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The distribution and abundance of Wolf Spiders (Araneae: Lycosidae) on Chapel Fell in the Northern Pennines

J.A. Durnford

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The Distribution and Abundance of Wolf Spiders (Araneae: Lycosidae) on Chapel Fell in the Northern Pennines

J.A.Durnford

A Dissertation Submitted in Partial Fulfilment of the Requirements for the Degree of Master of Science, Advanced Course in Ecology

Department of Biological Sciences

Durham University

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Acknowledgements

SUMMARY

The study is introduced with some background information on the Pennine moors and their animal communities with particular reference to spiders and general information on wolf spiders, in particular.

The study was carried out by pitfall trapping at 20 sites on Chapel Fell, 14 selected for differing vegetation and soil type, at around 600m in altitude and 6 on an altitude transect, with a wet and a dry sites at each of three altitudes.

Eight species of lycosid were caught. The numbers were approximately a quarter to a third of the all spiders caught during the early summer, but there was considerable variation (30%) between years.

The catch of lycosids varied over the study period, rising from single figures in early May to a peak of 637 in 1991 and 980 in 1992 during June or July, after which the numbers dropped again.

Catches from 1991 were examined for a six month period. These showed three peaks in abundance/ activity; the major one in July and two smaller ones in June and September.

The total numbers of each individual species caught varied between 65% of all lycosids to 0.1%. There were significant changes in the numbers of most species, between years.

Species richness for each site was worked out and a maximum of six and minimum of one species per site was found. Species diversity was calculated using Simpson's Index. Both of these measurements showed a tendency to increase between 1991 and 1992.

Their distribution between the sites was analysed by Detrended Correspondence Analysis (DECORANA) which suggested that species show preferences between sites, which are based on soil moisture variation and vegetation differences.

Altitude is also shown to affect species distribution; some species only occur in very small numbers at high altitudes, which are caught in hundreds lower down. Other

species show no significant variation. The wet and dry site on the altitude transect demonstrate that five out of seven show significant preferences with regard to moisture.

The lycosid *Alopecosa pulverulenta* was shown to have varying preferences with regard to soil moisture, depending on the soil type.

The ratio of males to females caught was approximately 9:1. There was an increase in the proportion of males caught in 1992 for most species, which could be related to activity occurring earlier in the seas that year.

The timing of the appearance of juvenile forms suggests two spiders *Alopecosa pulverulenta* and *Pirata piraticus* could have two year life-cycles in the uplands

In view of controversy, the value of using pitfall traps is discussed and it is concluded from studies that have been carried out that it was the best method available.

Suggestions are made to account for the patterns of distribution and abundance of lycosids on Chapel Fell, particularly interspecific competition or alternatively climatic factors. A longer study would be needed to reach any firm conclusions, because neither explanation can be ruled out by the results obtained.

INTRODUCTION

The uplands of Britain form a `backbone' of Palaeozoic rocks down the western side of the country from Scotland in the north, through the Lake District and Pennines, Wales and finally to Devon and Cornwall. Rainfall in these upland areas, particularly on the western sides is very high (Figure 1), and evaporation low, leading to water-logged soils and leaching of minerals. The resulting wet, low-nutrient conditions give rise to bog formation and plant communities that can survive mineral deficiencies; the moorlands (Pearsall, 1950).

The layer of peat acts as a barrier to restrict the availability of minerals further, so that the plant community at the surface is effectively isolated from the underlying rock as a source of nutrients. Although peat can develop "up to a considerable angle of slope" (Moore & Bellamy, 1974), mineral soils are present on steeper ground and where alluvial deposits form beside streams.

The northern Pennines, while not as high as the mountains of Scotland and Wales and the fells in the Lake District, in Cumbria, nevertheless rise to an altitude of nearly 900m (Cross Fell: 893m). Chapel Fell, which lies in County Durham, has a maximum altitude of 700m. High altitude leads to low temperatures, and comparisons have been made with tundra ecosystems in terms of productivity (Forrest, 1971). Rates of decomposition are slow: 90% turnover time for *Eriophorum/Calluna* moorland is estimated to be 60 years, compared to 100 years for Arctic tundra and 2 years for temperate grassland (Ridge & Varley, 1986).

Undecayed material builds up as peat so there is only a small proportion of primary production being passed on to consumers. Coulson and Butterfield (1978) have shown that "it is the intrinsic low decomposition rate of some of the plant species forming the community which leads to peat accumulation", *Eriophorum, Calluna* and especially *Sphagnum* species are particularly unrewarding and it is believed that the plants recycle nutrients within themselves, so that their litter is impoverished in nutrients. Thus, the adaptation of the plants to the harsh environment produces positive

Figure 1 Map of the British Isles showing the distribution of moorlands (left) and areas of high rainfall: over 1250mm per annum (right) (Pearsall, 1950)

Figure 2 A typical lycosid: *Alopecosa pulverulenta*

feedback in the cycle of low nutrient availability. Soil animals are also adapted to the conditions and do contribute to the breakdown of plant material in the summer, preparing the plant material for microorganisms (Standen, 1978).

The quality of food available to herbivores tends to be low. Animals may respond to this, combined with the direct effects of low temperatures, by slow growth rates and life-cycle modifications (for instance, some bugs and tipulids take longer to mature in the uplands than in the lowlands (Hodkinson, 1973; Coulson & Whittaker, 1978). Predators, for example carabid beetles, may also have longer life-cycles in the uplands and this is related not only to the low temperature, but also to food availability (Butterfield, 1986).

Animal communities vary depending on the soil type and plant communities. Mineral soils have a larger soil fauna than peat (Coulson & Whittaker, 1978) and Collembola, for instance, were more numerous on mineral soils (40-46000 per m²) than peat (23-33000 per m²). Spider densities did not show a similar distribution; 40-370 per m² for mineral soil and 130-300 per m² for peat. Generalized predators are not restricted in habitat type and can move from one to the other in search of food (Coulson, 1988). The numbers of Collembola and other prey species (e.g. Diptera) are in excess of the needs of the spiders present, so that lack of suitable food supply may not the limiting factor for spiders.

However, Cherrett (1964) found a clear correlation between spider numbers (97% of the species were Linyphiidae) and amount of potential prey, as "other readily visible arthropods" (sampled on four occasions through a year), so it is possible that their distribution is indirectly affected by poor quality of plant material as food supply, in the way that many other moorland arthropods clearly are, but that the pattern is not so clear because of their mobility.

There are a number of vertebrate predators on the moors, which may eat spiders. Frogs (Rana temporaria) are common and shrews (Sorex minutus and S. araneus) are important predators of arthropods, especially on the boundaries between soil types (Coulson, 1978) and spiders may constitute 1-2% of their diet (Bristowe, 1941). However, Edgar (1969) found little evidence that they eat spiders in woodland.

A number of insectivorous birds are also present; the meadow pipit (*Anthus pratensis*) probably being the most common, but spiders are minimal in the diet fed to nestlings (Coulson, 1978). No definite information is available about spider predation by vertebrates. Spiders do prey on each other both inter and intraspecifically, however, and it may be that the larger species/specimens are important predators of the smaller.

Very little is known about parasites of spiders in the uplands. Spiders are attacked by parasitic wasps (Pompilidae and Sphecidae), both as eggs and as adults (Foelix, 1982) and Bristowe (1958) cites the hunting wasp *Anoplius fuscus* as commonly affecting *Trochosa terricola* Thorell. These parasitoids may not affect spiders so much in upland areas, as they are frequently less active at higher altitudes (e.g. the parasite of the rush moth *Coleophora alticolella* is affected by altitude (Randall, 1982).

The spider community of Moorhouse Nature Reserve has been studied by Cherrett (1964) and was found to be sub-arctic in type (more similar to Iceland than lowland Britain), comprising over 70% Linyphiidae (by species). The numerical distribution of this family seems to be governed by the distribution of prey, but could /\ due to other factors affecting both spiders and prey, for instance he found that on a limestone grassland area, sheep grazed parts had half the (linyphiid) species and approximately half the numbers of ungrazed parts. Corcuera (1989) has analysed the distribution of all spiders on Chapel Fell, and found that species were grouped by microhabitat differences, principally vegetation density and grass cover.

Lycosids are the next largest group, in terms of species, found at high altitudes (other families occurring only as one or two species), although they have only a fraction the number of species, compared to the Linyphiidae. However, very large numbers of individuals may occur, which, combined with their relatively large physical size, makes it worthwhile to study them separately.

The Lycosidae or wolf spiders are a widespread group. They occur in most parts of the world including Europe, America and Australia. There are 36 British species in 9 genera. All British species occur also in Europe (Jones, 1983), but they are fewer than the mainland species, being an impoverished fauna, comparatively. *Pardosa*

amentata (Clerck) occurs in northern Norway (Otto & Svensson, 1982) and *Pirata piraticus* (Clerck) and *Pardosa pullata* (Clerck) occur in Denmark (Norgaard, 1951). Some species are very widespread, occurring on both sides of the Atlantic, for example, *Trochosa terricola* Thorell (Bultman & Uetz, 1982).

As a family, lycosids are medium sized (4-16mm approx.) cursorial spiders, that is, they do not spin webs to catch their prey, but either (most commonly) lie in wait for passers-by or actively chase them (Figure 2). Their eyesight, while not as good as that of the Salticidae, which largely hunt by sight, is certainly good enough to play an important part in prey capture, as "they can see moving objects at a distance of several feet" (Bristowe, 1958). Probably this is related to the fact that many lycosid species are diurnal in activity. In Norfolk, *Trochosa terricola*, however, shows activity patterns that vary with age, the juveniles being more active by day and adults by night (Workman, 1978).

Eyesight plays an important part in their mating behaviour, also, as the male lycosid commonly `courts' the female with visual displays. Many species have visually contrasting body parts specialized for display, notably the male *Pardosa nigriceps* (Thorell), which has thick black hair on its palps, or *Trochosa terricola* with a very dark first pair of legs.

Prey for wolf spiders consists mostly of soft bodied arthropods (Collembola, Diptera, Cicadina, Aphidina and Araneae), while the smallest instars may eat pollen and spores (Nentwig, 1987). Edgar (1969) found that Diptera, Hemiptera and Araneae made up 85% of the prey of *Pardosa lugubris* (Walkenaer) in Scotland, their relative importance varying with the season. In a study of *Pardosa amentata* in the Netherlands, Edgar (1970) found that Diptera made up 67% of the diet, followed by Collembola at 13%.

In most species of lycosids mating takes place in spring; the male actively seeks the female, which does not move around so much. The female constructs an egg sac from silk which, in most species, she carries around with her, either attached to her spinnerets or in her chelicerae (especially in the case of the larger species, such as *Alopecosa pulverulenta* (Clerck), because the egg sac is too large to carry off the

ground behind her (laboratory observation)). Some species, for example *Trochosa terricola*, however, retire to a burrow with their eggs (Workman, 1978). A second, smaller sac may be produced in late summer (Edgar, 1971; Workman, 1978).

The life-cycle length of wolf spiders varies depending both on the species and on the geographical location. Most of the smaller species have an annual life-cycle, but larger ones may be biennial, for example, *Trochosa terricola* (Workman, 1978) and this species may even overwinter a third time, if conditions for growth are unfavourable. Species which are annual in the south such as *Pardosa lugubris* may be biennial further north (Edgar, 1971).

