Habitat preferences of some spiders on heathland in southern England

R. Snazell

Institute of Terrestrial Ecology,
Furzebrook Research Station,
Wareham, Dorset BH20 5AS

Summary

Spiders were sampled for one year at 154 random points on an area of heathland. Twelve variables had been measured at each point for a previous study. These comprised 5 physical and 7 vegetational characters. Principal components analysis was applied to 45 of the more abundant species of spiders. This gave the relative positions of the optimum conditions of each species within a habitat hyperspace defined by the 12 principal components. Only the first 4 components are considered in this study, accounting for 85.38% of the total variation in the habitat. Most of the spider species showed a preference for the more moderate heathland habitats but 9 showed preferences for more extreme conditions. The implications of the distribution of these optimal habitats are discussed with reference to the co-existence of the spider species.

Introduction

Heathland in Dorset is characterised by the dominance of the ericaceous shrubs *Calluna vulgaris* (L.) Hull, *Erica cinerea* L. and *E. tetralix* L. *Calluna vulgaris* is usually associated with dry heath, *E. tetralix* with wet heath and *E. cinerea* with higher, drier areas. Fairly large quantities of the mat-forming *Ulex minor* Roth. are present on most dry sites between the *C. vulgaris* plants. *Molinia caerulea* (L.) Moench and *Agrostis setacea* Curt. are the dominant grasses, the former in the wet heath and bog and the latter on the high, dry ground. Grazing of the heath by mammals is insignificant, being restricted to small numbers of rabbits (*Oryctolagus cuniculus* (L.) . The geology, topography, climate, soil and flora of these heaths have been studied in detail by Good (1948) and Tansley (1939).

In 1961 and again in 1971, an 8 ha area of lowland heath in the Hartland Moor National Nature Reserve, near Wareham, Dorset (Grid ref. SY 942852) was sampled for ant species (Brian, 1964; Brian *et al.*, 1976). The area, situated on Bagshot Sands and Clays in the Poole Basin, comprised several discrete, mature heathland vegetation types including dry, humid and wet heath, and, along the north-eastern edge, a small amount of *Sphagnum* bog. The altitude ranged between 2 and 30 m above sea level, further increasing the habitat diversity. In the present work, the distribution of the spider species was studied by pitfall trapping at the random points used in Brian's studies, and the results analysed by principal components analysis.

Methods

In the ant surveys of 1961 and 1971 the 8 ha site was divided into hectare squares and 20 sampling points chosen at random within each square, using random numbers and co-ordinates for location. Because of the irregular shape of the site, 6 points were lost giving a total of 154. During July and August 1971 each point was surveyed for altitude, soil moisture, soil organic content and maximum height of the dominant ericaceous shrub, and for integrated temperature in July, using Pallman's sucrose inversion technique (Lee, 1969). The main plant species, seven in all, and the amount of "bare ground" were recorded as proportions of a circle of 1 m² centred on the sample point. In fact, bare ground also included lichen and moss cover, a factor which led to certain anomalies in the results.

Although the spiders were not sampled until 1974, the 1971 physical and vegetational data were considered relevant, as the heath during that period had reached a stable state. Thus it is assumed for this study that any changes in the habitat would have been negligible. The spiders were sampled using one pitfall trap placed as near as possible to each of the 154 marked sample points. The traps had a diameter of 7.3 cm and a depth of 10.5 cm with overflow holes at a depth of 3 cm, and contained a water/detergent mixture with a fungicide/bacteriocide. They were serviced at approximately monthly intervals for one year. The data for the entire year were combined as the temporal variation was not under consideration in this study.

In order to ascertain whether the presence of a great deal of bare ground in the trapping area would have the effect of artificially inflating the diversity of the catch, Margalef's index of diversity (Margalef, 1957) was calculated for each point. There was found

to be no significant correlation between the catch diversity and the amount of bare ground.

Forty-five species of spider were selected for analysis. These comprised the 20 most numerous species, plus a further 25 which were considered to be of potential interest, e.g. members of congeneric groups.

The data were then analysed to examine how the selected species differ in their habitat preferences. For each species in turn the weighted mean was calculated for each of the 12 habitat variables as follows:

$$y = (n_1 x_1 + n_2 x_2 + \ldots\ldots n_{154} x_{154})/N$$

where n_1 = no. of individuals of that species at site 1,

x_1 = value of the habitat variable at site 1,

and $N = n_1 + n_2 + \ldots\ldots n_{154}$ = total no. of individuals of that species taken.

