A discriminant analysis and logistic regression approach to the analysis of *Walckenaeria* habitat characteristics in grassland (Araneae: Linyphiidae)

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Summary

Field research in grasslands has shown that several species of *Walckenaeria* (Araneae, Linyphiidae) may coexist on the same site. The occurrence of members of this genus on 81 sites in north-east England was recorded by continuous pitfall trapping through 5 months in one of three years. Environmental data were collected for each site and used as habitat characteristics to identify the preferred habitats of the *Walckenaeria* species found, using descriptive discriminant analysis and logistic regression. The species appeared to have different vegetation density, altitude and soil moisture preferences. Species of a similar size were more widely separated in habitat characteristic space than those of dissimilar size. The results are discussed in the light of the known habitat preferences and ecology of these species.

Introduction

Attempting to understand why individual species of animal are found in some habitats but not in others has been one of the major fascinations of biologists since Darwin. With large animals such as vertebrates, habitat requirements are often easily characterised. As the size of animal considered becomes smaller, however, it often becomes more difficult both to study the animals themselves and to define habitat characteristics of importance. This is particularly true of spiders, where there has been considerably more research on the niche characteristics of the larger species of Lycosidae (Kuenzler, 1958; Vogel, 1972; Van der Aart, 1973) than on smaller species in other families, such as the Linyphiidae. In temperate grassland habitats, members of this family may form the dominant guild in the spider fauna; species lists in excess of 100 are not uncommon even in intensively disturbed pastures (Edwards *et al.*, 1975). It is also not uncommon to find grassland sites on which several species of the same genus coexist. There has been some research on identifying habitat characteristics of linyphiid species that build large and characteristic webs (Toft, 1987) and those of agricultural significance (Thornhill, 1983), but recorded habitat requirements of most species are usually little more than a summary of all of the possible habitats in which they may be found. Consequently, the mechanisms by which even the most closely related species coexist remain unknown.

Where experimentation is difficult, recourse has to be made to more indirect methods of study. Previous authors have collected species in habitats with known environmental or ecological gradients and identified the habitat preferences of individual species by reference to their occurrence along the gradient (e.g. sand dunes, Duffey, 1968). Other authors have used a variety of sophisticated multivariate techniques to identify important habitat characteristics and species preferences from such data sets as well as from others without clearly defined environmental gradients (Principal Components Analysis, Van der Aart, 1973, Snazell, 1982; Cluster Analysis, Maelfait & Seghers, 1986; Detrended Correspondence Analysis, Rushton *et al.*, 1987). In all of these studies it was concluded that vegetation structure and the moisture status of the sites studied were major factors influencing which species were present. None of these techniques could be used to define the habitat requirements of individual species except in a very general way. Techniques that are species- rather than community-centred are more likely to allow greater resolution of the habitat requirements of individual species. Two very different techniques of this type, Multiple Discriminant Analysis and logistic regression, have been used successfully in the study of habitat and niche characteristics in other organisms.

Discriminant analysis, in the widest sense, describes any activity connected with the task of classifying unknown objects into groups (James, 1985). According to Williams (1983) data for discriminant analysis typically consist of observations for which there is a grouping index and an associated vector of measurements. Discriminant analysis can be used predictively, where the objective is to predict the group to which an observation belongs, or alternatively descriptively, where the aim is to exhibit optimal separation of groups. Most ecological applications have been descriptive (Williams, 1983). In this paper measurements of site characteristics constitute the vector of measurements, the list of sites on which a species is found forms the group, and the aim is to find which combination of site variables describes the optimum discrimination between species. It is assumed that the original variables selected for inclusion in the analyses are of ecological significance to the species considered. Discriminant analysis has been used most extensively in the analysis of habitat characteristics and niche structure of vertebrates (e.g. Cody, 1979; Rice *et al.*, 1983). Although Rushton *et al.* (1989) used it successfully to analyse the effects of pasture improvement and management procedures on the structure of upland spider communities, the use of these techniques in spider ecology has not been widespread.

Logistic regression is a technique that has been used by plant ecologists (e.g. Austin *et al.*, 1984; Jongman *et al.*, 1987) to model species occurrence as a response to quantitative environmental variables. It is a Generalised Linear Modelling technique (McCullagh & Nelder, 1983) that is used in this context to fit gaussian and asymptotic response curves using presence-absence as the dependent variable and the environmental variable as the predictor. One of the main objectives is to predict species optima and tolerances along individual environmental gradients. Research by Ter Braak & Looman (1986) has demonstrated that this technique has a more general application than Weighted Averaging (which is also the basis of many ordination techniques) for determining species optima and tolerances, in part because it takes account of species'

absences as well as presences.

The aim of this study was to investigate the use of multiple discriminant analysis and logistic regression in the analysis of niche separation in coexisting species of *Walckenaeria* in grasslands in north-east England, with a view to understanding how these spiders coexist.

