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THE SPIDER (ARANEAE) GUILDS OF FOUR DIFFERENT VEGETATION TYPES WITH PARTICULAR REFERENCE TO PLANT STRUCTURE

by

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ABSTRACT

Four subsites were selected at the eastern end of Hedleyhope Fell, Tow Law, County Durham. These areas were chosen on the basis of differing vegetation types.

The study of spiders was conducted using pitfall trapping and sweep-netting with each sample collected five times, at fortnightly intervals, between May and July. The value of these sampling methods is considered, with the conclusion reached that they are the best techniques available, taking into account the restrictions imposed, for this type of investigation. A total of 2795 spiders were caught, comprising 10 families and 64 species. Chi-square tests, correlation and regression, percentages, Detrended Correspondence Analysis (DCA) and Simpson's diversity index were used when appropriate on the pitfall data. The totals caught via sweep-netting were too small to analyse statistically.

Species diversity and richness for both families and species showed considerable differences when the subsites were compared.

The distribution between subsites was analysed by DCA (DECORANA) and subsequent Chi-square tests. These critiques suggested that individual species showed preferences for certain subsites. This is demonstrated particularly well by the predominant Lycosid species whose subsite dispersal was markedly dissimilar.

The total numbers of spiders caught varied over the study period, rising to a peak in late June after which the numbers dropped again. The ratio of males : females was high at the beginning of the field work and remained so until it declined towards the end of the investigation. The overall male : female ratio was 2.1 : 1.

The sweep-net analysis illustrated that a different section of the fauna was being sampled by this technique, although catches were poor, and there was some bias towards certain species in some areas.

The vegetation was classified by species composition and architecture. Plant cover at each subsite was shown to be disparate according to the National Vegetation Classification (NVC) system. The architecture was analysed between subsites by DECORANA. This, followed by subsequent statistical tests, indicated that the plots were divergent in their physical arrangement in addition to their plant species composition.

The suggestion that significant differences between vegetation structure are a determinant of spider guilds is discussed. The reasons behind this community isolation are also considered, with particular reference to interspecific competition, prey availability and microclimatic factors. A longer study would be needed to reach any

firm conclusion as it is difficult to exclude any causal explanation of spider community relations with the results obtained over two and a half months.

1.0 INTRODUCTION

Hedleyhope Fell is an extensive unenclosed heathland on the edge of Tow Law (NZ 144413), which is situated at about 1000 feet (305 metres) above sea level. It is one of only two areas of heathland (the other being Waldridge Fell SSSI) which now survive in the area of central Durham between Stanley and Tow Law, where up until the 1950's quite extensive tracts of heathland occurred. It is estimated (Hopkins, 1982) that around 80 percent of the heathland has been lost from the area since 1950 due to reclamation, afforestation, opencast coal working and succession to birch wood. Hedleyhope Fell covers in excess of 100 acres and appears to be transitional between low altitude heathland and the moorland of higher altitudes. The phytosociology of the area has been described by Hughes & Huntley (1986).

The eastern end of Hedleyhope Fell is a mosaic of vegetation stands as a result of differing soil types and past mining activities. Four such regions were investigated, these being dominated by *Vaccinium myrtillus* (bilberry), grass (Graminaceae), *Calluna vulgaris* (heather) and *Pteridium aquilinum* (bracken) respectively. They were described both compositionally and architecturally as well as in terms of the resident spider fauna.

Spiders are ubiquitous predators in terrestrial ecosystems. They are generalist predators that primarily attack insects, but also eat other arthropods, including other Araneae. Spiders are even more strictly carnivorous than many other taxa of primarily predacious invertebrates such as centipedes and Carabid beetles. Potent neurotoxins enable spiders to kill prey rapidly. Victims usually are smaller than or similar in size to the spider, but many spiders subdue prey several times their own mass. All species of spiders spin silk, though not all spin webs. This is true of both sexes, although of web-builders the mature males eventually cease web-building and leave their web-sites in search of females. Male spiders usually mature before females and die earlier than their mates, who may live long enough to protect the egg-sac and, in some cases, care for the spiderlings. The spider persona varies in relation to how silk is used to capture prey. Differences and similarities between spider families in the use of silk generally reflect patterns in habitat utilisation and foraging behaviour, which influence the spider's role in its ecological web. The clearest distinction is between the web spinners and the wandering spiders, which make silk but do not spin webs.

Animal communities vary depending on the soil type and plant communities. Mineral soils, with their increased plant species diversity, have a larger soil fauna diversity (Coulson & Whittaker, 1978) with Collembola, for instance, being far more numerous on mineral soils although this does not seem to affect distribution of spiders disproportionally (Durnford, 1992). Collembola, followed closely by Diptera, are the most important prey species of spiders (Bristowe, 1958) and with up to two million spiders per acre being estimated to exist in nutritionally rich areas (Bristowe, 1958), the numbers of invertebrate prey need to be high. However, generalised predators are not restricted in habitat type and can move from one to another in search of food (Coulson, 1988). This is particularly true of spiders as most species have extremely efficient dispersal mechanisms (Duffey, 1956; Richter, 1970; Foelix, 1982).

This does not mean to say, however, that spiders are not limited in number by the availability of food and Cherrett (1964) found a clear correlation between spider abundance (albeit 97 percent were Linyphiidae) and amount of potential prey. He concludes that their distribution may be affected indirectly by poor quality of plant material influencing their invertebrate food supply, although the pattern may not be obvious because of spider mobility.

Despite food frequently being a limited resource, spiders do not often compete with other spiders for prey. This is not necessarily because spiders have assumed different roles but is absent because spider densities are below competitive levels (Wise, 1993). However, this does not mean that differentiation of roles via isolated ecological niches is not a result of competition at some stage in the evolutionary process. This is illustrated in work on wolf spiders by Nørgaard (1951) and Vlijm & Kessler-Geschiere (1967) and orb-web spinners by Enders (1974). Indeed, the divergence of closely related species by their habits would seem to be inherent in speciation mechanisms and whilst spider densities may be too low to initiate competition, this may not have been true for the ancestors of today's species.

Microclimate is extremely important in designing invertebrate communities (Cloudsley-Thompson, 1962). However, these factors may be of greater direct consequence for herbivorous or omnivorous orders than for generalist carnivores like the Araneae although spiders will be affected by prey abundance. A plant community with an increased invertebrate level will, in general, support an expanded spider fauna although not necessarily with a greater diversity (Uetz, 1991). Thus, microclimate considerations are difficult to separate from prey requirements, which in turn are hard to distinguish from vegetation characteristics, as far as spiders are concerned.

In respect of plant architecture Robinson (1981) introduced artificial substrates and documented their colonisation by spiders resident on the natural vegetation. He demonstrated that some spiders respond differentially to a variety of artificial structures placed in the field. Unfortunately, the connection between the behaviour of spiders on the three-dimensional arrangements and their responses to the architecture of natural vegetation is obscure and was not addressed by the researcher. The availability of web sites and the requirement for attachment points has been tested by several workers, in investigating the importance of free-standing vegetation for spider occupation. Cherrett (1964) concluded that two orb-weavers (*Meta merianae* and *Araneus cornutus*) chose certain habitat sites because these areas provided the necessary attachment elements for the supporting framework of the web whilst Schaefer (1978) illustrated that the Linyphiid (*Floronia bucculenta*) was limited in its distribution by the availability of low-lying, dense vegetation in which to build its web. A study to determine the effect of plant architecture on the whole of the spider community was undertaken by Hatley & MacMahon (1980) using modified sage brush (*Artemisia tridentata*) bushes. The outcome was clear : experimental manipulation of the vegetation affected spider community structure, although perhaps not to the extent that might have been predicted. This was mirrored in an experiment by Rypstra (1983) who found that increasing the heterogeneity of the vegetation structure was of utmost significance in achieving a greater spider diversity and density.

In a variety of analyses on the structure of the ground vegetation i.e. moss and leaf litter, Uetz (1975, 1976, 1979) found high levels of correlation between depth and density of litter and spider community complexity. Further work by Stevenson & Dindal (1982) and Bultman & Uetz (1982) using artificial and natural leaf litter levels indicated that the complexity of litter was also meaningful. Thus the importance of lower level vegetation for wandering spiders may be equal to the importance of potential web building sites for web spinners.

The effect of plant composition on the Araneae of a given area is also important, although the vegetation cover is usually examined inadvertently because of its underlying architectural complexity rather than a feature in itself. This is generally a valid assumption to make although, of course, any particular plant species displays different structural attributes as it matures (Barclay-Estrup, 1973). Bristowe (1939) also points out that some plants harbour a greater number and diversity of spiders. He notes that grasses (Graminaceae), heather (*Calluna vulgaris*) and Oaks (*Quercus* spp.) produce a richer haul for the ecologist than bracken (*Pteridium aquilinum*), willows (*Salix* spp.) and beech (*Fagus sylvaticus*). This may be a result, to some extent, of structural complexity but also to the fact that spiders do have an aversion to certain plants. This is because the chemotactic sense of Araneae in their leg tarsi causes certain plants to be repellent to them (Bristowe, 1939; Savory, 1964).

The importance of architecture and composition on the spider community, in terms of abundance and diversity, is therefore well established. However, most of the literature is simplified in this respect and does not take on board many of the ecological implications that these vegetation differences entail (such as microclimate, prey requirements, competition or predator pressure). As Wise (1993) concludes, the vegetation structure and properties of the leaf litter anchor the maze of trophic connections that forms the metaphor of the ecological web. There are no easy answers in attempting to untangle such a web.

This study will aim to elucidate vegetation differences between four adjacent subsites and relate these to the structure of resident spider guilds. Whilst experimental field measurement of microclimate, prey availability or interspecific competition interactions were not possible within the time framework of this investigation, conceivable causes of this isolation will be discussed in relation to the plant structure characteristics at each subsite. These processes, which are vital in understanding the full ecological scenario of spider distribution, have been ignored in much of the preceding literature.

2.0 METHOD

2.1 A Preliminary Investigation

2.1.1 Introduction

Prior to the main study a preliminary trial of the pitfall technique was conducted. The location of this trial was eventually to become the heather subsite (subsite 3) in the main study. Appropriate details will thus be described later. The aims were, by use of pitfall traps, to;

(i) Find a method to collect invertebrates but exclude large ground beetles (Carabids), shrews (*Sorex* spp.) and bumble bees (*Bombus* spp.).
(ii) Maximise spider capture, in respect of all other invertebrates, so that further population investigations may be undertaken.

2.1.2 Method

The trial investigation was carried out over a two-week period with traps being laid on 30th April and collected on 7th May and 13th May. Five sites were chosen with the same vegetation cover and underlying soil type (estimated by sight only). These sites were approximately equidistant, with two above the other three thus forming a trapezium. At each site six traps were laid in two rows with each about 2 metres from one another. The pitfalls consisted of plastic cups with an internal diameter of 68 millimetres and a depth of 74 millimetres. Chicken wire, of hexagonal diameter 16 millimetres, was cut into approximately 15 centimetre squares and used to cover half the traps (i.e. one row) to see if this would exclude large beetles, shrews and bumble bees. This mesh was secured by the use of metal staples. The three treatments used (hence two pitfalls at each site) were no treatment (i.e. cups left empty), 5% formalin and ethylene glycol (anti-freeze) - about 3 centimetres in each cup. The formalin treatment also contained a small amount of wetting agent (1% Teepol) to remove surface tension, hence preventing the invertebrates escaping. The pitfalls were emptied and replaced after a week, and then removed the following week, thus enabling analysis of a fortnights captures.

2.1.3. Results

2.1.3.1 Invertebrates Captured

The invertebrates caught were counted and identified down to order, class or family according to Chinery (1986). The list is given in Appendix 1. The spiders were identified down to species using Locket & Millidge (1951, 1953), Locket *et al* (1974), Roberts (1985a, 1985b, 1987) and Dalingwater (1986) and these are given in Appendix 2.

2.1.3.2 Shrew And Bee Capture

No shrews or bees were caught in any of the traps so it remains to be seen whether the mesh is adequate in excluding them.

2.1.3.3 The Effects Of The Mesh

(a) Large Carabids trapped;

Table 2.1 - The Effects Of Mesh Size And Preservative With Respect To Carabid Capture In Pitfall Traps

Site	**Trap Content**					
Letter	**O+**	**O-**	**F+**	**F-**	**G+**	**G-**
A	0	0	1	1	0	1
B	1	1	5	3	2	2
C	0	0	1	1	0	1
D	0	0	2	2	0	0
E	0	0	1	1	0	3
Total	1	1	10	8	2	7

O+ = No treatment plus mesh

O- = No treatment minus mesh

F+ = Formalin plus mesh

F- = Formalin minus mesh

G+ = Glycol plus mesh

G- = Glycol minus mesh

Total Carabids caught : With Mesh = 13 (44.8%)
Without Mesh = 16 (55.2%)

As far as the Carabids are concerned it appears the mesh does not exclude them completely. This conclusion is reached from numbers which are too small to analyse statistically but, obviously, large Carabids are being consistently caught in the meshed traps and therefore as a preventative measure this particular method is insufficient.

(b) Spiders trapped; With Mesh = 92 (49.5%)
Without Mesh = 94 (50.5 %)

Mesh size will have no effect as it is much larger than any spiders captured, either with or without mesh. This is reflected in the totals caught, as given above.

2.1.3.4 - The Effect Of The Different Preservative

Whilst the 'no treatment' traps are an admirable attempt at conservation (i.e. live trapping the invertebrates, identifying them and subsequently releasing them) it falls down practically on several fronts. Firstly, the numbers caught are insufficient to carry out a sustained analysis of invertebrate fauna. This may be due to predation by shrews, birds or other invertebrates or simply that the animals have the ability to scale the walls of the trap and escape. The latter explanation is more likely to be true as there was little difference between the covered and uncovered (should birds or shrews be predating it is unlikely they would have access to the covered traps). Secondly, the traps rarely stay dry (probably due to precipitation but possibly natural seepage or condensation) and thus death occurs irrespectively, often resulting in a 'slush' of dead animals in the trap which are difficult to identify.

Thus, having dismissed the 'no treatment' pitfalls, the traps containing formalin and glycol were analysed, grouping together large Carabids (C), spiders (S) and all other invertebrates (O). The results were as follows;

Table 2.2 - The Capture Of Different Invertebrate Groups With Respect To Pitfall Trap Preservative

Site	Formalin			Glycol		
Letter	O	C	S	O	C	S
A	58	2	10	39	1	21
B	70	8	12	80	4	16
C	56	2	12	76	1	18
D	150	4	19	70	0	13
E	91	2	15	99	3	20
Totals (%)	425 (83.2)	18 (3.5)	68 (13.3)	364 (79.0)	9 (2.0)	88 (19.0)

Totals individuals caught :- Formalin = 511
Glycol = 461

Chi-square analysis (between formalin and glycol treatments) gave significant differences for all three invertebrate categories ($\chi 2$ = 7.47 with two degrees of freedom) and, more importantly, for spiders and Carabids ($\chi 2$ = 4.92 with one degree of freedom). Thus, by referring back to the raw data in Table 2.2 it seems that glycol is the best treatment for this particular situation, with the least large Carabids trapped but a higher percentage of spiders. Glycol is also an advantage in that the spiders do not have a tendency, having been transferred for preservation in 70% alcohol, to curl their legs underneath the body as they do after being trapped in formalin, hence making identification without damage more difficult. However, on the other hand, formalin does not discolour the specimens as badly although colour is often not a reliable species specific characteristic.

2.1.4 Conclusion

The conclusion reached from this preliminary investigation was to use glycol-filled traps with a mesh covering. The cover will hopefully prevent shrews gaining access and drowning or being poisoned by the glycol and reduce the numbers of large Carabids caught. Finally, a note of caution must be expressed, in that the data is somewhat limited and these conclusions may not be applicable for other investigations.

2.2 The Study Site

Four subsites were investigated at the eastern end of Hedleyhope Fell (NZ 144413). The exact positions of these and the vegetation types are presented in Figure 2.1 which maps this part of the fell. The subsites chosen each represent an area in which differing plant species form the majority of the covering flora. A brief description of each is given below.

Subsite 1

Position On Fell: Top
Underlying Architecture: Moss/Leaf Litter
Dominant Vegetation : *Vaccinium myrtillus* (Bilberry)

Subsite 2

Position On Fell: Mid
Underlying Architecture: Moss/Leaf Litter
Dominant Vegetation : Graminaceae (Grass - Several Species)

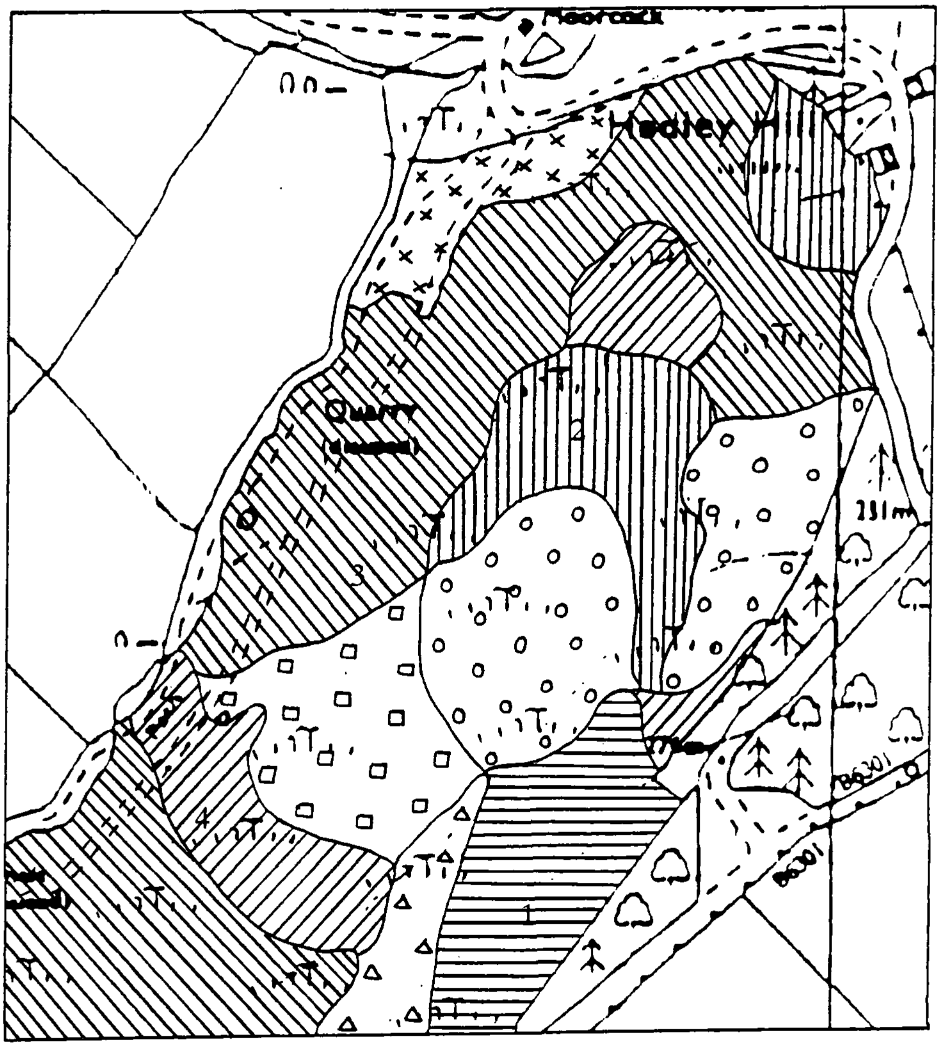
Subsite 3

Position On Fell: Mid-Lower
Underlying Architecture: Bare Ground
Dominant Vegetation : *Calluna vulgaris* (Heather)

Subsite 4

Position On Fell: Lower
Underlying Architecture: Moss/Leaf Litter
Dominant Vegetation : *Pteridium aquilinum* (Bracken)

Figure 2.1 Vegetation Mapping Of The Eastern End Of Hedleyhope Fell Showing The Positions Of The Four Subsites



1 = Subsite 1
2 = Subsite 2
3 = Subsite 3
4 = Subsite 4

▤ Bilberry Dominated (90%)
▥ Grassland Dominated (80%)
▧ Heather Dominated (80%)
▨ Bracken Dominated (90%)
× Gorse Dominated (90%)
○ 50% Grassland 50% Heather
△ 50% Grassland 50% Bracken
□ 50% Heather 50% Bracken

The subsites 1, 2, 3 and 4 are hence interchangeable with the terms bilberry, grassland, heather and bracken, and thus both numerical and dominant vegetation descriptions will be used accordingly throughout the following text.

2.3 The Sampling Of Araneae

2.3.1 Pitfall Trapping

Pitfall traps were set at each subsite in accordance with the results obtained from the preliminary investigation. The holes were bored and the six traps sunk in a 3 by 2 formation, each equidistant by approximately two metres from each other and covered by a hexagonal chicken wire grid (16 millimetre diameter). The position of the 3 by 2 grids is illustrated in Figure 2.1. In order that the invertebrates remained in the pitfalls ethylene glycol was used to a depth of approximately 30 millimetres. The catch is directly related to the edge length, in this case the circumference, of the trap (Luff, 1975) and to standardise this a constant size of trap was used. The dimensions are as for the preliminary study. Initially, the traps were emptied weekly to improve identification skills but later collection was only necessary every fortnight and thus all data is presented at two week intervals. The invertebrates captured were counted and placed into class, order or family with the exception of spiders which were identified down to species. The specimens were preserved and stored in 70% alcohol. If they were allowed to dry out *rigor mortis* would set in and identification would become extremely difficult. Some researchers, notably Duffey (1972), have advocated glycerine addition to the alcohol. However, the advantage of this is negligible for whilst maintaining the suppleness of the invertebrate it tends to clog up the hair resulting in identification problems. Most spiders are hairy and, as this study was mainly concerned with this order, 70% alcohol was considered the most appropriate preservative. All invertebrates were placed in plastic tubes containing the alcohol and a pencil label giving details of subsite, date and method of capture. Non-spiders were categorised as the traps were sorted. The spider fauna was examined in a watch glass containing alcohol and sand, for easy manoeuvrability, under a Motic microscope with a 6.4-40x magnification. The light source used was Schott KL 1500 electronic fibre optic lamp. The specimens were subsequently identified using the literature described in the preliminary investigation.