Alternatively, this may be expressed by:

$$y_{ij} = \frac{\sum\limits_{k=1}^{154} n_{ik} . x_{jk}}{\sum\limits_{k=1}^{154} n_{ik}}$$

for species i = 1,2......45,

for habitat variables j = 1,2......12,

where $\sum\limits_{k=1}^{154}$ is the summation of n_{ik} or $(n_{ik} . x_{jk})$ values for sample points k = 1,2......154.

This gives an i x j (i.e. 45 x 12) matrix describing the distribution of the 45 species within a hyperspace defined in terms of the 12 dimensions provided by the 12 habitat variables. The weighted means are used in preference to the unweighted means so as to represent better the average habitat where an individual is found. From this 45 x 12 matrix the correlation coefficients between the habitat variables (Table 1) are calculated. In cases such as this where the data sets show high intercorrelation, principal components analysis (Blackith, 1960; Pearce & Holland, 1960; Seal, 1964), may be used on the correlation matrix to select groups of variables showing high intercorrelation and to identify from them the major lines or components of the variation in the species habitat preferences. Each component

is characterised by a value or loading on each of the 12 habitat variables. The size and sign of these loadings show their relative contribution to each component, e.g. a high positive loading on soil moisture means that the positive extreme of that variation is a wet habitat. The variables with the highest loadings therefore contribute most to the variation and hence to the interpretation of that component.

A score for each species on each component was then calculated by multiplying its weighted mean for a habitat variable by the loading of that habitat variable on the component and summing the product over all the variables.

Component score = $y_1 c_1 + y_2 c_2 + \ldots\ldots y_{12} c_{12}$

where y_1 = weighted species mean for habitat variable 1,

and c_1 = loading of habitat variable 1 on that component.

Alternatively:

$$z_{i1} = \sum_{j=1}^{12} y_{ij} . c_{j1}$$

where z_{i1} is the component score for species i on component 1,

y_{ij} is the weighted mean for habitat variable j for species i,

and c_{j1} is the loading of habitat variable j on component 1.

Results

From the 154 traps, a total catch of some 25,000 adult spiders representing 173 species was obtained during the year. Forty-five of the most abundant species were selected for analysis.

The correlation matrix

The correlations (Table 1) show the major elements of a typical Dorset heathland. Wet low-lying areas dominated by *E. tetralix* and/or *M. caerulea*, a higher zone, drier and warmer, dominated by *C. vulgaris* and, at the highest altitudes, another warm, dry zone, this time dominated by *E. cinerea*.

As would be expected, the presence of a high proportion of bare ground gives high soil temperatures due to insolation. Conversely, a high proportion of long, dense vegetation, and the shade it produces,

gives lower ground temperatures. Bare ground and temperature both have positive correlations with altitude. However, both the dominant plants of the upper zone have negative correlations with temperature. This is probably due to the dense, tussock-forming habit of *A. setacea* creating an insulating layer and thus depressing the soil temperature. Also in the extremely bare high areas the effect of wind may also serve to depress temperatures. The same insulating effect is seen with *U. minor* which has a tight, mat-forming habit.

M. caerulea shows a strong negative correlation with temperature, but for different reasons. In this case it is present in rather wet areas so that much of the heat will be conducted away by ground water. Somewhat surprisingly *U. minor* shows an insignificant negative correlation with *C. vulgaris* but a large positive correlation with *E. cinerea.* Brian *et al.* (1976), using the same habitat data, but erecting the correlation matrix from the group means of six ant species, found an opposite effect. This might indicate that the *E. cinerea/U. minor* habitat is of more importance in the distribution of spiders than the *C. vulgaris/U. minor* grouping, the reverse being true for the ant fauna.

Principal components analysis

Four uncorrelated components were extracted for this study accounting for 85.38% of the total variation. The loadings of the individual habitat variables making up these components are shown in Table 2.

Component I

Component I, accounting for 30.56% of the total variation, has a high negative loading on temperature, moderate negative loadings on bare ground, *C. vulgaris* and *E. tetralix,* and moderate positive loadings on vegetation height, *E. cinerea* and the mat- and tussock-forming plants, *U. minor, A. setacea* and *M. caerulea.* Thus, this first component represents the variation from a cold, heavily vegetated habitat with much *U. minor* mat and *A. setacea* between quite tall bushes of *E. cinerea,* to a warm habitat with either *C. vulgaris* or *E. tetralix* and large areas of bare ground. Here we have the anomaly of *C. vulgaris* and *E. tetralix* both apparently being associated with bare ground. In fact, *E. tetralix* is associated with either *Sphagnum* spp. ɔor a damp lichen cover. As mentioned previously, these were recorded as bare ground in the original data. *M. caerulea* appears to have similar loadings to *E. cinerea,* rather than to *E. tetralix.* This rather unexpected phenomenon is probably due to a large area in the west of the site which, although of moderately high altitude, has impeded drainage giving a large amount of *M. caerulea* with some *E. cinerea* and *C. vulgaris.*