Materials and methods

Sample sites and sampling regime

Spider communities were sampled on 81 sites distributed throughout the counties of Northumberland, Durham, and Tyne and Wear, using pitfall trapping as outlined in Rushton *et al.* (1987). Sites were selected to cover a range of substrate and vegetation types encompassing as wide a range as possible of the different grasslands present in these three counties. Nine pitfall traps, consisting of polypropylene pots of 8.5 cm diameter by 10 cm depth and half filled with a 70% ethanol-5% glycerol solution were used on each site. Sites were sampled at monthly intervals from the end of April to the beginning of October in each year. At each sample date the contents of all 9 traps for each site were pooled and stored in sealed polypropylene containers before analysis. Trap contents were sorted in the laboratory where adult spiders were removed and stored in 70% ethanol before identification. Initially, fifty-four sites were sampled in 1985; eleven sites were sampled over the same sampling period during 1986 and the remaining sixteen in 1987, following the same procedure but using ethylene glycol as a trap preservative. Nomenclature follows Merrett, Locket & Millidge (1985).

Vegetation analysis

Two measures of vegetation were taken at 62 of the sites. The mean peak biomass of vegetation above 10 cm and mean peak vegetation height were estimated from 0.1 m quadrats during the summer of the year of sampling, following the methods outlined in Eyre *et al.* (1986). An index of vegetation density was then determined by dividing the mean plant biomass by the mean peak height for each site.

Site wetness and altitude

Two measures of site wetness were obtained for each site. Firstly, volumetric moisture content of the soil on each sample site was determined from four, 29 cm^3 cores taken from 5 cm depth when the soil was at field capacity in January of the year of sampling, following the methods outlined in Rushton *et al.* (1987). Secondly, estimates of the mean annual rainfall for each site were obtained from the records kept at the Meteorological Office in Newcastle upon Tyne. Where sample sites did not correspond to a meteorological station, estimates from the nearest available recording station were used, provided that the distance between the sample site and recording station did not exceed 10 km. An index of 'annual wetness' was determined for each site by combining the soil moisture content and rainfall data in a principal components analysis. Site scores for the first axis of the PCA (i.e. that which

accounted for the major axis of variation in the rainfall-soil moisture content data matrix) were then calculated and used as wetness scores. Site altitude was recorded to the nearest 10 m after consulting 1:50,000 Ordnance Survey maps.

Species characteristics

Differences in size and general morphology between species were investigated by direct measurement of physical features under the microscope using an eyepiece graticule. Cheliceral and carapace lengths were determined for between 10 and 15 adult females of each species. Males were not considered because these were generally less abundant in the catches. Where insufficient animals were available from the sites sampled (animals were not retained from the 1985 sampling season), specimens from similar habitats, but different regions (notably south-west Scotland) were used. Preliminary analysis indicated that there were no differences in respective mean sizes of any of the measured characteristics between sites sampled. The individual measures of each characteristic were then used to illustrate differences in the size of each species.

Discriminant analysis

The soil, vegetation and altitude characteristics for the sites on which each species was found were used as species 'descriptive variables' in linear stepwise multiple discriminant analyses (James, 1985) in an attempt to assess the extent to which the habitat preferences of each species could be distinguished in terms of the measured environmental variables on the sites on which they were found. The discriminating power of each environmental variable was assessed using the conditional F-ratio, which tests the differences between the species, with respect to each variable, conditional on those variables already considered. It is the F-ratio which is used in an analysis of covariance testing group differences using all variables selected as covariates (James, 1985).

Logistic regression

The presence and absence data for the individual species were used as response and the measured site characteristics as predictive variables in logit regression. Sigmoid and gaussian species response curves were fitted to the environmental data following the method outlined in Jongman *et al.* (1987) using the GLIM package (Baker & Nelder, 1978). The goodness-of-fit of

Species	Carapace	Chelicera	*n*
W. acuminata	75.4 ± 1.1	29.4 ± 0.5	12
W. nudipalpis	62.9 ± 0.9	25.4 ± 0.5	19
W. unicornis	53.8 ± 2.8	22.4 ± 1.7	5
W. cuspidata	52.1 ± 0.6	20.4 ± 0.4	10
W. vigilax	51.5 ± 0.3	19.1 ± 0.4	12
W. antica	51.6 ± 0.9	19.4 ± 0.6	10