The traps were first set on 21st May and collected until 20th July. The spiders caught were counted, identified down to species and recorded as male, female or immature.

Pitfall traps have a number of drawbacks which will be discussed later - they have a tendency to trap larger numbers of active, more mobile species and collections of Carabids and spiders caught are thought to be reduced in dense vegetation (Jenkins, 1990).

2.3.2 Sweep-Netting

As a supplementary collecting aid to pitfalls a sweep-net was used every fortnight, usually on the same day that the traps were emptied. The net consisted of a stout, canvas net with a metal tubed, semi-circular mouth of radius 185 millimetres. The purpose of this was to examine a different part of the spider population as sweep-netting samples species which spend most of their time in the higher vegetation rather than on the ground (Turnbull, 1973). All other invertebrates captured were released. One 'sweep' involved the net being moved over the vegetation just above ground level in a long arc movement. At each fortnightly interval four runs of fifty individual sweeps were undertaken at each subsite, covering as much of the area as possible, and thus a total of two hundred sweeps in each patch was achieved. The spiders were collected in plastic tubes and returned to the laboratory for preservation and examination as before. There were five sample dates from the first on 27th May to the last on 20th July. As with pitfall trapping sweep-netting presents the researcher with several problems and these will be argued further in the discussion.

2.4 The Vegetation Survey

2.4.1 Plant Species' Composition

The vegetation survey was based on the guidelines set out by English Nature (Smith *et al*, 1985) for Phase 2 quantification. This involved placing five 1x1 metre square fixed quadrats at all subsites, each marked by both a wooden stake (approximately 50 centimetres high) and a piece of red insulating tape. The stake, when driven into the ground, represented the top left hand corner of the quadrat with the tape attached to a suitable piece of tall vegetation (depending upon the availability of an appropriate plant) directly below the stake. These designations were made relative to the top of the fell and the road which runs along it. The reasons for having separate markers for each quadrat was twofold. Firstly, it enabled easier recognition of the fixed square, with two points to search for rather than one. Secondly, it was hoped to ensure that the quadrats position could still be found if one or other of the markers was disturbed as there is a reasonable amount of human activity at Hedleyhope Fell, particularly at weekends.

The fixed quadrats were surveyed using the Domin scale (Table 2.3) on three occasions (28th May, 17th June and 14th July). This produced a species list and a record of cover abundance for each quadrat during the study period. The vegetation was identified using Watson (1968), Rose (1981), Clapham *et al* (1987), Fitter *et al* (1989), Fitter *et al* (1992), Hubbard (1992) and Purvis *et al* (1992). This data set was the basis for comparison of plant communities between the subsites.

Other quantitative methods of vegetation description such as the Braun-Blanquet scale of sociability (Table 2.4) and the DAFOR rating (dominant; D, abundant; A, frequent; F, occasional; O and rare; R) were not used due to the limited time available. These methods are frequently used by English Nature as supplementary designations (Smith *et al*, 1985).

The accuracy of a survey of this nature is increased as the number of quadrats increase (Southwood, 1968) but time constraints meant that only five quadrats were used per subsite, thus representing 20 square metres at each locality. However, in order to gain a more comprehensive species list each subsite was searched further during all visits. This enabled the number of species in the quadrats to be calculated as a percentage of the total, hence giving an indication of the fixed quadrats' accuracy as subsite representatives.

The vegetation was surveyed during one day at three week intervals on three occasions. Every species observed within the quadrats was documented including bryophytes and lichens. Where it occurred, the percentage of bare earth was also recorded. As a result each subsite was allocated a status using the National Vegetation Classification (NVC) system via the VESPAN program (Malloch, 1985).

Other methods of surveying include line transects where all plants touching the line are recorded and point sampling, with a 1x1 metre frame, with 100 points where the number of contacts with the frame per species is registered. However, the fixed quadrat method allowed the succession of flora over the season to be less subjective whilst the Domin scale was considered sufficiently accurate given the time available.

Table 2.3 - The Domin Scale Of Vegetation Cover Abundance Estimates

Scale	Percentage Cover
+	Present in the stand adjacent to the quadrat but absent within the quadrat
1	< 4% Cover; rare, one or a few scattered individuals
2	< 4% Cover; scattered individuals
3	< 4% Cover; frequent
4	4% ≤ Cover ≤ 10%
5	10% < Cover ≤ 25%
6	25% < Cover ≤ 33%
7	33% < Cover ≤ 50%
8	50% < Cover ≤ 75 %
9	75% < Cover ≤ 90 %
10	90% < Cover ≤ 100%

Table 2.4 - The Braun-Blanquet Scale Of Sociability

Scale	Description
1	Growing once in a place, singly
2	Growing in groups or tufted
3	Growing in groups, small patches or cushions
4	Growing in small colonies, extensive patches or forming carpets
5	Growing in great crowds or pure populations

Tables 2.3 and 2.4 from Huntley (1981)

2.4.2 Plant Architecture

Architecture, in vegetation terms, describes the structure of a plant with respect to variables such as its height, the number of leaves and the position of branching stems. Numerous researchers have found a high correlation between invertebrate diversity and plant architecture and this is particularly true for spiders (e.g. Uetz, 1975; Hatley & MacMahon, 1980; Rypstra, 1983). The correlation between spiders with respect to plant architecture was investigated in this study.

The technique employed was the bayonet method as described by Poissonet *et al* (1973). This was adopted due to ease of use and accuracy when compared to other methods. The bayonet consists of an aluminium blade 100 centimetres high, 4.5 centimetres broad and 0.2 centimetres thick. The upper part is T-shaped to push the bayonet into the ground to a depth level with the zero on the vertical scale marked on one edge (in 1 centimetre divisions). From one limb of the handle a plum-line is suspended to ensure that each measurement is made vertically. The architecture is recorded by counting the number of touches along the right hand bevelled edge of the bayonet in each height class. The number of touches per species was also recorded. These height classes are 1 centimetre each from 0-10 centimetres (0-1cm, 1-2cm to 9-10cm) and then eighteen divisions of 5 centimetres between 10 and 100 centimetres.

The bayonet method was used in a 1x1 square metre fixed quadrat exactly three metres to the West of the stake marking the cover-abundance fixed quadrats. This measurement was consistent for each of the twenty quadrats. The purpose of this 3 metre gap was to ensure minimal disturbance (in respect of downtrodden plants, severed roots or stems and damaged leaves) to the original quadrats. For each of the twenty fixed 1x1 square metre bayonet quadrats ten randomly placed samples were recorded, giving a total of two hundred samples (fifty samples at each subsite). This resulted in twenty-eight divisions (0-1cm, 1-2cm to 95-100cm) recorded fifty times at each subsite. The architecture survey was conducted on the 27th May and 14th July and the subsequent data was used in the multivariate analysis of the vegetation structure between subsites.

2.5 Analysis

Analysis of the results involved Chi-square tests, correlation and regression, percentages, detrended correspondence analysis (DCA) and Simpson's (1949) diversity index where appropriate. The use of the analysis tools for different areas of the study will become apparent in the results. All tests involving differences from expected values were deemed to be significant at the 5% probability level. The formulas used were as follows;

Chi-Square

$\chi 2 = \sum [(O - E)^2] / E$

O = Observed value
E = Expected value

Correlation and Regression

$r = \sum(x - xm)(y - ym) / \sqrt{\sum(x - xm)^2\sum(y - ym)^2}$

r = Correlation Coefficient
x = Independent Variable Value
xm = Mean Of The x Value
y = Dependent Variable Value
ym = Mean Of The y Value

Regression Equation = $y = a + bx$

b = Regression Coefficient (Slope)

Simpson's Diversity Index

$D = N (N -1) / \sum n (n - 1)$

D = Diversity
N = Total Number Of Individuals
n = Number Of Individuals Of Each Species

This index is used because it has been shown to be the most precise and lacking in bias of four possible indices (Simpson, Shannon, Patil-Taillie and Margalef) and it is less insensitive to rare species or families than the Shannon Index (Giavelli *et al*, 1986). This latter point needs to be considered as several species of spider are likely to be found only once or a few times in a study such as this.

Detrended Correspondence Analysis (DCA)

Detrended correspondence analysis is an eigenvector ordination technique based on reciprocal averaging but correcting the faults of arch distortion and compression of the first axis ends found in principle components analysis (Gauch, 1982). DCA results in the production of an ordination diagram in which similar species or samples are near each other and dissimilar entities are far apart. Thus, clusters that are seen on the plots can be extracted and statistically analysed for significant differences. Gauch (1982) states that "DCA results are at least as good as, and usually superior to, other ordination techniques." For analysis of community, or indeed subcommunity, data, DCA ordinates samples and species simultaneously and effectively. Furthermore, DCA appears to be appropriate to the Gaussian community model and successful in applications of community analysis (Gauch, 1982). A more detailed review of the DCA process, incorporating technical details and considerations involving its usefulness, is outlined by Hill & Gauch (1980).

The data to be used in the DCA analysis was entered into the DECORANA (Hill, 1979) program. This computer package provides a species ordination as well as a sample ordination. The species or samples are given arbitrary values which allow them to be plotted on a graph so that relationships between species or samples can be distinguished.

3.0 RESULTS

3.1 Species' Lists

The invertebrates caught by means of pitfall trapping, and identified to class, order or family, are given in Appendix 3. The moss, lichen and vascular plant species recorded from each subsite are listed an Appendices 4 and 5. A species list of spiders captured is given as Appendix 6 (pitfalls) and Appendix 7 (sweep-net). In addition, a complete catalogue of all Araneae caught during the study period (i.e. a summation of captures from the preliminary study, pitfall trapping and sweep-netting) is shown as Appendix 8. This also shows the species for which there is no county record, as assembled by Bristowe (1939).

3.2 The Araneae Data

3.2.1 Inter-Subsite Analysis Of Pitfall Trap Data

3.2.1.1. Totals

The number of all spiders caught at each subsite during May, June and July were totalled. The results are given in Figure 3.1 showing subsite 2 (grassland) with the highest numbers caught and subsite 3 (heather) with the lowest. Totals of all combinations of subsites were tested by $\chi 2$ and are displayed in Table 3.1. All subsites, with the exception of 1 (bilberry) and 4 (bracken), are highly significant in their differences with respect to total spiders captured. This may well be a consequence of the vegetation dissimilarities. Conversely, the similarity of the bilberry and bracken subsites may be related to the vegetation architecture or composition. Such postulations shall be discussed later.

3.2.1.2 Species Richness And Diversity

The species richness is the number of species caught at each subsite whilst the species diversity is given by calculations derived from Simpson's (1949) index. The

Figure 3.1 The Total Number Of Spiders Caught At Each Subsite

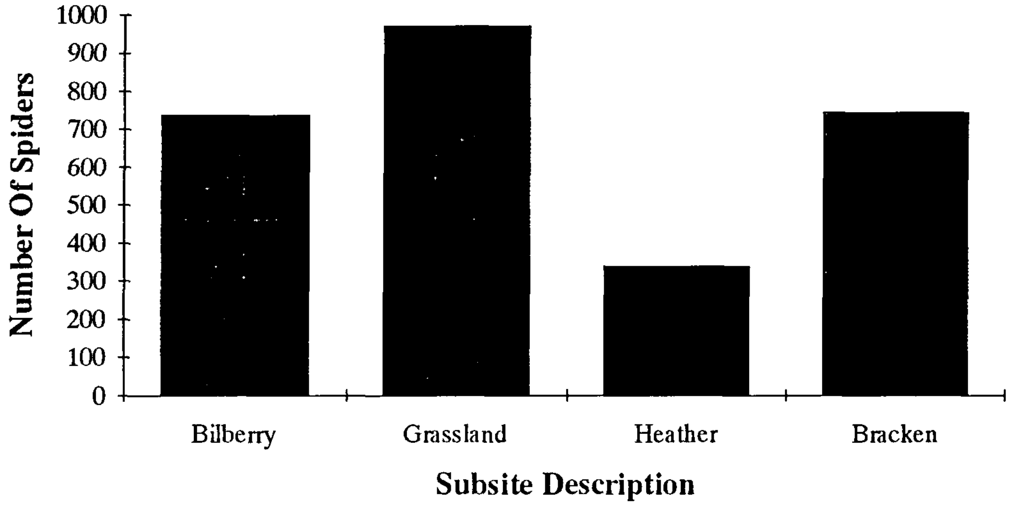


Table 3.1 - Chi-square Analysis Between Subsite Totals

Subsite	$\chi 2$ Value	Degrees Of Freedom	Significance Level
Bilberry v Grassland	**31.767**	**1**	**$p < 0.001$**
Bilberry v Heather	**146.942**	**1**	**$p < 0.001$**
Bilberry v Bracken	**0.043**	**1**	**Not Significant**
Grassland v Heather	**303.708**	**1**	**$p < 0.001$**
Grassland v Bracken	**29.485**	**1**	**$p < 0.001$**
Heather v Bracken	**151.783**	**1**	**$p < 0.001$**

results and calculations are presented in Table 3.2. The scores for species richness and diversity were correlated, r = 0.46344 for 2 degrees of freedom, which is not significant and hence there is no relationship between richness and diversity for the subsites. Additionally, a Chi-squared test shows that there is no between-subsite significant difference for species richness ($\chi2 = 0.46$ at 3 degrees of freedom).

Table 3.2 indicates that subsite 2 (grassland) is considerably less diverse in its species fauna than the other three subsites, which are similar. As this is the designated grassland site this relative impoverishment may be an outcome of the architectural simplicity of Graminaceae.

3.2.1.3 Family Richness and Diversity

The analysis of spider families was conducted on the same basis as species richness and diversity with the results shown in Table 3.3. Each family and the number of individuals contained therein (as a percentage of the total from all subsites) is given by Figure 3.2. This illustates the relative proportions of families at the individual subsites and thus how some groups show a preference for particular areas (e.g. Gnaphosids and Salticids mainly at the heather subsite). The family richness and diversity correlation, and the between-subsite Chi-squared test were not significant (r = 0.08837 with 2 degrees of freedom and $\chi2 = 0.7$ with 3 degrees of freedom respectively). Table 3.3 shows that subsite 2 (grassland), despite having the highest family richness, has the lowest family diversity. This can be explained by referring back to the raw data which illustrates that the grassland subsite contains many families but most have few representatives, the majority of spiders coming from two families; the Lycosidae (29.4%) and the Linyphiidae (65.1%) and therefore a family diversity of only 1.96. At the opposite end of the scale subsite 3 (heather) has a high family diversity of 3.35. This is because the numbers of spiders are more evenly spread through the range of families when compared with the spread of individuals at the other subsites. The ecological significance of this will be considered later.

3.2.1.4 The Predominant Lycosid Species

The most numerous Lycosid species (*Alopecosa pulverulenta*, *Pardosa nigriceps* and *Pardosa pullata*) represent 5.3%, 12.3% and 14.7% respectively of all

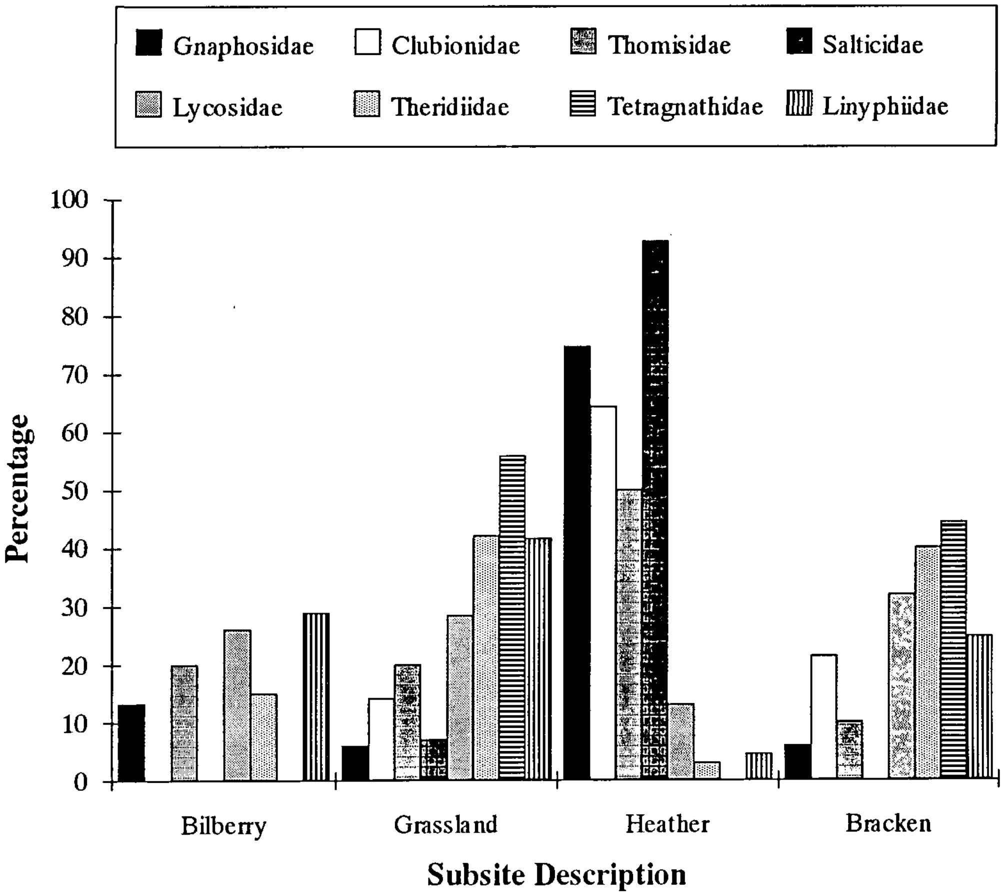
Table 3.2 - Inter-Subsite Species Richness And Diversity

Subsite Description	Species Richness	Species Diversity
Bilberry	33	12.60
Grassland	39	4.47
Heather	38	12.98
Bracken	39	11.46

Table 3.3 - Inter-Subsite Family Richness And Diversity

Subsite Description	Family Richness	Family Diversity
Bilberry	5	2.08
Grassland	8	1.96
Heather	7	3.35
Bracken	7	2.26

Figure 3.2 The Number Of Spiders In Each Family As A Percentage Of The Totals At All Subsites



the spiders caught. These large proportions were to be expected as highly mobile ground species have a greater probability of being captured by this method (Greenslade, 1964; Luff, 1975; Southwood, 1968). However, for inter-habitat analysis (as opposed to a population study) such comparison is valid (Topping and Sunderland, 1992), particularly as these species were caught in large numbers.

The results are presented in Figure 3.3 which shows that the dominant Lycosid species (in terms of number of individuals) are *Pardosa nigriceps* (bilberry and bracken subsites), *Pardosa pullata* (grassland subsite) and *Alopecosa pulverulenta* (heather subsite). Subsequent calculations in Table 3.4 illustrates highly significant differences between the subsites indicating that even closely related species have specific habitat preferences. The implications of this will be discussed later.

3.2.1.5 Other Differences In Species' Occurrence

Several interesting anomalies are seen from the raw data sets. These are briefly mentioned here and related to their ecological significance later.

(a) The *Lepthyphantes* genus

The *Lepthyphantes* genus is a group of small long-legged sheet web spinners (Linyphiidae) whose distribution appeared to be biased towards subsite 1 (bilberry) and away from subsite 3 (heather). This apparent skew was tested statistically and shown to be highly significant ($\chi2 = 200.71$ with 3 degrees of freedom, $p < 0.001$). The difference may be related to web-spinning conditions.

(b) *Silometopus elegans*

This species is also a sheet-web spinner which showed a considerable preference to subsite 2 (grassland). Of a total 384 specimens collected, 379 were at the grassland plot ($\chi2 = 1112.35$ with 3 degrees of freedom, $p < 0.001$). This may be a consequence of prey abundance, specific micro-habitat requirements or simply an area of high local abundance where dispersal has been poor.

Figure 3.3 The Distribution Of The Three Numerically Dominant Species Of Lycosidae

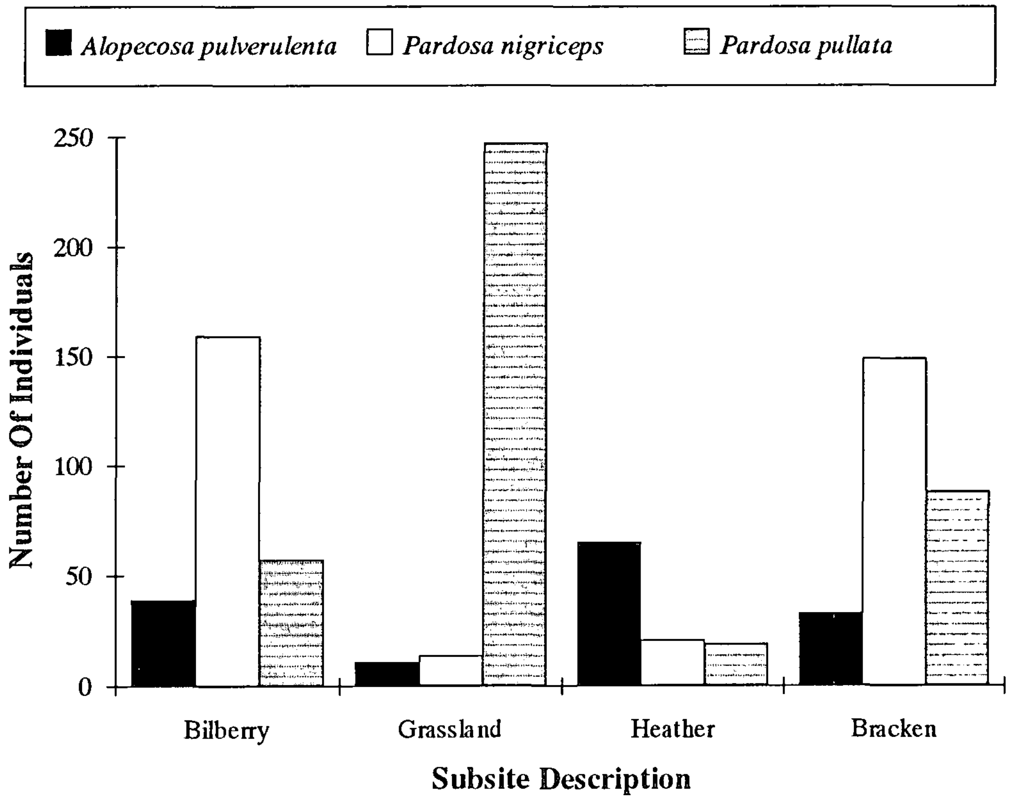


Table 3.4 - A Statistical Analysis Of The Distribution Of The Three Numerically Dominant Lycosid Species

Subsite Number	**χ^2 Value**	**Degrees Of Freedom**	**Significance Level**
Bilberry v Grassland	**255.679**	**2**	**$p < 0.001$**
Bilberry v Heather	**83.254**	**2**	**$p < 0.001$**
Bilberry v Bracken	**7.029**	**2**	**$p < 0.05$**
Grassland v Heather	**200.579**	**2**	**$p < 0.001$**
Grassland v Bracken	**198.271**	**2**	**$p < 0.001$**
Heather v Bracken	**97.260**	**2**	**$p < 0.001$**
All Subsites	**487.476**	**6**	**$p < 0.001$**

(c) *Evansia merens*

Evansia merens (Linyphiidae) is a spider that lives in the nests of Formicidae (Hymenoptera). This spider was collected exclusively at subsite 3 (heather) so it was perhaps to be expected that the ant population was found to be significantly higher ($\chi2 = 570.42$, 3 degrees of freedom, $p < 0.001$), with 48% of all ants being found here. *E.merens* is known to exist in the nest of *Lasius niger* (Roberts, 1985), and this species is frequent on Hedleyhope Fell (Jenkins, 1992).