Component II

The second component is only slightly less important than the first, with 27.08% of the variation. The major features of this component are the high negative loadings on soil moisture, *E. tetralix* and *M. caerulea* and the high positive loading on altitude. *C. vulgaris, E. cinerea* and *U. minor* also show moderate

		1	2	3	4	5	6	7	8	9	10	11	12
Altitude	1	100											
Soil moisture	2	−55.3	100										
Bare ground	3	*31.6*	−4.3	100									
Veg. height	4	*−34.9*	−18.9	−53.2	100								
Temperature	5	42.2	−9.8	82.7	−76.9	100							
C. vulgaris	6	5.2	*−35.0*	6.3	−10.9	*33.7*	100						
E. cinerea	7	56.8	−37.7	−9.2	2.5	−12.6	−56.7	100					
E. tetralix	8	−46.0	71.2	25.5	−44.8	28.5	−18.5	*−33.9*	100				
M. caerulea	9	−30.9	54.7	−18.4	11.7	−46.7	−82.5	16.1	18.5	100			
A. setacea	10	−27.9	11.3	−34.7	−2.5	*−33.4*	−71.1	68.7	−1.1	49.2	100		
U. minor	11	40.8	−60.9	−37.9	35.0	−31.7	−6.3	55.0	−79.6	−8.7	19.6	100	
P. aquilinum	12	−18.4	1.9	−26.5	*34.7*	−23.2	−6.2	−9.9	−20.2	5.7	9.7	8.0	100

Table 1: Correlation matrix. Coefficients (×100) of 12 habitat variables, based on weighted mean values for 45 spider species. For 43 degrees of freedom a value of 38.0 has 1% probability (bold type) and 29.4 has 5% probability (*italics*).

positive loadings. This, then, represents the variation from high, dry, moderately warm *C. vulgaris* or *E. cinerea*, with *U. minor*, to low-lying, wet areas of *E. tetralix* and *M. caerulea*. The height of the vegetation or the amount of bare ground are of little importance in this component.

Component III

Component III is still fairly important, with 20.39% of the variation. It has high positive loadings on *E. cinerea*, *A. setacea* and altitude, moderately high on bare ground and temperature, and high negative loadings on vegetation height and *C. vulgaris*. The variation shown by this component therefore is that from a high moderately warm habitat dominated by *E. cinerea* and *A. setacea*, but also having a fairly high proportion of bare ground, to one lower-lying and dominated by tall *C. vulgaris*, with a little *Pteridium aquilinum* (L.) Kuhn but very little bare ground.

Component IV

Component IV is of minor importance, accounting for only 7.35% of the variation. It is of interest, however, for the very high positive loading on *P. aquilinum*. Apart from moderate positive loadings on bare ground and temperature all other variables are of negligible importance. This component may represent areas of *P. aquilinum* in warm open situations with little preference for any other plant species. It is interesting that Component IV of Brian *et al.* (1976) was very similar both in loadings

Component	I	II	III	IV
% total variation	30.56	27.08	20.39	7.35
Variables				
Altitude	0.051	0.408	0.361	0.107
Soil moisture	−0.134	−0.487	0.056	0.016
Bare ground	−0.355	0.127	0.271	0.188
Veg. height	0.332	−0.047	−0.385	−0.035
Temperature	−0.408	0.217	0.250	0.226
C. vulgaris	−0.264	0.298	−0.380	−0.085
E. cinerea	0.325	0.157	0.413	−0.038
E. tetralix	−0.309	−0.370	0.146	−0.063
M. caerulea	0.208	−0.403	0.204	−0.022
A. setacea	0.320	−0.134	0.391	0.115
U. minor	0.368	0.309	−0.019	−0.103
P. aquilinum	0.154	−0.069	−0.226	0.929

Table 2: Principal components I-IV. Individual habitat variable loadings derived from correlation matrix.

and overall importance, indicating that this *P. aquilinum* habitat is significant both to the ant and the spider populations.

Habitat preferences of the spider species

Using the appropriate component loadings and the mean values of the 12 habitat variables, a single score for each spider species on each component was calculated (Table 3). Thus, it is possible to plot a relative position for each species within a hypothetical four-dimensional space which describes 85.38% of the variation within the habitat. The scores on each component indicate where the populations of the species are at their most dense with regard to that variation and therefore, it is assumed, at their optimum position.

