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# The habitat preferences of grassland spiders as identified using Detrended Correspondence Analysis (DECORANA)

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## Summary

Spider species lists from 54 grassland sites in the North-East of England are analysed using Detrended Correspondence Analysis (DECORANA). Management regime and site wetness are shown to be important environmental determinants of spider community structure in grasslands. Habitat preferences of individual species are discussed in the light of these results.

## Introduction

Identifying the causes of differences in the distributions of animal species is often a difficult task because there are usually too many variables to be considered at the same time. In the case of spider communities there may be as many as one quarter or more of the total British fauna present on one site or habitat type (e.g. Merrett, 1983). In these circumstances, recourse has to be made to multivariate techniques which can handle large and complex data sets at the same time as simplifying them so that major trends can be identified. In the past, multivariate techniques, such as Principal Components Analysis (P.C.A.), have been used in the analysis of spider communities (Aart, 1973; Snazell, 1982), but these techniques make considerable assumptions which are not often met by ecological data (see review in Gauch, 1982). More recently, however, new techniques have been developed specifically for the analysis of plant and animal communities which have overcome these inadequacies. One of these, Detrended Correspondence Analysis (DECORANA), an ordination technique devised by Hill (1979a), has been increasingly used by several authors and has been shown to be a valuable tool in the identification of important environmental determinants of the structure of other invertebrate communities (Wright *et al.*, 1984; Eyre, Ball & Foster, 1986; Eyre, Rushton *et al.*, 1986). This technique is particularly useful because it ordinates species as well as sites, thus allowing the interpretation of distribution patterns of individual species in terms of the same environmental factors.

Although DECORANA and related classification techniques such as Two-way Indicator Species Analysis (TWINSPAN, Hill, 1979b) have been used in arachnological research for some years, published reports such as that of Curtis & Stinglhammer (1986), are few. This paper describes work using the former ordination technique for identifying the habitat preferences of spider species in grassland. Species lists derived from pitfall trap catches from six months sampling of 54 grassland sites in North-East England are analysed using DECORANA. The principal environmental factors determining distributions of the spider communities are identified by comparing site ordination scores with measures of 6 environmental variables from each site and discussed in the light of current knowledge.

## Materials and methods

Spider communities were sampled on 54 grassland sites in Northumberland, Durham, and Tyne & Wear. The sites were selected to provide as wide a range of grassland types as possible within the region, covering a range of management regimes. Spiders were sampled using 70% ethanol-filled pitfall traps, emptied at monthly intervals from April to November 1985, as outlined in Eyre, Rushton *et al.* (1986).

Spiders were identified using Locket & Millidge (1953) and Roberts (1985) with the nomenclature of Merrett *et al.* (1985).

Four types of environmental factor, selected on the basis of their potential importance to spider communities, were measured for each site. These were:

### (i) *Extent of management*

The level of management occurring on each site was assessed by scoring, on a scale of 1 to 5, using the descriptions given in Table 1, following discussions with the relevant land owners and farm managers.

### (ii) *Vegetation*

Mean peak biomass of vegetation present was estimated for 23 of the sites during July 1985 as outlined in Eyre, Rushton *et al.* (1986).

### (iii) *Site wetness*

Site wetness was assessed on the basis of the mean

**Level 1**

Totally unmanaged grassland, not used agriculturally.

**Level 2**

Very poor permanent to rough pasture grazed only once or twice a year for 1-2 weeks in autumn. Hay not taken because sward dominated by tussocks and poor quality grass species such as *Holcus lanatus* L.

**Level 3**

Poorer quality permanent pasture, not dominated by *Lolium perenne* L., inorganic fertilisers not used and grazing usually for less than half of year (often with horses). Hay often taken.

**Level 4**

Intensively managed permanent leys, usually *L. perenne*, inorganic fertilisers used infrequently and grazed for more than 6 months of year. Silage may be taken but not hay.

**Level 5**

Intensively managed temporary leys, often part of an arable rotation, inorganic fertilisers used frequently, sown with *L. perenne* and grazed for more than 6 months of the year. Silage may be taken but not hay.

Table 1: Classification of the grassland sites sampled on the basis of the management regime in operation.

volumetric soil moisture content of four 29 $cm^3$ cores taken from each site when the soil was at field capacity in January 1986. Sites were assigned to one of 5 moisture classes covering the range from 0 to 100% volumetric soil moisture content, in increments of 20%.