Table 1: Measurements of carapace and cheliceral length in micrometer units and standard error for six coexisting species of *Walckenaeria*. (1 micrometer unit = 0.02 mm.)
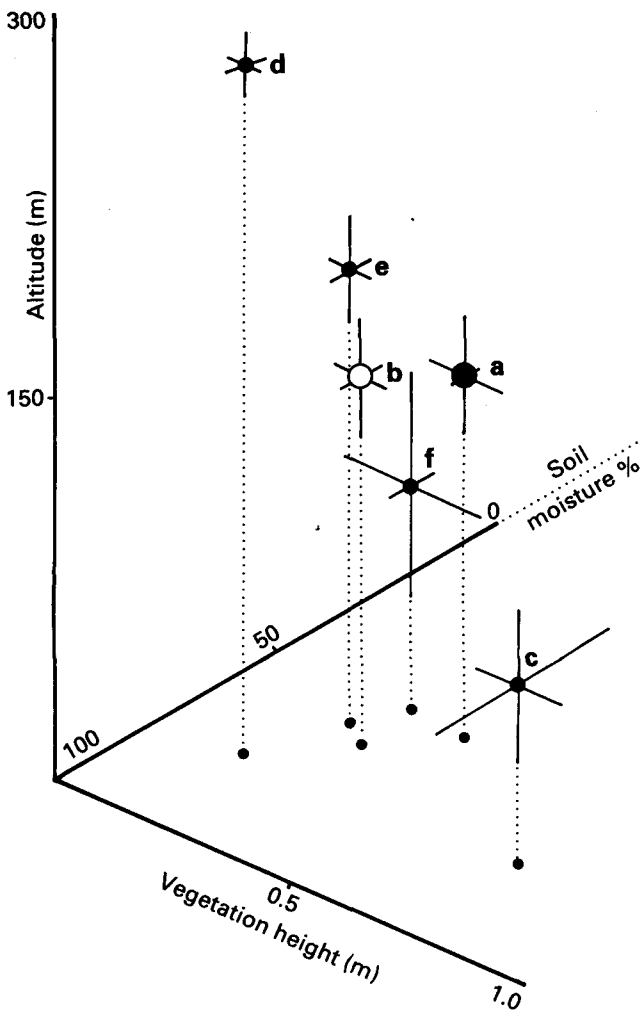
Fig. 1: Mean values and associated standard error for three characteristics of sites on which species of *Walckenaeria* were found. **a** = *W. acuminata;* **b** = *W. nudipalpis;* **c** = *W. unicornis;* **d** = *W. antica;* **e** = *W. vigilax;* **f** = *W. cuspidata.* Form of symbol refers to size class of species; large solid dot (●) largest, open circle (○) middle size, small solid dot (•) smallest size class (see text).

each model to the data was then assessed by determining the decrease in deviance arising from fitting species response curves to the environmental data, relative to that of the null model with no predicted relationship (the deviance test, McCullagh & Nelder, 1983). The deviance of the null model is equivalent to apportioning all of the variation to the random (error) component and is analogous to the total sum of squares in normal linear regression. The deviance of each fitted model is analogous to the residual sum of squares in linear regression. The major difference between the deviances in normal linear regression and those considered here is that in the former the error distribution is considered to be normal (with the variance independent of the mean) whereas in logit regression it is considered to be binomial. Consequently, the extent to which both models were a good description of the species incidence response to each environmental variable was assessed by testing whether the decrease in deviance following model fitting was significant, in a manner similar to the analysis of variance undertaken in stepwise multiple regression. If the decrease in

deviance was greater than the critical value of χ^2 at 95% levels of significance for n degrees of freedom (where n is the number of parameters included in the extended model — in this case, one from the null model to the logistic and one from the logistic to the gaussian) then the inclusion of that parameter was considered significant (McCullagh & Nelder, 1983; Ter Braak & Looman (1986). In practice this involved calculating the decrease in deviance from the null model to the logistic model to assess the goodness of fit of that model and then the subsequent decrease in deviance when this was extended by one parameter to the gaussian model. An alternative test of significance is to test whether the highest order individual regression coefficient in each model is significantly different from zero using a one-tailed t-test as detailed in Jongman *et al.* (1987).

Results

Species characteristics

Seven species of *Walckenaeria* were found on the sample sites. Of these, six, *W. acuminata* Blackwall (23 sites), *W. nudipalpis* (Westring) (19 sites), *W. vigilax* (Blackwall) (20 sites), *W. antica* (Wider) (10 sites), *W. unicornis* O. P.-Cambridge (8 sites) and *W. cuspidata* Blackwall (6 sites) were found sufficiently frequently to warrant further analysis. [The seventh species, *W. atrotibialis* (O. P.-Cambridge), was found on only two sites.] Mean carapace and cheliceral lengths of these species are given in Table 1. The most obvious feature is that the six species fell into three size groups and that the size difference between the three groups was relatively constant. The largest group comprised the smaller species *W. antica, W. cuspidata, W. unicornis* and *W. vigilax* which were very similar in size. The second group comprised *W. nudipalpis,* which was larger than all of the species in the small size group. Mean carapace and cheliceral length of this species was between 1.17 and 1.22 (mean for all species 1.20) and between 1.13 and 1.33 (mean for all species 1.24) times larger, respectively, than those of species in the small size group. The remaining group comprised *W. acuminata;* mean carapace length of this species was 1.20 and cheliceral length 1.16 times larger than that of *W. nudipalpis.* The results suggest that there was an approximately constant increase in size in these three groups of species.