Plotting Components I, II and III (Figs. 1 & 2) shows most of the spider fauna to be scattered throughout the more moderate habitats of the heath. However, 9 species show strong preferences for more extreme conditions. *Gnaphosa leporina* (L. Koch) (Code number 4) has high negative scores on Components I and II, showing a high degree of preference for low, wet, bare areas, including a *Sphagnum* or lichen carpet. Although *Pardosa pullata* (Clerck) (11) was taken at 121 of the 154 points it shows a higher preference for low, wet heath with *E. tetralix* and *M. caerulea* than any other species. However, it also requires a more heavily vegetated habitat than the previous species.

The thomisid *Xysticus erraticus* (Blackwall) (9) shows the most extreme preference for the high, dry *E. cinerea/A. setacea* zone of Component III. It is also common on dry, open chalk grassland in the south of England. *Alopecosa accentuata* (Latreille) (13) has the highest positive score on Component II of any species. It also has a moderate positive score on Component III and a moderate negative score on Component I. Therefore the habitat preference of this species, when on heathland, is for the high, dry, moderately bare ground in the *E. cinerea/A. setacea* zone. *A. accentuata* is also very common on chalk grassland, on the short, dry turf on steep slopes. *Walckenaera unicornis* O. P.-Cambridge (27) has a moderately high positive score on Component I and a similar negative score on Component III, indicating that this species prefers long, dense *C. vulgaris* at moderate height. *W. cuspidata* Blackwall (28) has the

Species	Code Number	Components I	II	III	IV	N
Family Gnaphosidae						
Drassodes cupreus (Blackwall)	1	−1.22	−1.05	1.16	0.65	332
Haplodrassus signifer (C. L. Koch)	2	−0.14	−0.05	0.19	−0.04	52
Zelotes latreillei (Simon)	3	−0.63	−1.57	1.39	0.32	98
Gnaphosa leporina (L. Koch)	4	−4.72	−3.31	2.22	−0.47	67
Family Clubionidae						
Agroeca proxima (O. P.-Cambridge)	5	0.07	−0.03	0.20	−0.24	8157
Scotina celans (Blackwall)	6	1.60	−0.54	−2.33	−1.45	65
S. gracilipes (Blackwall)	7	−1.94	1.82	0.23	−0.29	208
Family Zoridae						
Zora spinimana (Sundevall)	8	0.66	0.29	−0.37	−0.01	909
Family Thomisidae						
Xysticus erraticus (Blackwall)	9	−0.73	−1.63	3.03	0.25	28
Oxyptila atomaria (Panzer)	10	0.40	1.11	1.00	−0.14	136
Family Lycosidae						
Pardosa pullata (Clerck)	11	−1.88	−5.01	1.71	−0.05	1193
P. nigriceps (Thorell)	12	1.14	−0.15	−0.34	−0.20	2172
Alopecosa accentuata (Latreille)	13	−1.26	3.62	1.85	−0.23	69
Trochosa terricola Thorell	14	−0.67	−0.56	−0.19	0.31	640
Family Pisauridae						
Pisaura mirabilis (Clerck)	15	−0.40	0.90	−1.11	−0.42	241
Family Agelenidae						
Hahnia nava (Blackwall)	16	−1.94	1.79	−0.89	1.98	102
Family Mimetidae						
Ero cambridgei Kulczynski	17	−0.09	2.09	0.42	−0.06	36
E. furcata (Villers)	18	1.33	−1.38	1.65	0.50	53
Family Theridiidae						
Episinus truncatus Latreille	19	−1.68	2.58	−0.05	−0.25	99
Robertus lividus (Blackwall)	20	1.40	1.22	0.95	−0.44	225
Pholcomma gibbum (Westring)	21	2.36	−0.08	0.74	−0.12	257
Family Tetragnathidae						
Pachygnatha degeeri Sundevall	22	−1.71	0.44	0.41	0.35	232
Family Linyphiidae						
Ceratinella brevipes (Westring)	23	1.28	0.38	−2.46	−0.72	170
Walckenaera acuminata Blackwall	24	−1.05	0.40	−0.76	−0.14	587
W. antica (Wider)	25	−0.78	1.31	−0.59	−0.64	379
W. cucullata (C. L. Koch)	26	1.73	−2.34	−1.08	0.37	101
W. unicornis O. P.-Cambridge	27	3.20	0.25	−3.21	0.14	26
W. cuspidata Blackwall	28	6.11	0.42	5.20	−1.31	29
Gonatium rubens (Blackwall)	29	1.67	−0.97	−0.31	4.98	451
Maso sundevalli (Westring)	30	−0.69	−1.48	−3.29	−0.92	28
Peponocranium ludicrum (O. P.-Cambridge)	31	0.83	0.47	−0.59	−0.26	814
Pocadicnemis pumila (Blackwall)	32	2.88	−3.76	0.27	−0.32	107
Hypselistes jacksoni (O. P.-Cambridge)	33	−2.70	−4.62	−2.29	−0.60	36
Cnephalocotes obscurus (Blackwall)	34	−0.10	1.41	0.76	0.35	188
Tiso vagans (Blackwall)	35	−0.84	0.08	−0.91	−0.66	963
Tapinocyba mitis (O. P.-Cambridge)	36	−1.31	1.87	−0.25	0.38	87
Jacksonella falconeri (Jackson)	37	3.06	−0.78	−1.56	0.35	68
Gongylidiellum vivum (O. P.-Cambridge)	38	−0.16	0.68	−0.45	−0.39	614
Savignya frontata (Blackwall)	39	−2.26	1.23	0.15	−0.36	50
Agyneta subtilis (O. P.-Cambridge)	40	0.06	1.51	−0.71	−0.01	517
Centromerita concinna (Thorell)	41	−2.96	0.44	0.88	−0.41	1042
Stemonyphantes lineatus (Linnaeus)	42	−0.63	2.57	0.15	0.60	29
Lepthyphantes zimmermanni Bertkau	43	3.10	0.04	−1.32	0.04	145
L. mengei Kulczynski	44	0.06	0.11	1.06	−0.32	912
L. ericaeus (Blackwall)	45	0.55	0.29	−0.55	−0.14	416