### (iv) *Soil type*

Soil organic matter content, pH and % sand content were determined for each of the four cores used in the soil moisture content determination, following the methods of Allen *et al.* (1974).

### *Ordination*

Detrended correspondence analysis (DECORANA, Hill, 1979a) was used to ordinate the sites in four axes, using abundance figures and species lists derived from pooling trap catches from each month for each site. All species recorded from each site were incorporated in the analysis and no down-weighting (terminology of Hill, 1979a) was used to reduce the significance of rarely recorded species on the ordination. Principal parameters influencing the distribution of species amongst sites were then identified by comparing site ordination scores for each axis with the measured site characteristics, as in Wright *et al.* (1984). Spider habitat preferences were then assessed in terms of these environmental parameters by considering the occurrence of individual species throughout the data set and their respective ordination scores in DECORANA axis space.

## Results

### *Identification of environmental factors influencing the ordinations*

Eigenvalues for the ordination, which give some indication of the amount of community variation explained by each axis, were 0.624, 0.435, 0.220 and 0.128 for the first to fourth axes respectively. These results suggest that the first two axes explained most of the between-site differences in spider communities. A brief description of 15 sites, representative of the range of grasslands sampled, is given in Table 2. Included for comparison are axis 1 and axis 2 ordination scores, volumetric soil moisture content and management class. The Axis 1 scores for the sites appeared to be related to management, since the most intensively managed sites had the highest axis scores and the unmanaged sites the lowest, as shown by sites 1-3 and 13-15 respectively (Table 2). A histogram showing the mean axis 1 score for all sites in each of the 5 management classes (Fig. 1a) indicates a clear increase in axis score with an increase in the level of management. When sites were ranked on the basis of the amount of vegetation biomass present and their axis 1 scores there was a significant correlation ($r_{\text{Spearman}} = 0.443$, $p < 0.02$), suggesting that for those sites from which vegetation samples had been taken, axis score was also related to vegetation biomass as well as management.

Axis 2 scores appeared to be more related to site wetness, since the marshy sites like sites 9 and 11 had

| | Grid ref. | Grassland type | Management class | Axis 1 score | Soil water % | Moisture class | Axis 2 score |
|---|---|---|---|---|---|---|---|
| **1** | NZ127682 | Temporary rye grass ley | 5 | 418 | 31.4 | 2 | 189 |
| **2** | NZ203917 | as above | 5 | 395 | 44.4 | 3 | 185 |
| **3** | NZ2190 | as above | 5 | 322 | 45.2 | 3 | 162 |
| **4** | NZ064848 | Ancient ridge & furrow pasture | 4 | 312 | 48.0 | 3 | 146 |
| **5** | NZ133658 | Permanent, cut but ungrazed | 4 | 272 | 38.3 | 2 | 100 |
| **6** | NZ134658 | as above | 4 | 237 | 35.3 | 2 | 61 |
| **7** | NY834922 | Permanent upland sheep grazing | 3 | 266 | 65.6 | 4 | 133 |
| **8** | NZ198628 | Permanent horse grazing | 3 | 257 | 45.6 | 3 | 131 |
| **9** | NZ195735 | Permanent, hay meadow | 3 | 131 | 74.0 | 4 | 330 |
| **10** | NZ167636 | Permanent, autumn grazed | 2 | 211 | 42.9 | 3 | 116 |
| **11** | NZ198629 | Permanent, tussocky horse grazed | 2 | 198 | 65.9 | 4 | 303 |
| **12** | NZ288941 | Autumn grazed dune grassland | 2 | 176 | 4.8 | 1 | 107 |
| **13** | NZ131661 | Unmanaged, rough neutral grassland | 1 | 104 | 46.6 | 3 | 132 |
| **14** | NZ195735 | Unmanaged, marshy grassland | 1 | 130 | 69.2 | 4 | 266 |
| **15** | NZ3132 | Unmanaged, magnesian limestone grassland | 1 | 60 | 50.2 | 3 | 144 |

Table 2: DECORANA axis 1 and axis 2 scores for a selection of sites covering the range of grassland sampled.

the highest scores and the driest sites, like site 12, had the lowest. A histogram showing the mean axis 2 scores for sites in each of 5 volumetric soil moisture content classes (Fig. 1b) indicates that axis 2 score increased with site wetness.

Site scores for axes 3 and 4 of the ordination plot were not immediately identifiable with any of the measured environmental parameters and since the eigenvalues for both ordinations were very low they are not considered further in this analysis.