3.2.1.6 Detrended Correspondence Analysis (DCA) Of Species

The analysis, using the DECORANA program (Hill, 1979), was carried out using the species found at each of the four subsites, with the sample occurrences combined. The DCA data is represented graphically in Figure 3.4 and shows the species falling into four groups (which coincidentally are found along the positive and negative areas of the two axes). The four groups of species are shown below. The numbers of spiders in each group at each subsite were counted (by reference to the raw data) and analysed statistically by a Chi-square test (between subsites for each group). The results are presented in Table 3.5 which shows that there are significant differences between the subsites for all groups. It is also apparent that the groups 1 to 4 correspond to the subsites 1 to 4 (i.e. group 1 has the highest total at subsite 1, group 2 at subsite 2 *etc*). The exception is group 3 which does not have the highest catch at subsite 3, although here the numbers form the highest proportion for subsite 3 as compared to the other groups. This indicates that the species form distinct communities within each of the study areas and that these communities are all different. Furthermore, it can be argued that the groups 1 to 4 correspond to the spider guilds at the subsites 1 to 4, in both composition and proportion (i.e. the group 1 guild is representative of the bilberry subsite, the group 2 guild of the grassland subsite *etc*). This may be related to the vegetation differences, both structural and compositional, of the chosen plots. Such implications will be discussed later in conjunction with results from the foliage analysis.

The spider species in each group are given a numerical code in Figure 3.4 as shown below. The family belonged to plus the total number of each species caught (at all subsites) is shown in parentheses. The family abbreviations are as follows;

Figure 3.4 - The DCA Plot Of Spider Species

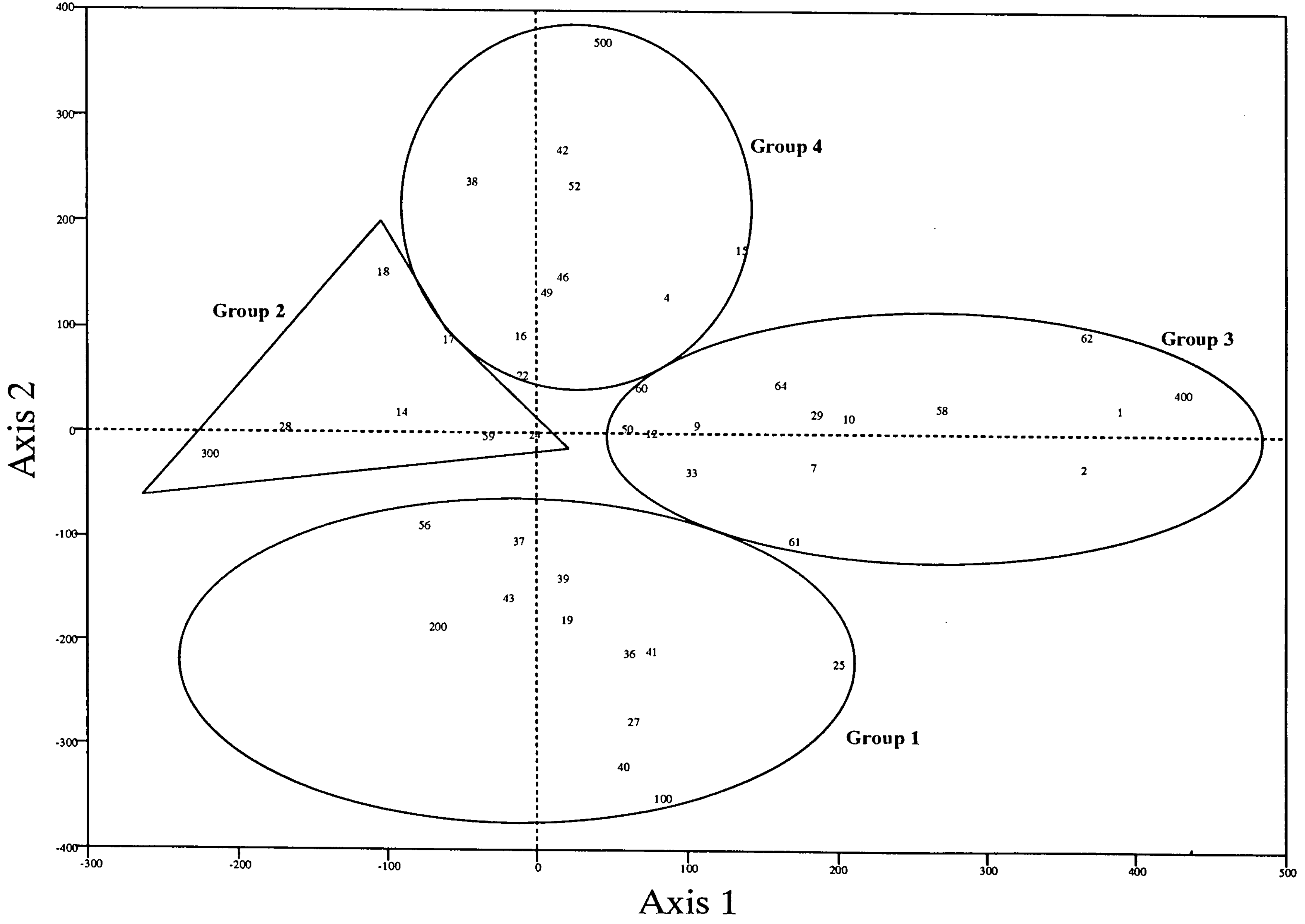


Table 3.5 - Chi-square Analysis Of The Associations Of Species Between Subsites As Given By Figure 3.4 (All With 3 Degrees Of Freedom)

Group	Number Of Spiders In Each Group				Chi-Square Value Between Plots	P Value
	Subsite 1 (Bilberry)	Subsite 2 (Grassland)	Subsite 3 (Heather)	Subsite 4 (Bracken)		
1	278	91	10	57	379.725	$p < 0.001$
2	86	719	26	138	1276.932	$p < 0.001$
3	231	44	225	201	133.939	$p < 0.001$
4	81	81	15	261	306.000	$p < 0.001$

Gn = Gnaphosidae
Cl = Clubionidae
To = Thomisidae
Sa = Salticidae
Ly = Lycosidae
Te = Theridiidae
Tt = Tetragnathidae
Li = Linyphiidae

Group 1

19	*Agyneta conigera* (Li : 77)
100	*Bolyphantes luteolus* (Li : 2)
25	*Centromerus prudens* (Li : 3)
27	*Ceratinella brevipes* (Li : 44)
200	*Gongylidiellum vivum* (Li : 4)
200	*Hypomma bituberculatum* (Li : 2)
36	*Lepthyphantes ericaeus* (Li : 74)
37	*Lepthyphantes mengei* (Li : 131)
39	*Lepthyphantes tenebricola* (Li : 5)
40	*Lepthyphantes tenuis* (Li : 11)
41	*Lepthyphantes zimmeranni* (Li : 36)
43	*Micrargus herbigradus* (Li : 43)
100	*Pocadicnemis juncea* (Li : 4)

100 = 23 and 51
200 = 34 and 35

Group 2

300	*Agyneta olivacea* (Li : 2)
300	*Baryphyma trifons* (Li : 1)
24	*Centromerita concinna* (Li : 3)
300	*Centromerus sylvaticus* (Li : 1)
28	*Cnephalocotes obscurus* (Li : 18)

18	*Pachygnatha degeeri* (Tt : 9)
14	*Pardosa pullata* (Ly : 411)
17	*Robertus lividus* (Te : 94)
56	*Tabinocyba pallens* (Li : 39)
59	*Trichopterna thorelli* (Li : 7)
300	*Silometopus elegans* (Li : 384)

300 = 20, 21, 26 and 54

Group 3

10	*Alopecosa pulverulenta* (Ly : 148)
1	*Drassodes cupreus* (Gn : 25)
29	*Diplostyla concolor* (Li : 3)
400	*Erigonella hiemalis* (Li : 1)
400	*Euophrys aequipes* (Sa : 10)
400	*Evansia merens* (Li : 1)
33	*Gonatium rubens* (Li : 15)
2	*Haplodrassus signifer* (Gn : 69)
9	*Heliophanus flavipes* (Sa : 2)
400	*Micaria pulicaria* (Gn : 1)
400	*Minyriolus pusillus* (Li : 1)
400	*Oedothorax retusus* (Li : 1)
12	*Pardosa nigriceps* (Ly : 343)
400	*Pardosa palustris* (Ly : 9)
50	*Peponocranium ludicrum* (Li : 7)
400	*Tabinocyba praecox* (Li : 1)
58	*Tiso vagans* (Li : 8)
60	*Walckenaeria acuminata* (Li : 22)
61	*Walckenaeria antica* (Li : 9)
62	*Walckenaeria monoceros* (Li : 6)
64	*Walckenaeria unicornis* (Li : 12)
7	*Xysticus cristatus* (Th : 7)

400 = 3, 8, 13, 31, 32, 45, 48 and 57

Group 4

22	*Bathyphantes parvulus* (Li : 144)
4	*Clubiona diversa* (Cl : 3)
500	*Clubiona pallidula* (Cl : 1)
500	*Clubiona reclusa* (Cl : 1)
500	*Dismodicus bifrons* (Li : 2)
38	*Lepthyphantes pallidus* (Li : 3)
42	*Meioneta saxatilis* (Li : 26)
500	*Microlinyphia pusilla* (Li : 1)
46	*Monocephalus fuscipes* (Li : 5)
500	*Oedothorax gibbosus* (Li : 1)
500	*Pardosa amentata* (Ly : 2)
49	*Pelecopsis mengei* (Li : 95)
16	*Pholcomma gibbum* (Te : 4)
52	*Pocadicnemis pumila* (Li : 118)
500	*Saaristoa abnormis* (Li : 3)
500	*Sintula cornigera* (Li : 1)
15	*Trochosa terricola* (Ly : 27)
500	*Walckenaeria nudipalpis* (Li : 1)

500 = 5, 6, 11, 30, 44, 47, 53, 55 and 63.

In addition to the above, this part of the investigation has indicated that whilst the spider communities are different at each subsite, they form a gradation from one subsite to the next. This is clearly shown in Figure 3.4 where the groupings are seen as changing by degree from one subsite to another and not as discrete entities.

3.2.2 Inter-Date Analysis Of Pitfall Trap Data

The main investigative area was a between-subsite analysis incorporating vegetation composition and its architecture. However, as the pitfalls were retrieved at fortnightly intervals this enabled a seasonal aspect to be considered as the research continued through May, June and July.

3.2.2.1 Totals

The results are shown as a graph in Figure 3.5. Totals between dates were tested by Chi-square and are shown in Table 3.6. There is much difference between the collection dates, the majority being significant. As a general trend it appears that the numbers of spiders reach a peak in late June to early July before declining in late July. However, at the last collection on 20th July all the traps were flooded due to unusually high rainfall over the preceding fortnight. This would have reduced the catch considerably (Standen, pers. comm.) and hence a spurious trend may be exposed. The diminishing number at this date was also generally reflected in the other invertebrate groups.

3.2.2.2 The Male To Female Ratio

During the spring most spiders are mature (91.02% in this case) thus sexing them is not a problem as the male palp and the female epigyne are fully formed. Two sets of data were examined in this aspect of the study.

Firstly, the results of the total male : female ratio is presented in Figure 3.6. Chi-squared tests between the dates, for each sex, show significance (for males $\chi2 = 60.382$, for females $\chi2 = 34.074$; both with 12 degrees of freedom and $p < 0.001$). There is a clear swing to females being captured in greater numbers (hence indicating greater mobility) at the last sample date. Although the total number of spiders collected on the 20th July was significantly lower than earlier in the year, the ratio of males to females will be representative, particularly as the catch was still high (264 individuals).

Secondly, the sex ratio for each family was considered in order to ascertain if one group was influencing the overall scenario (Figure 3.7). A correlation between males and females of each family showed the significance level to be $p > 0.05$ ($r = 0.861$ with 6 degrees of freedom). Thus there is no correlation between the male and female ratio of different families, indicating that some families may be biasing the total ratio (e.g Lycosidae = 4.4:1, Linyphiidae = 1.8:1, Gnaphosidae = 0.8:1). It is also important to realise that Figure 3.7 presents only the percentage male : female ratio and that for some families the numbers caught were very low (for example Clubionids (5 individuals) and Thomisids (7)) whilst others were high (e.g. Lycosids (938) and

Figure 3.5 The Number Of Spiders Captured With Respect To Date

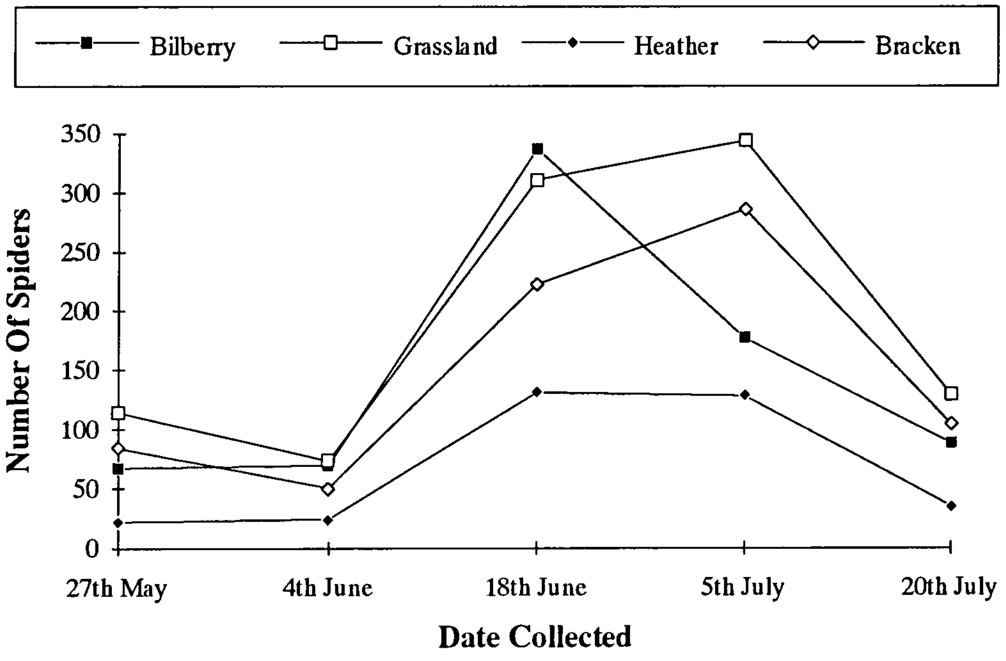


Table 3.6 - A Statistical Analysis Of The Total Number Of Spiders At Each Collection

Date	χ^2 value	Degrees Of Freedom	Significance Level
27th May v 4th June	10.022	1	$p < 0.01$
4th June v 18th June	506.348	1	$p < 0.001$
18th June v 4th July	2.250	1	Not Significant
5th July v 20th July *	259.675	1	$p < 0.001$
All Dates	87.837	12	$p < 0.001$

* = The Pitfalls Collected On The 20th July Were Flooded

Figure 3.6 The Change In The Male To Female Ratio Over The Study Period

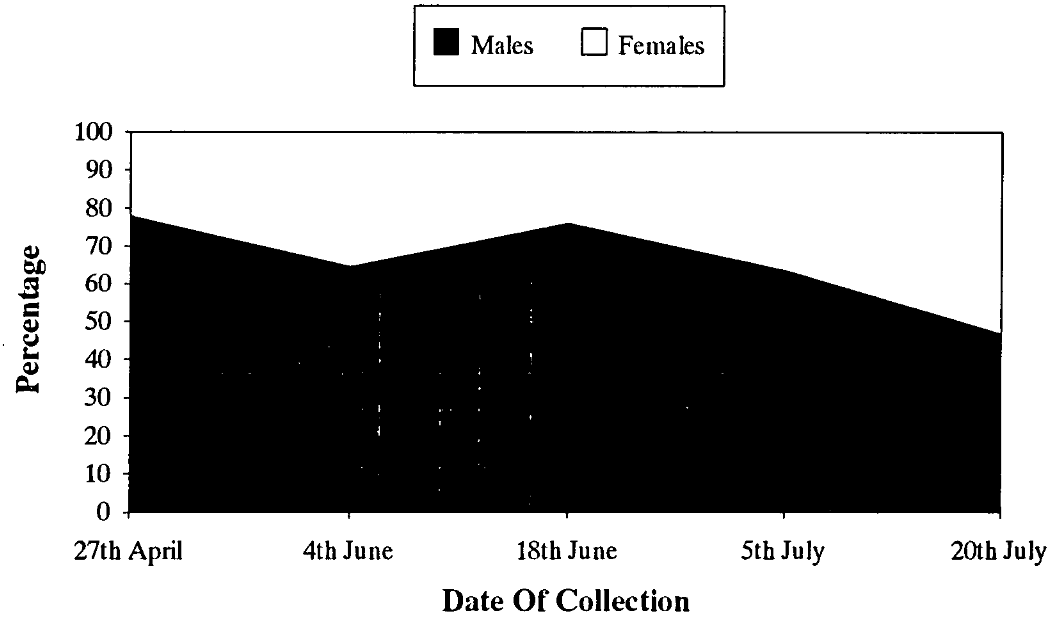
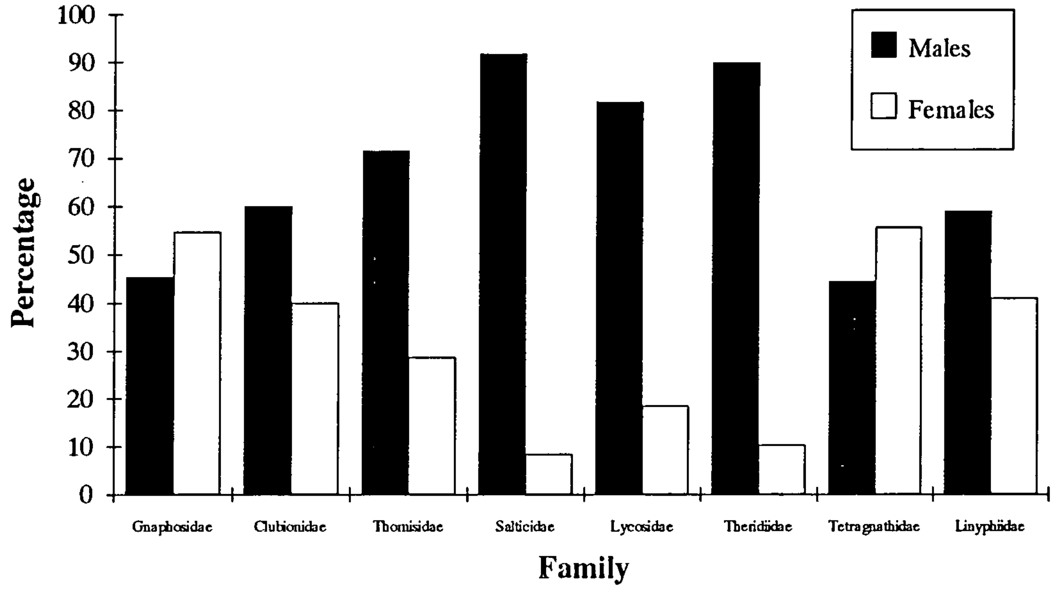


Figure 3.7 The Percentage Male : Female Ratio For Each Spider Family



Linyphiids (1382)). Thus, interpretations based purely on total spiders caught should be treated with some caution.

3.2.3 Sweep-Net Analysis

The sweep-net collections (numbers and sexes) are given in Appendix 7. Despite the low numbers caught (and hence lack of statistically valid interpretations) due to wet vegetation keeping spiders closer to the ground, several points of note do arise.

Firstly, two families are represented which are completely absent from the pitfall collections - the Araneidae and Dictynidae. Of the latter the vast majority were netted at the heather subsite (97.4%).

Secondly, three species from other families were captured exclusively by this technique, namely *Philodromus aureolus* (Thomisidae), *Erigone dentipalpis* and *Kaestneria pullata* (both Linyphiidae).

These captures seem to indicate that different families, in addition to particular species, occupy separate levels in the vegetation. Such conjectures will be discussed later.

3.3 The Vegetation Survey

3.3.1 Plant Species' Composition

The fixed quadrats that were surveyed three times (in order not to miss any vegetation which is brief in its appearance on the fellside) represented 63%, 72%, 69% and 65% respectively of the total number of plant species identified at subsites 1 to 4.

