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The zonation and ecology of a sand-dune spider community

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Summary

The plant and spider communities of Raven Meols sand dunes, Merseyside, were investigated using quadrats, pitfall traps and sweep-nets. Four major coastal plant zones were identified in the study: embryo dunes, pure *Ammophila*, mixed *Ammophila,* and dune grassland. Pin-frame analysis revealed that the number of plant species increased significantly with distance from the sea. Vegetation height, distance between hit and percentage bare ground, although significantly different, did not display the expected zonational sequence. Sweep-net samples suggested that the upper stratum of vegetation is a poorly used niche among spiders (0.03 spiders m^{-2}). Pitfall catch data recorded 1078 individuals from 59 species. A DECORANA biplot of the pitfall trap data identified three main clusters: frontal (embryo and pure *Ammophila* dunes), mixed *Ammophila*, and dune grassland. Axis 1 of the DECORANA was positively correlated with ranked distance from the strandline, whilst axis 2 was correlated with the structural and diversity variables of the vegetation. The spider communities identified were found to contain wide-ranging species as well as specialists of frontal dune sites. The ecology of some of these is discussed with particular reference to *Oedothorax*, *Erigone*, *Bathyphantes* and *Lepthyphantes* species, and *Zelotes latreillei*.

Introduction

Despite being a harsh environment, sand dunes are rich in invertebrates, with about 30% (188 species) of the British spider fauna represented (Duffey, 1968), and 53 species being strongly associated with coasts (Ratcliffe, 1977). Arachnologists have examined spider communities in relation to the seral succession of plant communities on sand dunes (e.g. Lowrie, 1948; Barnes, 1953; Perttula, 1984). Several factors influence the spider communities found, including plant diversity, cover, life form and distribution (Duffey, 1968; Uetz, 1991), as well as temperature, humidity and wind velocity (Almquist, 1973a,b).

On the south Lancashire sand dunes, Mackie (1967) and Felton (1993) found that, although the majority of spiders collected are common throughout Britain, two notably rare coastal specialists occur. These are *Attulus saltator* (Simon) (Salticidae) and *Argenna patula* (Simon) (Dictynidae) which inhabit open sandy places and the strandline (Felton, 1993). The aim of this paper is to explore the relationships between the structure and diversity of the four major plant zones and the spider communities which are found in each of those areas.

Study site

Raven Meols Local Nature Reserve (LNR), Merseyside (Grid ref. SD 283055) is part of the Sefton coast sand-dune system in north-west England. Typically, *Ammophila arenaria* (Linnaeus) dominates the mobile and semi-fixed dunes, reducing in abundance as sand deposition decreases towards the stable dune grassland further from the sea. Previous disturbance has created a mosaic of vegetation communities, some of which have been impoverished by plantations of pine and asparagus (Edmondson

& Gateley, 1989) and more recently by the effects of recreation (Haughton, 1992).

Methods

Five sites of 16 m^2 were chosen in each of the four major coastal zones: embryo dune (E), pure *Ammophila* (A), mixed *Ammophila* (M), and dune grassland (G). At each of the 20 sites, a random quadrat (0.5 m^2) and a 100 pin pin-frame (each pin marked at 5 mm intervals) were placed above the vegetation. Pins were slowly worked through to the ground recording the number of hits, vegetation height, number of plant species present, and the distance between each hit, to give an indication of structure (i.e. thatch within the stand). When either a thick moss layer at ground level or bare sand was touched, recording ceased and the substrate was noted. Eight plastic pitfall traps (80 × 60 mm) were placed 2 m apart in a 4 × 2 grid formation at each of the 20 sites and were filled with an aqueous solution of 10% ethylene glycol and 5% formalin. The vegetation directly around the traps was cleared to allow free access to them. The traps were emptied fortnightly for 6 weeks (19 July–1 September 1993). Comparisons were not made of abundance between species nor between males and females of the same species, in recognition of the limitations of pitfall trapping (Uetz & Unzicker, 1976). Instead, differences in the catch of surface-active spiders were examined. Sweep-netting of the vegetation in each plot was carried out three times, once during each pitfall trap collection period. The vegetation was completely swept once for each of the 16 m^2 areas, and the catch was immediately pootered into an aqueous solution of Steadman's B solution. Detrended Correspondence Analysis (DECORANA) is an indirect gradient ordination technique (Hill, 1979) used here to explore the differences and similarities between sites in terms of their spider communities. Non-specific rank means tests were used to determine whether the vegetation structure differed significantly between sites. Spearman's rank correlation coefficients were used to explore the relationship between the zonation of the spider community (measured by the axis 1 and 2 scores from the DECORANA) and the vegetation data.