### *Axis 1 and axis 2 ordination scores of individual species*

A total of 145 species was caught over the period of sampling, of which 49 were caught frequently (on more than approximately 5 sites of the total 54). Axis 1 and axis 2 ordination scores for these species are given in Table 3. A graphical representation of the scores showing the relationships between the species is shown in Fig. 2.

The most important feature in all of the plots is the wide scatter of species across the ordination. The range of scatter in both axes was greater than 200 units of axis score. Each unit of axis score is a measure of species turnover (termed standard deviations of species turnover by Hill, 1979a) where ranges in excess of 400 indicate that species do not occur together. Of these 49 species a conspicuous group of 6, *Savignya frontata* (Blackwall), *Milleriana inerrans* (O. P.-C.), *Erigone dentipalpis* (Wider), *E. atra* (Blackwall) and *Oedothorax fuscus* (Blackwall), had axis 1 scores higher than 300, suggesting that they preferred the more open, highly managed, temporary ley sites. At the other extreme, 9 species, *Pardosa nigriceps* (Thorell), *P. lugubris* (Walck.), *Gonatium rubens* (Blackwall), *Pocadicnemis pumila* (Blackwall), *Gongylidiellum vivum* (O. P.-C.), *Kaestneria pullata* (O. P.-C.), *Lepthyphantes zimmermanni* Bertkau, *L. tenebricola* (Wider) and *L. ericaeus* (Blackwall), had axis 1 scores below zero, indicating a strong preference for undisturbed, well vegetated sites. The wide separation in axis scores indicates that these two groups of species did not occur together with any frequency on the sites sampled. Between these two extremes was another large group of species with scores around 200, of which *Xysticus cristatus* (Clerck), *Pardosa palustris* (Linn.), *P. amentata* (Clerck), *Pachygnatha degeeri* Sundevall, *Walckenaeria nudipalpis* (Westring) and *Monocephalus fuscipes* (Blackwall) were typical, which had preferences for moderately disturbed sites such as hay meadows.

The range in axis 2 scores for these 49 species was not as large as that for axis 1, indicating that there was considerably less variation in the distribution of species across the range of sites sampled, that could be attributable to this axis. Nonetheless, the axis 2 score for one species, *Pirata piraticus* (Clerck) was in excess of 425 and this, when compared with the lowest score of −16 for *P. palustris*, indicates that these species were at the extreme ends of the site wetness preference continuum. Three other species, *P. amentata, Pachygnatha clercki* Sundevall and *Bathyphantes gracilis* (Blackwall), had axis scores greater than 350, suggesting that they also preferred wet sites. Few of the remaining species had very low axis 2 scores, although a large group typified by *Alopecosa pulverulenta* (Clerck), *X. cristatus, Pachygnatha degeeri* and *Tiso vagans* (Blackwall), had scores below 100 suggesting that they were tolerant of relatively dry conditions.

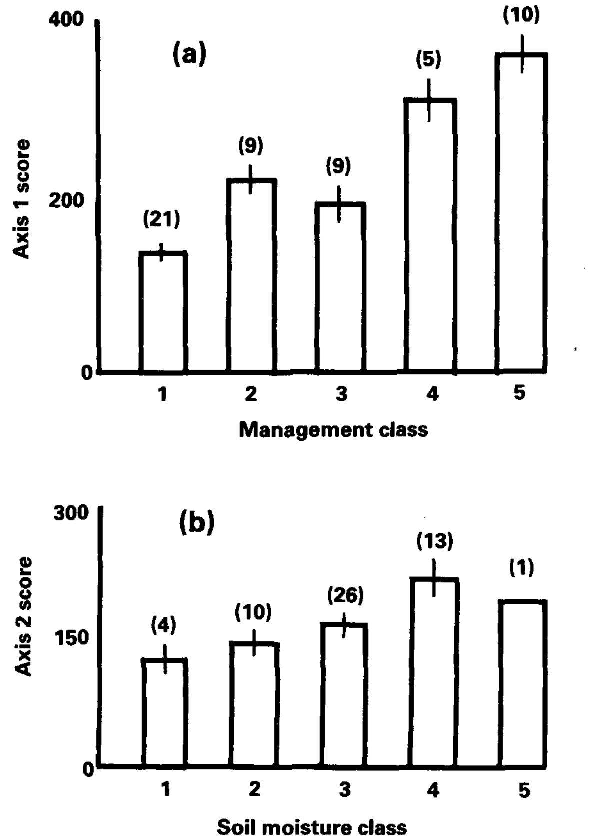

Fig. 1: Comparisons of DECORANA ordination scores against site management class and measured site wetness class.