Table 3: Individual component scores for 45 of the most abundant species. N = total number of individuals. Nomenclature as in Locket, Millidge & Merrett (1974).

most extreme habitat preferences of all the spiders in this study. It has very high positive scores on both Components I and III, indicating a very strong preference for areas which are cool and heavily vegetated with *E. cinerea, A. setacea,* or other mat-forming plants.

Maso sundevalli (Westring) (30) has a similar high negative loading on Component III to *W. unicornis* (27). However, it prefers considerably less dense, tall *C. vulgaris,* having a low, negative score on Component I. *Pocadicnemis pumila* (Blackwall) (32) shows a marked preference for fairly low-lying damp areas with good ground cover, plenty of the mat-forming plants, but also some long vegetation, although with little preference for any one of the ericaceous shrubs. *Hypselistes jacksoni* (O. P.-Cambridge) (33) is well known to be restricted to wet marshes or bog habitats. This is borne out by the position plotted here. Components I and II show a low-lying, wet, open habitat while III indicates fairly long vegetation.

Component IV is of little importance, most of the spider species having very low scores in it. The only species much affected by this variation is *Gonatium rubens* (Blackwall) (29) which has a very high positive score. It is the only species with an apparent preference for this warm, open, grassy habitat with *P. aquilinum* present.

The tendency towards partitioning of the habitat by members of certain groups, or guilds (Root, 1973; Uetz, 1977) of spiders, and also by some congeneric pairs, is well illustrated. Of the four most common gnaphosid species, *Drassodes cupreus* (Blackwall) (1) and *Zelotes latreillei* (Simon) (3) seem to prefer moderately low, damp, bare conditions, while *Haplodrassus signifer* (C. L. Koch) (2) shows little preference for any of the more extremes of variation. *G. leporina* (4), as stated above, is found in the low, wet, bare *Sphagnum* of the valley bog. *D. cupreus* and *Z. latreillei* have somewhat similar preferences and are also phenologically similar. However, size differences (Enders, 1975, 1976) and possibly differences in diurnal foraging strategies may reinforce the differences in habitat preference.

Agroeca proxima (O. P.-Cambridge) (5) was the most common spider taken in this study, 8157 individuals occurring in the 154 traps. It showed a slight preference for dry *C. vulgaris* heath, but was found in small numbers in all habitats. Also within this guild are the two *Scotina* species, *S. celans* (Blackwall) (6) and *S. gracilipes* (Blackwall) (7). The preferences of these two species are rather different, the former preferring more heavily vegetated, damp areas with tall *C. vulgaris,* whereas *S. gracilipes* is found in dry, more open, vegetation.

Within the lycosid group, the congeneric pair of *Pardosa pullata* (11) and *P. nigriceps* (Thorell) (12) are well separated with the former preferring wet, fairly open situations and the latter, dry, well vegetated areas of long heather, it being a more arboreal species. *Alopecosa accentuata* (13) is a spider of the high, dry *E. cinerea/A. setacea* zone, whereas the other guild member of equivalent size (*Trochosa terricola* Thorell) (14) shows no preference for the more extreme habitats.