Site habitat characteristics

The mean values of altitude, vegetation height and soil moisture content for the sites on which these species were found are shown in Fig. 1. *W. antica* was

Species	acuminata	nudipalpis	unicornis	antica	vigilax
W. nudipalpis	11.5				
W. unicornis	42.3	52.3			
W. antica	53.2	46.4	92.6		
W. vigilax	20.7	13.9	62.9	36.3	
W. cuspidata	21.3	22.8	45.3	67.6	31.8

Table 2: Separation of individual *Walckenaeria* species in three dimensions of habitat space.

found on sites at higher altitudes, whereas *W. unicornis* was found on lower sites. The remaining species formed a group at intermediate mean site altitudes. Similarly, *W. unicornis* was generally found on sites with longer vegetation whereas the remaining species were found on sites with shorter vegetation. All species appeared to favour moist sites in preference to dry, with mean soil moisture contents in excess of 50%.

The axes of this plot were scaled to the same units (0-100) and the means for each habitat characteristic for each species used to determine the species separation in the three dimensions of the habitat-characteristic space. The separation in the three dimensions was calculated using the 2nd Minkowski metric and the data are presented in Table 2. The most obvious feature of these data is the wide separation in space of species of similar size, relative to that between dissimilar-sized species. The mean distance between similar-sized species was significantly greater ($t = 2.403$, $p < 0.05$) than that for species of dissimilar size, suggesting that similar-sized species were found in different habitats whereas dissimilar species coexisted in the same habitat.

Multiple discriminant analysis

The results of the multiple discriminant analysis indicated that altitude was the most significant discriminating variable between the groups of sites on which each species was found when all species were considered ($F = 4.488$, $p < 0.01$). Soil moisture content, vegetation height and vegetation biomass were also significant ($F = 3.286$, $p < 0.05$; $F = 3.745$, $p < 0.05$; and

$F = 3.139$, $p < 0.05$ respectively) but these were not significant when included as the second variable in subsequent analyses. When the two larger species (*W. acuminata* and *W. nudipalpis*) were removed from the analysis the discriminating power of the altitude variable was increased ($F = 8.985$, $p < 0.001$), indicating that there was considerably more separation in the types of habitat occupied by the smaller species. None of the other variables added significantly to the discriminating power of this first variable in subsequent steps in the analysis although volumetric soil moisture content and vegetation height were also significant discriminators in their own right ($F = 4.618$, $p < 0.01$ and $F = 5.510$, $p < 0.01$, respectively).

Logistic regression

Of the three water and three vegetation variables used in each analysis, vegetation density, volumetric soil moisture content and altitude gave rise to more significant regressions than the remaining variables; regression coefficients for the best fit of the gaussian and sigmoidal logit curves for the individual species incidence data against these three variables are shown in Tables 3-5, respectively. Also shown are the deviances of the null model for comparison with those obtained when the model was extended sequentially to the logistic and then to the gaussian models.

Curves showing the predicted probability of occurrence of each species plotted against the three environmental variables for each of the significant regressions are shown in Figs. 2a, b and 3 for vegetation density, soil moisture content and altitude respectively. The calculated t values and significance levels, for both of the regression coefficients and the deviances, are given in parentheses in each table. *W. acuminata* and *W. unicornis* had significant unimodal response curves to the vegetation density variable, with broadly similar optima (x^2 from the null to the gaussian model of 10.73 and 11.59 respectively), whereas *W. nudipalpis* and *W. antica* had significant sigmoidal response curves, with the probability of occurrence increasing with increasing vegetation density ($x^2 = 9.62$ and 8.8 respectively). Similarly, *W. acuminata* showed a significant unimodal response to soil moisture content, with an optimum of 60% ($x^2 = 7.1$), and *W. antica* and *W. nudipalpis* had significant sigmoidal response curves, the probability of encountering both increasing with increasing soil moisture content ($x^2 = 19.9$ and 9.2 respectively). For *W. vigilax* the regression coefficient for the asymptotic curve was also significant, whereas the deviance was not ($x^2 = 3.1$). *W. antica* and *W. vigilax* showed sigmoidal responses to altitude, the probability of occurrence increasing with altitude ($x^2 = 19.1$ and 7.4 respectively).