Information on the abundance and distribution of lycosids may be masked by the much larger numbers of Linyphiid species. The two families may be affected by different factors, because of differing lifestyles (for instance, lycosid spiders have been found to be adversly affected by litter depth, while other families are positively affected (Uetz, 1979). In considering the Lycosidae separately, it is hoped to gain insight into their relative importance within the moorland invertebrate community in terms of the numbers in which they occur and how they are distributed within the habitat. Information can be obtained on the temporal occurrence and life-cycles of the lycosids at high altitude, for comparison with lowland communities.
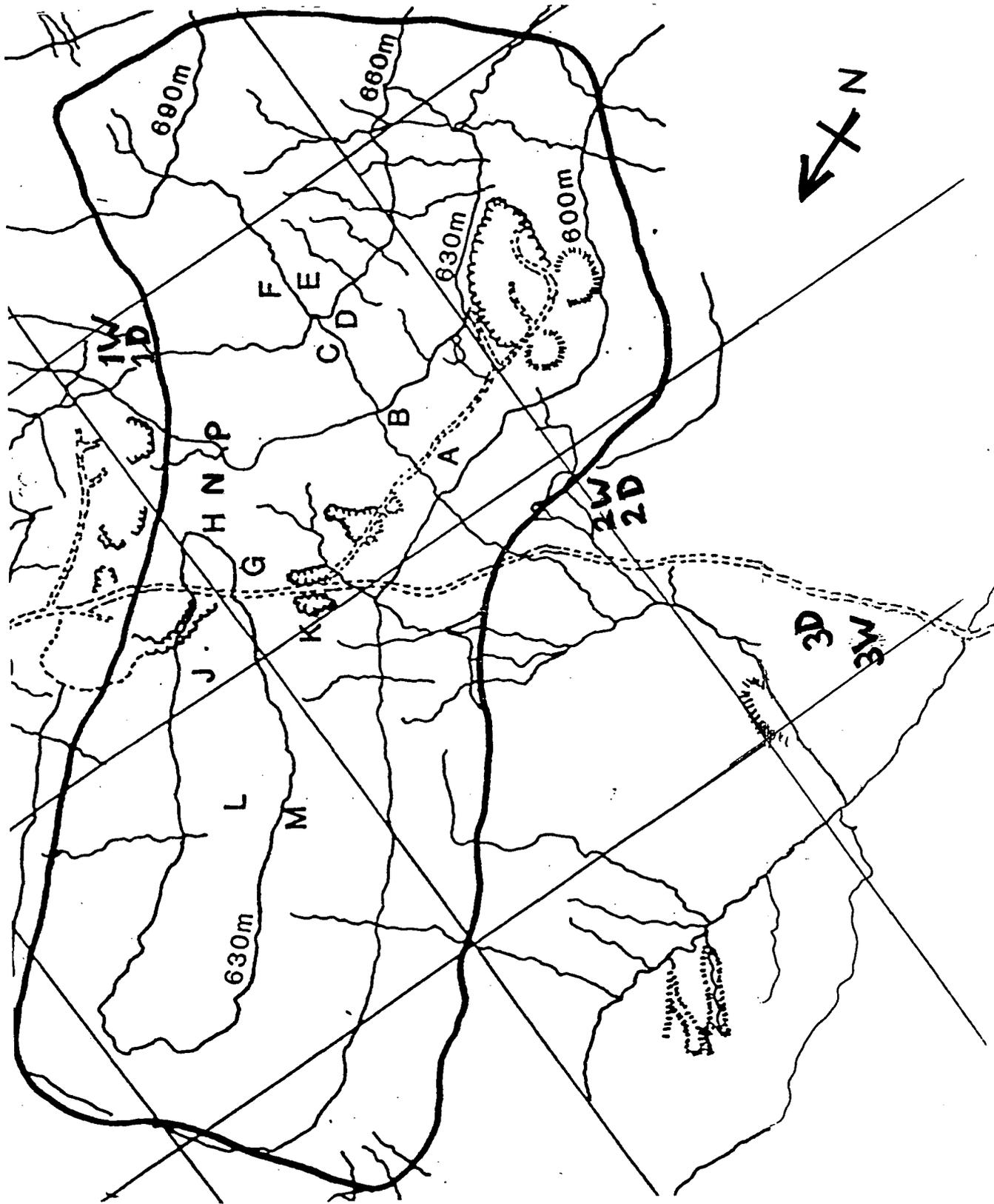
METHODS

Study Area

The main area of this study lies on the side of Chapel Fell (National Grid reference NY 863349) in the northern Pennine uplands at altitudes of 600 - 650m. Chapel Fell lies on a watershed, so that while the northern slopes drain into the river Wear, the south facing slopes (on which the study sites lie) drain, via Langdon Beck, into the Tees.

The underlying rocks are Upper Carboniferous, belonging to the Upper Limestone Group. They are about 180m thick and are composed of sandstones, grits and shales with coal seams and limestone bands (Johnson, 1978) and there are quarries near the sites. Most of the area is covered by blanket peat, but there are also patches of mineral soil, forming a mosaic of soil types.

The climate is harsh. Rainfall is about 1500mm per year (figures from the weather station at Widdybank Fell, altitude 510 metres (Pigott, 1978), which is within 8 km of Chapel Fell), with rain falling on an average 240 days per year, and figures, referring to 1975 and before, demonstrate that at that time, no month had evaporation exceeding rainfall, though there may be dry years (e.g. 1989) at infrequent intervals. Frequent cloud cover lowers the solar radiation received and the temperatures are lower than nearby lowlands on average, as is usual in the uplands. Frosts occur in most months of the year and snow is common in all months except May to September.

Wind adds to the harshness of the climate. The air is rarely still and high winds are frequent. The mean yearly wind speed at Widdybank was 5.5m/s (1968-1975), while at the summit of Great Dun Fell (847m) it was 10m/s. Chapel Fell is intermediate between these two sites in terms of altitude and exposure, so will fall between them in terms of wind.

Figure 3 Map of study area on Chapel Fell, with all sites marked

Trapping methods and materials

The invertebrates were trapped by means of pitfalls, which were set out on 14 main sites in straight lines with 10 traps per site and 2m between each trap. The traps were set in late April and thereafter the contents were collected fortnightly, throughout the summer (this is part of a on-going study).

On 6 additional altitude transect sites, there were also 10 traps per site, but they were at 1m intervals, and they were collected weekly, from early May to mid-July 1992.

The contents of the traps were sorted and all lycosid spiders were identified to species, using both Locket and Millidge (1951) and Roberts (1985). Nomenclature follows the latter.

A small comparative survey was done by hand searching, attempting to calculate the actual density of spiders per metre, so that the relevance of the pitfall trap figures might be established.

The pitfall traps on the main sites consisted of plastic jars with mouths approximately 4.5cm wide, containing water with 2% formalin (to preserve the specimens) and a little Teepol (to break the surface tension and avoid escapes). On the additional sites plastic cups 6cm wide, with similar contents, were used.

Soil analysis

5 soil samples, about 12cm deep, were taken at each site by means of a corer, diameter 2.5cm. Green vegetation was removed, then the soil water and organic content were ascertained.

Water content

The wet soil was weighed, then dried in an oven at 100°C, until a constant weight was obtained. The moisture content was then expressed as a percentage of the wet weight.

Water content % = Weight loss/ Initial weight x 100

Organic content

The oven dried soil was crumbled and mixed thoroughly. Then a sample of roughly 10g was taken, weighed and the organic content burned off in a muffle furnace at 450°C for 4 hours. The sample was reweighed and the organic content was calculated as a percentage of dry weight.

Organic content % = Weight loss/ Dry weight x 100

Soil temperature

At each altitude on the additional sites the soil temperature was measured weekly. The measurement was taken at about 10cm depth, to avoid recording diurnal fluctuations in surface temperature.

Site Descriptions

The sites were chosen to reflect the different soil types and also the range of vegetation types that occur in the study area. A survey of the vegetation at each site was carried out. Their position is shown on Figure 3.

Main study sites

Site A

Soil type: Mineral

Organic content: 26%

Water content: 27%

Vegetation: *Juncus* grassland

Juncus squarrosus is the dominant plant having 25% cover. There are numerous grasses including *Deschampsia flexuosa, Agrostis tenuis, Anthoxanthum odoratum* and *Festuca ovina*. There is a large amount (20%) of *Galium saxitile* and a small amount of *Eriophorum angustifolium*.

Site B

Soil type: Deep, wet peat

Organic content: 95%

Water content: 84%

Vegetation: *Eriophorum* tussocks

Eriophorum vaginatum is the dominant plant with 40% cover. There is a large amount of the grass *Deschampsia flexuosa* (20%) and a noticeable amount of *Vaccinium myrtillus* (12%) and *Eriophorum angustifolium*.

Site C

Soil type: Alluvial mineral

Organic content: 38%

Water content: 30%

Vegetation: *Nardus* grassland

The dominant plants on this narrow (5m) streamside strip are grasses, principally *Deschampsia flexuosa* (30%) with *Nardus stricta* (20%). Other grasses are also common, including *Anthoxanthum odoratum* (20%), *Festuca ovina* and *Agrostis tenuis* (10%), while small amounts of *Juncus effusus* grow close by.

Site D

Soil type: Shallow peat

Organic content: 94%

Water content: 80%

Vegetation: *Vaccinium* hummocks

The dominant plant is *Eriophorum vaginatum* (30%) which grows with *Deschampsia flexuosa* (20%) and a small amount of *E. angustifolium*, between the conspicuous hummocks of *Vaccinium myrtillus*, *V. vitis-idaea* and *Empetrum nigrum*.

Site E

Soil type: Blanket peat

Organic content: 95%

Water content: 85%

Vegetation: *Eriophorum/Calluna*

The dominant plant on this site is *Eriophorum vaginatum* with nearly 70% cover and there is a large amount of *Calluna vulgaris* (30%)

Site F

Soil type: Alluvial mineral

Organic content: 42%

Water content: 32%

Vegetation: *Nardus* grassland

There is a strip of grassland, about 5m wide, dominated by *Nardus stricta* (40%) with some *Agrostis tenuis* beside a stream, where the traps are set. Nearby the vegetation graduates into a blanket peat community, with first some *Vaccinium myrtillus* and *Eriophorum vaginatum* and then increasing amounts of *Calluna* until it is dominant.

Site G

Soil type: Blanket peat

Organic content: 99%

Water content: 79%

Vegetation: *Eriophorum/Calluna*

Eriophorum vaginatum is the dominant plant with about 40% cover, while *Calluna vulgaris* is very common (30%), and there is a good amount (20%) of *Deschampsia flexuosa*

Site H

Soil type: Eroded peat hags

Organic content: 94%

Water content: 66%

Vegetation: *Calluna/Eriophorum* `islands'

Calluna vulgaris is the dominant plant having 40% cover, but *Eriophorum vaginatum* (20%) and *E. angustifolium* (20%) together are similarly abundant. *Erica tetralix* is also present in moderate amounts (12%).

Site J

Soil type: Wet peat

Organic content: 95%

Water content: 75%

Vegetation: *Eriophorum/Calluna*

Eriophorum vaginatum (50%) and *Calluna vulgaris* (20%) dominate at this site, where they occur as drier hummocks with wetter areas with abundant sphagnum and some *E. angustifolium* and *Narthecium ossifragum*.

Site K

Soil type: Wet peat

Organic content: 98%

Water content: 88%

Vegetation: *Eriophorum* tussocks

This site is similar to Site B with *Eriophorum vaginatum* the dominant species (40%), but here *Deschampsia flexuosa* is co-dominant (40%) and there is little other grass, whereas there is a considerable amount (20%) of *E. angustifolium*.

Site L

Soil type: Mineral, with high organic content

Organic content: 68%

Water content: 48%

Vegetation: Grassland.

Festuca ovina is the dominant grass (30%), with a considerable amount of *Nardus stricta* (20%). *Galium saxitile* is abundant (20%) and *Juncus squarrosus* frequent (12%).

Site M

Soil type: Peat

Organic content: 96%

Water content: 77%

Vegetation: *Juncus* grassland.

Juncus squarrosus attains nearly 50% cover here, while *Deschampsia flexuosa* is also important (30%) and there is some *Festuca ovina* and *Eriophorum vaginatum.*

Site N

Soil type: Eroded peat hags (similar to Site H)

(Organic and water content - No figures available for this site)

Vegetation: *Eriophorum/Calluna* `islands'.

The vegetation is similar to Site H.

Site P

Soil type: Eroded peat hags (Similar to Site H)

(Organic and water content - No figures available for this site)

Vegetation: *Eriophorum/Calluna* `islands'.

The vegetation is similar to Site H.

Additional altitude transect sites

There were two sites at each of three altitudes; one was a wet stream-side site and the other was on close-by, drier ground. When the sites were selected, in early spring, it was intended that similar sites would be found at each altitude. However, although the wet sites were comparable, the dry sites were not as close vegetationally as had been hoped. Plants were identified using Rose (1981) and Hubbard (1968).

Site 1W

Altitude: 650 m

Soil type: Peat

Organic content: 86%

Water content: 85%

Vegetation: Mossy.

A spring arises within a few metres of this site. There is a blanket of moss, both of *Sphagnum* and *Polytrichum* species. There are clumps of *Juncus effusus* nearby, and also small amounts of grass (*Deschampsia flexuosa* and *Festuca ovina*).

Site 1D

Altitude: 650m

Soil type: Peat

Organic content: 93%

Water content: 77%

Vegetation: *Vaccinium* hummocks.