The two *Ero* species, *E. cambridgei* Kulczynski (17) and *E. furcata* (Villers) (18) exhibit very different preferences with regard to Component II, the former occurring in the higher, drier areas with rather less ground cover than the latter, which also prefers far more moist conditions. Of the 9 species of *Walckenaera* recorded during the trapping period, 5 were present in high enough numbers to use in the analysis. Two of these, *W. acuminata* Blackwall (24) and *W. antica* (Wider) (25) plot fairly close together on all three axes although the former shows a preference for slightly more moist conditions. In this case, co-existence may be facilitated by prey size specialisation (Uetz, 1977). The remaining species show progressively greater preference for cooler, more heavily vegetated habitat, *W. cucullata* (C. L. Koch) (26) in lower wetter situations, *W. unicornis* (27) in long *C. vulgaris,* and *W. cuspidata* (28) in dense *E. cinerea/A. setacea.*

Discussion

The use of pitfall traps in this study was dictated by the need for a maximum catch of spiders in order to perform the statistical analyses. The generally low population density and the high mobility of many of the more important cursorial species meant that methods such as quadrat sampling and vacuum netting were unsuitable.

There is a great deal of discussion of the validity of using pitfall trap data in quantitative ecological studies. However, when used specifically in studies

of relative abundance within the same broad vegetation types the data can be used to obtain the required comparisons. Although one is in fact measuring a product of density and activity, the "Aktivitatsdicht" of Heydemann (1961), the "penetration" of Breymeyer (1966) or the "active density" of Uetz & Unzicker (1976), if it is assumed that the behaviour of a species is generally similar in what are similar habitats and that climatic conditions will affect all habitats similarly, then the data obtained will give a reasonably accurate estimate of relative abundance.

Microclimate is a major influence in determining microhabitat selection in spiders (Vogel, 1972; Almquist, 1970, 1973; Tretzel, 1952). The physical structure of the habitat also has a profound effect on habitat selection (Duffey, 1966; Luczak, 1963; Curtis, 1979; Curtis & Bignal, 1980; Robinson, 1981).

In this study the physiognomy of the vegetation was not measured directly. However, each major vegetation type used has a particular intrinsic structure. Thus the measurements taken do reflect the physical structure closely. The relative positions of the spider species in the matrix indicate their optimum habitat conditions. However, because of the high environmental tolerance and great mobility, both cursorial and aeronautic, of many species it is possible for them to be trapped, albeit in lower numbers, while dispersing, or searching for prey or mates, at a considerable distance from their optimal habitats, even in positively inimical environments. Thus these distributions may reflect responses of the populations to competition for prey, or mates, rather than purely a preference for microhabitat or microclimate.

The temporal variation of the spider species was not included in this study as their phenology in the
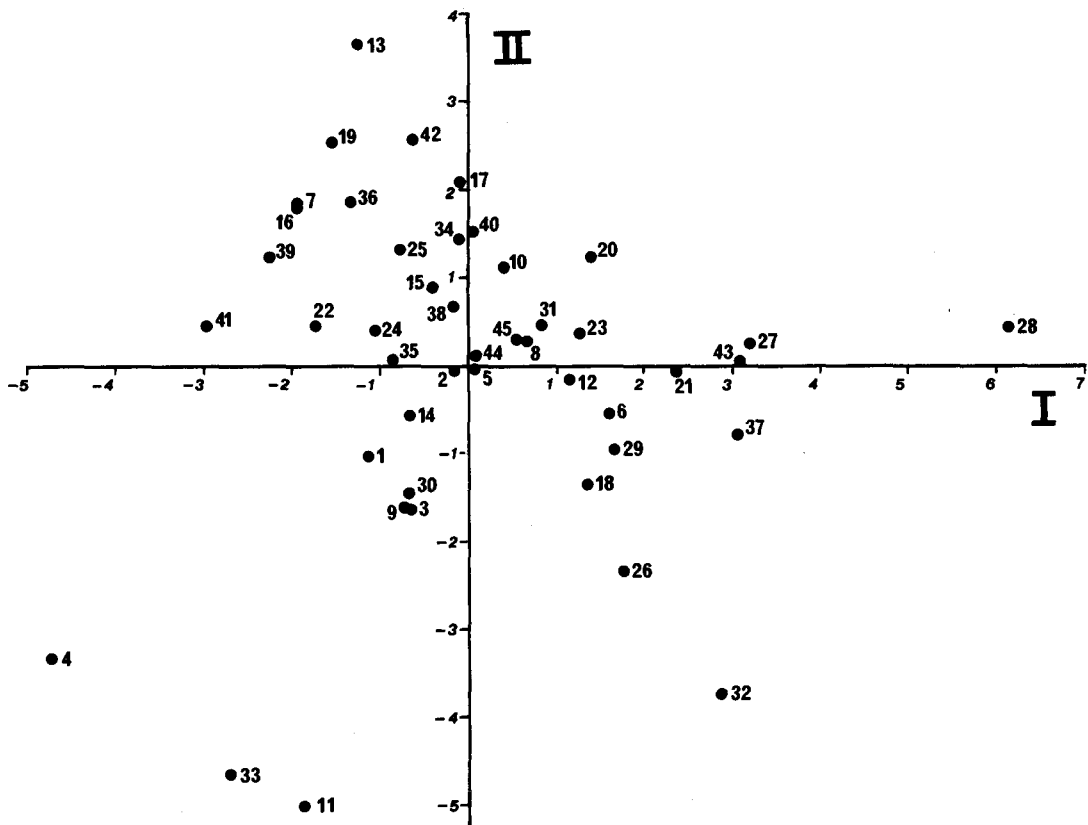