3.3.1.1 National Vegetation Classification (NVC) Of The Subsites

The Domin scores of each quadrat were entered into the VESPAN program (Malloch, 1985). The nearest three classifications of each subsite (as a subcommunity) are given, together with the percentage correlation to that subcommunity, in Table 3.7. Thus the four subsites are different in plant composition although the bilberry and

Table 3.7 - The National Vegetation Classification (NVC) Of Each Subsite

Subsite	NVC Code	Code Description	C.S.
1	U2	*Deschampsia flexuosa* grassland	63.6
	U20c	*Pteridium aquilinum-Galium saxatile* community: Species-poor subcommunity	56.1
	H9d	*Calluna-Deschampsia flexuosa* heath: *Galium saxatile* subcommunity	55.7
2	U4b	*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland: *Holcus-Trifolium*	54.4
	W23a	*Ulex europaeus-Rubus fructicosus* scrub: *Anthoxanthum odoratum* subcommunity	50.8
	U4	*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	50.3
3	H9	*Calluna-vulgaris-Deschampsia flexuosa* heath	48.0
	U2	*Deschampsia flexuosa* grassland	46.8
	H1	*Calluna vulgaris-Festuca ovina* heath	44.4
4	U20c	*Pteridium aquilinum-Galium saxatile* community: Species-poor subcommunity	62.7
	W16	*Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland: 2 subcommunities	57.9
	U2	*Deschampsia flexuosa* grassland	57.5

C.S. = The Coefficient Of Similarity To That Subcommunity bracken subsites exhibit some affinity in having two coinciding categories (U2 and U20c) in the three highest coefficients of similarity to their subcommunities.

3.3.2 Plant Architecture

The heights of the most abundant groups of vegetation (less dominant plants were classed as 'other vegetation') were plotted as the number of touches for that group or species. Each subsite has two plots, these representing the two dates on which the architecture was surveyed (27th May and 14th July). These are given in Figures 3.8 - 3.11.

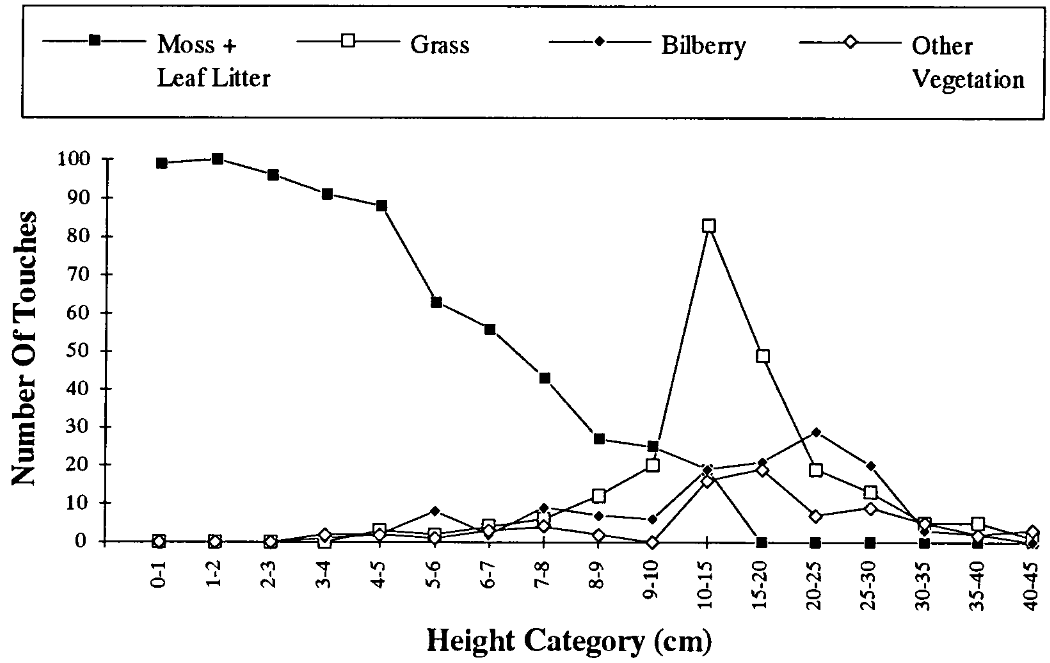
The most notable height change is apparent for the grass and bracken categories, the latter being low shoots in late May but by July becoming a forest of overhanging fronds up to and above 100 centimetres high. Thus the phenomonen is most noticable at the bracken subsite. This speed of growth, and hence shading of the underlying flora, has major ecological implications. However, even at the last date of pitfall collection the ground flora was still thriving and the lack of light appeared to have no effect during the study period. The importance of shading for the ground plants, and subsequently other organisms, is probably only noticeable later in the season. The other immediately obvious point to be gained from Figures 3.8 - 3.11 is the absence of leaf litter on the *Calluna* heath. The layer of moss and leaf litter may be important in maintaining a suitable microhabitat for many spiders. This considerations will be discussed later in connection with the spider associations at each subsite.

3.3.2.1 Detrended Correspondence Analysis (DCA) Of Architecture

Further study was conducted in order to try and isolate any significant differences between the subsites. The vegetational height categories were used in a DECORANA (Hill, 1979) analysis shown in Figure 3.12. From this plot four groups can be isolated and these are given below together with the height category that each code represents. The total number of touches from all subsites for that division is shown in brackets. The number of touches were obtained through reference to the raw data sets.

Figure 3.8 The Vegetation Heights At Subsite 1 (Bilberry)

Subsite 1 Date 1 (27th May)



Subsite 1 Date 2 (14th July)

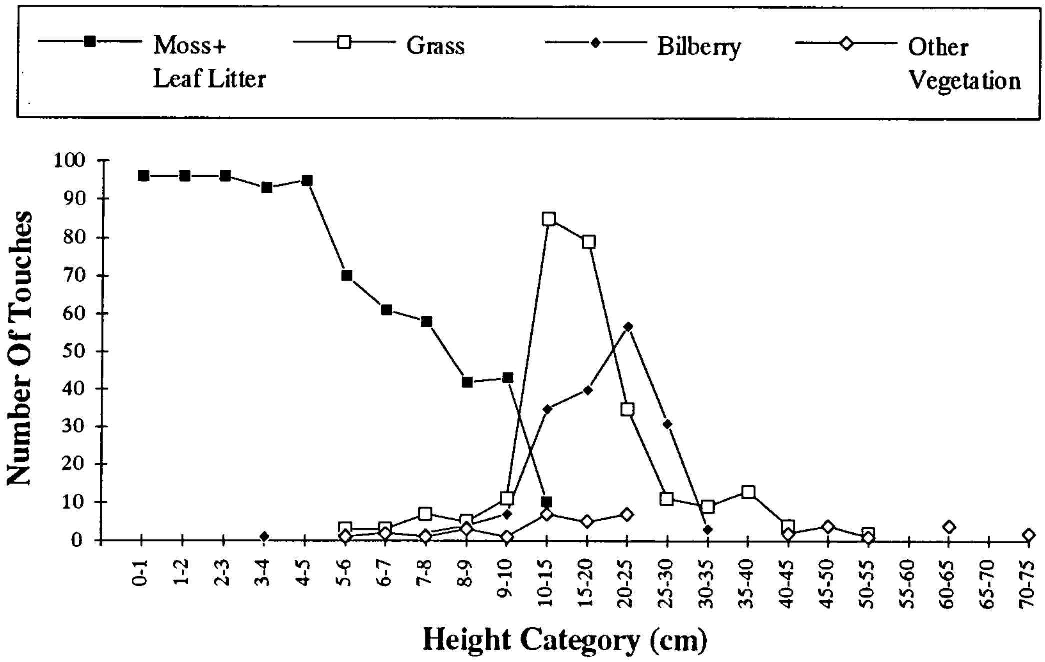
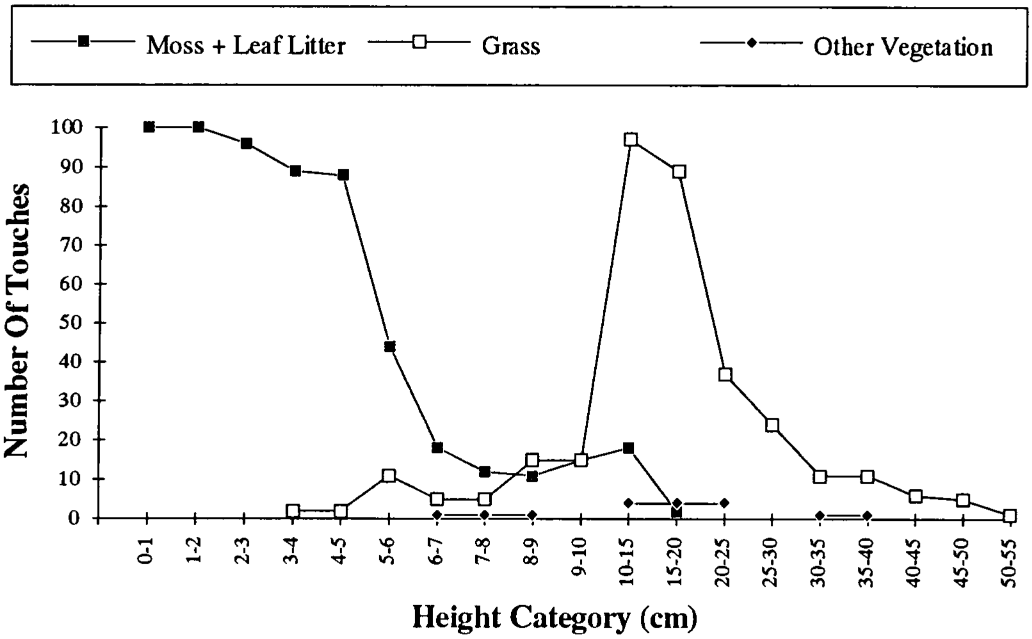


Figure 3.9 The Vegetation Heights At Subsite 2 (Grassland)

Subsite 2 Date 1 (27th May)



Subsite 2 Date 2 (14th July)

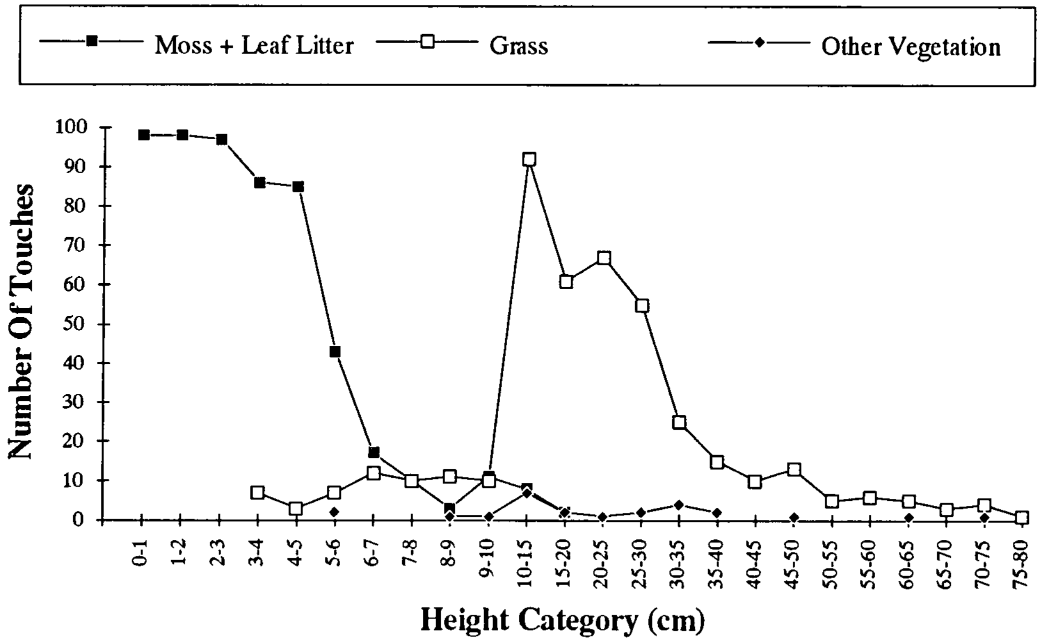
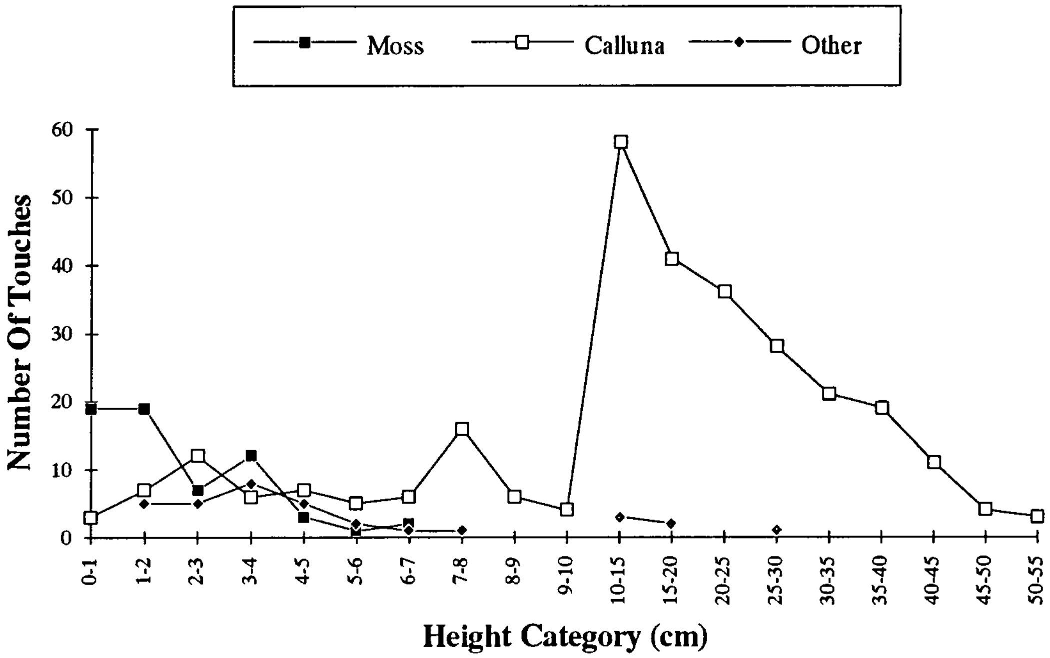


Figure 3.10 The Vegetation Heights At Subsite 3 (Heather)

Subsite 3 Date 1 (27th May)



Subsite 3 Date 2 (14th July)

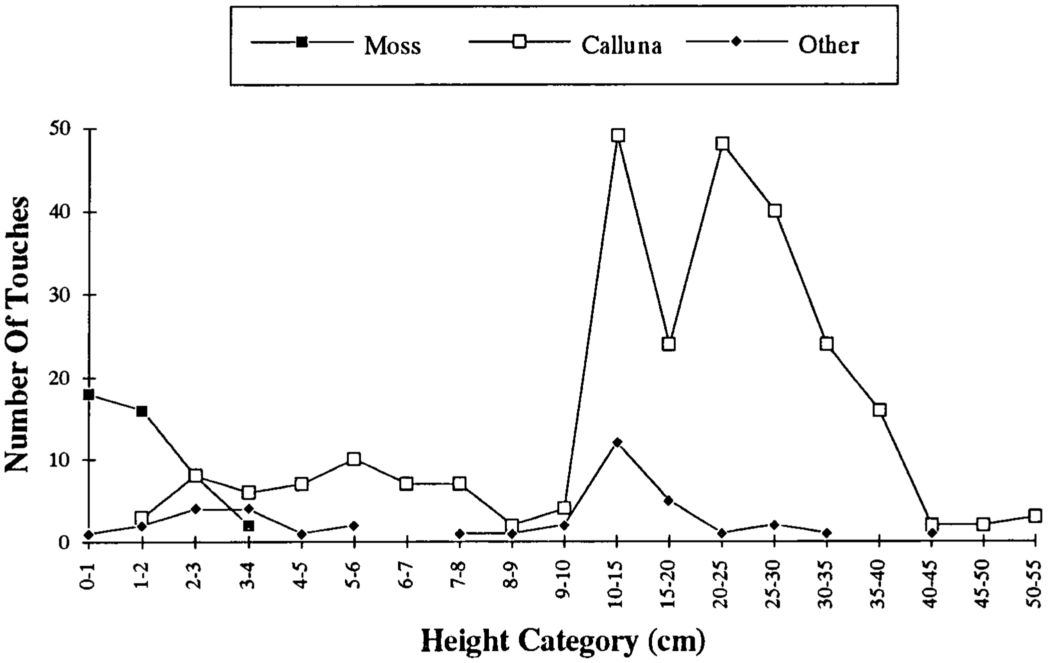
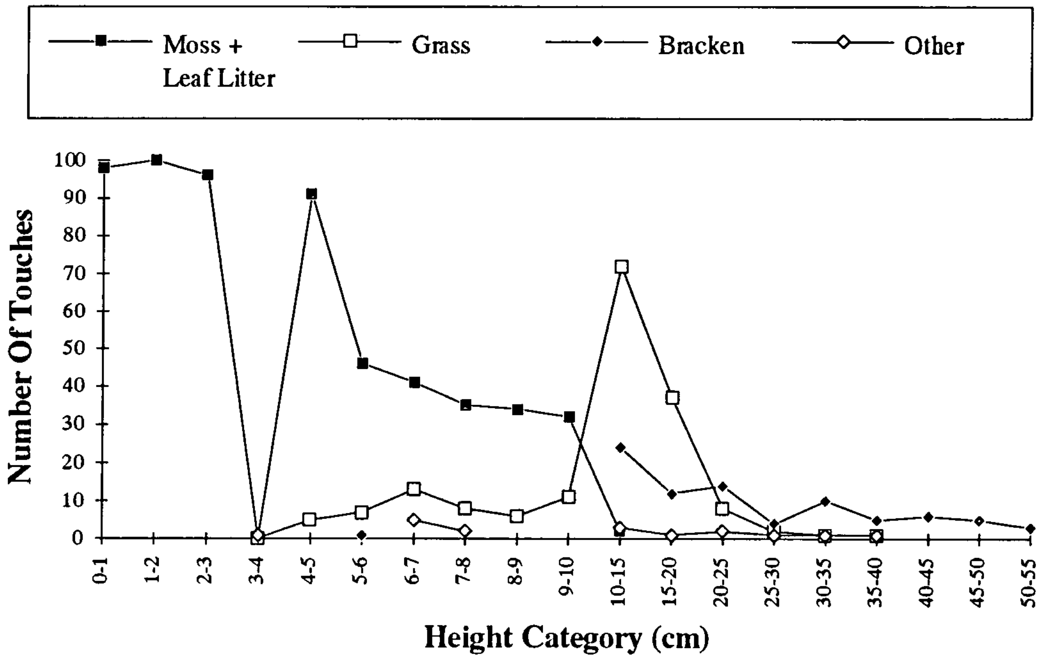


Figure 3.11 The Vegetation Heights At Subsite 4 (Bracken)

Subsite 4 Date 1 (27th May)



Subsite 4 Date 2 (14th July)

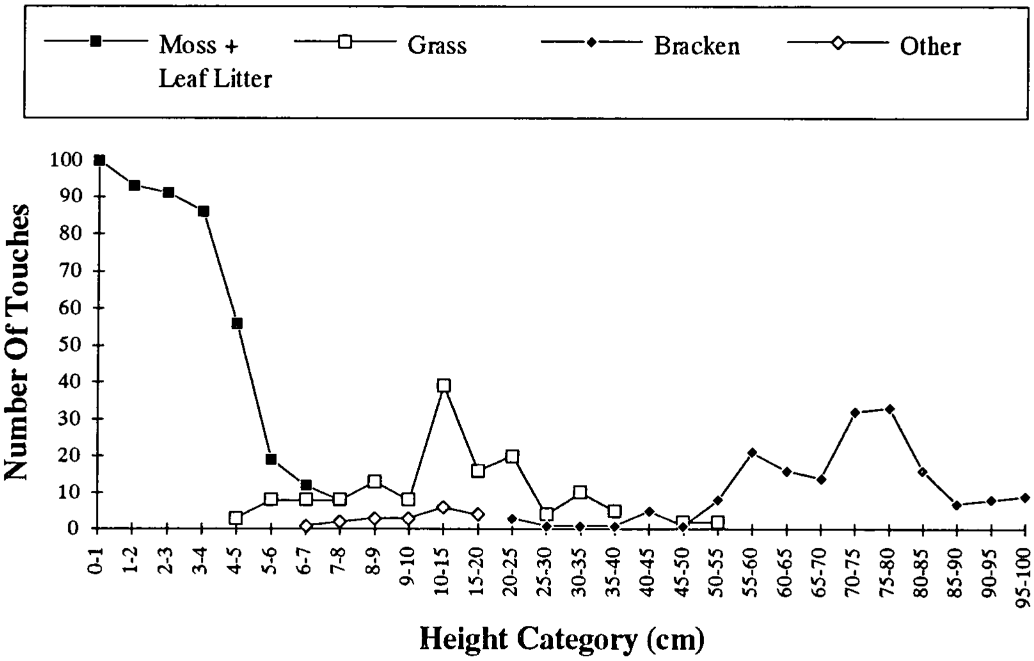
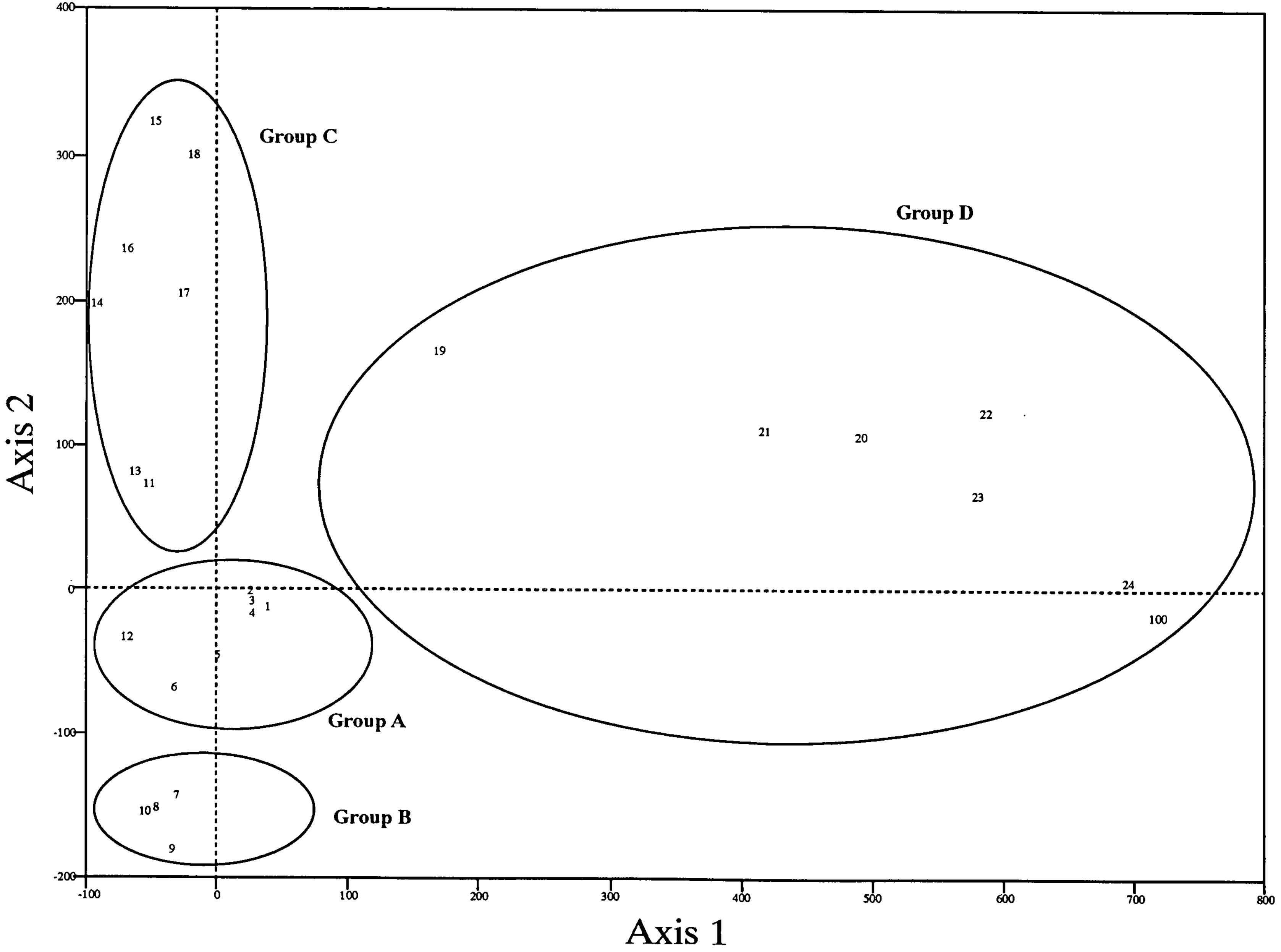