This site is within a few metres of the previous one, on slightly higher ground. *Vaccinium myrtillus* grows in hummocks along with crowberry *Empetrum nigrum* and a little *Calluna vulgaris*. Grass grows between the hummocks, largely *Deschampsia flexuosa* with some *Festuca ovina* and *Anthoxanthum odoratum*, along with patches of *Sphagnum*. Towards the top end of the site grass cover replaces the hummocks. Lichen (*Cladonia* sp.) is frequent.

Site 2W

Altitude: 550m

Soil type: Wet peat

Organic content: 96%

Water content: 88%

Vegetation: Mossy.

This site forms a very damp area several metres wide along the bank of a stream. There is complete moss cover of *Polytrichum* and *Sphagnum* species and large amounts of *Juncus effusus* and some *J.squarrosus* close-by. Also present are small amounts of *Eriophorum vaginatum* and the grasses *Deschampsia flexuosa* and *Festuca ovina.*

Site 2D

Altitude: 550m

Soil type: Mineral, but with considerable organic matter.

Organic content: 71%

Water content: 69%

Vegetation: Grassland.

This site is on rising ground a few metres away from Site 2W. Grasses include abundant *Nardus stricta* and *Festuca ovina* and some *Anthoxanthum odoratum.* There is a great deal of *Galium saxitile* and some *Potentilla erecta* and patches of *Polytrichum.*

Site 3W

Altitude: 450m

Soil type: Wet peat

Organic content: 93%

Water content: 88%

Vegetation: Mossy.

Mosses (both *Sphagnum* and *Polytrichum*) cover the majority of this site, which is in a flat boggy area beside Langdon Beck. There is a considerable amount of *Equisetum palustre*. Higher plants present include large amounts of *Juncus effusus, J. squarrosus, Eriophorum vaginatum* and grasses, including *Festuca ovina*. The bright yellow flowers of *Potentilla erecta* are noticeable.

Site 3D

Altitude: 450m

Soil type: Peat

Organic content: 86%

Water content: 69%

Vegetation: Grassland.

Situated on rising ground a short distance from Site 3W, this site had a particularly thick litter layer. The commonest grasses are *Nardus stricta* and *Deschampsia flexuosa*, while *Molinia caerulea* is present. There are a few *Juncus squarrosus* plants. On the lower side *Sphagnum, Polytrichum* and sedge *Eriophorum vaginatum* were present.

RESULTS

Species list of Lycosidae found at the study sites

Alopecosa pulverulenta (Clerck)

Pardosa amentata (Clerck)

Pardosa nigriceps (Thorell)

Pardosa palustris (Linnaeus)

Pardosa prativaga (L. Koch)

Pardosa pullata (Clerck)

Pirata piraticus (Clerck)

Trochosa terricola Thorell

Overall Totals

The number of all spiders caught at all the sites (A - P) in May, June and July 1991 and 1992 were totalled, as were the number of lycosids. The results are given in Table 1.

Table 1

Totals of all spiders and wolf spiders caught at sites A to P, in

May, June and July 1991 and 1992

	Total		%
	Spider	Lycosid	lycosids
1991	8397	1742	20.7
1992	7296	2344	32.1
Change	-13.1%	+30.1%	

The total number of spiders caught decreased significantly ($X^2 = 77$, 1 d.f.[Yates'correction applied], p<0.001) between the years, while the number of lycosids increased significantly ($X^2 = 88$, 1 d.f., p<0.001) from 20.7% in 1991 to 32.1% in 1992. The change in the numbers of spiders and lycosids and their relative proportions is shown in Figure4.

Fortnightly totals

The percentage of lycosids in the catches of spiders were measured in fortnightly periods during the early summer in 1991 and 1992. These results are given in Table 2. There was a significant difference between the numbers of spiders caught these time periods in each year ($X^2 = 2266$, d.f. = 5, p<0.001) and also in the numbers of lycosids ($X^2 = 676$, d.f. = 5, p<0.001).

Figure 5 shows how the numbers of lycosids captured differed between the two years. In 1991 there was a small peak in numbers in mid-June, followed by a slight fall, then a much larger peak in mid-July. In 1992 there is a more rapid increase in numbers to a single, major peak in mid-June, which is higher than the year before, after which there is steady decline to a lower level than the year before.

In fact, if the total number of spiders (Figure 6) is compared to the number of lycosids (Figure 5), there is a similar pattern of fluctuations within each year, except for the 29 May 1991 data, which do not show this relationship. Between the years, however, quite different patterns are in evidence, with peaks and troughs completely unsynchronized.

However, the lycosids are not a relatively constant proportion of the total spiders, but increase from a very small percentage at the beginning of the period to over a third of total spiders captured in June/July. (Figure 7). While the maximum proportion in both years is not very different, the increase is earlier in 1992, and sharper, but numbers drop more rapidly.

Figure 4 Comparative proportions of all spiders to lycosids in 1991 and 1992

□ All spiders
▨ Lycosids

numbers

1991   1992
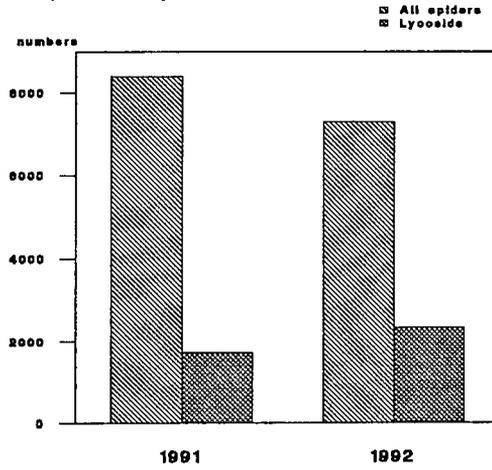
Figure 5 Numbers of all lycosids caught at Sites A to P in May, June and July 1991 and 1992

lycosid numbers

-♦- 1991
—■—1992

8 May   29 May   13 June   28 June   10 July   24 July
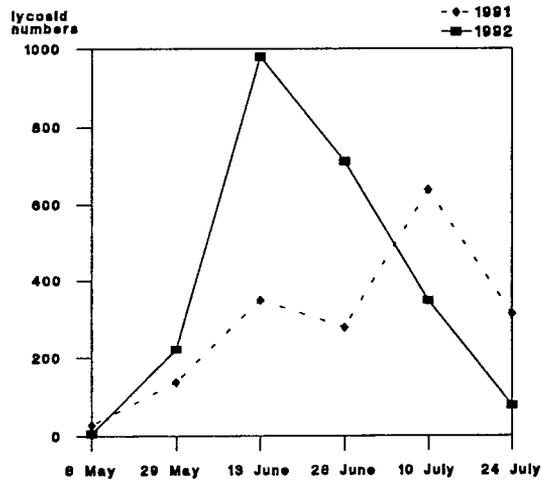
Figure 6 Numbers of all spider species caught on Sites A to P in May, June and July 1991 and 1992

-♦- 1991
—■—1992

spider numbers

8 May   28 May   13 June   28 June   10 July   24 July
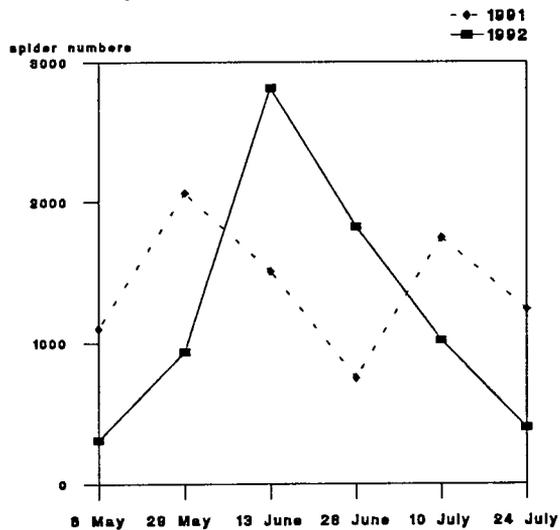
Table 2

Numbers of spiders and lycosids caught in each fortnightly period

during May, June and July 1991 and 1992

Date	1991			1992		
	Spider	Lycosid	%	Spider	Lycosid	%
8 May	1099	28	2.5	309	6	1.9
29 May	2063	137	6.6	937	222	23.7
13 June	1505	349	ʼ23.2	2811	980	34.9
28 June	750	278	37.1	1825	711	39.0
10 July	1744	637	36.5	1017	347	34.1
24 July	1236	313	25.3	397	78	19.6

Total for six month period

In order to determine lycosid abundance/activity and how this relates to total spider numbers throughout a longer period, spiders were counted for a six month period of 1991 (Figure 8). The whole spider population shows three abundance peaks and two considerable troughs. The lycosid numbers also display three peaks, though two of these are rather small, and the first is not in synchrony with the very large peak in spider abundance in late May. It is also noticeable that while spiders as a whole remain active in considerable numbers at the beginning and end of this period, the activity of lycosids commences at a very low level, and falls away to virtually none by the end of October.

Figure 7 Lycosids in early summer 1991
and 1992 as percentages of total
spiders in that year

- ♦ 1991
—■— 1992

8 May 29 May 13 June 28 June 10 July 24 July
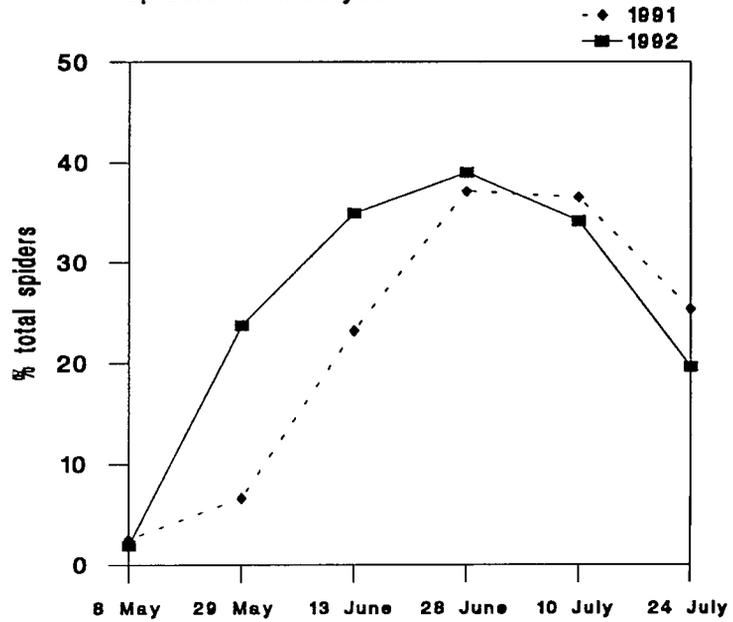
Figure 8 Total numbers of all spiders and
lycosids compared over a period of 6 months

- ♦- total spiders
—■— lycosids

spider nos

8 May 29 May 13 June 28 June 10 July 24 July 8 Aug. 20 Aug 18 Sept 23 Oct.
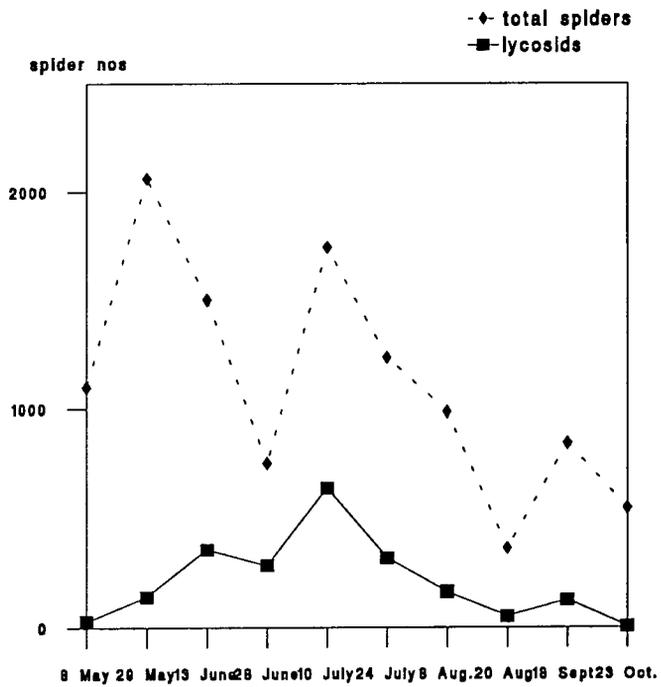
Totals of lycosid species

The total numbers of each species from the family Lycosidae found in the traps is very variable both between species (some are very rare and occur only in single figures, while others occur in hundreds), and within species from year to year when some show marked increases (e.g. eightfold increase in *P. pullata*) and decreases (e.g. the numbers of *A. pulverulenta* halved). The total numbers of each species for 1991 and 1992 and their relative proportions (as percentages) are shown in Table 3, as well as the significance of the changes.