Discussion

Previous authors have criticised the use of pitfall traps in invertebrate ecology (Southwood, 1978), as catches are influenced by factors other than population density, such as activity. Whilst pitfall traps may not give true estimates of population density, they do how-

Model:	i) Gaussian			ii) Logistic		iii) Null
Species	B0	B1	B2	B0	B1	
W. acuminata	−1.521	8.966	−8.833	−1.077	2.776	
Standard error	0.452	3.127	4.070	0.369	1.245	
Significance	(*t*=2.170, *p*<0.02)			(*t*=2.229, *p*<0.02)		
Deviance	71.4			76.2		81.8
		−5.1			−5.6	
W. nudipalpis	−1.432	0.248	6.426	−1.633	3.858	
Standard error	0.461	4.297	7.804	0.425	1.375	
Significance	(*t*=0.823, NS)			(*t*=2.806, *p*<0.005)		
Deviance	65.9			66.8		76.4
		−0.9			−9.6	
W. unicornis	−4.144	16.080	−17.770	−2.594	2.790	
Standard error	1.213	7.223	10.470	0.581	1.438	
Significance	(*t*=1.697, *p*<0.05)			(*t*=1.940, *p*<0.05)		
Deviance	37.1			43.9		47.7
		−6.8			−3.7	
W. cuspidata	−2.543	2.096	−1.377	−2.467	1.094	
Standard error	0.672	4.420	5.511	0.583	1.630	
Significance	(*t*=0.24, NS)			(*t*=0.671, NS)		
Deviance	38.9			39.0		39.4
		−0.1			−0.4	
W. antica	−2.370	0.152	5.698	−2.707	4.142	
Standard error	0.636	4.368	6.277	0.596	1.516	
Significance	(*t*=0.907, NS)			(*t*=2.732, *p*<0.005)		
Deviance	44.9			45.9		54.8
		−1.0			−8.9	
W. vigilax	−1.057	4.073	−5.370	−0.837	0.496	
Standard error	0.406	3.156	4.680	0.353	1.148	
Significance	(*t*=1.147, NS)			(*t*=0.432, NS)		
Deviance	76.2			77.8		77.9
		−1.6			−0.1	

Table 3: Coefficients for GLM regression of incidence of different species of *Walckenaeria* against vegetation density on sample sites. Residual deviance of each model and decrease in deviance following incorporation of further parameters into model also given.

1.0

A

Probability

0.5

b
d

a

c

0.5   1.0
Vegetation density (g cm⁻¹)

1.0

B

Probability

d
b
e

0.5

a

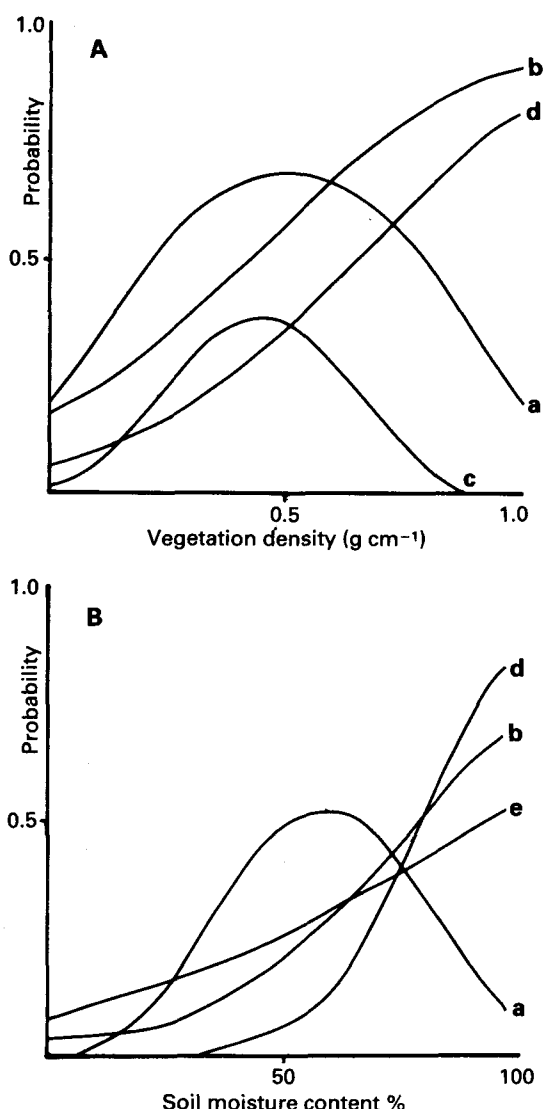50   100
Soil moisture content %

Fig. 2: Predicted response curves of individual species of *Walckenaeria* to different observed habitat characteristics. Only those curves considered significant by the deviance test and/or with significant regression coefficients are shown (see text for explanation). Letters refer to species as in Fig. 1. **A** = Vegetation density; **B** = Volumetric soil moisture content.

ever give a good indication of what spider species are present, often comparing well with the results obtained from other sampling techniques such as D-vac suction sampling (Merrett, 1983).