Fig. 1: Position of species in component space (Components I and II). Code numbers as in Table 3.

study area is well known (Merrett, 1967, 1968, 1969). Temporal segregation may be a means of reducing competition between species, which in this work have been shown to have similar habitat preferences. *H. signifer* (2) and *A. proxima* (5), for example, plot very closely on all three axes. However, the former is active from May to mid-August while the latter is active from mid-August until mid-December. This form of segregation is not seen in the case of such ubiquitous species as *P. pullata* (11) and *P. nigriceps* (12) which, although having very different habitat preferences, show considerable environmental tolerance and are relatively common over much of the area studied. *P. pullata* was not taken in the highest, driest parts and *P. nigriceps* was only present in quite small numbers in the bog. The small differences in behaviour, *P. nigriceps* being more arboreal than *P. pullata*, do not seem

fully to explain the great overlap in their distributions, both ecological and temporal.

Acknowledgements

References

ALMQUIST, S. 1970: Thermal tolerances and preferences of some dune living spiders. *Oikos* 21: 230-236.

ALMQUIST, S. 1973: Habitat selection by spiders on coastal sand dunes in Scandia, Sweden. *Entomol.Scand.* 4: 134-154.

BLACKITH, R. E. 1960: A synthesis of multivariate techniques to distinguish patterns of growth in grasshoppers. *Biometrics* 16: 28-40.
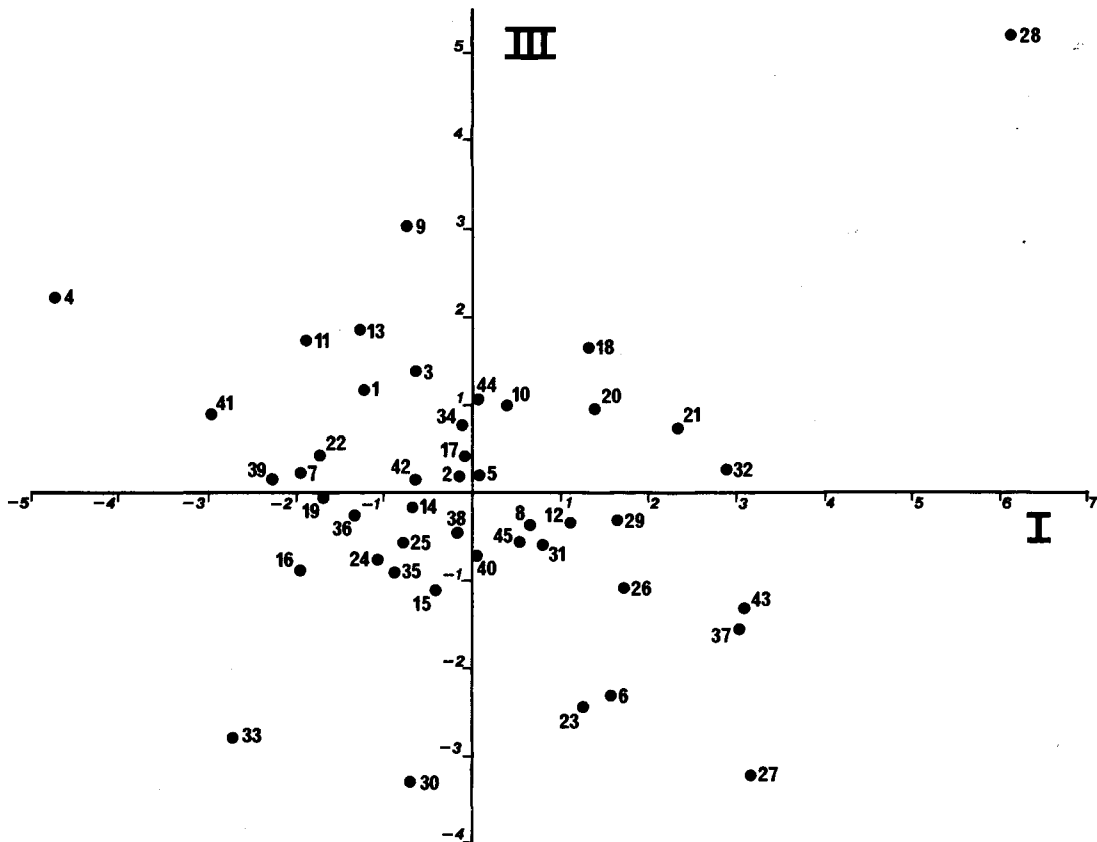