Most species increased between the years, except for *A. pulverulenta*, which declined by half, and fell from a dominant position, representing two-thirds of lycosids in 1991 to less than a quarter in 1992 (*T. terricola* also decreased, although the numbers of this species were so small, random fluctuation could account for this.). In 1992 the dominant position was held by *P. piraticus* representing half the lycosids, whereas in 1991 it contributed a quarter of the total. *Pardosa amentata* and *Pardosa nigriceps* occurred as rare species only in 1992.

The numbers of each species caught varied with the time period as can be seen in Figure 9. Most species occur in a similar manner (reflected in the overall pattern, Figure 5). In 1991 there was a slow start, then increasing numbers, while in 1992 there was an earlier and higher peak, after which numbers fell. *A. pulverulenta* has an early and high peak in 1991 as well, but its numbers in that year continue to rise whereas in 1992, they fall markedly

Table 3

Totals of each lycosid species from Sites A to P, May to July 1991 and 1992 and the percentage of lycosids and all spiders they represent

Species:	1991			1992		
	Total	% lycosids	% spiders	Total	% lycosids	% spiders
Alopecosa pulverulenta	933	65.3	13.0	485***	21.4	7.0
Pardosa amentata	0	-	-	2	0.1	0.03
Pardosa nigriceps	0	-	-	2	0.1	0.03
Pardosa palustris	32	2.2	0.4	48ns	2.1	0.7
Pardosa prativaga	10	0.7	0.1	121***	5.3	1.8
Pardosa pullata	56	3.9	0.8	403***	17.8	5.8
Pirata piraticus	391	27.4	5.5	1201***	53.0	17.4
Trochosa terricola	7	0.5	0.1	4ns	0.2	0.06

(Significant abundance change between years *** = p<0.001, ns = not significant)

Figure 9 Numbers of 6 lycosid species caught in early summer in 1991 and 1992.
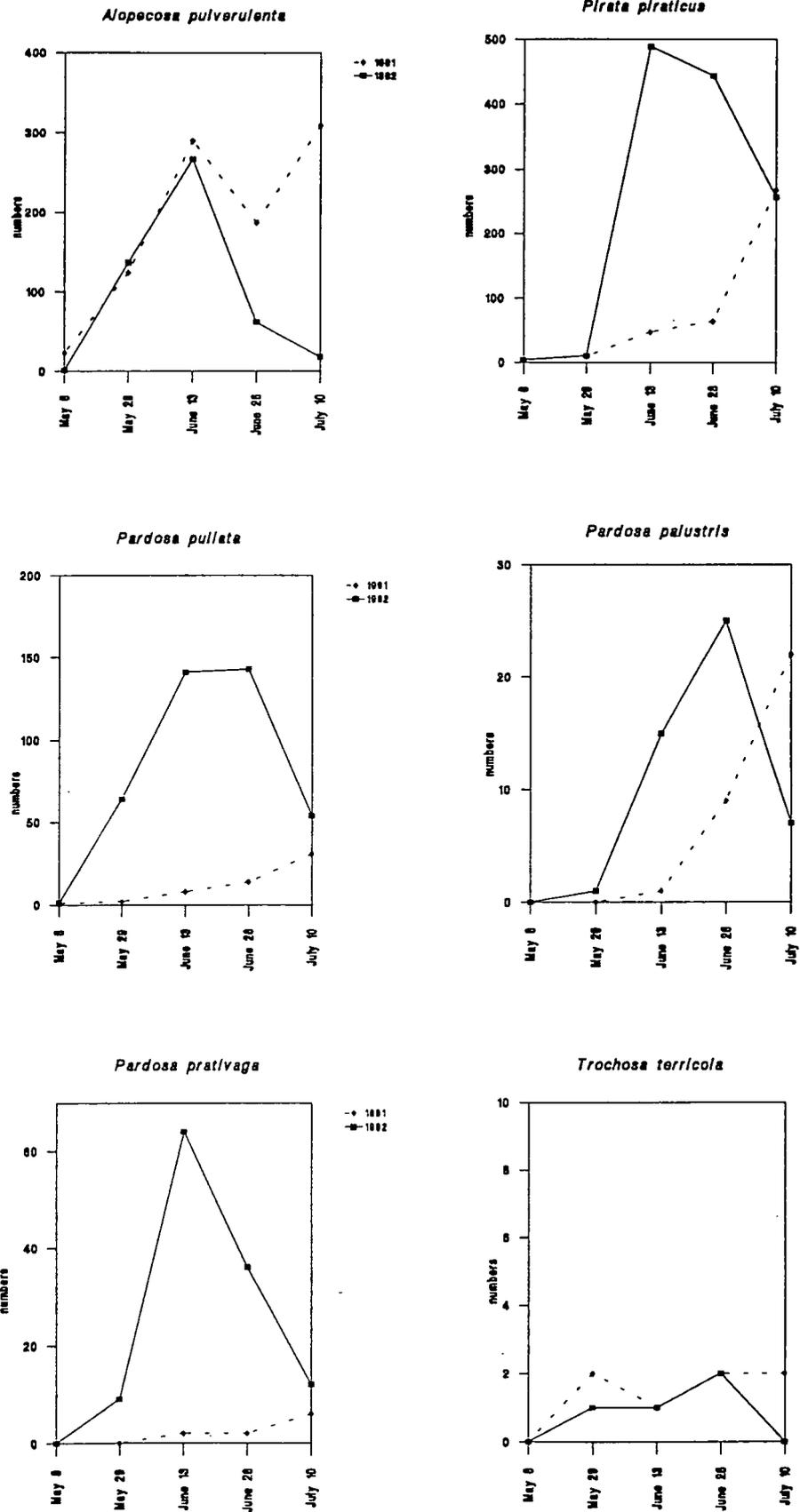
Distribution of all lycosids by site

Numbers of all species are not evenly distributed between the sites, varying from tens (sites H, N, P) to several hundred (sites F, J, K,). The totals at each site are different for the two years and the rank by numbers is not the same, except for site K, which had the greatest number in both years, and sites P, N and H, which had least in both years. These changes are a reflection of the fact that individual species change markedly in number between years.

Species richness and diversity in relation to site

Simpson's index was used to calculate species diversity for each site. The formula used was

$$D = \frac{N(N-1)}{\sum n(n-1)}$$

(D = diversity, N = total number of individuals, n = number of individuals of each species)

This index has been shown to 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 than the Shannon Index (Giavelli, Rossi & Sartore, 1986), which needs to be considered as several species of lycosid are represented by few individuals per site.

Table 4 gives the results for diversity and also species richness for all the sites (A to P) for the early summer of 1991 and 1992. There was a significant change both in species richness (t = 3.48, d.f. = 13, p<0.01) and in diversity (t = 4.18, d.f.= 13, p<0.01). Diversity increased on most sites, except B and K, where there was a fall (Figure 10). Species richness did not decrease at any of the sites between the two years, in fact, it increased on 9 out of the 14 sites (Figure 11). The scores for species richness and diversity were correlated:

1991   r = 0.627, d.f. = 12:   p< 0.02,

1992   r = 0.237, d.f. = 12:   not significant.

Therefore, the diversity does not always correlate with species richness. The year it did correlate, 1991, had lower species richness on all but two sites.

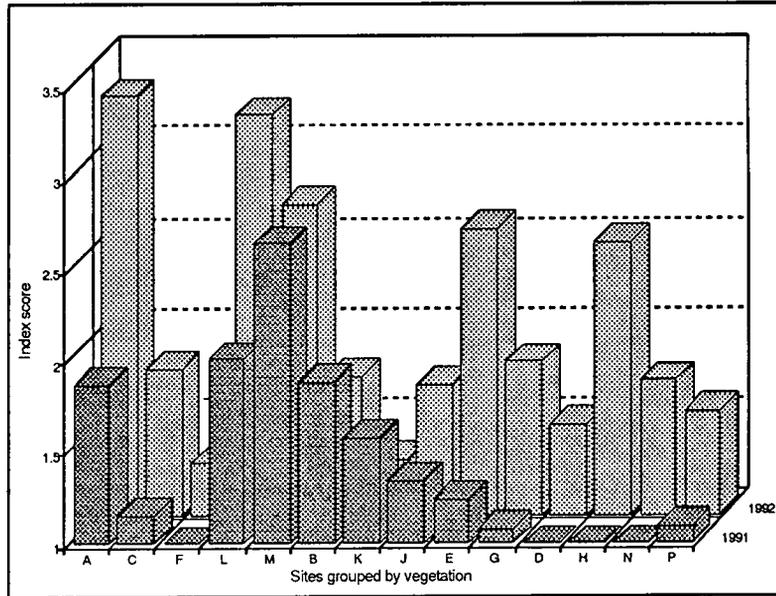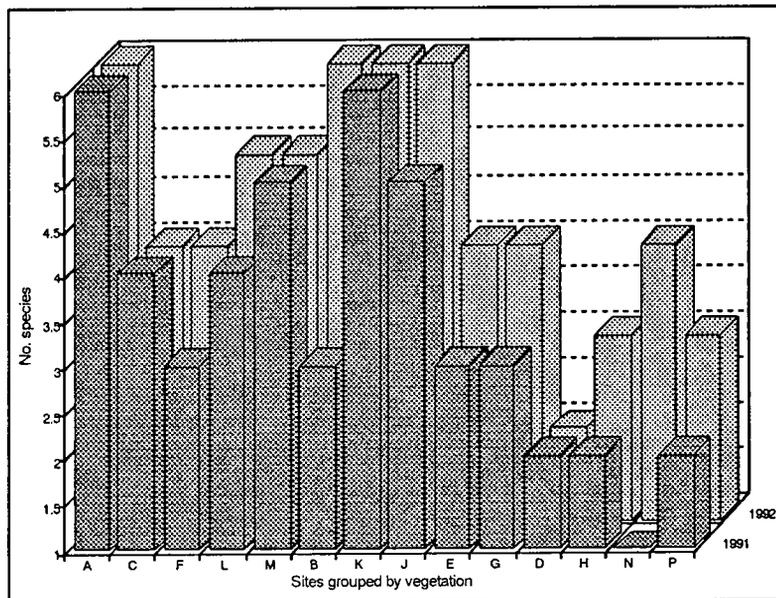Figure 10 Species Diversity (Simpson's Index) on Sites A to P grouped by vegetation

Figure 11 Species richness on Sites A to P, grouped by vegetation

Table 4

Species richness and diversity (Simpson's Index) of lycosids

from Sites A to P in 1991 and 1992

Site	Species richness		Diversity	
	1991	1992	1991	1992
A	6	6	1.87	3.30
B	3	6	1.88	1.75
C	4	4	1.15	1.79
D	2	2	1.00	1.50
E	3	4	1.23	2.57
F	3	4	1.00	1.28
G	3	4	1.08	1.84
H	2	3	1.00	2.50
J	5	6	1.34	1.71
K	6	6	1.57	1.30
L	4	5	2.01	3.20
M	5	5	2.65	2.71
N	1	4	1.00	1.73
P	2	3	1.09	1.57

Distribution of individual species by site

Detrended Correspondence Analysis (DECORANA) (Hill, 1979) was used to investigate the distribution of the individual species. The ordination of all sites according to the species present for 1991 and 1992 are given in Figures 12a & b. The sites clump in the same way in both years (though DECORANA has reversed the value of Axis 1), with two small groups comprising sites B, J, K and sites A, L, M and a larger group of the other eight sites (C, D, E, F, G, H, N, P).

In order to identify the factors that were important to the Axes, variables for each site were correlated to the axis score for that site, as described by Rushton, Topping and Eyre (1987). Axis 1 was found to correlate significantly with soil moisture ($r = 0.63$, d.f. $= 12$, $p<0.02$) and Axis 2 correlated significantly with species diversity (Simpsons' Index scores) ($r = 0.84$, d.f. $= 12$, $p< 0.001$).