Whilst the inadequacies of the sampling technique may not, therefore, have had much influence on the results, the conclusions that can be drawn from them appear to be dependent on the techniques used to analyse the data. The results of the discriminant analysis suggested that although vegetation and moisture were significant discriminators, altitude was the most important habitat characteristic distinguishing species in this genus. The regression analyses, on the other hand, suggested that vegetation density and soil moisture were important and that only two species showed significant responses to altitude. This difference reflects in part the mechanics of each technique.

There are several problems associated with applying

discriminant analysis to ecological data. One major limitation is that the technique requires a set of mathematical assumptions that are rarely met by the data (see Williams, 1983). The extent to which the data set met these assumptions was not evaluated, but there are several other more likely causes of this failure. Firstly, whilst vegetation type and soil moisture status have been shown to be important habitat characteristics for these species (e.g. Snazell, 1982) it is possible that the measures of both factors used in this study were too crude to allow resolution between individual species preferences for the characteristics they were supposed to represent. The fact that the significance of both the vegetation and altitude discriminating variables increased when the analysis was confined to species of the same size class indicates, however, that the crudity of the habitat measurements was not the only factor influencing the results of the discriminant analyses. One possible explanation for this increase (and hence the apparent failure of the discriminant analysis to distinguish between the habitat preferences of all species) is that the large and small species of *Walckenaeria* had overlapping habitat preferences. This will be considered more fully below.

An important prior consideration in the use of Generalised Linear Modelling techniques in ecology is the model adopted to describe the species response to the environmental variable being considered. There are numerous examples in the ecological literature which indicate that unimodal response curves are more appropriate ecological response models than are simple linear

Model:	i) Gaussian			ii) Logistic		iii) Null
Species	B0	B1	B2	B0	B1	
W. acuminata	−5.607	0.1946	−0.00165	−1.101	0.01306	
Standard error	2.592	0.9590	0.00085	0.687	0.01245	
Significance	(*t*=1.95,*p*<0.05)			(*t*=1.04, NS)		
Deviance	101.6			107.2		108.7
		−5.6			−1.5	
W. nudipalpis	−2.047	−0.1600	−0.00055	−3.607	0.04550	
Standard error	1.910	0.0712	0.00064	0.969	0.01614	
Significance	(*t*=0.85, NS)			(*t*=2.83,*p*<0.005)		
Deviance	80.6			81.3		90.5
		−0.7			−9.2	
W. unicornis	0.647	−0.0859	0.00074	−1.349	−0.01482	
Standard error	1.405	0.5889	0.00058	0.970	0.01919	
Significance	(*t*=1.28, NS)			(*t*=0.77, NS)		
Deviance	54.5			55.9		56.5
		−1.4			−0.6	
W. cuspidata	−9.976	0.3086	−0.00289	−2.320	−0.00074	
Standard error	6.854	0.2592	0.00236	1.153	0.02124	
Significance	(*t*=1.22, NS)			(*t*=0.03, NS)		
Deviance	44.8			47.7		47.7
		−2.9			−0.0	
W. antica	−3.659	−0.0374	0.00108	−7.416	0.09402	
Standard error	3.657	0.1287	0.00111	1.812	0.02672	
Significance	(*t*=0.97, NS)			(*t*=3.52,*p*<0.005)		
Deviance	47.3			48.0		67.9
		−0.7			−19.9	
W. vigilax	−1.468	−0.0094	0.00031	−2.286	0.02448	
Standard error	1.565	0.0591	0.00054	0.814	0.01413	
Significance	(*t*=0.58, NS)			(*t*=1.73,*p*<0.05)		
Deviance	91.3			91.6		94.7
		−0.3			−3.1	

Table 4: Coefficients for GLM regression of incidence of individual species of *Walckenaeria* against volumetric soil moisture content of sample sites. Residual deviances of each model and decrease in deviance following incorporation of additional parameters into model also given.

1.0

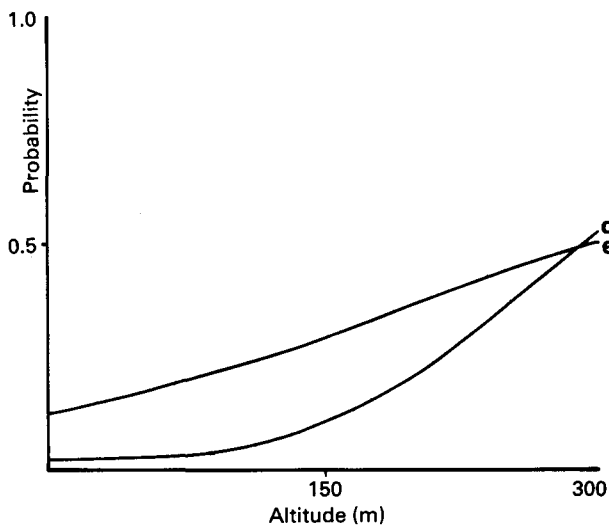Probability

0.5

150   300

Altitude (m)