Figure 3.12 - The DCA Plot Of
Vegetation Height Categories



Group A

1	0-1 cm (630)
2	1-2 cm (632)
3	2-3 cm (613)
4	3-4 cm (585)
5	4-5 cm (546)
6	5-6 cm (357)
12	15-20 cm (561)

Group B

7	6-7 cm (281)
8	7-8 cm (270)
9	8-9 cm (213)
10	9-10 cm (217)

Group C

11	10-15 cm (695)
13	20-25 cm (421)
14	25-30 cm (260)
15	30-35 cm (129)
16	35-40 cm (104)
17	40-45 cm (52)
18	45-50 cm (38)

Group D

19	50-55 cm (30)
20	55-60 cm (30)
21	60-65 cm (26)
22	65-70 cm (17)

23	70-75 cm (39)
24	75-80 cm (34)
100	80-85 cm (16)
100	85-90 cm (7)
100	90-95 cm (8)
100	95-100 cm (9)

100 = 25, 26, 27 and 28

Each of the architectural height category groups were extracted and compared to the raw data for the total number of touches at the individual subsites. Chi-squared tests were subsequently conducted to expose any significant differences between the subsites and the results are presented in Table 3.8. It is apparent from this that there are statistical differences between the subsites so far as these groups of height categories are concerned. These findings can be related to the groupings of spider species (i.e. groups 1 to 4) that show significant differences between the chosen plots and hence it appears that certain communities of spiders are associated with particular architectural design.

Much of the significance of group A is due to the lack of leaf litter at subsite 3 (heather). As mentioned earlier this could relate to the probable lower humidity and reduced temperatures on the ground, hence influencing the Araneae community structure. Another possibility is that the prey species may be different here and hence this area is more suited to particular spiders.

The group B height categories peak in number of touches at the bilberry and trough at the heather subsites, indicating that the vegetation is relatively thick and sparse respectively at these plots. It may be that the dense vegetation provides a preferable habitat for the sheet-web spinners (Linyphiidae) whilst the decreased foliage is more suited to faster moving ground spiders.

Group C shows a gradation of touches from subsite 1 to subsite 4. Whilst the Chi-square value between the chosen areas is the lowest of all the groups it is still highly significant and the importance can be illustrated by looking at subsite 3 (heather). In all the groups of height classes extracted the vegetation is at its most sparse in the heather area - with the exception of this group. Hence the dense vegetation of group C here (in relation to the other height groups) may be of value to the spider inhabitants of this area.

Table 3.8 - Chi-square Analysis Of The Associations Of Vegetation Height Classes Between Subsites As Given By Figure 3.12 (All With 3 Degrees Of Freedom)

Group	Number Of Touches In Each Group				Chi-Square Value Between Plots	P Value
	Subsite 1 (Bilberry)	Subsite 2 (Grassland)	Subsite 3 (Heather)	Subsite 4 (Bracken)		
1	1318	1218	290	1098	673.708	$p < 0.001$
2	475	185	60	261	370.971	$p < 0.001$
3	556	519	376	248	140.616	$p < 0.001$
4	9	27	6	174	360.333	$p < 0.001$

The categories represented by group D are almost non-existent at all subsites except for subsite 4 (bracken). The significance between regions is likely to be almost entirely due to the high proportion of touches at the bracken subsite. The high vegetation (all *Pteridium aquilinum*) is probably of little direct importance to the spider community although indirectly, via the canopy effect as suggested above, it may have grave consequences for the ecology of this subsite.

The speculations presented here shall be discussed in more depth later with reference to the work of other ecologists in this field.

4.0 DISCUSSION

4.1 The Araneae Data

4.1.1. Methodology

4.1.1.1 Pitfall Trapping

Pitfall trapping is extensively used to study the occurrence, abundance and activity of surface-active arthropods. Pitfall traps are inexpensive, setting them requires little effort, many species can be trapped and large catches often result. They also sample continuously and are therefore not prone to the problems of spot sampling in time. Resulting catches have been used to describe phenology (Merrett, 1967, 1968, 1969), estimate abundance (Duffey, 1962a, 1962b; Baars, 1979), elucidate diurnal activity cycles (Blumberg & Crossley, 1988) and to compare species assemblages (Culin & Yeargan, 1983). However, there has been a great deal of difference of opinion about the validity of pitfall trapping as a means of sampling invertebrate populations so an assessment of the use of this method is worthwhile. It undoubtedly has a number of drawbacks such as a tendency to trap more mobile spiders (thus not reflecting the comparative abundance of the sedentary species) and not accounting for the density of individuals in the population. Greenslade (1964) was uncertain about their effectiveness as a trap for the Carabidae because of escape rates and vegetation differences affecting the catches whilst Grüm (1971) described the influence of Carabid activity changes, due to prevailing weather conditions, on trap captures. Further doubt is cast on pitfall trap efficiency because of variation in capture from habitat to habitat (Mitchell, 1963) and species to species (Greenslade, 1964). Other authors, however, have been more positive, especially in relation to cursorial spiders. Uetz & Unzicker (1976), Baars (1979), Topping and Sunderland (1992) and, in a review of preceding literature, Southwood (1968) have all found favour with this technique. Uetz & Unzicker (1976) recommend the use of pitfalls over other sampling methods for the assessment of wandering spider guilds whilst Topping & Sunderland (1992), using both pitfall trapping and absolute density sampling of spiders in a 17 hectare field of winter wheat, declared that pitfalls are useful in creating an index for interpreting differences between sample areas. A study of the Carabid fauna of Kralo Heath (Province of Drenthe, Holland) by Baars (1979) reaches a similar conclusion.

Nevertheless, all these analyses underline the need to exercise caution in interpreting the resulting data. The research suggests that community comparisons using pitfall traps are valid if the following conditions are met. Firstly, that the trapping is continuous, over a long period of time, and the comparison of communities should be made on the basis of samples taken in the same seasons and in the same general climatic regime. Secondly, these comparisons must take into account the possibility of obstruction to movement by various habitat factors. Thirdly, pitfall trapping should be supplemented by a second method (for example hand-searches, sweep-nets or beating trays). Finally, some thought must go into reducing the known sources of error. Such examples include trap placement, design and attractant or repellent qualities of the trap content. Ideas on overcoming these three problems are discussed in some depth by Luff (1975), Uetz & Unzicker (1976) and Curtis (1980) respectively. These considerations represent the underlying view of research involving pitfall trapping although even here there are disagreements as exemplified by Halsall & Wratten (1980) whose work on Carabidae found few differences between differing substrates, traps and seasons. As far as this investigation is concerned every effort was made to conform to these conditions but for some, such as the long time span, it was simply not possible.

The crux of this matter, however, must surely be to isolate an alternative method that eliminates the deficiencies of pitfall trapping. Some of the more commonly used replacements are outlined below. At present, despite the reservations about pitfalls upheld by many, there is no other method that provides the ecologist with a quick, continuous and practical way of sampling the Araneae fauna of a given area. It is also not unimportant when resources are limited that they are cheap and easy to transport. The interpretation of results should be treated with some caution for the reasons described above but pitfall trapping is extremely useful in studies examining relative abundance such as community comparisons (Topping & Sunderland, 1992), species diversity (Uetz, 1976, 1979), habitat breadth (Uetz, 1991) and niche overlap (Uetz & Unzicker, 1976).

Thus, in view of this evidence and the drawbacks of other sampling techniques, pitfall trapping is probably the best available method for investigating spider sub-communities of a semi-upland site.

4.1.1.2 Sweep-Netting

The sweep-net is a cherished instrument of the arachnologist and in general it yields large numbers of specimens that are vulnerable to it (Turnbull, 1973). However, there are two major problems with it. Firstly, it cannot accurately sample very short or very dense vegetation (Southwood, 1968) and secondly, the sweep-net is extremely weather dependent as a wet net reduces invertebrates to an unidentifiable vegetation-animal slush. Other problems related to these but important in their own right to legitimate sampling are habitat differences (which may contain similar spider communities but vegetation differences skew the sweep-net capture) and changes in the vertical distribution of the spiders. Enders (1974) showed that orb-web building spiders remain lower in the vegetation during the juvenile stages whilst Foelix (1982) points out that smaller spiders in general stay closer to the ground regardless of species. Luczak (1966) showed that wandering spiders moved up and down in the vegetation structure depending on time of day and the physical properties of the microhabitat during that period. In addition it is well known (Johnson *et al*, 1957; Southwood, 1968) that the vulnerability of even closely related species to sweep-net capture is greatly variable.

This does not mean that the sweep-net is an ineffective way of collecting spider community data and several researchers endorse this method. For example Luczak & Wierzbowiska (1959) concludes that the selectivity of this technique is always of a similar type and does not give deformations in the overall picture of quantitative dynamics of ground flora spiders. Thus, whilst sweep-netting may be inefficient at sampling for population estimates it is a valid procedure for community comparisons. As for pitfall trapping the sweep-net is practical, cheap and no alternative is immediately obvious. The validity is, of course, only maintained if certain criteria are met. These include the synchronisation of similar weather conditions, time of day and number of sweeps made. In addition, the interpretation of results should be confined to the section of the vertical strata that the net samples.

4.1.1.3 Conclusion

The two methods described above, plus that of the beating tray (which records spiders from the upper shrub and tree layers hence its exclusion from this study), have been regarded as the three principal tools for sampling spider populations (Turnbull, 1973). Many alternative or auxiliary techniques are often utilised. The more common supplementary tools include capture and recapture (Dondale *et al*, 1970; Hallander, 1967), visual hand searches (Luczak, 1953; Kajak, 1960; Jenkins, 1990) and a variety of air or vacuum suction devices (Turnbull, 1966; Turnbull & Nicholls, 1966; Van Hook, 1971; Topping & Sunderland, 1992). A full review of arthropod sampling applications is given in Southwood (1968). As noted by Turnbull (1973) and Foelix (1982) there are no easy answers to sampling problems and every study must be considered as separate, requiring individual consideration depending on the particular information to be obtained.

In conclusion I believe that, despite the advantages - and disadvantages - that certain of these other methods may have over the ones used, pitfall trapping supplemented by sweep-netting is an invaluable combination for investigating this aspect of Araneae ecology, i.e. the comparison of spider communities in adjacent but vegetationally different stands.

4.1.2 Inter-Subsite Pitfall Data

As a preliminary text to this section, a consideration of the lifestyles of different spider families is worthwhile to outline the biases that may occur as a result of the trapping methods used. The Lycosidae will always be caught in large numbers via pitfall trapping merely because of their feeding strategy. This usually involves moving fast and catching the prey, purely by outrunning it. At the other extreme the sedentary spiders i.e. the web-builders (Araneidae, Tetragnathidae, Theridiidae, Dictynidae and Linyphiidae) will inevitably be under-represented in pitfall catches. The Araneidae and Tetragnathidae are orb-web weavers (Roberts, 1985a), the Dictynidae construct mesh-webs (Bristowe, 1958) whilst the Theridiidae create irregular tangle webs (Roberts, 1985a). The Linyphiidae spin sheet or hammock webs in which to trap their prey (Roberts, 1985b). The families with 'intermediary' strategies are often caught in low numbers but would appear to be more prone, as their ground activity is greater, to capture. As they are non-web builders they are termed, along with the Lycosidae, wandering spiders. This perhaps suggests that these families (the ones captured in this study being Gnaphosidae, Clubionidae, Thomisidae and Salticidae) to be of very low relative number in the population fauna if the assumption is made that they are caught in greater proportion than is their actual representation in the community. These four families each have a slightly different method of attacking their prey although all utilise a certain amount of the 'sit and wait' tactic, either under a stone or in dense vegetation (Bristowe, 1958). The generalised family traits of these groups, so far as prey capture is concerned, are outlined here as described by Bristowe (1958), Roberts (1985a) and Wise (1993). The Salticidae ('jumping' spiders) stalk their prey and then, as the name suggests, pounce whilst the Thomisidae ('crab' spiders) rely on ambush followed by a fast sideways scuttle. The other two families (Clubionidae and Gnaphosidae) are closely related and have similar hunting ecologies, both being short-sighted night hunters which stalk stealthily but can run rapidly when the prey is in range.

These characteristics are generally true for each family but, as with most biological phenomena, there are exceptions too numerous to mention here. Another way in which data may be biased is caused by differences of behaviour between sexes - the males of any particular species are more mobile during mate-searching (Topping & Sunderland, 1992) and the females whilst looking for an egg-laying site (Duffey, 1956). This is further complicated by the different mating seasons of spiders (Merrett, 1967, 1968, 1969). A more specific example is the Linyphiid genus *Erigone*, the males of which do not build a web but spend their lives searching for females and foraging for prey en route (Topping & Sunderland, 1992). However, despite these anomalies, the data is invaluable as a relative index for comparing differences between communities provided it is appreciated that the samples do not depict a population estimate of the subsites.

4.1.2.1 Totals

In isolation, the total number of spiders caught at each subsite explains very little although two points of interest do arise. Firstly, the lack of significant difference between subsites 1 (bilberry) and 4 (bracken) which may be a result of their similarity in relation to the vegetation classification. Secondly, the most spiders were caught at subsite 2 (grassland) and the least at subsite 3 (heather). This appears to contradict evidence that less open areas catch fewer individuals because of overhanging vegetation (Jenkins, 1990). However, pitfall sampling gives no indication of the absolute numbers at each subsite. Thus, although subsite 2 (grassland) shows three times as many spiders caught as subsite 3 (heather), the actual population density may be ten times greater, so in actuality the pitfalls are catching a higher proportion of the community in the heather area. Alternatively, the situation could be reversed for whatever reason, perhaps spiders are simply less mobile on the more exposed (and hence an increase in predation risk) heather region, although there is no evidence for this. This note of caution must be expressed and heeded throughout the interpretations of the pitfall data.

4.1.2.2 Spider Richness And Diversity

The richness, abundance and diversity of the spider fauna are usually greater in vegetation associated with later stages of ecological succession or in plant communities with greater structural complexity (Uetz, 1991). This has been illustrated in a variety of habitat types including deserts (Chew, 1961), grasslands (Duffey, 1962a, 1962b), meadows (Kajak, 1960, 1962), prairies (Muma & Muma, 1949), sand dunes (Duffey, 1968) and forests (Bultman & Uetz, 1982; Bultman *et al*, 1982).

In this study species and family richness are not significantly different between subsites indicating that the plots have a similar complexity or age. Nevertheless, the species diversity shows much fluctuation and is especially low at subsite 2 (grassland). This could be a result of the simplicity of Graminaceae which shows little structural complexity. A possible explanation of the species richness not being significantly different at this subsite in relation to the other plots, is the so-called 'edge effect.' Where subsites are small many species may encroach in low numbers such that they are present but do not form an integral part of the subcommunity. This may also be the case for family richness.

The highest diversity of spiders were found on the heather heath (subsite 3). This result opposes previous work by Uetz (1975, 1976, 1979) which found a positive correlation between depth of deciduous forest leaf litter and diversity in wandering spiders i.e. non-web builders, for both species and families. He attributed this to an increased diversity of microhabitat and hunting strategies available to the fauna. However, species (and family) richness and diversity are also known to be correlated with overall vegetation complexity. Greenstone (1984) found a significant correlation between vegetative tip-height diversity (a measure of potential attachment points for webs) and the diversity of web-building species whilst Rypstra (1986) compared web spider abundance in a temperate forest (Pennsylvania) with tropical forests (Peru and West Africa). Vegetation density was consistently the best predictor at all sites, with prey abundance and micro-climate significant additional variables.

Thus, it appears that the vegetational complexity as a whole is the over-riding factor giving the heather high diversity values. This would be in accordance with the discontinuity compared to other areas of the fell; patches of moss, grass and a variety of other herbs in addition to the characteristic bare ground possibly give the spider fauna the opportunity to become increasingly diverse, if not numerically more abundant.

4.1.2.3 The Predominant Lycosid Species

The plethora of research on the Lycosidae seem to form a disproportional percentage of ecological studies concerning the Araneae. This is hardly a surprise as they are caught in large numbers (probably as a consequence of their high mobility), are easy to identify (due to size, immediate recognisability and low number of species - only 36 from 9 genera in Britain) and form a constituent part of virtually every community.

The three species scrutinised here (*Alopecosa pulverulenta*, *Pardosa nigriceps* and *Pardosa pullata*, in order of increasing abundance) were the most abundant Lycosids trapped. This may have been because the activity of these species peaked during the study period as they do on heathlands in the south of England (Merrett, 1968). Other Lycosids captured are known to be more active during other months of the year. For example *Trochosa terricola* has two mobility peaks, both outside this study period, in April and October (Merrett, 1968).

However, whilst this may account for the high abundances it does not explain the distribution patterns. The *Pardosa* genus (formerly *Lycosa*) is a group of rapidly moving hunting spiders with all except *Pardosa nigriceps* confining their activities to ground level (Roberts, 1985a). *Pardosa nigriceps* is usually found on low vegetation such as gorse (*Ulex europaeus*) or heather and is the only species in this genus to exhibit arboreal tendencies (Locket & Millidge, 1951). Thus, there is ecological separation with *Pardosa pullata* living in the 0-5 centimetre band and *Pardosa nigriceps* operative at 20-30 centimetres (Duffey, 1963). This has also been correlated with preference for damp (*Pardosa pullata*) and drier (*Pardosa nigriceps*) places (Vlijm & Kessler-Geschiere, 1967). On the face of it, therefore, *Pardosa pullata* should be a far more frequent capture - relative to *Pardosa nigriceps* - in all areas containing leaf litter, as its ground hugging existence makes it more liable to be pitfall trapped. Despite this not being the case an explanation can be given by linking the spiders' behaviour to the chosen plots. Subsites 1 (bilberry) and 4 (bracken) had little overhanging vegetation and thus *Pardosa nigriceps* would be more likely to fall in the traps relative to the overlying grass at subsite 2 because it is known to prefer shorter, drier vegetation that it can run across the top of (Williamson, 1949; Vlijm & Kessler-Geschiere, 1967). Hence, greater capture in the bilberry (subsite 1) and bracken (subsite 4) areas. *Pardosa pullata* on the other hand prefers longer damper vegetation in which to inhabit (Williamson, 1949; Vlijm & Kessler-Geschiere, 1967) as at the grassland site. Thus each species dominates in its preferred habitat. Subsite 3 (heather heath), where *Alopecosa pulverulenta* is the numerically abundant Lycosid, is more difficult to comprehend, particularly as there is little available work on this species. A possible explanation, as suggested by Durnford (1992), is that *Alopecosa pulverulenta* at 5-10 millimetres (Locket & Millidge, 1953; Roberts, 1985a) is a larger spider than the *Pardosa* species' at 4-7 millimetres (Locket & Millidge, 1953; Roberts, 1985a) and is preying on them, thus keeping the numbers lower. Another possible answer which may be associated with size, is that *Alopecosa pulverulenta* is a better competitor in this habitat, perhaps for available prey, or that the microclimate is more favourable compared to the smaller *Pardosa* species. As the heather area is dominated by bare ground the smaller spiders may have greater problems with desiccation, as they have a proportionally larger surface area over which to lose water. This is unlikely to be a factor here though as Hedleyhope Fell appears to be very wet, with a high precipitation level. In other years, however, it may become more important as it can be very dry for short periods (Standen, pers. comm.).

The ecological isolation of these three species, whatever the causal mechanism(s), provides a good opportunity to investigate the theory of mutual exclusiveness i.e. that no two species living in the same habitat have identical ecology (Gause, 1934). However, the implications will be discussed later in order that architectural divisions and vegetational composition differences can be incorporated into the argument.

4.1.2.4 Other Differences In Species' Occurrence

(a) The *Lepthyphantes* genus

I have not been able to find any work expressly associated with this genus. The constituent spiders are widespread throughout the British Isles and are abundant in virtually every locality, although there is some species preference for particular habitats, for example *Lepthyphantes pallidus* in moss and grass on high ground and *Lepthyphantes ericaeus* in dry heathery places (Locket & Millidge, 1953; Roberts, 1987). The high numbers caught at the bilberry subsite were presumably indicative of a favourable microhabitat, possibly reflecting the abundance of web-building sites. *Vaccinium myrtillus* would provide ideal scaffolding for sheet web construction with sturdy support from its tough stems which are close to the ground yet not very dense. The peak of touches is at 10-15 centimetres for grass and 20-25 centimetres for bilberry as given in the architecture survey by Figure 3.8. These levels are known to be frequented by Linyphiids as webs are often found between about 10 and 40 centimetres (Bristowe, 1939). A more specific example is given by Schaefer (1978) who concluded that the Linyphiid *Floronia bucculenta* was limited in its distribution by the availabilty of low-lying, dense vegetation in which to constuct its web.