Figure 12   DECORANA ordination of Sites A to P
in   a) 1991

b) 1992
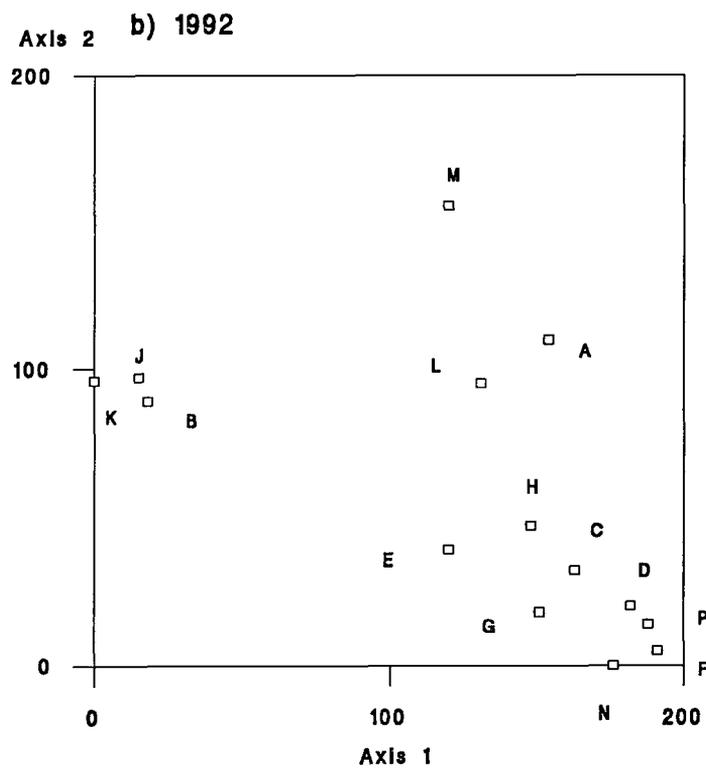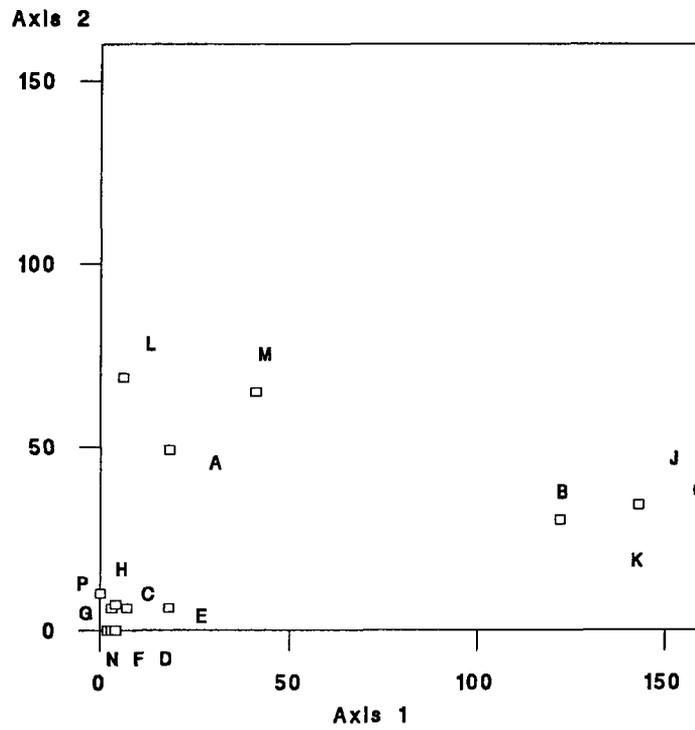
Both years' data sites were then ordinated on the same axes so that the changes between the years could be assessed (Figure 13). Most sites have changed in a similar direction relative to both axes, although B, K and E have not changed as much as the others relative to Axis 2. Site J alone has remained the same relative to Axis 1, but has changed relative to Axis 2.

DECORANA ordinations of the species for each year are given in Figures 14a & b. Once again Axis 1 is reversed between the two years. The species do not clump into groups in either year and the ordination is somewhat different each year. Leaving out of consideration the rare species (less than 10 individuals), it can be seen that *A. pulverulenta*, *P. piraticus* and *P. pullata* are in the same relative position, but that *P. prativaga* has changed particularly on Axis 1 and that *P. palustris* is in a completely different position on both axes. This reflects a large increase by this species on the group of sites B,J,K.

These groups represent sites that differ in vegetation, though not in a completely straightforward manner: Group 1 (BJK) are the wettest peat sites with *Eriophorum* tussocks and *Sphagnum*; Group 2 (ALM) are the larger grassland sites and Group 3 are the drier, heathery peat sites (DEGHNP) and the narrow streamside mineral sites (CF), which border them. Table 5 gives the numbers of each species in the three site groups for the two years.

Only *Pardosa pullata* had highly significant changes in numbers in all three groups of sites. *A. pulverulenta* did not change on Group 1 sites, but fell by one third on Group 2 sites and by over one half on Group 3 sites (though it remained a numerous species, even so). *Pardosa palustris* changed significantly only on the Group 1 sites. *Pardosa prativaga* increased fourteenfold on the grassland sites (Group 2), a highly significant change. Although, statistically it increased significantly on Group 1 sites as well, the numbers (2 to 9) are so small it is not clear they are biologically significant. *Pirata piraticus* doubled in number on Groups 2 and 3, but the numbers involved are small, whereas the highly significant increase on Group 1 site represents a trebling of already high representation.

Figure 13   DECORANA ordination of Sites A to
P for 1991 and 1992 combined

Figure 14 DECORANA ordination of
all species caught on Sites A to P In
a) 1991

Axis 2

Axis 1

b) 1992

Axis 2

Axis 1
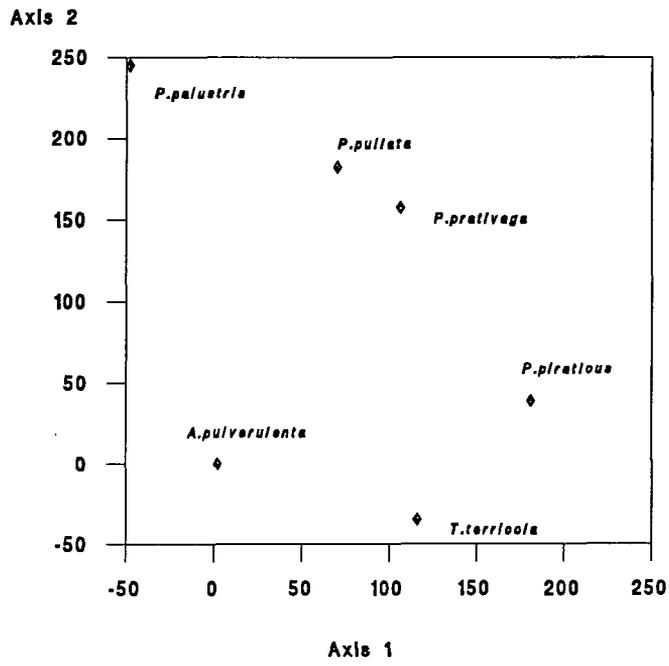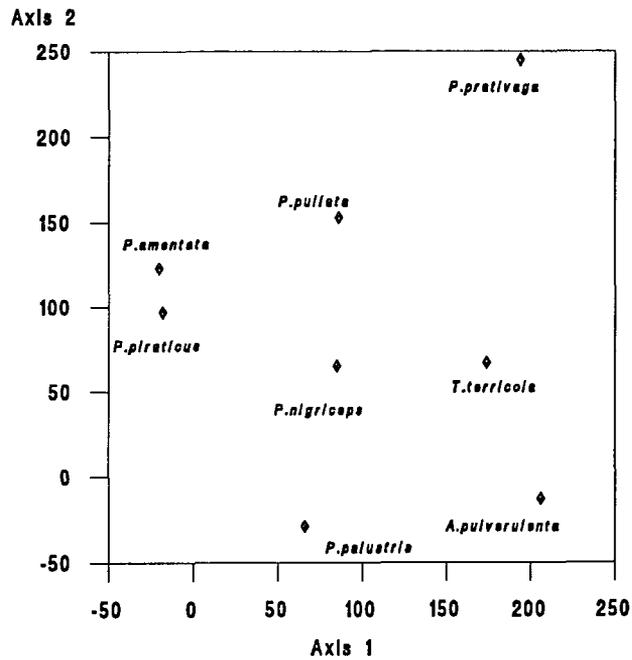
Table 5

Species numbers from sites divided into 3 groups by

DECORANA ordination

		Alopecosa pulverulenta	*Pardosa palustris*	*Pardosa prativaga*	*Pardosa pullata*	*Pirata piraticus*	*Trochosa terricola*
Group 1 (BJK)							
	1991	89	3	2	8	373	2
	1992	73	23	9	140	1159	1
		ns	***	*	***	***	
	change	-18%	+666%	+350%	+1650%	+210%	
Group 2 (ALM)							
	1991	162	23	8	43	7	1
	1992	105	18	112	201	18	1
		***	ns	***	***	*	
	change	-35%	-21%	+1300%	+367%	+157%	
Group 3 (CDEFGHNP)							
	1991	682	6	0	5	11	1
	1992	307	7	0	62	24	2
		***			***	*	
	change	-55%	-17%		1140%	+118%	

(Significant changes between years: *** = $p<0.001$, * = $p<0.05$, ns = not significant)

Altitude sites

The species distribution along the altitude transect is given in Table 6, and also whether the species occurred on the wet or dry site at that altitude. Numbers for most of the *Pardosa amentata, P. palustris* and *T. terricola* show a weighting in favour of lower altitudes, which is probably valid because these spiders only occurr in very low numbers at all A-P sites (600-650m) (n = 9 is the maximum number at any of these sites). *A. pulverulenta, P. piraticus* and *P. prativaga* are more prevalent in the middle site.

Table 6

Differences in species distribution at 3 altitudes sites with either

high or lower soil moisture in May, June and July 1992

Species	Total	650m	550m	450m	Wet	Dry	X^2
Alopecosa pulverulenta	209	28	160	21	94	115	ns
Pardosa amentata	15	0	1	14	14	1	***
Pardosa palustris	81	6	12	63	66	15	***
Pardosa prativaga	6	0	6	0	0	6	
Pardosa pullata	1520	33	816	671	562	958	***
Pirata piraticus	746	15	535	196	730	16	***
Trochosa terricola	292	0	3	289	110	182	***

(Significant differences: *** = $p < 0.001$, ns = not significant)

Although the differences are statistically significant between the altitudes it is neccessary to be rather wary in interpreting them, because the results are based on so

few sites. In the case of *A. pulverulenta,* for instance, the 650m sites caught 28, but Site F at a similar altitude caught 139 (mean catch A-P = 35) and the same applies to *Pirata piraticus* of which 226 were caught at Site J (630m) and 760 at Site K (600m). Mean temperatures at each altitude for mid-May to mid-July were: 650m, 12°C; 550m, 13°C; 450m, 14.5°C.

Significantly different distributions are shown on the two sites at each altitude by all species except *A pulverulenta,* which was present on both types in similar quantites *(Pardosa prativaga* was too rare to test). In some species there was a very marked preference, for instance, *P. piraticus* was forty-five times as common on the wet site. *Pardosa amentata* and *P. palustris* also favour the wetter site. Others occur in quantity on both wet and dry sites, but with a bias to one; *P.pullata* and *T. terricola* have significantly more on the dry sites, but they occur in hundreds on the wet.
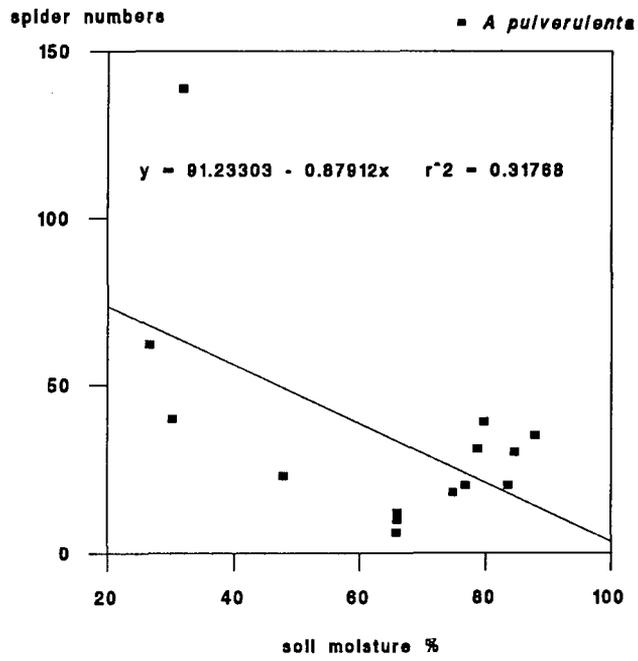
Distribution of *Alopecosa pulverulenta* in relation to soil moisture

Alopecosa pulverulenta shows a significant negative correlation with soil moisture (r = 0.56, d.f. = 12, p<0.05), when all sites (A to P) are taken into account (Figure 15a). This is in accord with the position of this species on the DECORANA ordination (at the extreme position on the axis correlated with soil moisture). However, if the mineral soil sites (ACFL) are left out and only the peat sites plotted then the situation is reversed and a significant positive correlation with soil moisture is found (r = 0.83, d.f. = 8, p<0.01) as seen in Figure 15b. *A.pulverulenta* has been shown to be relatively resistant to dessication (Cherrett, 1964), but perhaps the different properties of dry mineral soil, which maintains its capillarity and dry peat, which becomes water repellant could be a factor. Also, the correlation with moisture could be result of a third unknown factor (such as available prey).