Fig. 3: Predicted response curves of individual species of *Walckenaeria* to altitude. Only those curves considered significant by the deviance test and/or with significant regression coefficients are shown (see text for explanation). Letters refer to species as in Fig. 1.

models. The sigmoidal response curve used here, is a special case since it is essentially one side of a normal response curve and there may be sound ecological reasons why the remaining half of the curve does not exist. In this study for intance, it would have been impossible to have volumetric soil moisture contents in excess of $1g\ cm^{-3}$, so whilst the probabilities of occurrence of some species may have increased to 97% soil moisture content, they could not possibly increase beyond this point. The adoption of unimodal rather than bi- or trimodal response models, however, is more open to debate, since there are known examples of these responses. Hill (1977) suggested, however, that a good ecological variable minimises the occurrence of bimodal species distributions. It is likely that the variables considered in this study were "good" since they have been demonstrated to be the most important determinants of spider community structure on these sites (Rushton *et al.*, 1987). Consequently, I suggest that the unimodal and sigmoidal response curves used here serve as reasonable models to explain the response of individual spider species to these environmental gradients.

Given this what do the results of this study tell us about the ecology of the *Walckenaeria* species and how do they equate with those of previous studies? Firstly, it is obvious that some of the species had overlapping habitat preferences, e.g. *W. unicornis* and *W. acuminata* had very similar response curves to vegetation density, as did *W. nudipalpis* and *W. antica*. Neither of the species in each pair were of similar size. Snazell (1982) showed that *W. acuminata* and *W. antica* had similar habitat preferences on heathland in southern England and suggested that they avoided interspecific competition because they differed in size. Size difference has been cited as a means by which spiders avoid competition in guilds (Uetz, 1977) and in taxonomically closely related species (Enders, 1974, 1975, 1976), the mechanism allowing coexistence being differ-

ences in the prey size range utilised by each species. Food-related morphological adaptation has been cited as a means by which closely related species avoid competition in many groups of animals (see Hutchinson, 1959). More specifically, a constant minimum difference in the ratio of linear measures of body size of 1.3, as one moves from one species to the next, is believed to ensure that the prey size ranges of adjacent species do not overlap greatly. It is impossible to determine the extent to which competition for prey has influenced body size differences between these *Walckenaeria* species, but Wilson (1975) concluded that constant minimum size differences of this type would not generally apply to arthropod predators, effectively because a size ratio of 1.3 would not guarantee that prey size ranges did not overlap. Whilst prey size range may not be important it is possible that morphological adaptations may have occurred in response to some other limiting resource, such as suitable sites for building webs. Rypstra (1983) demonstrated that population densities of other linyphiid spiders were dependent on the availability of suitable sites for web construction.

Although size differences may be a means by which some species of *Walckenaeria* avoid competing, there is no evidence to suggest that competition between any of these species actually occurs, and as with much previous research in spider ecology the importance of competition is open to debate (Wise, 1984). Nonetheless, the results of this study do indicate that the habitat preferences of the similar-sized species were

Model:	i) Gaussian			ii) Logistic		iii) Null
Species	B0	B1	B2	B0	B1	
W. acuminata	−0.581	0.0004	0.000003	−0.618	0.0015	
Standard error	0.440	0.0075	0.000025	0.364	0.0022	
Significance	(*t*=0.12, NS)			(*t*=0.68, NS)		
Deviance	108.2			108.2		108.7
		0.0			−0.5	
W. nudipalpis	−1.206	−0.0013	0.000005	−1.307	0.0015	
Standard error	0.501	0.0085	0.000028	0.420	0.0024	
Significance	(*t*=0.17, NS)			(*t*=0.62, NS)		
Deviance	90.7			90.1		90.5
		+0.6			−0.4	
W. unicornis	−1.658	0.0015	0.000031	−1.437	0.0058	
Standard error	0.593	0.0126	0.000051	0.492	0.0041	
Significance	(*t*=0.60, NS)			(*t*=1.41, NS)		
Deviance	53.7			54.1		56.5
		−0.4			−2.4	
W. cuspidata	−1.916	0.0054	0.000007	−1.968	0.0035	
Standard error	•0.652	0.0131	0.000046	0.567	0.0041	
Significance	(*t*=0.15, NS)			(*t*=0.85, NS)		
Deviance	46.8			46.9		47.6
		−0.1			−0.7	
W. antica	−4.555	0.0123	0.00001	−4.777	0.0168	
Standard error	1.635	0.0184	0.00005	1.135	0.0048	
Significance	(*t*=0.20, NS)			(*t*=3.5, *p*<0.005)		
Deviance	47.8			48.8		67.9
		−1.0			−19.1	
W. vigilax	−2.246	0.0130	0.00002	−1.944	−0.00678	
Standard error	0.665	0.0959	0.00002	0.479	0.00259	
Significance	(*t*=1.00, NS)			(*t*=2.62, *p*<0.01)		
Deviance	86.8			87.3		94.7
		−0.5			−7.4	