(b) *Silometopus elegans* and *Evansia merens*

Once again suggestions as to why these species should congregate at a particular subsite (*Silometopus elegans* on the grassland and *Evansia merens* on the heather) are generally speculation due to the dearth of specific publications. *Silometopus elegans* is found, if rather uncommonly, in wet grass, moss and undergrowth (Locket & Millidge, 1953; Roberts, 1987). This may explain the predilection to the grassland subsite but the reasons for this are unclear. This species heavily outnumbers other Linyphiids (which presumably have similar micro-habitat requirements) so this conglomeration is likely to be a 'hot-spot' where dispersal has been poor although Duffey's (1956) work at Wytham Wood (near Oxford) demonstrates that the dispersal of hammock-web spinners is usually very efficient. Many other Linyphiids are described by Locket & Millidge (1953) and Roberts (1987) as being 'locally abundant' and this is possibly the case with *Silometopus elegans*.

Evansia merens is a myrmecophilous spider and hence has a requirement for Formicidae. Bristowe (1939) has shown that the rare discovery of such spiders not associated with the nests of ants is because of dispersal activity only. Thus the distribution of *Evansia merens* is skewed towards areas of high ant populations as at the heather subsite. An interesting side issue here is the possible interspecific competition between ants and spiders as both are generalist predators and therefore likely to be competing for the same food supply. There is only likely to be this type of competition among non-web builders and ants as web constructors, in general, trap a different part of the insect fauna (winged invertebrates instead of apterous ones). The published studies of this interaction are sparse and even these produce conflicting views. Van der Aart & de Witt (1971) believe that, via an investigation on ants and hunting spiders (i.e. the non-web building families of Lycosidae, Gnaphosidae, Ctenidae, Pisauridae and Clubionidae) in Holland (in an area adjacent to the Hague and Wassener), that the relationship between Formicidae and Araneae is of a competitive nature whilst Breymeyer (1966) reaches an opposite conclusion. In respect of this study it is perhaps the combination of low spider numbers and high numbers of ants at subsite 3 (heather) that are a reflection of the interspecific competition between these two highly successful orders. This is pure speculation, however, and these anomalies may be more indicative of the preference of ants to bare ground.

4.1.2.5 The Detrended Correspondence Analysis (DCA) Of Species

The DECORANA analysis showed there to be different spider communities at each subsite. It seems probable that these are due to structural and compositional vegetational differences (Uetz, 1991). This effect may be direct, as specific structures are needed for activities such as web-building (Cherrett, 1964; Enders, 1974) or indirect, with certain requirements for physical properties (light, temperature, humidity *etc*) or prey availability (Turnbull, 1973) being correlated with vegetation structure. This analysis merely illustrates that there are different spider associations at each subsite, and in isolation is of limited use. In-depth discussion will be deferred until section 4.3.

4.1.3 Inter-Date Pitfall Data

4.1.3.1 Totals

Spiders are no different to any other group of organisms in that their main activity is concentrated around the time of maximal productivity i.e. spring and summer. This is hardly earth-shattering news, particularly as they are generalist predators and as such are governed by the cycles of abundance and activity of their prey. This study merely provides a snap-shot of an annual fluctuation and there is little to be gained without continuous sampling throughout the year. However, the large increase in spiders caught from early June to late July is particularly noticeable and July is indeed the month where a sharp incline is noted (Duffey, 1962a, 1962b; Bultman & Uetz, 1984; Topping & Sunderland, 1992). This is obviously a generalisation and it is worth noting that different species, even those that are closely related, mature at different times. This may be important in avoiding interspecific competition particularly as younger spiders are known to occupy lower levels in the vegetation (Enders, 1974). The significance of this, because of the resultant increase in activity and hence a larger pitfall capture, is outlined below. The decline in numbers from the last sample date is completely unexpected and probably entirely due to the flooded traps, as there is no published evidence for a reduction in Araneae at this time, although there is a higher proportion of juveniles in the population. Spiderlings are notoriously good escapees from pitfalls (Uetz, 1991) and with males dying shortly after mating (Savory, 1964; Bristowe, 1958) this could explain the decrease in captures.

4.1.3.2 The Male To Female Ratio

The male : female ratio provides interesting discussion as males outnumber females heavily in all but the final collection. This is consistent with the research of other spider ecologists. Tretzel (1955) attributed the high percentage of males during the spring to male-searching as they give up their webs and become mobile in the search for a mate. This behaviour has been well documented by Savory (1964) and Bristowe (1958). Following mating, males die and females exhibit post-copulatory dispersal (Merrett, 1967), usually in the quest for a suitable oviposition location (Duffey, 1956). Thus, as pitfalls reflect the activity of invertebrates, the males are seen to increase followed by a peak in female capture (as seen to a certain extent in this investigation). However, a word of warning should be expressed at this point. The male : female ratio is, on the whole, clearly greater in all families (Figure 3.7) but the overall proportion does not take account of the relative numbers between these groups. For instance the high number of Lycosidae probably influences the whole picture as they have a greater weighting, by number, than many of the other families, Thus, the changes in ratio may be more indicative of the assemblages of Lycosids and Linyphiids than the population as a whole.

4.1.4 Sweep-Net Data

Despite the lack of captures for this sampling method and hence the invalidity of interpreting the data statistically, some trends are apparent and these can be compared to the published research. Turnbull (1973) outlines the susceptibility of certain families to sweep-netting with the most vulnerable (some Linyphiidae, Araneidae, Dictynidae and Theridiidae) likely to be caught in large numbers whilst others are rare (Clubionidae and Gnaphosidae). This is to be expected as the sweep-net is sampling the lower shrub level where the microhabitat is favourable for some species and families. The data gleaned from this investigation supports this assumption with the families Dictynidae and Araneidae, plus three species from other families (Thomisidae and Linyphiidae), caught exclusively in the net. However, Turnbull (1973) also points out that this method only provides a glimpse of the spider fauna as the vulnerability of animals is controlled by their vertical distribution which can change with the development stage of the plant or spider and hour to hour changes in temperature, humidity, air movement and insolation. A further consideration is dampness as wetter conditions confer lower habitation in the vegetation. This is reflected by the relatively high numbers caught in the heather (subsite 3). *Calluna vulgaris* is structurally sparse and dries out much faster after a shower or in the morning (following heavy dew) than the other regions. Hence the Araneae are found, and therefore captured by sweep-netting, more consistently at this level in comparison to the other subsites.

4.2 The Vegetation Survey

4.2.1 Methodology

The sampling of vegetation by using a scale to represent the percentage of that plant present has long been recognised as valid, providing the quadrats are randomly positioned in that particular stand of vegetation (Poore, 1956; Grime, 1979; Smith *et al*, 1985). Most work on phytosociology incorporates a percentage cover technique to quantify the plant composition and in this respect the investigation is no different. The number of species found in the quadrats as a percentage of the total species was high, indicating that the quadrats are a good represenetation of the flora at each subsite. Much the same applies for the definition of vegetation architecture although the bayonet method was a divergence from the norm which is to use point quadrats. These two methods reach the same conclusion and it is simply personal preference for the former that the bayonet was used. This is because I believe that the edge of the instrument removes any doubt as to whether a touch has been made or not whereas the point quadrat method may introduce some subjectivity.

4.2.2 Plant Species Composition And Architecture

Plant species composition and architecture are both different between the subsites, as shown by the National Vegetation Classification and DECORANA analyses respectively. However, these conclusions simply illustrate that there are anomalies between the subsites and not how they relate to spider communities. Discussion of these areas will be deferred until section 4.3 when the spider guilds at each subsite will be related to the vegetation differences. The incorporation of Araneae data into the argument will give a clearer picture of why foliage structure is important in determining the distribution of this invertebrate group.

4.3 The Relationship Between Plant Structure And Spider Communities

4.3.1 The Vegetation Cover

The role played by phytosociology in determining spider communities encompasses a degree of controversy as several arachnologists have interpreted their findings in dissimilar ways.

Luczak (1963) chose the web-building spiders of the field and canopy layers of a young pine (*Pinus sylvestris*) forest upon which to base his study. Despite superficial differences the pines constituted three distinct phytosociological habitats each of which contained the same association of web spiders.

The majority of work, however, exposes separate plant communities as having a specific group of spiders associated with them. In a study of the dune spider composition along the shores of Lake Michigan, Lowrie (1948) noted that the spider community altered as the structure of the vegetation community changed with dune succession. Duffey (1962a, 1962b) scrutinised the microdistribution of spiders on a limestone grassland (Wytham Wood, Berkshire) and was able to correlate the distribution of individual species with habitat features, including plant species composition. The work of Cherrett (1964) on the occurrence of spiders on moorland at Moorhouse Nature Reserve, Westmorland concluded that different habitat forms supported differing spider fauna for the Argiopidae (orb-web spinners), Lycosidae (wolf spiders) and the Linyphiidae (sheet or hammock web builders). Another analysis by Barnes & Barnes (1955) revealed that the spider community of a given vegetational arrangement may stay remarkably constant from area to area. This was illustrated by their work on the succession of abandoned farmland throughout the south-eastern United States which found relative spider abundance and species present to be very similar in what they termed the 'abstract broomsedge community.'

Further research has compared spider populations in adjacent but dissimilar plant associations and found marked differences (Macfadyen, 1954; Kajak, 1960; Lowrie, 1963). Much has been discovered on the relationship between vegetation and spider communities, but in the majority of work a consideration is made of the architectural aspects as well. Thus, whilst a brief deliberation is offered below, a more comprehensive discussion incorporating all aspects of the plant structure will be given later.

The classification of data into a recognised form (National Vegetation Classification) enables the subsites to be formally appreciated as sub-communities in their own right. This means that the original choice on a purely visual basis is an efficient way of isolating vegetational differences. At the highest coefficient of similarity (CS) the subsites are distinct but there is considerable overlap in classification between the bilberry and bracken dominated areas with the U2 and U20c codes both found in the top 3 CS values for these subsites. However, the bilberry and bracken subsites do have certain phytosociological differences and the resident spider guilds exhibit considerable disparity, indicating that they are separate subcommunities, although perhaps with superficial similarities.

4.3.2 The Vegetation Architecture

This section will overlap to some extent with 4.3.1 as it is very difficult to isolate vegetation configuration from species composition as, in general, a certain plant species will have a particular growth form. This though, is a simplification to a certain extent in that the same species will vary in architecture with age. Barclay-Estrup (1973) illustrates this well in work on heather succession where areas that are homogenous in *Calluna vulgaris* cover fluctuate widely in their structural suitability for arthropods. The study of Hedleyhope Fell examined four subsites that were heterogeneous in plant composition (see 4.3.1) and architecture, the latter being shown as a result of the DECORANA analysis on distribution of height categories at each subsite. These architectural differences can be related to the different spider communities and thus used to explain why some species and families prefer a particular combination of height levels. The following section will discuss both the hypothesis that dissimilar plant communities contain disparate spider associations and also, having established this, the ecological reasoning behind this isolation.

Vegetation provides 'home and table' for invertebrates (Richards, 1983), but they also require shelter and perhaps less easily defined attributes. The more diverse the plant architecture of a plant community the more numerous are its niches (Krebs, 1985). A niche of an animal is its place in the biotic environment and its relations to food and enemies (Elton, 1927). The vertical structure and density of the sward determines the microclimate of that area and hence the number of available niches. This in turn will determine the abundance and diversity of species present. These variables are equally important to spiders as to any other invertebrate group.

The finely branching and close proximity of moss stems and litter produces a large number of microhabitats i.e. niches. Spiders can move vertically through the perpendicular moisture gradient from the damper lower layers to the drier upper layers to find the most favourable level. Much previous research has focused on the influence of deciduous forest leaf litter on spider communities (Uetz, 1975, 1976, 1979). This established that species richness and diversity is correlated with litter depth, hence a 10 centimetre depth of litter would contain a different community to an area of 5 centimetre litter depth. As pointed out by Foelix (1982) each zone has a characteristic microclimate, various niches for retreat and a different spectrum of prey animals. Thus, the importance of large areas of bare ground at subsite 3 (heather) is illustrated as species with a microhabitat requirement for leaf litter, for whatever reason, will be absent. Whilst this may encourage species that prefer bare ground, the loss of many niches that come with the establishment of a layer of moss and dead foliage has impoverished this region, at least in respect of numbers caught although not in species or family diversity.

Since the influence of habitat structure is complicated by interaction with associated variables (microclimate *etc*), several experimental studies have sought to separate these differences. Stevenson & Dindal (1982) and Bultman & Uetz (1982) compared spider communities in both artificial litter (which does not serve as a trophic base for the decomposer arthropod community) and natural litter of varying structure, Stevenson & Dindal (1982) found that species and family guild diversity was greater in curled natural leaves and curled filter paper than in flat leaves or filter paper. They also found that although all litter types supported approximately the same proportion of hunting and web-building spiders, complex (curled) litter supported greater density of a Theridiid web-builder, *Enoplognatha ovata*, whose three-dimensional web and retreats are more common among curled leaves. Bultman & Uetz (1982), using vinyl plastic and natural leaves, found that structural complexity of litter significantly affected abundances of some forest floor spiders, in particular web-building species. Variation in litter nutritional content and complexity only slightly affected species composition and richness. These results suggest that litter depth is more influential than structural complexity or nutritional content of litter in organising the ground Araneae fauna. This can be related to the lack of litter (hence reduction of abundance of spiders) at the heather subsite although the diversity is high when it would be expected to be the lowest. However, this may be a consequence of complexity at a point other than ground level. The litter was also recorded as being slightly deeper at subsites 1 (bilberry) and 4 (bracken) and this indeed is correlated with both species and family diversity which are higher here than at the other litter subsite (the grassland area). In general, therefore, this study falls into line with other work on litter depth in different habitats.

Several other investigators have manipulated the structure of above-ground habitats to test the influence of habitat complexity on spider communities. Hatley & MacMahon (1980) experimentally altered the vegetative structure of sagebrush communities by respectively clipping branches to reduce, and tying branches together to increase, complexity. The number of spider species, spider guilds and guild importance values were significantly higher in shrubs with branches tied together, and lower in shrubs with clipped branches. This suggests that structurally more complex herbs can support a more diverse spider community. Rypstra (1983) tested the influence of availability of prey and web attachment structures for spiders in field enclosures in a Pennsylvania woodlot. Although both variables influenced the density and diversity of spiders, the influence of structure (in the form of wooden orange crates) was more pronounced and consistent overall. Thus, the low diversity at the grassland subsite may be indicative of the architectural simplicity of grass.

Several authors have suggested that the relationship between spiders and vegetative structure reflects 'species stratification' or habitat resource partitioning as a means of reducing interspecific competition. Luczak (1966) outlines the distribution of wandering spiders (Salticidae, Clubionidae and Thomisidae) in the field layer and pines of Poland and concludes that interspecific competition is keeping the species apart. Uetz (1977) reaches a similar verdict for wandering spiders in Delaware whilst Enders (1974) shows vertical stratification to be important in separating orb-web spiders (Araneidae) in North Carolina. Another example of this is given by Nørgaard (1951) via a study on *Pardosa pullata* and *Pirata piraticus*, two wolf spiders apparently co-habiting bogs where *Sphagnum* moss is found. However, *Pardosa pullata* keeps almost exclusively to the surface of the moss whereas *Pirata piraticus* prefers the more secluded stem region of the moss. Continuous monitoring shows that the temperature fluctuates a great deal on the surface of the moss but very little inside. The adaptation to differing temperature regimes allows the two species to live in the same habitat. A further point expressed in much of this work (Luczak, 1966; Turnbull, 1973; Enders, 1974; Uetz, 1977) is the intraspecific variation in distribution of many spiders. This may vary with age (juveniles tend to remain closer to the ground), size, breeding season, time of day and prevailing weather conditions. The latter two parameters are linked with changes in microclimate.

These studies and others (Turnbull, 1960; Olive, 1980; Brown, 1981), plus the other Lycosid work described earlier, appear to support the Gaussian hypothesis that only one species can occupy a distinct ecological niche. However, it cannot be stated as a general rule that only a single species will live in a given habitat. The American wolf spiders *Pardosa carolinensis* and *Pardosa timuqua* live in the same habitat, hunt the same type of prey and are both active at night (Kuenzler, 1958). Other species, particularly among the jumping spiders, migrate back and forth between different vegetative zones (Luczak, 1966).

In general though, the specific preference of many spiders to different levels of vegetation is shown in similar stands of vegetation (Robinson, 1981). It is therefore no surprise that separation should occur in areas of differing plant composition and architecture and hence the formation of individual spider guilds. The fact that the DECORANA height category analysis and spider groups respectively removed and subsequently analysed were significantly different between subsites indicates that each plot has a characteristic spider guild and vegetation structure. This gives an adequate explanation of the data evaluated with each association of species showing a preference for a specific habitat.

From the literature discussed above the impression gained is that some authors believe interspecific competition to be of maximal importance in determining the eventual spider community while others favour the microhabitat preferences. In reality both are probably correct as virtually all habitats are different and require individual attention to elucidate the causal factors of the community composition. In this investigation it may be that interspecific competition is of greatest importance as competition is increased in even moderately harsh environments because there are less natural enemies controlling numbers than in more favourable places (Connell, 1980).

Hedleyhope Fell could be considered as moderately severe climatically as precipitation is high, winds are strong and temperatures low. The predation pressure is therefore possibly low in relation to lower-lying sites with only a few moorland and heath vertebrates such as birds (mainly meadow pipit - *Anthus pratensis* but also linnet - *Carduelis cannabina*, whinchat - *Saxicola rubetra* and partridge - *Perdix perdix*), amphibians (common frog, *Rana temporaria*) and mammals (the shrews *Sorex minutus* and *Sorex araneus*) present in any significant number. Shrews and frogs are known to be important predators of spiders (Coulson, 1978) and may constitute 1-2 percent of their diet (Bristowe, 1941). The insectivorous meadow pipit is probably the most common bird present but spiders are minimal in the diet fed to nestlings (Coulson, 1978). Very little is known of the interactions between other invertebrates and Araneae but spiders do prey on each other, both inter and intraspecifically (Bristowe, 1958) and it may be that the larger species are important predators of the smaller. Parasites of spiders are probably minimal although spiders are attacked by parasitic wasps (Pompilidae and Sphecidae) both as eggs and adults (Foelix, 1982) and Bristowe (1958) cites the hunting wasp *Anoplius fuscus* as commonly affecting the wolf spider *Trochosa terricola*. However, these parasitoids may not affect spiders so much at this semi-upland site as they are frequently less active at higher altitudes. An example are the Hymenopteran parasites of the rush moth *Coleophora alticolella* which is rendered ineffective by increased elevation (Randall, 1982).

4.4 Conclusion

The assumption that spiders are highly mobile creatures with excellent dispersal mechanisms (Duffey, 1956; Richter, 1970; Foelix, 1982) leads to the hypothesis that, potentially, the spider fauna of a given habitat could be the same as any other. This, of course, is a very simplistic view because the communities are open to a whole host of ecological pressures which may or may not be operative on such assemblages. In this investigation different spider guilds have been demonstrated at each of the subsites so it is therefore appropriate to consider the possible causes of this separation. One such mechanism is plant architecture which is significantly different between the subsites. Another is plant composition, which has also been studied, with the adjacent subcommunities classified as different by the National Vegetation Classification system. Hence these two aspects of vegetational dissimilarity are at least a partial cause of the segregation of the spider communities.

This conclusion is supported by much of the ecological research concerned with the distribution of Araneae (e.g. Turnbull, 1973; Uetz, 1991). How important this contribution is remains to be seen. Nevertheless, given their dependence on environmental structure (e.g. web construction sites, microclimate) and their unique perceptual biases (spiders receive information through mechanoreceptors), spiders are likely to be highly sensitive to the physical arrangement of objects in space and therefore are excellent organisms with which to examine questions about the ecological role of habitat structure.

As a final remark in respect of the investigation at Hedleyhope Fell, I shall contend that the relative proportions of spiders collected at the subsites are representative of a particular vegetation cover and group of architectural characteristics and that these communities are different from each other, at least for the time period studied. Thus, it is fair to conclude that the spider fauna of these habitats is governed to some extent by the underlying vegetational attributes.

REFERENCES

Baars, M.A. (1979). Catches in pitfall traps in relation to mean densities of Carabid beetles. *Oecologia*, **41**, 25-46.

Barclay-Estrup, P. (1973). Arthropod populations in a heathland as related to cyclical changes in the vegetation. *Entomologist's Monthly Magazine*, **109**, 79-84.

Barnes, R.D. & Barnes, B.M. (1955). The spider population of the abstract broomsedge community of the southeastern piedmont. *Ecology*, **36**, 658-666.

Blumberg, A.Y. & Crossley, D.A. (1988). Diurnal activity of soil-surface arthropods in agroecosystems : design for an inexpensive time-sorting pitfall trap. *Agriculture, Ecosystems and Environment*, **20**, 159-164.

Breymeyer, A. (1966). Relations between wandering spiders and other epigeic predatory Arthropoda. *Ekologia Polska (A)*, **14**, 26-67.

Bristowe, W.S. (1939). *The Comity Of Spiders. Volume I.* Ray Society : London. 228 pp.

Bristowe, W.S. (1941). *The Comity Of Spiders. Volume II.* Ray Society : London. 560 pp.

Bristowe, W.S. (1958). *The World Of Spiders.* Collins : London. 304 pp.

Brown, K.M. (1981). Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia*, **50**, 380-385.

Bultman, T.L. & Uetz, G.W. (1982). Abundance and community structure of forest floor spiders following litter manipulation. *Oecologia*, **55**, 34-41.

Bultman, T.L. & Uetz, G.W. (1984). Effect of structure and nutritional quality of litter on abundances of litter-dwelling arthropods. *American Midland Naturalist*, **111**, 165-172

Bultman, T.L., Uetz, G.W. & Brady, A.R. (1982). A comparison of cursorial spider communities along a successional gradient. *Journal of Arachnology*, **10**, 23-35.

Cherrett, J.M. (1964). The distribution of spiders on the Moor House National Nature Reserve, Westmorland. *Journal of Animal Ecology*, **33**, 27-48.