NON-SPECIFIC TEST

Comparison of:	d.f.	*H*	*P*	Rank order
species across zones	3	15.02	**	G>M>E:A
height across zones	3	10.93	*	A>E>G>M
distance across zones	3	14.93	**	A>E>M>G
ground across zones	3	15.84	**	E:A>G>M

Table 1: Analysis of the vegetation quadrat data using the rank means test (Meddis, 1984). $n = 5$ in each of the four zones, * = $P < 0.05$, ** = $P < 0.01$.

Results

The vegetation varied significantly across the dunes (Table 1). Although the number of species increased with distance from the sea, this was not true for all variables. The distance between each hit, stand height and bare ground coverage showed differences which were not in sequence with increased distance from the sea.

The sweep-net samples were very small (0.03 spiders m^{-2}) despite a total area of 960 m^2 having been swept. Only 29 individuals from 13 species (7 families) were found. The commonest, *Tibellus oblongus* (Walckenaer), occurred in all zones, but never exceeded three individuals in any one zone. Three species, exclusive to the sweep-net samples, are typical species of the upper strata of low vegetation: *Tetragnatha extensa* (Linnaeus) (Tetragnathidae), *Heliophanus flavipes* (Hahn) (Salticidae), and *Philodromus aureolus* (Clerck) (Philodromidae). The pitfall trap survey yielded 1078 individuals of 58 species (Table 2). Of these, 24 species (31 individuals) are not listed in Table 2 because they occurred less than three times in total. Of the commoner species, *Lepthyphantes tenuis* (Blackwall) occurs in all zones, *Scotina gracilipes* (Blackwall) occurs mainly in the mixed *Ammophila* stands, but is present in all four zones and *Arctosa perita* (Latreille), shows a distinct habitat preference for the more frontal dunes. *Zelotes latreillei* (Simon) occurs in the more stable dune areas, together with six of the seven species of lycosid. Linyphiids exploit all zones, but *Oedothorax fuscus* (Blackwall) and *Erigone* species show a preference for the bare and unstable frontal dunes.

The DECORANA biplot (Fig. 1) shows a separation of the grassland spider communities from the other sites along axis 1. Axis 2 reveals

Spider species	**Embryo**	**Pure *Ammophila***	**Mixed *Ammophila***	**Grassland**	**Totals**
Gnaphosidae					
Drassodes cupreus	1	1	4	2	8
Drassodes pubescens		2	7	1	10
Zelotes electus	1		3		4
Zelotes latreillei			19	13	32
Liocranidae					
Scotina gracilipes	67	60	223	2	352
Philodromidae					
Tibellus oblongus	4	2			6
Salticidae					
Euophrys frontalis	3		6	2	11
Lycosidae					
Pardosa monticola			2	1	3
Pardosa pullata		1	2	5	8
Pardosa nigriceps		1	12	4	17
Xerolycosa miniata		2	37		39
Alopecosa pulverulenta			1	8	9
Trochosa terricola				9	9
Arctosa perita	98	49	1	1	149
Mimetidae					
Ero cambridgei	1	1		1	3
Theridiidae					
Theridion bimaculatum	1	4		1	6
Enoplognatha ovata	3	1			4
Tetragnathidae					
Pachygnatha degeeri				19	19
Linyphiidae					
Walckenaeria antica			12		12
Walckenaeria atrotibialis				3	3
Gonatium rubens				4	4
Peponocranium ludicrum			10		10
Pocadicnemis pumila			4	2	6
Oedothorax fuscus	36	1			37
Pelecopsis nemoralis	2	6	4		12
Tiso vagans		3	3		6
Erigone dentipalpis	15			1	16
Erigone atra	7	6		1	14
Erigone promiscua	2	3			5
Bathyphantes gracilis	5	13	4	10	32
Bathyphantes parvulus			4	4	8
Lepthyphantes tenuis	24	28	39	45	136
Lepthyphantes mengei		1	1	8	10
Lepthyphantes flavipes	16	5	18	8	47
Total individuals[a]	286 (298)	190 (198)	416 (420)	155 (162)	1047
Total species[a]	17 (27)	20 (27)	22 (25)	24 (30)	

Table 2: Total number of spider species in each zone, from the pitfall trap survey.
[a]Those species, and their totals, which are excluded from this table (< 3 individuals) are given in parentheses.

