	1	3	1	2	2	5	4	4	2
	Megaloptera			2			1				
	Lepidoptera	6	9	8		1	1	3	4		4
	Diptera	105	212	46	182	173	71	32	45	56	32
	Siphonaptera										
	Hymenoptera	40	36	11	13	11	8	1	3	9	4
	Coleoptera	66	73	122	99	122	148	46	161	301	225
Gastropoda	Pulmonata	3					2	3	1		1

15/06/94		Pasture					Heather				
Altitude (m)		360	400	440	480	500	360	400	440	480	500
Oligochaeta		25	9	4	1	2		1	4		2
Arachnida	Pseudoscorpionida										1
	Araneae	290	384	301	247	225	134	67	94	179	67
	Opiliones	4	2	2	5	3	6	26	28	77	53
	Acari	41	52	47	25	18	54	34	67	103	73
Diplopoda	Chordeumatid						2				
Chilopoda	Geophilomorpha										
	Lithobiomorpha										
Insecta	Collembola	452	735	291	457	345	40	18	5	16	20
	Othoptera										
	Hemiptera	5	14	13	22	2	1	3	18	17	8
	Megaloptera										
	Lepidoptera	6	16	5	6	2	2	2	1	5	2
	Diptera	195	136	78	142	115	13	7	51	46	29
	Siphonaptera										
	Hymenoptera	33	51	45	30	32	14	6	11	22	24
	Coleoptera	125	132	189	176	220	120	55	102	299	207
Gastropoda	Pulmonata	1	1			1	11	1			

30/06/94		Pasture					Heather				
Altitude (m)		360	400	440	480	500	360	400	440	480	500
Oligochaeta		33	9	4	2	1		2			
Arachnida	Pseudoscorpionida										
	Araneae	180	367	272	198	184	100	70	82	120	63
	Opiliones	5	2	1	1	5	33	27	63	125	122
	Acari	44	37	97	23	23	53	33	81	140	62
Diplopoda	Chordeumatid						4				
Chilopoda	Geophilomorpha								1		
	Lithobiomorpha									1	
Insecta	Collembola	235	654	295	263	310	28	10	11	29	20
	Othoptera										
	Hemiptera	4	11	4	1		7	10	13	13	2
	Megaloptera							1		3	3
	Lepidoptera	4	11	10	1		7	6	1	2	2
	Diptera	214	209	223	166	159	33	10	55	45	52
	Siphonaptera								4		1
	Hymenoptera	82	75	58	28	40	14	7	26	25	22
	Coleoptera	102	125	219	168	179	98	40	116	471	206
Gastropoda	Pulmonata		3	1			8				

	14/07/94	Pasture					Heather				
	Altitude (m)	360	400	440	480	500	360	400	440	480	500
Oligochaeta		22	4	5		2					
Arachnida	Pseudoscorpionida						2			1	2
	Araneae	118	164	188	150	141	103	67	29	97	45
	Opiliones	5	2		4	3	80	63	88	144	153
	Acari	85	79	125	101	50	86	24	39	50	74
Diplopoda	Chordeumatid										
Chilopoda	Geophilomorpha										
	Lithobiomorpha				1						
Insecta	Collembola	189	498	240	473	379	62	17	5	8	14
	Othoptera			5		1					
	Hemiptera	9	8	10	7	4				1	
	Megaloptera	4									3
	Lepidoptera	3	5	4	3	2	3	1	1	1	4
	Diptera	271	232	237	289	409	65	27	43	53	183
	Siphonaptera									1	4
	Hymenoptera	123	91	199	138	114	28	6	16	17	17
	Coleoptera	110	160	298	184	184	139	30	57	253	224
Gastropoda	Pulmonata	2	1	1			2				