Fig. 2: Position of species in component space (Components I and III). Code numbers as in Table 3.

BREYMEYER, A. 1966: Relations between wandering spiders and other epigeic predatory Arthropoda. *Ekol.pol.* (A), **14**: 27-71.

BRIAN, M. V. 1964: Ant distribution in a southern English heath. *J.Anim.Ecol.* **33**: 451-461.

BRIAN, M. V., MOUNTFORD, M. D., ABBOTT, A. & VINCENT, S. 1976: The changes in ant species distribution during 10 years post-fire regeneration of a heath. *J.Anim.Ecol.* **45**: 115-133.

CURTIS, D. J. 1979: *Upland spiders – sampling study winter 1973-79:* 1-20. Nature Conservancy Council, South West (Scotland) Region report.

CURTIS, D. J. & BIGNAL, E. 1980: Variations in peat bog spider communities in relation to environmental heterogeneity. *Int.Congr.Arachnol.* **8**: 81-86.

DUFFEY, E. 1966: Spider ecology and habitat structure. *Senckenberg.biol.* **47**: 45-49.

ENDERS, F. 1975: The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae and Salticidae). *Am.Nat.* **109**: 737-763.

ENDERS, F. 1976: Size, food finding and Dyar's constant. *Environ.Entomol.* **5**: 1-10.

GOOD, R. D'O. 1948: *A geographical handbook of the Dorset flora.* Dorset Natural History and Archaeological Society.

HEYDEMANN, B. 1961: Untersuchungen über die Aktivitats und Besiedlungsdichte bei epigäischen Spinnen. *Verh.dt.zool.Ges.Saarbrücken* **1961**: 538-556.

LEE, R. 1969: Chemical temperature integration. *J.appl. Meteorol.* **8**: 423-430.

LOCKET, G. H., MILLIDGE, A. F. & MERRETT, P. 1974: *British spiders* 3: 1-314. Ray Society, London.

ŁUCZAK, J. 1963: Differences in the structure of communities of web-building spiders in one type of environment (young pine forest). *Ekol.pol.* (A), **11**: 159-221.

MARGALEF, D. R. 1957: Information theory in ecology. Transl. from paper in *Mems R.Acad.Cienc.Artes Barcelona* **23**: 373-449.

MERRETT, P. 1967: The phenology of spiders on heathland in Dorset. I. Families Atypidae, Dysderidae, Gnaphosidae, Clubionidae, Thomisidae and Salticidae. *J. Anim.Ecol.* **36**: 363-374.

MERRETT, P. 1968: The phenology of spiders on heathland in Dorset. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. *J.Zool., Lond.* **156**: 239-256.

MERRETT, P. 1969: The phenology of linyphiid spiders on heathland in Dorset. *J.Zool., Lond.* **157**: 289-307.

PEARCE, S. C. & HOLLAND, D. A. 1960: Some applications of multivariate methods in botany. *Appl.Statist.* **9**: 1-7.

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

ROOT, R. B. 1973: Organization of a plant arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecol.Monogr.* **43**: 95-124.

SEAL, H. L. 1964: *Multivariate statistical analysis for biologists:* 101-122. Methuen, London.

TANSLEY, A. G. 1939: *The British Islands and their vegetation.* Cambridge.

TRETZEL, E. 1952: Zur Ökologie der Spinnen (Araneae). *Sber.phys.-med.Soz.Erlangen* **75**: 36-131.

UETZ, G. W. 1977: Co-existence in a guild of wandering spiders. *J.Anim.Ecol.* **46**: 531-542.

UETZ, G. W. & UNZICKER, J. D. 1976: Pitfall trapping in ecological studies of wandering spiders. *J.Arachnol.* **3**: 101-111.

VOGEL, B. R. 1972: Apparent niche sharing of two *Pardosa* species (Araneida: Lycosidae). *Armadillo Paps.* **7**: 1-13.