Proportions of lycosid males and females

In both years the number of males was significantly greater than females (1991:X^2 = 845, 1992: X^2 =1592, d.f.=1, p<0.001), in 1991 there were eight times more males than females caught, and in 1992, there were twelve times as many. The total number of

Figure 15 Relationship of Alopecosa
pulverulenta with soil moisture on
a) all Sites A to P

spider numbers   ■ *A pulverulenta*

150

y = 91.23303 - 0.87912x   r^2 = 0.31768

100

50

0

20   40   60   80   100

soil moisture %

b) Peat sites only

spider numbers   ■ *A pulverulenta*

40

y = -64.80218 + 1.13556x   r^2 = 0.69617

30

20

10

0

60   70   80   90

soil moisture %
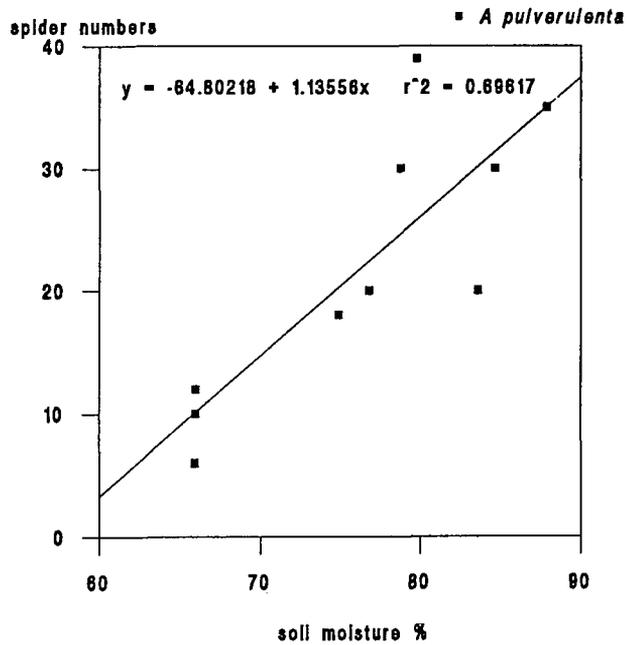
males in 1991 (May to July) was 1249 (89%), and of females was 158 (11%). For the same period of 1992 the numbers are males: 2068 (92%), and females: 177 (8%). The increase in the number of males between the two years was proportionally greater. (Figure 16).

Proportion of males to females in each species

In all individual species, numbers of males were greater than females, as well, though the actual amount was variable. Table 7 gives the numbers of each species in both years, divided according to sex and shows which numerical changes were significant.

The numbers of each species have not changed in the same way; both male and female A. pulverulenta decreased significantly, but females (by two-thirds) proportionally more than males (by half). All the other species showed significant increases, except Trochosa terricola which remained very rare, and male Pardosa palustris which showed no change, though the females increased. In most cases the proportional change in male and female numbers of an individual species is similar to the overall change in proportions between years, that is, a slight increase in males and decrease in females. However, P.pullata has shown a greater change, from a higher proportion of females to males than lycosids as a whole, (females, 14%: males, 86%) in 1991, to a smaller proportion (females, 5%: males, 95%) in 1992, because the numbers of females merely doubled, whereas the males increased seven-fold. The changes in some of the species (not those with very low numbers) are illustrated in Figure 18.

Figure 16   Male and Female lycosids caught
in 1991 and 1992 showing the change in
proportions between the years

numbers

☐ Male
▨ Female

2000

1000

0

1991   1992
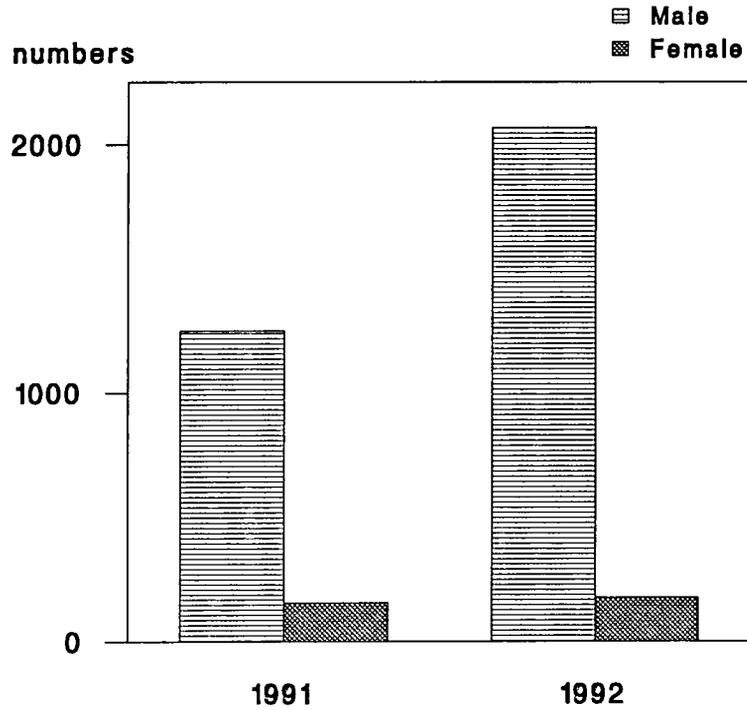
Figure 17   Male and female lycosids showing
the period (May to July) when they were
caught

numbers

—☐—Male 91   —◇—Female 91
- ■ -Male 92   - ♦ -Female 92

1000

800

600

400

200

0

8 May   29 May   13 June   28 June   10 July
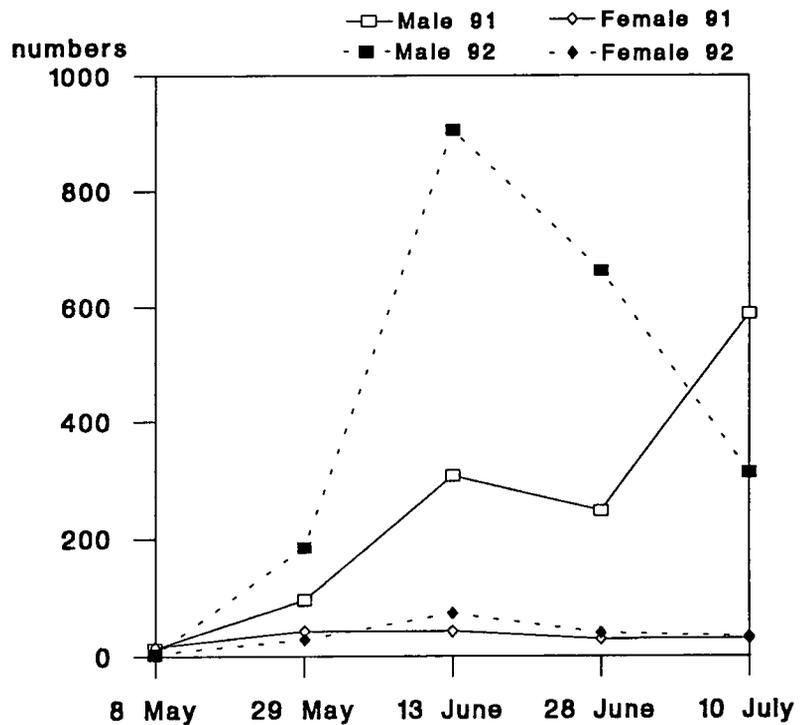
Figure 18 The proportion of Males
and Females in four lycosid species
and how this changed between 1991
and 1992

a) Alopecosa pulverulenta

1991

1992

b) Pardosa palustris

1991

1992
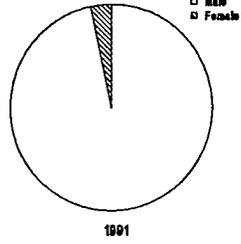
c) Pardosa pullata
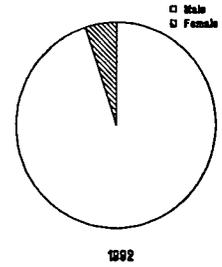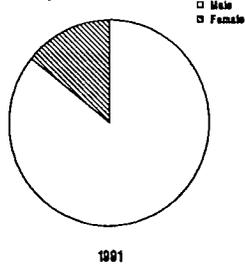
1991

1992

d) Pirata piraticus
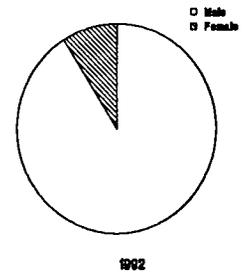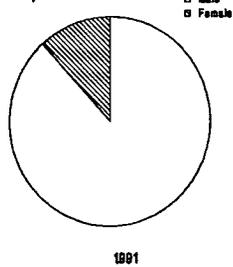
1991

1992

Table 7

Numbers of each sex for all lycosid species caught on Sites A to

P in May, June and July, 1991 and 1992

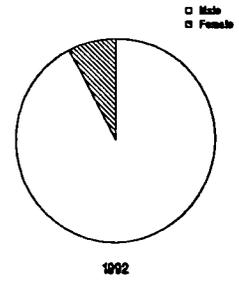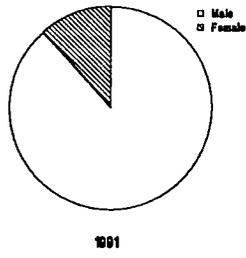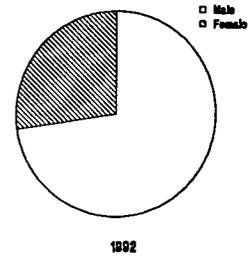|	1991		1992		% change	
	M	F	M	F	M	F
Alopecosa pulverulenta	824	109	444 ***	37 ***	-46	-66
Pardosa amentata	0	0	2	0		
Pardosa nigriceps	0	0	2	0		
Pardosa palustris	30	1	32 ns	12 **	+7	1100
Pardosa prativaga	10	0	121 ***	0	+1110	
Pardosa pullata	48	8	373 ***	20 *	+667	+150
Pirata piraticus	345	46	1090 ***	108 ***	+216	+135
Trochosa terricola	4	1	4	0		

(Significant change in numbers between years: *** = $p<0.001$, ** = $p<0.01$ * = $p<0.05$, ns = not significant)

Changes over 3 months

The number of females in 1991 rose in May (Figure 17) and then remained fairly steady, whereas in 1992 there was a peak in early June at roughly double the maximum of 1991, then a decline to a similar level. The number of males did show a peak in mid-June, but the numbers many times greater than the females and differed quite a lot

between the years. By late May, in 1992, there were double 1991 numbers and in June treble. However, in July the 1992 numbers fell to half of 1991, which had continued to rise.

Life cycle information

Alopecosa pulverulenta and *Pirata piraticus* were examined for lifecycle information, both because they occur in sufficient numbers, and also because they are distinctive in the juvenile stage (only one species of each genus occurs in the study area) which *Pardosa* species are not. The timing of the appearance of different age classes of spider is given in Table 8.