(a) Mean axis 1 score ± 1 S.E. for sites in each of the five management classes described in Table 1.

(b) Mean axis 2 score ± 1 S.E. for sites in five soil moisture content classes.

1 = 0-19% volumetric soil moisture content
2 = 20-39% " " " "
3 = 40-59% " " " "
4 = 60-79% " " " "
5 = 80-100% " " " "

In both figures numbers in parentheses refer to number of sites in each class.

The genus with the greatest number of representatives encountered during the course of the study was *Lepthyphantes*, with 6 species. The range in scores was great, particularly for axis 1, suggesting that these species had very different habitat preferences. *L. tenuis* (Blackwall) had the highest axis 1 score (246) suggesting that it preferred short vegetation, followed by *L. pallidus* (O. P.-C.) (206) and ranging through *L. mengei* (Kulczynski), *L. ericaeus* (Blackwall) and *L. zimmermanni* Bertkau to *L. tenebricola* (Wider) which had the lowest score (−93) and a preference for longer vegetation.

## Discussion

The results suggest that management regime and site wetness are the major factors influencing spider communities on the grassland sites sampled in this study. The importance of management has long been recognised (see Duffey *et al.*, 1974) and practices such as grazing (Duffey, 1962; Cherrett, 1964) and cutting regimes (Kajak, 1962; Edwards *et al.*, 1975) have been shown to affect the structure and diversity of grassland spider communities. Management is considered to affect spider communities by altering the structural diversity of the habitat (Duffey, 1978; Greenstone, 1984) and experimental manipulation of vegetation structure has been shown to affect spider communities in scrub ecosystems (Hatley & Macmahon, 1980). At the simplest level, agricultural grassland management reduces structural diversity by removal of the vegetation itself. Duffey (1962) illustrated this in limestone grassland, where differential grazing left pockets of high spider species diversity in otherwise barren areas subjected to higher grazing pressure. Clearly, much of the difference in spider community structure reflected in the axis 1 ordination scores between management classes 1 and 5 is attributable to the presence of different amounts of vegetation. The fact that class 4 sites had lower axis 1 scores than class 5 sites even though the vegetation cutting, grazing and fertiliser regimes were similar, suggests that there were other factors influencing the spider communities on these sites.