Chew, R.M. (1961). Ecology of the spiders of a desert community. *Journal of the New York Entomological Society*, **69**, 5-41.

Chinery, M. (1986). *A Field Guide to the Insects of Britain and Northern Europe.* Collins : London. 352 pp.

Clapham, J.E, Tutin, T.G. & Moore, D.M. (1987). *Flora of the British Isles.* Cambridge University Press : Cambridge. 690 pp.

Cloudsley-Thompson, J.L. (1962). Microclimate and the distribution of terrestrial arthropods. *Annual Review of Entomology*, **7**, 199-222.

Connell, J.H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**, 131-138.

Coulson, J.C. (1978). Terrestrial animals. In : *Upper Teesdale : The Area and its Natural History.* Edited by Clapham, A.R. Collins : London. 258 pp.

Coulson, J.C. (1988). The structure and importance of invertebrate communities on peatlands and moorlands, and effects of environmental and management changes. In : *Ecological Change in the Uplands.* Edited by Usher, M.B. & Thompson, D.B.A. Blackwell : Oxford. 450 pp.

Coulson, J.C. & Whittaker, J.B. (1978). The ecology of moorland animals. In : *Production Ecology of British Moors and Montane Grasslands.* Edited by Heal, O.W. & Perkins, D.F. Springer-Verlag : Berlin. 354 pp.

Culin, J.D. & Yeargan, K.V. (1983). Comparative study of spider communities in alfafa and soybean ecosystems : ground-surface spiders. *Annals of the Entomological Society of America*, **76**, 832-838.

Curtis, D.J. (1980). Pitfalls in spider community studies (Arachnida, Araneae). *Journal of Arachnology*, **8**, 271-280.

Dalingwater, J.E. (1986). *A Short Key to British Spider Families*. Unpublished. 4 pp.

Dondale, C.D., Redner, J.H., Farrell, E., Semple, R.B. & Turnbull, A.L. (1970). Wandering hunting spiders in a meadow. *Bulletin of the Museum of Natural History (Nature)*, **41**, 61-64.

Duffey, E. (1956). Aerial dispersion in a known spider population. *Journal of Animal Ecology*, **25**, 85-111.

Duffey, E. (1962a). A population study of spiders in limestone grassland : description of study area, sampling methods and population characteristics. *Journal of Animal Ecology*, **31**, 571-599.

Duffey, E. (1962b). A population study of spiders in limestone grassland. The field layer fauna. *Oikos*, **13**, 15-34.

Duffey. E. (1963). Ecological studies on the spider fauna of the Malham Tarn area. *Field Studies*, **1(5)**, 65-87.

Duffey, E. (1968). An ecological analysis of the spider fauna of sand dunes. *Journal of Animal Ecology*, **37**, 641-674.

Duffey, E. (1972). Ecological surveys and the arachnologist. *Bulletin of the British Arachnological Society*, **2**, 69-82.

Durnford, J.A. (1992). *The Distribution and Abundance of Wolf Spiders (Araneae : Lycosidae) on Chapel Fell in the Northern Pennines*. Unpublished MSc Thesis : University of Durham. 45 pp.

Elton, C.S. (1927). *Animal Ecology*. Sidgwick & Jackson : London. 208 pp.

Enders, F. (1974). Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. *Ecology*, **55**, 317-328.

Fitter, R., Fitter, A.H. & Blamey, M. (1989). *The Wild Flowers of Britain and Northern Europe.* Collins : London. 336 pp.

Fitter, R, Fitter, A.H. & Farrer, A. (1992). *Grasses, Sedges, Rushes and Ferns of Britain and Northern Europe.* Collins : London. 256 pp.

Foelix, R.F. (1982). *Biology Of Spiders.* Harvard University Press : Cambridge, Massachusetts. 308 pp.

Gauch, H.G. (1982). *Multivariate Analysis In Community Ecology.* Cambridge University Press : Cambridge. 298 pp.

Gause, G.F. (1934). *The Struggle for Existence.* Williams & Wilkins : Baltimore. 164 pp.

Giavelli, G., Rossi, O. & Sartore, F. (1986). Comparative evaluation of four species diversity indices related to two specific ecological situations. *Field Studies*, **6**, 429-438.

Greenslade, P.J.M. (1964). Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, **33**, 301-310.

Greenstone, M.H. (1984). Determinants of web spider species diversity : vegetation structural diversity vs prey availability. *Oecologia*, **62**, 299-304.

Grime, J.P. (1979). *Plant Strategies and Vegetation Processes.* Wiley : Chichester. 222 pp.

Grüm, L. (1971). Remarks on the differentiation in Carabidae mobility. *Ekologia Polska (A)*, **19**, 47-56.

Hallander, H. (1967). Range and movements of the wolf spiders *Pardosa chelata* (O.F. Muller) and *Pardosa pullata* (Clerck). *Oikos*, **18**, 145-50.

Halsall, N.B. & Wratten, S.D. (1988). The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology*, **13**, 293-299.

Hatley, C.L. & MacMahon, J.A. (1980). Spider community organization : seasonal variation and the role of vegetation architecture. *Environmental Entomology*, **9**, 632-639.

Hopkins, J.J. (1982). *Site Evaluation of Hedleyhope Fell, Nr. Tow Law, County Durham.* Unpublished. 2 pp.

Hill, M.O. (1979). *DECORANA: A Fortran Program For Detrended Correspondence Analysis And Reciprocal Averaging.* Cornell University : New York. 52 pp.

Hill, M.O. & Gauch, H.G. (1980). Detrended correspondence analysis: An improved ordination technique. *Vegetatio*, **42**, 47-58.

Hubbard, C.E. (1992). *Grasses: A Guide to their Structure, Identification, Uses and Distribution in the Britsh Isles.* Penguin : London. 480 pp.

Hughes, J.C. & Huntley, B. (1986). A phytosociological study of a mid-altitude heath in County Durham, Northern England. *Nordic Journal of Botany*, **6**, 811-829

Huntley, B. (1981). *Continental Phytosociology - Collection of Field Data.* Unpublished. 2 pp.

Jenkins, P.M. (1990). A study of the flora and fauna of magnesian grassland (of Thrislington plantation SSSI) with particular reference to plant architecture and invertebrates. Unpublished MSc Thesis : University of Durham. 78 pp.

Jenkins, P.M. (1992). *A Study of the Coleoptera, Araneae and Hemiptera of Hedleyhope Fell and Translocated Blanket Bog at Tow Law, County Durham.* Unpublished. 38 pp.

Johnson, C.G., Southwood, T.R.E. & Entwistle, H.M. (1957). A new method of extracting arthropods and molluscs from grassland and herbage with a suction apparatus. *Bulletin of Entomological Research*, **48**, 211-218.

Kajak, A. (1960). Changes in the abundance of spiders in several meadows. *Ekologia Polska (A)*, **8**, 199-228.

Kajak, A. (1962). Comparison of spider fauna in artificial and natural meadows. *Ecologia Polska (A)*, **10**, 1-20.

Krebs, C.J. (1985). *Ecology : The Experimental Analysis of Distribution and Abundance.* Harper & Row : New York. 800 pp.

Kuenzler, E.J. (1958). Niche relations of three species of Lycosid spiders. *Ecology*, **39**, 494-500.

Locket, G.H. & Millidge, A.F. (1951). *British Spiders: Volume 1.* Ray Society : London. 310 pp.

Locket, G.H. & Millidge, A.F. (1953). *British Spiders: Volume 2.* Ray Society : London. 450 pp.

Locket, G.H., Millidge, A.F. & Merrett, P. (1974). *British Spiders: Volume 3.* Ray Society : London. 316 pp.

Lowrie, D.C. (1948). The ecological succession of spiders in the Chicago area dunes. *Ecology*, **29**, 334-351.

Lowrie, D.C. (1963). Effects of grazing and intensive collection on a population of the green lynx spider. *Ecology*, **44**, 777-781.

Luczak, J. (1953). Zespoly pajaków lesnych. *Ekologia Polska*, **1**, 57-94.

Luczak, J. (1963). Differences in the structure of communities of web spiders in one type of environment (young pine forest). *Ekologia Polska (A)*, **11**, 159-221.

Luczak, J. (1966). The distribution of wandering spiders in different layers of the environment as a result of interspecies competition. *Ekologia Polska (A)*, **14**, 233-244.

Luczak, J. & Wierzbowska, T. (1959). Analysis of the likelihood of material in relation to the length of a series in the sweep method. *Bulletin of the Academy of Polish Science (2)*, **7**, 313-318.

Luff, M.L. (1975). Some features influencing the efficiency of pitfall traps. *Oecologia*, **19**, 345-357.

Macfadyen, A. (1954). The invertebrate fauna of Jan Moyen Island. *Journal of Animal Ecology*, **23**, 261-297.

Malloch, A.J.C. (1985). *Vespan: A Fortran Program For Handling And Analysis Of Vegetation And Species Distribution.* University Of Lancaster : Lancaster. 131 pp.

Merrett, P. (1967). The phenology of spiders on heathland in Dorset. 1. Families Atypidae, Dysderidae, Gnaphosidae, Clubionidae, Thomisidae and Salticidae. *Journal of Animal Ecology*, **36**, 363-374.

Merrett, P. (1968). The phenology of spiders on heathland in Dorset. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. *Journal of Zoology (London)*, **156**, 239-256.

Merrett, P. (1969). The phenology of Linyphiid spiders on heathland in Dorset. *Journal of Zoology (London)*, **157**, 289-307.

Mitchell, B. (1963). Ecology of two Carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). II. Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. *Journal of Animal Ecology*, **32**, 377-392.

Muma, M.H. & Muma, K.E. (1949). Studies on a population of prairie spiders. *Ecology*, **20**, 485-503.

Nørgaard, E. (1951). On the ecology of two Lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish Sphagnum bog. *Oikos*, **3**, 1-21.

Olive, C.W. (1980). Foraging specialisations in orb-weaving spiders. *Ecology*, **61**, 1133-1144.

Poissonet, P.S., Daget, P.M., Poissonet, A. & Long, G.A. (1973). Rapid point survey by bayonet blade. *Journal of Range Management*, **25**, 313.

Poore, M.E.D. (1956). The use of phytosociological methods in ecological investigations. *Journal of Ecology*, **44**, 28-50.

Purvis, O.W., Coppins, B.J., Hawksworth, D.C., James, P.W. & Moore, D.M. (1992). *The Lichen Flora of Great Britain and Ireland.* Natural History Publications : London. 710 pp.

Randall, M. (1982). The dynamics of an insect population throughout its altitudinal distribution : *Coleophora alticolella* (Lepidoptera) in northern England. *Journal of Animal Ecology*, **51**, 993-1016.

Richards, P.W. (1983). The three dimensional structure of tropical rain forests. In : *Tropical Rainforest : Ecology and Management. Special Publication No. 2. British Ecological Society.* Blackwell : London. 461 pp.

Richter, C.J.J. (1970). Aerial dispersion in relation to habitat in eight wolf spider species (*Pardosa*, Lycosidae, Araneae). *Oecologia*, **5**, 200-214.

Roberts, M.J. (1985a). *The Spiders of Great Britain and Ireland. Volume 1: Introduction; Classification and Nomenclature; Key to the Families; Description of Species - Atypidae to Theridiosomatidae.* Harley : Colchester. 229 pp.

Roberts, M.J. (1985b). *The Spiders of Great Britain and Ireland. Volume 3: The Colour Plates - Atypidae to Linyphiidae.* Harley : Colchester. 256 pp.

Roberts, M.J. (1987). *The Spiders of Great Britain and Ireland. Volume 2: Description of Species - Linyphiidae; Checklist of the British Species.* Harley : Colchester. 204 pp.

Robinson, J.V. (1981). The affect of architectural variation in habitat selection on a spider community: An experimental field study. *Ecology*, **62(1)**, 73-80.

Rose, F. (1981). *The Wild Flower Key; British Isles and North West Europe - A Guide to Plant Identification in the Field, With and Without Flowers.* Penguin : London. 480 pp.

Rypstra, A.L. (1983). The importance of food and space in limiting web-spider densities ; a test using field enclosures. *Oecologia*, **59**, 312-316.

Rypstra, A.L. (1986). Web spiders in temperate and tropical forests : relative abundance and environmental correlates. *American Midland Naturalist*, **115**, 42-51.

Savory, T.H. (1964). *Spiders and Other Arachnids.* English Universities Press : London. 92 pp.

Schaefer, M. (1978). Some experiments on regulation of population density in *Floronia bucculenta* (Araneidae : Linyphiidae). *Symposia of the Zoological Society of London*, **42**, 203-210.

Simpson, E.H. (1949). Measurement of diversity. *Nature*, **163**, 688.

Smith, I.R., Wells, D.A & Welsh, P. (1985). *Botanical Survey and Monitoring Methods for Grasslands.* Nature Conservancy Council : Peterborough. 26 pp.

Southwood, T.R.E. (1968). *Ecological Methods With Particular Reference to the Study of Insect Populations.* Chapman and Hall : London. 392 pp.

Stevenson, B.G. & Dindal, D.L. (1982). Effect of leaf shape on forest-litter spiders : community organization and microhabitat selection of immature *Enoplognatha ovata* (Clerck) (Theridiidae). *Journal of Arachnology*, **10**, 165-178.

Topping, C.J. & Sunderland, K.D. (1992). Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology*, **29**, 485-491.

Tretzel, E. (1955). Intragenerische Isolation und interspezifische Konkurrenz bei Spinnen. *Zietschrift für Morphologie der Tiere*, **44**, 43-162.

Turnbull, A.L. (1960). The spider population of a stand of oak (*Quercus robur* L.) in Wytham Wood, Berks., England. *Canadian Entomologist*, **92**, 110-124.

Turnbull, A.L. (1966). A population of spiders and their potential prey in an overgrazed pasture in eastern Ontario. *Canadian Journal of Zoology*, **44**, 557-583.

Turnbull, A.L. (1973). Ecology of the true spiders (Araneomorphae). *Annual Review of Entomology*, **18**, 305-348.

Turnbull, A.L. & Nicholls, C.F. (1966). A 'quick trap' for area sampling in grassland communities. *Journal of Economic Entomology*, **59**, 1100-1104.

Uetz, G.W. (1975). Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. *Environmental Entomology*, **4**, 719-724.

Uetz, G.W. (1976). Gradient analysis of spider communities in a streamside forest. *Oecologia*, **22**, 373-385.

Uetz, G.W. (1977). Coexistence in a guild of wandering spiders. *Journal Of Animal Ecology*, **46**, 531-541.

Uetz, G.W. (1979). The influence of variation in litter habitats on spider communities. *Oecologia*, **40**, 29-42.

Uetz, G.W. (1991). Habitat structure and spider foraging. In : *Habitat Structure - The Physical Arrangement of Objects in Time and Space*. Edited by Bell, S.S., McCoy, E.D. & Mushinsky, H.R. Chapman and Hall : London. 452 pp.

Uetz, G.W. & Unzicker, J.D. (1976). Pitfall trapping in ecological studies of wandering spiders. *Journal of Arachnology*, **3**, 101-111.

Van der Aart, P.J.M. & de Wit, T. (1971). A field study on interspecific competition between ants (Formicidae) and hunting spiders (Lycosidae, Gnaphosidae, Ctenidae, Pisauridae, Clubionidae). *Netherlands Journal of Zoology*, **21(1)**, 117-126.

Van Hook Jr., R.I. (1971). Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. *Ecological Monographs*, **41**, 1-26.

Vlijm, L. & Kessler-Geschiere, A.M. (1967). The phenology and habitat of *Pardosa monticola*, *P. nigriceps* and *P. pullata* (Araneae, Lycosidae). *Journal of Animal Ecology*, **36**, 31-56.

Watson, E.V. (1968). *British Mosses and Liverworts.* Cambridge University Press : Cambridge. 495 pp.

Williamson, M.H. (1949). A preliminary note on the ecology of Lycosids (Araneae). *Entomologist's Monthly Magazine*, **85**, 92-93.

Wise, D.H. (1993). *Spiders in Ecological Webs.* Cambridge University Press : Cambridge. 328 pp.

APPENDICES

Appendix 1 - The Invertebrates Caught During The Preliminary Study

Order, Class or Family	Trap Treatment and Cover						
	O+	O-	F+	F-	G+	G-	Total
Acarina	1	0	1	0	0	0	2
Araneae	16	14	29	39	47	41	186
Coleoptera (total)	9	13	49	49	31	38	189
Carabidae (<3cm)	4	5	16	12	9	3	49
Carabidae (>3cm)	1	1	10	8	2	7	29
Coccinellidae	0	1	0	0	0	0	1
Curculionidae	0	0	1	3	2	2	8
Staphylinidae	1	3	11	15	8	21	59
Larvae	1	1	3	1	0	1	7
Other Coleoptera	2	2	8	10	10	4	36
Collembola	1	0	12	14	7	4	38
Dermaptera	0	0	0	0	1	1	2
Diplopoda	2	1	2	8	4	4	21
Diplura	0	0	0	5	0	0	5
Diptera (total)	0	2	8	10	9	8	37
Larvae	0	1	1	0	0	0	2
Other Diptera	0	1	7	10	9	8	35
Hemiptera (total)	3	1	15	10	16	22	67
Homoptera	1	1	6	4	10	16	38
Heteroptera	2	0	9	6	6	6	29
Hymenoptera (total)	8	9	144	109	119	94	483
Formicidae	8	8	140	102	116	93	467
Other Hymenoptera	0	1	4	7	3	1	16
Isopoda	2	3	7	5	3	5	25
Lepidoptera (total)	1	0	2	1	4	2	10
Larvae	1	0	1	1	3	2	8
Other Lepidoptera	0	0	1	0	1	0	2
Oligochaeta	0	0	0	1	0	0	1
Opiliones	1	0	1	3	1	1	7
Total	44	43	270	254	242	220	1073

O+ = Nothing Plus Mesh
O- = Nothing Minus Mesh
F+ = Formalin Plus Mesh
F- = Formalin Minus Mesh
G+ = Glycol Plus Mesh
G- = Glycol Minus Mesh

Appendix 2 - The Spider Species Caught During the Preliminary Study

Family Gnaphosidae

Drassodes cupreus	3f
Haplodrassus signifer	3f
Micaria pulicaria	2m
Gnaphosidae (Immature)	27

Family Salticidae

Euophrys aequipes	1m
Salticidae (Immature)	2

Family Theridiidae

Robertus lividus	1f

Family Clubionidae

Agroeca proxima	1f
Clubionidae (Immature)	3

Family Thomisidae

Thomisidae (Immature)	1

Family Lycosidae

Alopecosa pulverulenta	2m
Pardosa pullata	3m
Trochosa terricola	59m 12f
Lycosidae (Immature)	11

Family Linyphiidae

Bolyphantes luteolus	1m
Centromerus prudens	5f
Cnephalocotes obscurus	1m
Erigonella hiemalis	1m
Gonatium rubens	4f
Lepthyphantes ericaeus	2m
Lepthyphantes mengei	1m
Lepthyphantes tenuis	1f
Leptothrix hardyi	1f
Micrargus herbigradus	1f
Monocephalus fuscipes	1m
Peponocranium ludicrum	3m
Pocadicnemis pumila	1f
Tabinocyba pallens	1m
Tabinocyba praecox	1m
Tiso vagans	5m
Walckenaeria acuminata	8f
Walckenaeria antica	2f
Walckenaeria monoceros	13f
Linyphiidae (Immature)	2

m = male
f = female

Total Number Of Spiders Captured = 186

Appendix 3 - The Invertebrates Caught In Pitfall Traps During The Main Study Period

Order, Class or Family	Subsite Description				Total
	Bilberry	Grassland	Heather	Bracken	
Acarina	**17**	**95**	**16**	**18**	**146**
Araneae	**738**	**971**	**340**	**746**	**2795**
Chilopoda	**1**	**0**	**17**	**8**	**26**
Coleoptera (total)	**134**	**335**	**541**	**221**	**1231**
Cantharidae	6	4	2	0	12
Carabidae	41	72	97	53	263
Curculionidae	5	4	4	2	15
Elateridae	17	6	6	6	35
Siliphidae	0	0	0	1	1
Staphylinidae	33	162	378	113	686
Larvae	8	51	19	19	97
Other Coleoptera	24	36	35	27	122
Collembola	**306**	**514**	**114**	**411**	**1345**
Dermaptera	**0**	**0**	**5**	**0**	**5**
Diplopoda	**112**	**81**	**41**	**185**	**419**
Diplura	**0**	**0**	**53**	**4**	**57**
Diptera	**86**	**149**	**128**	**85**	**419**
Gastropoda	**2**	**6**	**0**	**1**	**9**
Hemiptera (total)	**77**	**47**	**32**	**13**	**169**
Heteroptera	3	3	0	1	7
Homoptera	74	44	32	12	162
Hymenoptera (total)	**81**	**444**	**508**	**185**	**1218**
Formicidae	32	363	499	146	1040
Apidae	0	0	0	1	1
Mutillidae	1	0	1	0	2
Symphyta Larvae	3	8	0	1	12
Vespidae	1	0	0	1	2
Other Hymenoptera	44	73	8	36	161
Isopoda	**22**	**19**	**59**	**158**	**258**
Lepidoptera (total)	**3**	**5**	**3**	**1**	**12**
Larvae	3	5	0	1	9
Other Lepidoptera	0	0	3	0	3
Oligochaeta	**0**	**5**	**1**	**2**	**8**
Opiliones	**199**	**29**	**8**	**21**	**257**
Orthoptera	**0**	**1**	**18**	**0**	**19**
Pseudoscorpiones	**0**	**1**	**0**	**1**	**2**
Trichoptera	**0**	**0**	**1**	**1**	**2**
Total	**1778**	**2702**	**1885**	**2061**	**8426**

Appendix 4 - The Plant Species Identified At Subsites 1 (Bilberry) And 2 (Grassland)

Subsite 1 (Bilberry)

Agrostis capillaris
Arrhenatherum elatius
Deschampsia caespitosa
Digitalis purpurea
Erica tetralix
Festuca rubra
Holcus lanatus
Hypnum cupressiforme
Juncus squarrosus
Nardus stricta
Pteridium aquilium
Vaccinium myrtillus
Anthoxanthum odoratum
Calluna vulgaris
Deschampsia flexuosa
Empetrum nigrum
Festuca ovina
Galium saxatile
Holcus mollis
Juncus effusus
Luzula campestris
Oxalis acetosella
Rumex acetosella