Table 8

Numbers of juvenile and adult *Pirata piraticus* and *Alopecosa pulverulenta* divided into fortnightly periods May to July 1991

| | *Alopecosa pulverulenta* | | | | | *Pirata piraticus* | | | | |
| | M | | F | | | M | | F | | |
	Ad	Sub	Ad	Sub	Imm	Ad	Sub	Ad	Sub	Imm
23 April	0	12	0	6	0	0	1	0	0	0
8 May	0	11	0	12	0	0	1	0	3	0
29 May	74	13	33	4	0	0	4	0	5	0
13 June	264	0	26	0	0	30	1	15	1	0
28 June	168	0	17	0	2	55	0	9	0	0
10 July	295	0	10	0	4	252	0	14	0	1

(M = male, F = female, Ad = adult, Sub = subadult, Imm = earlier instar, but not 1st.)

It is clear that neither females nor juveniles are as active as males, but the timing of when juveniles are caught can provide information. At first only subadults occur in both species, then there are mostly adults with a few subadults, but by the next fortnight there are only adults. This would be in line with an annual life-cycle. However, younger immature spiders start to appear which are not first instar spiderlings hatched from this year's eggs. Egg sacs have only recently been laid and take several weeks to hatch (23 days at room temperature in the laboratory for *Pirata piraticus* and a month for *Alopecosa pulverulenta*). In late August and September only female adults are present, some still producing egg sacs well into the autumn. There are two sizes of immature *Pirata piraticus* at this time, first instar spiderlings (which occur in large numbers when caught, as the whole brood is trapped at once, as they are being carried by the mother) and also much larger, but not subadult, instars. Few first instar *Alopecosa pulverulenta* were caught at all, but there were some largish juveniles.

DISCUSSION

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. Greenslade (1964) was uncertain about their effectiveness as a trap for beetles, because of escape rates and vegetation differences affecting the catches. Turnbull (1973) reviews several methods of trapping and concludes that "there are no easy answers to sampling problems", even though he himself had developed a relatively effective method of capturing invertebrates using suction from within a ground-hugging tent (Turnbull, 1966).

Other authors have been more positive, especially in relation to cursorial spiders. Uetz and Unzicker (1976) conclude that "comparison of the methods has shown pitfall trapping to provide a closer estimate of the number of species in a community". They take into account the fact that cursorial spiders run away when an investigator approaches and this affects samples that are collected directly. Similar conclusions are reached by Curtis (1980) who in addition points out that inactive individuals may fail to respond to extraction by heat gradient in a Tullgren funnel. He tested four kinds of pitfall trap and found those containing detergent and formalin to be most efficient.

Topping and Sunderland (1992) reach an opposite conclusion, though they are more concerned with density estimates, than species presence. They do assume, without justification, that suction sampling gives an accurate density estimate, in fact, they refer to `actual density' for this method, even though their quadrats were delimited by a plastic ring, rather than the more effective tent used by Turnbull (1966). It seems clear that there is the possibility of underestimating the most active spiders by this method, which they do not seem to have considered at all, in spite of collecting 298 male *Pardosa palustris* in their pitfalls and 1 by suction. Another problem with vacuum sampling is that it provides only a `snapshot' view, where pitfalls act continuously. This is particularly important with animals which are periodic in their activity, as lycosid spiders are, because it reduces `operator error' in choosing an inappropriate sampling

time. Lycosid spiders are not spread out in their distribution when they are active, (unlike web spiders), but may occur in large numbers, possibly congregating, in one place at one time and then being absent. Pitfall traps have been considered to measure activity and abundance together (Vlijm & Kessler-Geschiere, 1967) and they have been widely used, so comparisons can be made, with reservations, with other work that has been done. It is not unimportant when resources are limited that they are cheap and easy to use.

In view of the evidence from others, and observation of lycosid behaviour, I would conclude that pitfall traps can give useful information about these spiders, provided the limitations are taken into account. They measure activity to a marked degree (hence the over- representation of males) and it is not clear how large an area they sample as lycosids are capable of travelling considerable distances, relative to their size. They may even attract spiders, particularly if males are following the `trail' of a female that falls in. It is necessary to consider them relative samples of the population, not absolute ones. Given the different drawbacks of other sampling methods available, it is probably the best available method for studying lycosids in the uplands.

When a closely related group of species is under investigation the degree of ecological separation and the reasons for it need to be considered. This group of species is only a small part of the animal community or even the spider community in the area. Although there are few other hunting spiders present on Chapel Fell (*Clubonia lutescens* was found in small numbers on the peat hag sites where lycosid numbers were low), it is not clear that they represent a whole guild; "an assemblage of species utilizing a particular resource or group of resources in a functionally similar manner" (Giller, 1984), because it seems likely that other invertebrate predators in the moorland ecosystem, notably carabid beetles, would have to be considered in this definition.

However, the term is used by Uetz (1977) to refer just to spiders (although the habitat he dealt with had a much greater number of species from more families), so it seems reasonable to relate his findings to the Chapel Fell lycosids, to convey the ecological relationship for comparative purposes. Uetz (1977) found evidence of temporal segregation among the spiders of Delaware. There is possible evidence of this

on Chapel Fell, in that *Alopecosa pulverulenta* becomes active earlier than any of the smaller spiders. In 1991, it was active in April, and in both years well over 100 were caught in late May, many more than any of the smaller species. The same is true of *Trochosa terricola* on the lower altitude sites, but this difference between the larger and smaller spiders could also be due to the physiological necessities of a larger size, for instance needing longer to grow to a stage that can survive the winter. *Pardosa palustris* could also be showing temporal separation, because its peak of abundance/activity is later than any of the others (Figure 9) and on the lower altitude site where it occurred in quite large numbers, it only did so after *T. terricola* numbers had fallen, which was not the case with *Pardosa pullata*.

There is some evidence of altitudinal separation of the two larger spiders as *A. pulverulenta* is rare on the low altitude site where *T. terricola* is common (there would need to be more sites surveyed to be definite on this), and the latter is rare on all the high altitude sites. Goodier (1970) found similar differences on Snowdon, as did Pearson and White (1964) in Denbighshire, but here again it may be that *T. terricola* is outside its range on the higher sites physiologically. It could be, then, that *A. pulverulenta* is showing competitive release on the high altitude sites, and this is why it is so common there. It is an ubiquitous species in the British Isles, but as far as can be ascertained from published figures for example in Merrett (1968) for Dorset heaths and Duffey (1968), it is not so common in lowland habitats. Coulson *et al.* (1984) found it 'abundant' on upland peat and grassland sites in Yorkshire, (but this only meant more than 10 specimens) and Duffey (1963) in the uplands (above 450m) near Malham Tarn found comparable numbers to Chapel Fell. However, the figures are not conclusive, and competition between species as a cause of separation and the existence of competitive release needs to be assessed carefully with use of removal experiments to prove its existence (Connell, 1980).

But while Connell (1980) is dubious about how far competition is responsible for diversification of species, he does believe that this is most likely to happen in 'moderately harsh physical environments', because there are less natural enemies controlling numbers than in more favourable places, but the environment is not

so harsh as to reduce numbers below the level where resources need to be competed for (for example, in the High Arctic, the lycosid *Alopecosa exasperans* does not face interspecific competition (Kevan & Danks, 1986)). The conditions prevailing on Chapel Fell could be described as only moderately harsh in this way, because the lycosid spiders occur in some sites in very large numbers indeed (more than 800 specimens on Site K in 1992, for instance). It is noticeable that the numbers of the smaller lycosids rose in the year when *Alopecosa pulverulenta* fell in numbers and interference competition or direct competition for other food is a possible explanation for this. It would be necessary to monitor removal experiments in years of different weather conditions to prove or rule this out.

Many authors have accepted that competition either in the present or in the past is the main cause of diversification, because it is believed competition will not allow two animals to occupy the same niche (Gause, 1934). Lack (1971) working on birds found that species were separated by what they fed on and where they fed, and that this was reflected in different body size and beak size and shape. He related these differences to the effects of competition in the past. There is very little information on niche separation of this sort with regard to lycosid spiders. *Trochosa terricola* and *Alopecosa pulverulenta* have a larger body size than *Pirata piraticus* (medium sized) and the *Pardosa* species, smaller still, but about the same size as each other. *Pardosa nigriceps* has been shown to live higher in the vegetation than others of its genus (Duffey, 1963; Vlijm & Kessler-Geschiere, 1967), where they are present together. Norgaard (1951) found a similar vertical separation in a *Sphagnum* bog between *Pardosa pullata* on the surface and *Pirata piraticus* within the stalk layer. There is no evidence of separation between these generalist predators on prey type, but presumably the larger species can take prey that elude the smaller. The DECORANA species ordination results from the present study show species scattered and not clumped, which suggests separation. On a gradient of soil moisture, *Pirata piraticus* is not separated from *Pardosa amentata* in the year when they both occur. This is in agreement with the findings of Rushton, Topping and Eyre (1987) with regard to these species. However, *Pardosa palustris* does not show a simple relationship: in one year (1991) it appears on

the opposite end of the moisture axis to *P. piraticus* as Rushton *et al.* found, but the next year it exhibits a position in the middle. That it does not invariably prefer the dry sites is supported by findings from the wet and dry sites at different altitudes in 1992, where *P. palustris* significantly preferred the wet site. This apparent discrepancy between the years shows the necessity of being cautious in interpreting results based on short-term surveys, because it would be easy to oversimplify the situation, when in reality there is a complex interaction of factors.

The DECORANA ordination of the sites suggests by clumping that species are showing preferences and that these preferences persist from year to year. Most species increased most in 1992 on the site where they had highest numbers in 1991, suggesting that these are preferred sites. However, although preference exists and species exist in larger numbers on their preferred sites, giving sample sizes in the hundreds, there is considerable overlap and they clearly co-exist on these sites as the figures for species richness indicate (for instance, on Site A in 1992, 6 species were caught, with 3 (*A. pulverulenta, P. prativaga* and *P. pullata*) each numbering over 40 specimens. Wise (1984) cites many examples of field work which suggest competition between spider species may be spasmodic occurring when food levels are low. If food for lycosids is abundant on the moors, which it could well be considering the numbers of Collembola present, more than 100,000 per m² (Cragg, 1961), then it is not surprising that species can coexist.

There is no evidence that spider populations are limited by heavy predation or parasitism at this altitude. It is possible that the larger spider *Alopecosa pulverulenta* is affecting the populations of smaller species by predation, as the numbers of all smaller species caught were much increased from 1991 (496 specimens) to 1992 (1782 specimens), while *A. pulverulenta* decreased by approximately half. The mechanism must not involve the actual breeding capacity of the *Pardosa* species, because large numbers of *A. pulverulenta* were present in 1991 when the increased stock of *Pardosa* were bred. The former spider does become active earlier in the spring, however, so could have an effect by predation on subadult *Pardosa* at that time, limiting the numbers that reach breeding age, in years when it is very common. Information

showing a link between the populations of large and small spiders in this way would need to be available for many more years to progress beyond speculation. The populations could equally well be affecting each other in reverse (i.e. adult *Pardosa* eating immature *A. pulverulenta*) or each being affected differently by environmental factors.

Andrewartha and Birch (1954) proposed that animal populations are not regulated by density-dependant mechanisms, but that the numbers fluctuate with environmental conditions. While there has been much bitter argument and innumerable papers on the subject of population regulation (Hairston, Smith & Slobodkin, 1960; Ehrlich & Birch, 1967, *et cetera.*), the sensible conclusion seems to be that density dependant mechanisms like competition, affect animals more in the centre of their range where conditions are most favourable, whereas independent mechanisms like climatic factors are more important at the edge of ranges and in harsh environments where animals are surviving with difficulty. An example of this is the bug *Neophilaenus lineatus* (Whittaker, 1971), which is regulated by density dependant mechanisms in the centre of its range (Oxford), but is controlled by the timing of the first frost of autumn in the Pennines. Another is the rush-moth *Coleophora alticolella*, which is controlled by parasites in the lowlands, but in the uplands by the amount of seed its food plant sets, which depends in turn on the summer temperature (Coulson, 1978). None of the lycosids on Chapel Fell are specialist upland fauna, so it seems likely that edge of range effects could be limiting some of the populations.