| | Axis 1 | Axis 2 | Code number |
|---|---|---|---|
| Clubionidae | | | |
| *Clubiona reclusa* O. P.-C. | 209 | 280 | 1 |
| *C. neglecta* O. P.-C. | 229 | 76 | 2 |
| Thomisidae | | | |
| *Xysticus cristatus* (Clerck) | 203 | 86 | 3 |
| Lycosidae | | | |
| *Pardosa palustris* (Linn.) | 231 | –16 | 4 |
| *P. pullata* (Clerck) | 47 | 171 | 5 |
| *P. amentata* (Clerck) | 216 | 355 | 6 |
| *P. nigriceps* (Thor.) | –138 | 208 | 7 |
| *P. lugubris* (Walck.) | –93 | 181 | 8 |
| *Alopecosa pulverulenta* (Clerck) | 59 | 89 | 9 |
| *Trochosa ruricola* (Degeer) | 190 | 71 | 10 |
| *T. terricola* Thor. | 124 | 112 | 11 |
| *Arctosa perita* (Latr.) | 203 | 144 | 12 |
| *Pirata piraticus* (Clerck) | 154 | 425 | 13 |
| Theridiidae | | | |
| *Robertus lividus* (Black.) | 124 | 168 | 14 |
| Tetragnathidae | | | |
| *Pachygnatha degeeri* Sund. | 227 | 77 | 15 |
| *P. clercki* Sund. | 232 | 366 | 16 |
| Linyphiidae | | | |
| *Walckenaeria acuminata* Black. | 53 | 168 | 17 |
| *W. nudipalpis* (Westr.) | 199 | 268 | 18 |
| *W. vigilax* (Black.) | 299 | 248 | 19 |
| *Dicymbium tibiale* (Black.) | 146 | 264 | 20 |
| *Dismodicus bifrons* (Black.) | 37 | 251 | 21 |
| *Hypomma bituberculatum* (Wider) | 123 | 301 | 22 |
| *Gonatium rubens* (Black.) | –150 | 199 | 23 |
| *Pocadicnemis pumila* (Black.) | –67 | 207 | 24 |
| *Oedothorax fuscus* (Black.) | 333 | 206 | 25 |
| *O. retusus* (Westr.) | 226 | 297 | 26 |
| *Silometopus elegans* (O. P.-C.) | 12 | 332 | 27 |
| *Tiso vagans* (Black.) | 231 | 78 | 28 |
| *Monocephalus fuscipes* (Black.) | 244 | 313 | 29 |
| *Gongylidiellum vivum* (O. P.-C.) | –44 | 136 | 30 |
| *Micrargus herbigradus* (Black.) | 157 | 257 | 31 |
| *Savignya frontata* (Black.) | 362 | 125 | 32 |
| *Diplocephalus latifrons* (O. P.-C.) | 158 | 78 | 33 |
| *Milleriana inerrans* (O. P.-C.) | 469 | 164 | 34 |
| *Erigone dentipalpis* (Wider) | 445 | 164 | 35 |
| *E. atra* (Black.) | 396 | 216 | 36 |
| *Meioneta rurestris* (C. L. Koch) | 400 | 164 | 37 |
| *M. saxatilis* (Black.) | 21 | 150 | 38 |
| *Bathyphantes gracilis* (Black.) | 260 | 357 | 39 |
| *B. parvulus* (Westr.) | 51 | 263 | 40 |
| *Kaestneria pullata* (O. P.-C.) | –32 | 204 | 41 |
| *Diplostyla concolor* (Wider) | 103 | 74 | 42 |
| *Lepthyphantes tenuis* (Black.) | 246 | 191 | 43 |
| *L. zimmermanni* Bertkau | –32 | 265 | 44 |
| *L. mengei* Kulcz. | 26 | 71 | 45 |
| *L. tenebricola* (Wider) | –93 | 181 | 46 |
| *L. ericaeus* (Black.) | –23 | 235 | 47 |
| *L. pallidus* (O. P.-C.) | 206 | 60 | 48 |
| *Microlinyphia pusilla* (Sund.) | 224 | 240 | 49 |

Table 3: Individual axis 1 and axis 2 DECORANA species scores for the 49 species trapped on more than 5 of the 54 sites sampled. Code numbers refer to position of each species in Fig. 2.

Firstly, sites in class 5 lacked a litter layer because all of the swards were between 5 and 10 years old. Secondly, these sites had also been subjected to intense disturbance by autumn ploughing when they were reseeded. The spider fauna of the class 5 sites was species poor and dominated by highly mobile and invasive species (with high axis 1 ordination scores) such as *E. atra*, *E. dentipalpis* and *O. fuscus* which are often the first species to colonise new habitats such as arable fields (Thornhill, 1983) and newly reclaimed polders (Meijer, 1977). Class 4 sites, on the other hand, whilst also being dominated by these species, also had many of the smaller species with axis 1 scores around 250 such as *M. fuscipes* (244), *Oedothorax retusus* (Westring) (226) and *T. vagans* (237). It is possible that these species prefer sites with a litter layer that provides a greater abundance of prey, or sites more suitable for web construction. On the other hand, these species may simply be slow at recolonising sites following ploughing.

For the sites in other management classes, with lower axis 1 scores and subjected to less intense management, it is probable that the timing and frequency of vegetation removal were more important in determining the spider communities present. The frequency of removal of vegetation was higher on management class 3 sites than on class 2 sites because the latter were grazed only in autumn whereas the former were cut for hay in late spring and then grazed for the remainder of the season. Clearly, the vegetation on class 2 sites would remain longer for more of the year than on class 3 sites. This is reflected in the species lists for classes 3, 4 and 5, where species such as *P. pumila* and *P. nigriceps* which are known to favour long vegetation (Aart, 1973; Snazell, 1982) were abundant on unmanaged class 1 and class 2 sites but were found on only 2 of the class 3 sites.