Subsite 2 (Grassland)

Agrostis canina
Alopecurus pratense
Arrhenatherum elatius
Centaurea nigra
Cirsium arvense
Cirsium vulgare
Cynosurus cristatus
Deschampsia caespitosa
Dicranum sp.
Equisetum arvense
Festuca ovina
Fraxinus excelsior
Geranium pratense
Holcus lanatus
Hypnum crassifornum
Juncus effusus
Lycopodium sp.
Plantago lanceolata
Ranunculus repens
Rosa canina
Senecio jacobaea
Trifolium repens
Urtica dioeca
Vicia sepium
Agrostis capillaris
Anthoxanthum odoratum
Calluna vulgaris
Cerastium fontanum
Cirsium palustre
Crataegus monogyna
Dactylis glomerata
Deschampsia flexuosa
Empetrum nigrum
Equisetum littorale
Festuca rubra
Galium saxatile
Helictotrichon pubescens
Holcus mollis
Hypochoeris radicata
Lathyrus pratensis
Poa pratensis
Potentilla erecta
Rhytidiadelphus squarrosus
Rumex acetosa
Taraxacum officinale agg.
Ulex europaeus
Veronica chamaedrys

Appendix 5 - The Plant Species Identified At Subsites 3 (Heather) And 4 (Bracken)

Subsite 3 (Heather)

Achillea millifolium
Agrostis canina
Anthoxanthum odoratum
Betula pubescens
Chamaenerion angustifolium
Cirsium palustre
Cynosurus cristatus
Deschampsia caespitosa
Dicranum sp.
Empetrum nigrum
Festuca rubra
Holcus mollis
Hypochaeris radicata
Lotus corniculatus
Hieracium sp.
Nardus stricta
Plantago lanceolata
Trifolium pratense
Ulex europaeus
Vicia sepium
Alopecurus pratensis
Agrostis capillaris
Arrenatherum elatius
Calluna vulgaris
Cirsium arvense
Crataegus monogyna
Dactylis glomerata
Deschampsia flexuosa
Digitalis purpurea
Festuca ovina
Galium saxatile
Hypnum cupressiforme
Leontodon sp.
Lycopodium sp.
Holcus lanatus
Pinus sylvestris
Potentilla erecta
Taraxacum officinale agg.
Vaccinium myrtillus

Lichens present at subsite 3;

Bacidia muscorum
Cladonia coccifera
Cladonia furcata
Hypogymnia physodes
Baeomyces rufus
Cladonia coniocraea
Cladonia portentosa
Hypogymnia tubilosa
Cladonia arbuscula
Cladonia floerkeana
Cladonia squamosa
Porpidia macrocarpa

Subsite 4 (Bracken)

Agrostis canina
Anthoxanthum odoratum
Cardamine pratensis
Cirsium arvense
Cirsium vulgare
Deschampsia flexuosa
Empetrum nigrum
Festuca ovina
Galium aparine
Hieracium sp.
Holcus mollis
Juncus effusus
Potentilla erecta
Pteridium aquilinum
Rosa canina
Rumex acetosa
Urtica dioeca
Vicia sepium
Agrostis capillaris
Calluna vulgaris
Chamaenerion angustifolium
Cirsium palustre
Deschampsia caespitosa
Digitalis purpurea
Equisetum littorale
Festuca rubra
Galium saxatile
Holcus lanatus
Hypnum cupressiforme
Oxalis acetosella
Polygalia serpyllifolia
Ranunculus repens
Rubus sp.
Trifolium repens
Vaccinium myrtillus
Viola riviniana

Appendix 6 - The Spider Species Captured In Pitfall Traps During The Main Investigation

Clubionidae

Clubiona diversa
Clubiona pallidula
Clubiona reclusa
Clubionidae (Immature)

Saltícidae

Euophrys aequipes
Heliophanus flavipes
Salticidae (Immature)

Gnaphosidae

Drassodes cupreus
Haplodrassus signifer
Micaria pulicaria
Gnaphosidae (Immature)

Thomisidae

Xysticus cristatus
Thomisidae (Immature)

Theridiidae

Pholcomma gibbum
Robertus lividus

Lycosidae

Alopecosa pulverulenta
Pardosa amentata
Pardosa nigriceps
Pardosa palustris
Pardosa pullata
Trochosa terricola
Lycosidae (Immature)

Tetragnathidae

Pachygnatha degeeri

Linyphiidae

Agyneta conigera
Agyneta olivacea
Baryphyma trifons
Bathyphantes parvulus
Bolyphantes luteolus
Centromerita concinna
Centromerus prudens
Centromerus sylvaticus
Ceratinella brevipes
Cnephalocotes obscurus
Diplostyla concolor
Dismodicus bifrons
Erigonella hiemalis
Evansia merens
Gonatium rubens
Gongylidiellum vivum
Hypomma bituberculatum
Lepthyphantes ericaeus
Lepthyphantes mengei
Lepthyphantes pallidus
Lepthyphantes tenebricola
Lepthyphantes tenuis
Lepthyphantes zimmeranni
Leptothrix hardyi
Meioneta saxatilis
Micrargus herbigradus
Microlinyphia pusilla
Minyriolus pusillus
Monocephalus fuscipes
Oedothorax gibbosus
Oedothorax retusus
Pelecopsis mengei
Peponocranium ludicrum
Pocadicnemis juncea
Pocadicnemis pumila
Saaristoa abnormis
Silometopus elegans
Sintula cornigera
Tabinocyba pallens
Tabinocyba praecox
Tiso vagans
Trichopterna thorelli
Walckenaeria acuminata
Walckenaeria antica
Walckenaeria monoceros
Walckenaeria nudipalpis
Walckenaeria unicornis
Linyphiidae (Immature)

Appendix 7 - The Spider Species Captured During Sweep-Netting

Family and Species	Number and Gender	Subsite Description	Date
Dictynidae			
Dictyna arundinacea	2m 1f	Heather	27th May
	1f	Grassland	4th June
	2m 3f	Heather	4th June
	3m 7f	Heather	17th June
	1m	Heather	5th July
	4f	Heather	20th July
Dictynidae (Immature)	2	Heather	4th June
	1	Heather	17th June
	6	Heather	5th July
	6	Heather	20th July
Clubionidae			
Clubionidae (Immature)	1	Heather	4th June
Thomisidae			
Philodromus aureolus	1f	Heather	27th May
	1f	Bracken	4th June
Thomisidae (Immature)	1	Heather	4th June
	1	Heather	17th June
	1	Heather	20th July
Tetragnathidae			
Pachygnatha degeeri	1m	Grassland	27th May
Araneidae			
Araneidae (Immature)	1	Bracken	27th May
	1	Heather	4th June
	2	Bracken	17th June
	2	Grassland	5th July
	1	Heather	5th July
	2	Bracken	20th July
Linyphiidae			
Agyneta conigera	1f	Bracken	4th June
Baryphyma trifons	1m	Grassland	17th June
Erigone dentipalpis	1f	Heather	20th July
Kaestneria pullata	1m	Bilberry	4th June
Trichopterna thorelli	1m	Grassland	27th May
Walckenaeria unicornis	1f	Bilberry	17th June
Linyphiidae (Immature)	3	Bracken	4th June
	1	Grassland	17th June
	1	Bracken	17th June
	1	Grassland	20th July
	1	Bracken	20th July

m = male   f = female

Appendix 8 - The Complete List Of Spider Species Captured Throughout The Study Period

Clubionidae

Agroeca proxima •
Clubiona diversa •
Clubiona pallidula
Clubiona reclusa
Clubionidae (Immature)

Dictynidae

Dictyna arundinacea
Dictynidae (Immature)

Theridiidae

Pholcomma gibbum •
Robertus lividus

Gnaphosidae

Drassodes cupreus
Haplodrassus signifer •
Micaria pulicaria
Gnaphosidae (Immature)

Thomisidae

Xysticus cristatus
Philodromus aureolus •
Thomisidae (Immature)

Salticidae

Euophrys aequipes •
Heliophanus flavipes •
Salticidae (Immature)

Lycosidae

Alopecosa pulverulenta
Pardosa amentata
Pardosa nigriceps
Pardosa palustris •
Pardosa pullata
Trochosa terricola
Lycosidae (Immature)

Tetragnathidae

Pachygnatha degeeri

Araneidae

Araneidae (Immature)

Linyphiidae

Agyneta conigera •
Agyneta olivacea •
Baryphyma trifons •
Bathyphantes parvulus
Bolyphantes luteolus
Centromerita concinna •
Centromerus prudens
Centromerus sylvaticus
Ceratinella brevipes
Cnephalocotes obscurus •
Diplostyla concolor
Dismodicus bifrons
Erigone dentipalpis
Erigonella hiemalis •
Evansia merens
Gonatium rubens
Gongylidiellum vivum •

Hypomma bituberculatum
Kaestneria pullata
Lepthyphantes ericaeus •
Lepthyphantes mengei
Lepthyphantes pallidus •
Lepthyphantes tenebricola •
Lepthyphantes tenuis
Lepthyphantes zimmeranni
Leptothrix hardyi •
Meioneta saxatilis •
Micrargus herbigradus •
Microlinyphia pusilla
Minyriolus pusillus •
Monocephalus fuscipes •
Oedothorax gibbosus •
Oedothorax retusus

Pelecopsis mengei •
Peponocranium ludicrum •
Pocadicnemis juncea
Pocadicnemis pumila
Saaristoa abnormis
Silometopus elegans •
Sintula cornigera
Tabinocyba pallens •
Tabinocyba praecox •
Tiso vagans
Trichopterna thorelli •
Walckenaeria acuminata
Walckenaeria antica
Walckenaeria monoceros •
Walckenaeria nudipalpis
Walckenaeria unicornis
Linyphiidae (Immature)

• = Not Recorded In County Durham (Bristowe, 1939)

Appendix 9 - The Spider Species Caught In Pitfall Traps At Subsite 1 (Bilberry) During The Main Study

FAMILY AND SPECIES	**NUMBER, DATE AND SEX OF SPIDERS CAPTURED**				
	27th May	**4th June**	**18th June**	**5th July**	**20th July**
Gnaphosidae (Total)			(9)	(7)	(4)
Drassodes cupreus			1m		
Haplodrassus signifer			6m 2f	4m 1f	
Gnaphosidae (Immature)				2	4
Thomisidae (Total)			(1)	(1)	
Xysticus cristatus			1f	1m	
Lycosidae (Total)	(25)	(19)	(139)	(57)	(21)
Alopecosa pulverulenta	4m	1m 1f	29m 2f	1m 1f	
Pardosa nigriceps	11m 2f	11m 2f	84m 5f	26m 5f	5m 8f
Pardosa pullata	7m	3m 1f	16m 3f	16m 6f	2m 3f
Trochosa terricola	1m				
Lycosidae (Immature)				2	3
Theridiidae (Total)	(2)	(4)	(6)	(3)	
Pholcomma gibbum	1m				
Robertus lividus	1m	4m	6m	3m	
Linyphiidae (Total)	(40)	(46)	(182)	(109)	(63)
Agyneta conigera			33m 2f	11m	1m
Bathyphantes parvulus			6m	27m	6m 1f
Bolyphantes luteolus	1m			1f	
Centromerus prudens				1f	1f
Ceratinella brevipes	4m	4m 1f	13m 7f	1m 5f	2f
Diplostyla concolor			1m		
Gonatium rubens		1f	1f	4f	

(continued over)

Gongylidiellum vivum			2m		
Hypomma bituberculatum		1m			
Lepthyphantes ericaeus	11m 5f	4m 2f	18m 4f	8m 1f	1m
Lepthyphantes mengei	10m 2f	5m 6f	18m 7f	8f	1m 6f
Lepthyphantes tenebricola			3m		
Lepthyphantes tenuis	1f	5m 2f	1m 1f		
Lepthyphantes zimmeranni	1f	1f	8m 4f	7f	3m 5f
Meioneta saxatilis				1m	1m
Micrargus herbigradus	2m 3f	3m 1f	5m 5f	3m	2f
Pelecopsis mengei		1m	4m 2f	11m	2m 1f
Pocadicnemis juncea			3m 1f		
Pocadicnemis pumila			4m 1f	3m 1f	6m 1f
Silometopus elegans		1m			
Tabinocyba pallens		1m 4f	2m 5f	2f	
Walckenaeria acuminata			2f	1f	1f
Walckenaeria antica			2f		1f
Walckenaeria unicornis			1m 2f		
Linyphiidae (Immature)		3	14	13	21
Total (Adults)	**53m 14f**	**44m 22f**	**264m 59f**	**116m 44f**	**28m 32f**
Total (Immatures)	**0**	**3**	**14**	**17**	**28**
TOTAL (OVERALL)	**67**	**68**	**337**	**177**	**88**

m = male
f = female

Appendix 10 - The Spider Species Caught In Pitfall Traps At Subsite 2 (Grassland) During The Main Study

FAMILY AND SPECIES	**NUMBER, DATE AND SEX OF SPIDERS CAPTURED**				
	27th May	**4th June**	**18th June**	**5th July**	**20th July**
Gnaphosidae (Total)	(1)			(1)	
Gnaphosidae (Immature)	1			1	
Clubionidae (Total)	(1)				(1)
Clubiona diversa	1f				
Clubionidae (Immature)					1
Thomisidae (Total)	(1)				(1)
Xysticus cristatus	1m				
Thomisidae (Immature)					1
Salticidae (Total)			(1)		
Heliophanus flavipes			1m		
Lycosidae (Total)	(48)	(12)	(82)	(104)	(39)
Alopecosa pulverulenta	1f		5m 4f	1m	
Pardosa nigriceps	1m 1f	1m	5m 1f	4m	1m
Pardosa pullata	36m 6f	4m 6f	53m 12f	87m 7f	30m 6f
Trochosa terricola	1m 1f	1m	1m		
Lycosidae (Immature)	1		1	5	2
Theridiidae (Total)	(7)	(7)	(19)	(8)	(1)
Pholcomma gibbum				1f	
Robertus lividus	5m 2f	7m	18m 1f	6m 1f	1m

(continued over)

Tetragnathidae (Total)	(2)		(1)	(1)	(1)
Pachygnatha degeeri	1m 1f		1f	1m	1m
Linyphiidae (Total)	(54)	(54)	(208)	(230)	(86)
Agyneta conigera			8m	8m 2f	1m
Agyneta olivacea			1m	1f	
Baryphyma trifons			1m		
Bathyphantes parvulus			3m 1f	24m 5f	6m 1f
Centromerita concinna	1f				1f
Centromerus sylvaticus				1f	
Ceratinella brevipes		1m	1f	2f	
Cnephalocotes obscurus	1m 2f	1f	2m 1f	5m 3f	1m
Gonatium rubens			1f	1f	
Gongylidiellum vivum			1m	1m	
Hypomma bituberculatum			1m		
Lepthyphantes ericaeus	1f	1m 2f	2m 1f	1f	
Lepthyphantes mengei	3m 3f	1m 1f	9m 3f	10m 6f	2m 3f
Lepthyphantes pallidus			1m		
Lepthyphantes tenebricola			1m		
Lepthyphantes tenuis		1f			
Meioneta saxatilis			3m		
Micrargus herbigradus	1m		3m 1f	7m	2m
Monocephalus fuscipes			1f	1f	
Pelecopsis mengei		1f	2m 2f	1m 6f	1m 5f
Peponocranium ludicrum	1m	2m	1f		
Pocadicnemis pumila		4m	5m	1f	1m
Silometopus elegans	28m 4f	20m 7f	89m 47f	37m 96f	2m 49f
Tabinocyba pallens	2m 5f	1m 5f	2f	2f	3f
Tiso vagans			1m	1m	
Trichopterna thorelli	1m		3f	1m	
Walckenaeria acuminata	1f	2f	1f	1f	1m
Walckenaeria antica		1f	1f		
Walckenaeria unicornis					1f
Linyphiidae (Immature)		3	8	6	6
Total (Adults)	**82m 30f**	**43m 27f**	**216m 86f**	**194m 138f**	**50m 69f**
Total (Immatures)	**2**	**3**	**9**	**12**	**10**
TOTAL (OVERALL)	**114**	**73**	**311**	**344**	**129**

m = male
f = female

Appendix 11 - The Spider Species Caught In Pitfall Traps At Subsite 3 (Heather) During The Main Study

FAMILY AND SPECIES	**NUMBER, DATE AND SEX OF SPIDERS CAPTURED**				
	27th May	**4th June**	**18th June**	**5th July**	**20th July**
Gnaphosidae (Total)	(5)	(7)	(34)	(49)	(17)
Drassodes cupreus	1m	1f	1m 2f	2m 14f	2f
Haplodrassus signifer	1m	4m	12m 11f	7m 17f	3m 1f
Micaria pulicaria				1m	
Gnaphosidae (Immature)	3	2	8	8	11
Clubionidae (Total)		(1)	(2)	(6)	
Clubiona diversa		1m			
Clubionidae (Immature)			2	6	
Thomisidae (Total)			(2)	(2)	(1)
Xysticus cristatus			1m	1m 1f	
Thomisidae (Immature)			1		1
Salticidae (Total)	(2)		(8)	(2)	(1)
Euophrys aequipes			7m 1f	2m	
Heliophanus flavipes					1m
Salticidae (Immature)	2				
Lycosidae (Total)	(8)	(6)	(63)	(49)	(5)
Alopecosa pulverulenta		1m	34m 3f	26m 1f	
Pardosa nigriceps		2m	10m 5f	3m	1f
Pardosa palustris			2m	5m 2f	
Pardosa pullata	1m 2f	2m	4m 2f	5m 3f	
Trochosa terricola	5m	1m	1m 1f		1f
Lycosidae (Immature)			1	4	3

(continued over)

Theridiidae (Total)				(1)	
Robertus lividus				1m	
Linyphiidae (Total)	(7)	(10)	(22)	(19)	(11)
Agyneta conigera		1m	1m	1m	
Bathyphantes parvulus				1m	2m
Centromerita concinna		1f			
Centromerus prudens			1f		
Ceratinella brevipes			1m		
Cnephalocotes obscurus	1m				
Diplostyla concolor	1m				
Erigonella hiemalis			1m		
Evansia merens				1f	
Gonatium rubens				3f	
Lepthyphantes ericaeus	1m 1f		1f		
Lepthyphantes mengei		1f		1m	
Minyriolus pusillus					1m
Monocephalus fuscipes		1m			
Oedothorax retusus			1m		
Pelecopsis mengei			1f		
Peponocranium ludicrum	2m	1m			
Silometopus elegans			1m	1m	
Tabinocyba praecox					1f
Tiso vagans			3m 1f	2m	
Trichopterna thorelli			2f		
Walckenaeria acuminata			3f	1f	1f
Walckenaeria antica		1f	1f	2f	
Walckenaeria monoceros		2f	1f	2f	
Walckenaeria unicornis	1m	2m	1m		
Linyphiidae (Immature)			2	4	6
Total (Adults)	**14m 3f**	**16m 6f**	**81m 36f**	**59m 47f**	**7m 7f**
Total (Immatures)	**5**	**2**	**14**	**22**	**21**
TOTAL (OVERALL)	**22**	**24**	**131**	**128**	**35**

m = male
f = female

Appendix 12 - The Spider Species Caught In Pitfall Traps At Subsite 4 (Bracken) During The Main Study

FAMILY AND SPECIES	NUMBER, DATE AND SEX OF SPIDERS CAPTURED				
	27th May	**4th June**	**18th June**	**5th July**	**20th July**
Gnaphosidae (Total)			(1)		
Drassodes cupreus			1f		
Clubionidae (Total)			(2)	(1)	
Clubiona diversa			1m		
Clubiona pallidula			1f		
Clubiona reclusa				1m	
Thomisidae (Total)			(1)		
Xysticus cristatus			1m		
Lycosidae (Total)	(64)	(19)	(87)	(112)	(38)
Alopecosa pulverulenta	5m		16m	12m	
Pardosa amentata			2m		
Pardosa nigriceps	36m 3f	12m 1f	21m 6f	36m 25f	5m 4f
Pardosa pullata	11m 3f	4m 1f	33m 7f	14m 14f	1f
Trochosa terricola	6m	1m	2m	1m	3f
Lycosidae (Immature)				10	25
Theridiidae (Total)	(1)	(7)	(15)	(15)	(2)
Pholcomma gibbum				1m	1m
Robertus lividus	1f	4m 3f	14m 1f	13m 1f	1m
Tetragnathidae (Total)			(3)	(1)	
Pachygnatha degeeri			1m 2f	1f	

(continued over)

Linyphiidae (Total)	(19)	(24)	(113)	(157)	(64)
Agyneta conigera			4m	1m 1f	2f
Bathyphantes parvulus			7m 1f	42m 1f	10m
Ceratinella brevipes			1m		1f
Cnephalocotes obscurus	1m				
Diplostyla concolor					1f
Dismodicus bifrons			1f	1f	
Gonatium rubens			2f	2f	
Lepthyphantes ericaeus		1m	5m	2f	1f
Lepthyphantes mengei	2m 2f	3m	9m 2f	2m 5f	
Lepthyphantes pallidus			1m	1m	
Lepthyphantes tenebricola	1m				
Lepthyphantes zimmeranni		2f		1m 1f	2m 1f
Meioneta saxatilis			5m	10m	6m
Micrargus herbigradus		1f	2m 1f	1m	
Microlinyphia pusilla			1m		
Monocephalus fuscipes	1m 1f				
Oedothorax gibbosus	1m				
Pelecopsis mengei	1m 4f	1m 2f	1m 11f	3m 15f	3m 14f
Pocadicnemis pumila	1m	4m 4f	24m 3f	33m 9f	10m 3f
Saaristoa abnormis			1m	2m	
Silometopus elegans		1m 1f			
Sintula cornigera			1m		
Tabinocyba pallens	1f	2f	2f		
Walckenaeria acuminata		1f	2f	2f	2f
Walckenaeria monoceros				1f	
Walckenaeria nudipalpis				1f	
Walckenaeria unicornis	3m			1m	
Linyphiidae (Immature)		1	26	19	8
Total (Adults)	**69m 15f**	**31m 18f**	**153m 43f**	**175m 82f**	**38m 33f**
Total (Immatures)	**0**	**1**	**26**	**29**	**33**
TOTAL (OVERALL)	**84**	**50**	**222**	**286**	**104**

m = male
f = female