Some of the species are more common at the lower altitudes and these are probably limited by temperature. In 1992, a warmer year, more species appear at the higher altitudes (*Pardosa amentata* and *P. nigriceps*) and others increase in numbers at higher altitude sites (*P. palustris*). *Pirata piraticus* is well adapted to the climate (Norgaard [1951] describes immature specimens surviving in frozen *Sphagnum* heads) and lives in considerable numbers at high altitude on its preferred sites, which are those with a high water table. Dry weather is most likely to limit this species as its tolerance of desiccation is low (Cherrett, 1964). Species numbers from more years and a firm conclusion about the length of its life-cycle in the uplands are needed, but rainfall in the

summer of 1990 and 1991 (82 and 73 mm, averaged over 3 months), exceeded that of 1989 and 1992 (42 and 53 mm). Numbers of *Pirata piraticus* from 1993 and clarification of life-cycle length, could, then provide the evidence of a link between summer wetness and high numbers, or refute it.

The problem of inconclusive evidence on life-cycle length also occurs with *Alopecosa pulverulenta*. It is even more difficult to link this species to particular environmental conditions, as it is the most tolerant species present on Chapel Fell. Caught on all sites in both years in numbers above 10, except Site H in 1992, it numbered more than 30 at 10 sites in 1991 and 7 sites in 1992. However, its numbers fluctuate markedly between years, which suggests that if the length of its life-cycle in the uplands could be established a link to environmental changes might be also. For instance, if it does have a 2 year life-cycle then the high 1991 numbers can be linked to breeding in the dry summer of 1989, but if it is univoltine then a link with summer weather seems less likely as 1990 and 1991 had relatively similar weather at this time. Further information is needed to prove anything definite.

That the weather does affect timing of breeding in the lycosid family is shown by the earlier peak of activity/abundance in 1992, which coincided with a particularly warm, sunny May (more than 1989, 1990 or 1991). Comparisons with other work on phenology of lycosids show that in southern Britain there tends to be a peak of activity/abundance in late May/ early June (Williams, 1962; Merrett, 1968) and that the same applies in moorland of north Wales (Pearson & White, 1964). As the peak of abundance in 1991 is not until July, it suggests that breeding activity may be very variable in the uplands, depending on the weather. July breeding is obviously not too late in the season, as increased numbers survived into 1992.

The results of this study, therefore, give evidence that ecological separation does occur between the lycosid species on Chapel Fell, but the species are not mutually exclusive. It seems probable that the harsh physical environment is limiting the populations below the level where competition for resources needs to occur except in some particularly favourable times, but information from more years and further experimental work would be necessary to establish definite causation.

REFERENCES

Andrewartha, H.G. and Birch, L.C. (1954). *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.

Bristowe, W.S. (1941). *The Comity of Spiders*, Vol. 2. Ray Society, London.

Bristowe, W.S. (1958). *The World of Spiders*. Collins, London.

Bultman, T.L. and Uetz, G.W. (1982). A comparison of cursorial spider communities along an successional gradient. *J. Arachnol.*, 10, 23-33.

Butterfield, J.E.L. (1986). Changes in life-cycle strategies of *Carabus problematicus* over a range of altitudes in northern England. *Ecol. Entomol.*, 11, 17-26.

Cherrett, J.M. (1964). The distribution of spiders on Moorhouse National Nature Reserve, Westmorland. *J. Anim. Ecol.* 33, 27-48.

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

Corcuera, P. (1989). The distribution of spiders on Chapel Fell. MSc. dissertation, Durham University.

Coulson, J.C. (1978). Terrestrial Animals. *Upper Teesdale: the area and its Natural History*. (Ed. by Clapham, A.R.), pp. 122-9, Collins, London.

Coulson, J.C. (1988). The structure and importance of invertebrate communities on peatlands and moorlands, and effects of environmental and management changes. *Ecological Change in the Uplands*. (Ed. by M.B. Usher, & D.B.A. Thompson), pp. 356-380.

Coulson, J.C. and Butterfield, J.E.L. (1978). An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *J. Ecol.* 66, 631-650.

Coulson, J.C., Butterfield, J.E.L., Barratt, B.I.P. and Harrison,S.(1984). The spiders and Harvestmen of some peat and upland grassland sites in Yorkshire. *Naturalist*, 109, 103-110.

Coulson, J.C. and Whittaker, J.B. (1978). The ecology of moorland animals. *Production Ecology of British Moors and Montane Grasslands* (Ed. by O.W.Heal & D.F.Perkins), pp. 53-93. Springer-Verlag, Berlin.

Cragg, J.B. (1961). Some aspects of the ecology of moorland animals. *J. Anim. Ecol.,* **30,** 205-223

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

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. *J. Anim. Ecol.,* **37,** 641-74.

Edgar, W.D. (1969). Prey and predators of the Wolf spider *Lycosa lugubris. J. Zool., Lond.* **159,** 405-411.

Edgar, W.D. (1970). Prey and feeding behaviour of adult females of the Wolf spider *Pardosa amentata* (Clerck). *Neth. J. Ecol.* **20,** 487-491.

Edgar, W.D. (1971). The life, abundance and seasonal movement of the wolf spider, *Lycosa (Pardosa) lugubris,* in central Scotland. *J. Anim. Ecol.,* **40,** 303-332.

Erlich, P.R. and Birch, L.C. (1967). The `balance of nature' and `population control'. *Am. Nat.* **101,** 97-107.

Foelix, R.F. (1982). *Biology of Spiders.* Harvard University Press, London.

Forrest, G.I. (1971). Structure and Production of North Pennine Blanket Bog Vegetation. *J. Ecol.* **59,** 453-479.

Gause, G.F. (1934). *The Struggle for Existence.* Williams and Wilkins, Baltimore.

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

Giller, P.S. (1984). *Community Structure and the Niche.* Chapman and Hall, London.

Goodier, R. (1970). Notes on mountain spiders from Wales. *Bull. Br. Arach. Soc.,* **1,** (6) 85-7, (7) 97-100.

Greenslade, P.J.M. (1964). Pitfall trapping as a means for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.,* 33, 301-310.

Hairston, N.G., Smith, F.C. and Slobodkin,(1960). Community structure, population control, and competition. *Am. Nat.* 94, 421-425.

Hill, M.O. (1979). *DECORANA - A Fortran Program for Detrended Correspondence Analysis and Reciprocal Averaging.* Cornell University, Ithaca, New York.

Hodkinson, I.D. (1973). The population dynamics and host plant interactions of *Stophingia ericae* (Curtis) (Homoptera: Psylloidea). *J. Anim. Ecol.,* 42, 565-83.

Hubbard, C.E. (1968). *Grasses.* Penguin Books, London.

Jones, R. (1983). *Spiders of Britain and Northern Europe.* Country Life Books, London.

Johnson, G.A.L. (1978). Geology. *Upper Teesdale : the area and its Natural History.* (Ed. by Clapham, A.R.), pp.122-9, Collins, London.

Kevan, P.G. and Danks, H.V. (1986). Arctic Insects. *The Arctic and its Wildlife.* (Ed. by Sage, B.) pp. 72-77. Croom Helm, London.

Lack, D. (1971). *Ecological Isolation in Birds.* Blackwell Scientific Publications, Oxford.

Locket, G.H. and Milledge, A.F.(1951). *British Spiders.* Vol 1. Ray Society.

Merrett, P. (1968). The phenology of spiders in heathland in Dorset. *J. Zool. Lond.,* 156, 239-256.

Moore, P.D. and Bellamy, D.J. (1974). *Peatlands.* Elek, London.

Nentwig, W. (1987). The Prey of Spiders. *Ecophysiology of Spiders.* (Ed. by W. Nentwig), pp. 249-263. Springer-Verlag, Berlin.

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

Otto, C. and Svensson, B.S. (1982). Structure of communities of ground living spiders along altitudinal gradients. *Holarct. Ecol.* 5, 35-47.

Pearsall, W.H. (1950). *Mountains and Moorlands.* New Naturalist Series, Collins, London.

Pearson, R.G. and White, E. (1964). The phenology of some surface active arthropods of moorland country in north Wales. *J. Anim.Ecol.*, **33**, 245-262.

Pigott, C.D. (1978) Climate and Vegetation. *Upper Teesdale: the area and its Natural History.* (Ed. by Clapham, A.R.) pp. 102-121, Collins, London.

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

Ridge, I. and Varley, P. (1986). *Ecology.* Unit 3. The Open University Press, Milton Keynes.

Roberts, M.J. (1985). *The Spiders of Great Britain and Ireland.* Vols 1 & 3. Harley Books, Colchester.

Rose, F. (1981). *The Wildflower Key.* Frederick Warne.

Rushton, S.P., Topping, C.J., and Eyre, M.D. (1987). The habitat preferences of grassland spiders as identified using Detrended Correspondence Analysis (DECORANA). *Bull. Br. arachnol. Soc.* **7** (6), 165-170.

Standen, V. (1978). The influence of soil fauna on decomposition by mico-organisms in blanket bog litter. *J. Anim. Ecol.* **47**, 25-38.

Topping, C.J. and 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. *J. Appl. Ecol.,* **29**, 485-491.

Turnbull, A.L. (1966). A population of spiders and their potential prey in an over grazed pasture in eastern Ontario. *Can. J. Zool.,* **44**, 557-83.

Turnbull, A.L. (1973). Ecology of the true spiders (Araneomorphae). *Ann. Rev. Entomol.,* **18**, 305-348.

Uetz, G.W. (1977). Coexistence in a guild of wandering spiders. *J. Anim.Ecol.,* **46**, 531-541.

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

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

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

Whittaker, J.B. (1971). Population changes in *Neophilaenus lineatus* (L.) (Homoptera:Cercopidae) in different parts of its range. *J. Anim. Ecol.,* **40,** 425-43.

Williams, G. (1962). Seasonal and diurnal activity of harvestmen (Phalangida) and spiders (Araneida) in contrasted habitats. *J. Anim. Ecol.,* **31,** 23-42.

Wise, D.H. (1984). The role of competition in spider communities: In sights from field experiments with a model organism. *Ecological Communities.* (Ed. by Stong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B.) pp. 42-53. Princeton University Press, Princeton, New Jersey.

Workman, C. (1978). Life-cycle and population dynamics of *Trochosa terricola* Thorell (Araneae: Lycosidae) in a Norfolk grass heath. *Ecol. Entomol.,* **3,** 329-340.

Appendix 1. Species numbers from Sites A to P 1991

Site Species	A	B	C	D	E	F	G	H	J	K	L	M	N	P	Total
Alopecosa pulverulenta	63	25	136	85	61	217	80	24	17	47	70	29	32	47	**933**
Pardosa palustris	5	0	2	0	0	0	2	0	1	2	16	2	0	2	**32**
Pardosa prativaga	5	0	0	0	0	0	0	0	1	1	1	2	0	0	**10**
Pardosa pullata	13	2	3	0	1	0	0	1	3	3	17	13	0	0	**56**
Pirata piraticus	1	53	2	1	6	1	1	0	131	189	0	6	0	0	**391**
Trochosa terricola.	1	0	3	0	0	1	0	0	0	2	0	0	0	0	**7**
Total	**88**	**80**	**146**	**86**	**68**	**219**	**83**	**25**	**153**	**244**	**104**	**52**	**32**	**49**	**1429**

Appendix 2. Species numbers from Sites A to P 1992

Species \ Site	A	B	C	D	E	F	G	H	J	K	L	M	N	P	Total
Alopecosa pulverulenta	62	20	40	39	30	139	31	6	18	35	23	20	10	12	485
Pardosa amentata	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Pardosa palustris	6	9	3	0	2	0	1	0	8	6	9	3	1	0	48
Pardosa prativaga	45	0	0	0	0	0	0	0	5	4	10	57	0	0	121
Pardosa pullata	60	30	16	10	7	17	7	3	44	66	36	105	0	2	403
Pardosa nigriceps	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2
Pirata piraticus	2	173	1	0	16	1	4	1	226	760	1	15	1	0	1201
Trochosa terricola.	1	1	0	0	0	0	0	0	0	0	0	0	1	1	4
Total	176	234	60	49	55	158	43	10	302	872	79	200	13	15	2266

Appendix 3. Species numbers from altitudinal Sites 1W to 3D 1992

Site Species	1W	1D	2W	2D	3W	3D	Total
Alopecosa pulverulenta	19	9	70	90	5	16	**209**
Pardosa amentata	0	0	1	0	13	1	**15**
Pardosa palustris	5	1	7	5	54	9	**81**
Pardosa prativaga	0	0	0	6	0	0	**6**
Pardosa pullata	18	15	363	453	181	490	**1520**
Pirata piraticus	15	0	527	8	188	8	**746**
Trochosa terricola	0	0	2	1	108	181	**292**
Total	**57**	**25**	**968**	**563**	**351**	**705**	**2869**