Table 5: Coefficients for GLM regression of incidence of individual *Walckenaeria* species against altitude of sample sites. Residual deviances and decrease in deviance following incorporation of further parameters into model also given.

significantly more widely separated in the soil moisture-vegetation-altitude habitat space than were the dissimilar-sized species. It is possible that the smaller *Walckenaeria* species avoid competition by utilising different habitats. The differences in the habitat preferences of most of these species were marked, except for *W. antica* and *W. vigilax* which appeared to prefer moist, high altitude sites. There were differences in the species' responses to these two variables, however, since *W. vigilax* was more likely to be found at lower altitudes and on drier sites than *W. antica*. Furthermore, there was a strong positive relationship between vegetation density and probability of being caught for *W. antica* whereas there was no apparent relationship with vegetation for *W. vigilax*, suggesting that these species did have different habitat preferences.

The extent to which the predicted vegetation and moisture preferences of the individual *Walckenaeria* species were in agreement with those suggested by previous research varied according to the species. They were in general agreement for *W. nudipalpis* and *W. vigilax* since these species are generally associated with very wet habitats (Almquist, 1984; Maelfait & Seghers, 1986; Roberts, 1987), and also for *W. unicornis* which is usually associated with well-vegetated sites (Snazell, 1982; Almquist, 1984). Merrett & Snazell (1983) suggested that this latter species favoured the drier sites in their study, and Duffey (1968) caught it on yellow dune, a notably dry environment. Whilst the results of this study suggested that this species favoured well (but not densely) vegetated sites, there was no evidence of moisture preference for wet or dry sites. The fact that this species is to some extent semi-arboreal (Merrett & Snazell, 1983) would suggest that soil moisture content need not necessarily be an important habitat characteristic for this species, and therefore one might not expect there to be any observed relationship with this variable. The most obvious difference between the results of this study and those of previous authors was the apparent moisture preferences of *W. antica*. Previous authors have concluded that this species prefers dry rather than wet, well-vegetated sites (Palmgren, 1976; Roberts, 1987) and that site moisture status was the major habitat characteristic distinguishing it from *W. alticeps* (Denis), a species from which *W. antica* has only recently been separated. *W. alticeps* was not taken on any of the sites sampled in this study and it has not been taken subsequently on 15 similar wet peat upland sites in S.W. Scotland. It is possible that *W. antica*, being more eurytopic than *W. alticeps* (Palmgren, 1976), is able to utilise habitats more usually associated with the latter species if it is absent. Whilst this explanation may seem plausible, the extent to which this and the other hypotheses suggested in this discussion may be true, cannot be established from the results of survey work of the type described here. Use of the analytical techniques described may suggest hypotheses that should be tested, but these can only be investigated by experimentation designed to test whether species compete for resources or show marked habitat preferences, like that undertaken by Rypstra (1983) and Toft

(1987). Whilst this work is difficult it is undoubtedly the best approach to understanding the ecology of this interesting and attractive genus of spiders.

Acknowledgements

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Nomenclatural Notes

The following application has been received by the International Commission on Zoological Nomenclature and was published in *Bull.zool.Nom.* **47**(3) on 28 September 1990. Comments or advice are invited for publication in *Bull.zool.Nom.* and should be sent to the Executive Secretary, ICZN, c/o The Natural History Museum, Cromwell Road, London SW7 5BD.

Case 2734 **Thalassochernes Beier, 1940 (Arachnida, Pseudoscorpionida): proposed designation of Chelifer taierensis With, 1907 as the type species.** By Mark S. Harvey.

> *Abstract.* The purpose of this application is the designation of the nominal species *Chelifer taierensis* With, 1907 as the type species of the pseudoscorpion genus

Thalassochernes Beier, 1940. In his definition of *Thalassochernes*, Beier had misidentified the species he was studying as *Chelifer pallipes* White, 1849.

The following Opinions were published by the International Commission on Zoological Nomenclature in *Bull.zool.Nom.* **47**(3) on 28 September 1990.

Opinion 1611 *Heliophanus kochii* Simon, 1868 (Arachnida, Araneae): specific name conserved.

Opinion 1612 *Attus penicillatus* Simon, 1875 (currently *Sitticus penicillatus;* Arachnida, Araneae): specific name conserved.

Editor