The second major component influencing the distribution of species across the range of sites sampled was site wetness. Merrett & Snazell (1983) demonstrated that site wetness is an important factor influencing spider communities in heathland. The site wetness preferences of certain species, notably those of the lycosids and some of the linyphiids, e.g. *Hypomma bituberculatum* (Wider), as predicted from the axis 2 scores of the ordination are in broad agreement with those suggested by previous studies. For other species this was not the case. The axis 2 ordination score for *B. gracilis,* for instance was high, suggesting a preference for wet conditions, yet this species is very common in many habitats such as arable fields (Thornhill, 1983) which are not usually wet. It is likely that the high axis 2 score for this species reflects other aspects than site wetness of the sites sampled. Most of the wet sites sampled in this study were unmanaged and in consequence had rank vegetation. It is possible that the high axis 2 score for this species reflects a non-management mediated vegetation component that is prevalent on wet sites and only appears in the second axis of the ordination. One method of investigating the preferences of this and similar species would be to restrict ordination to limited parts of the data set, in this case management class 5 sites. In this way habitat preferences within more restricted habitat types could be elucidated more easily.

Even given these constraints it is obvious that DECORANA ordination is a potentially useful tool for identifying important environmental factors influencing spider communities. It is obvious that this technique can also be used to a certain extent to identify the habitat preferences of the spider species themselves. What is now needed is a more detailed analysis of the mechanisms by which factors such as vegetation structure influence the distribution of each of these species in the field. Only in this way can we increase our understanding of the components of what Duffey (1978) terms the "ecological strategies" of spiders.

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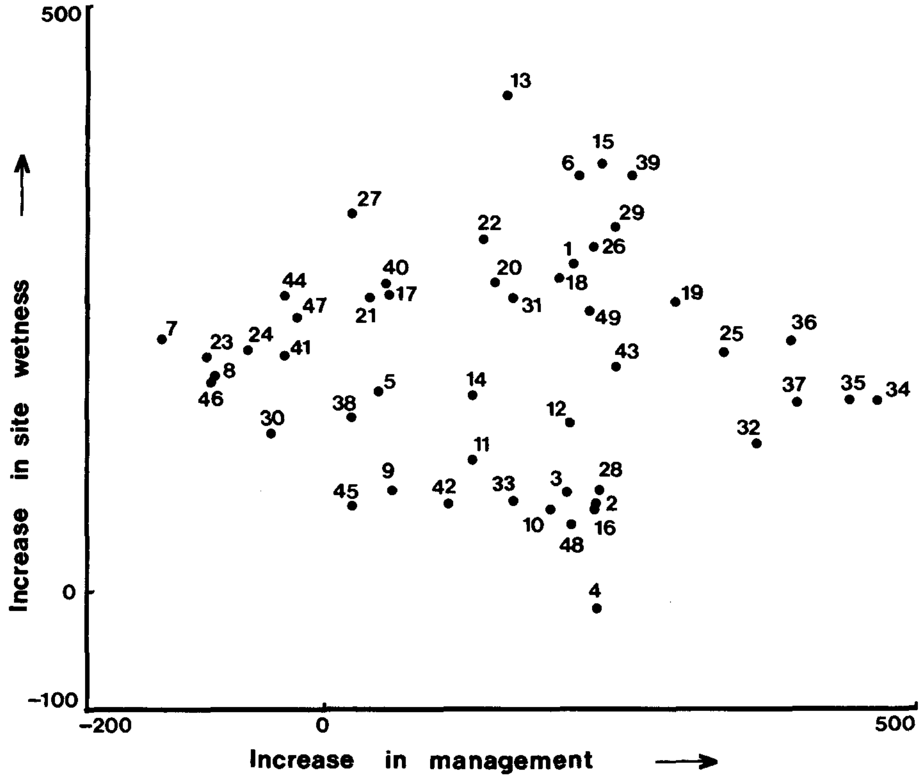

Fig. 2: Axis 1 by axis 2 plots of DECORANA ordination scores for 49 spider species. Numbers refer to species code numbers in Table 3.

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## Nomenclatural Note

Opinion 1426 of the International Commission on Zoological Nomenclature (1987, *Bull.zool.Nom.* **44**(1): 59-60) places the names *Argyrodes* Simon, 1864 and *Robertus* O. Pickard-Cambridge, 1879 on the Official List of Generic Names in Zoology. Also *argyrodes* Walckenaer, 1841 as published in the binomen *Linyphia argyrodes* (specific name of the type species of *Argyrodes* Simon, 1864) and *neglectus* O. Pickard-Cambridge, 1871 as published in the binomen *Neriene neglecta* (valid name at the time of the ruling for the type species of *Robertus* O. Pickard-Cambridge, 1879) are placed on the Official List of Specific Names in Zoology. Opinion 1426 also places the names *Argyrodes* Guenée, 1845 and *Ctenium* Menge, 1871 on the Official Index of Rejected and Invalid Generic Names in Zoology.

Herbert W. Levi