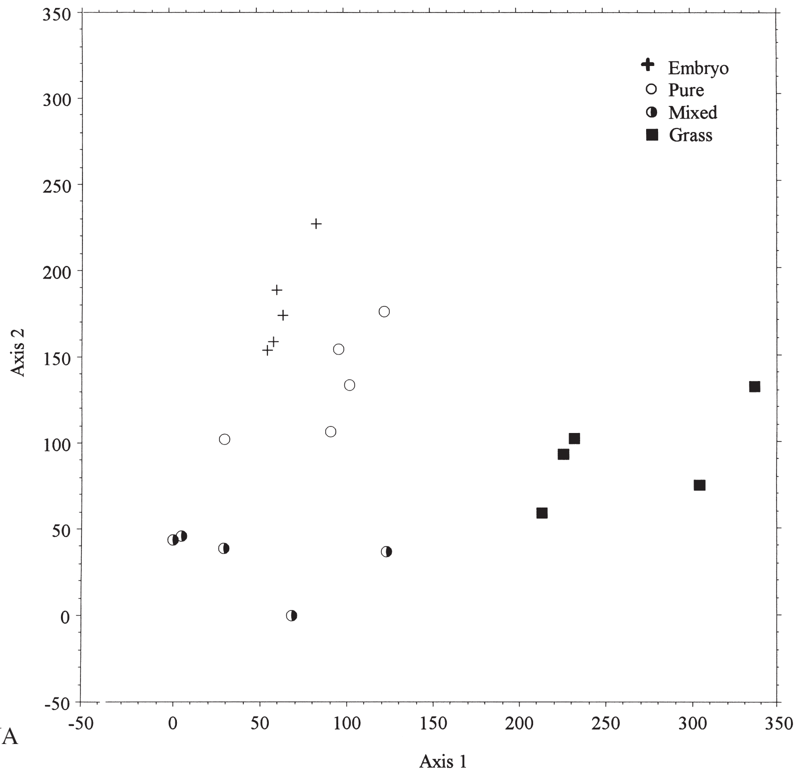

Fig. 1: Biplot of DECORANA axis 1 and axis 2 scores.

that the mixed *Ammophila* spiders can be split from the frontal communities, but that the two frontal communities remain clustered. This produces three spider community types: "frontal" (embryo and pure *Ammophila* communities), "mixed", and "grassland".

Axis 1 and 2 DECORANA scores were correlated with the vegetation data and the ranked distance from the strandline (Table 3). Axis 1 was positively correlated with ranked distance from the sea. Axis 2 was negatively correlated with ranked distance from the strandline and plant diversity, and positively correlated with the structure of the vegetation, its stand height and the percentage of bare ground at the base of the vegetation.

Discussion

Malloch (1985) described a model for sand dunes, where fore-dunes are the first habitat zone from the strandline and the sequence continues until dune grassland, heath and, ultimately, scrub can be found. Payne (1983) described this sequence at Ainsdale, which lies north of Raven Meols. In the present study, these habitat zones were clearly demonstrated, with more vertical spaces between the vegetation and increased height and bare ground cover in the

	Total Species	**Mean distance between hit**	**Mean stand height**	**% bare ground**	**Ranked distance from strandline**
Axis 1	0.314	–0.298	–0.024	0.142	0.477 *
Axis 2	–0.695 **	0.516 *	0.508 *	0.846 ***	–0.674 **

Table 3: Spearman's rank correlation co-efficients between DECORANA axis 1 and axis 2 scores and environmental variables. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

frontal dunes. As the plant communities change towards the fixed dunes, the stands tend to have compact vegetation of a relatively low stand height and bare ground cover (Table 1). A similarity between the two frontal zones (Fig. 1) has been noted by others (Duffey, 1968; Van der Aart, 1973) and it seems likely that xerophilic species tolerant of shifting sand (e.g. *Arctosa perita*) are specialists characterizing these two zones (Bell & Haughton, 1995). This frontal spider group is distinct from that in the mixed *Ammophila* cluster possibly due to increased vertical structure, height and bare ground cover in the frontal dunes. The distance from the sea, a multi-faceted and complex variable, distinguishes the dune grassland from the other two zones. The importance of vegetation structure to the distribution of spiders (Duffey, 1968; Van der Aart, 1973) leads to more individuals, guilds and species occurring with increasing habitat complexity (Hately & MacMahon, 1980). Habitat preference of spiders indicates that some are more tolerant of vertical structures than horizontal ones (Robinson, 1981), and display a strong association with bare ground (Bell & Haughton, 1995), vegetation tip height (Greenstone, 1984) and density (Rypstra, 1986). Habitat structure is closely linked to microclimatic influences which determine spider distribution (Almquist, 1973a,b). Undoubtedly the interplay between these factors are the major determinants of the three major dune spider community clusters.

Linyphiidae exploit all zones, although at a species level zonation is more complex. Mackie (1967) suggested that there may be a build-up of linyphiids on the leeward side of yellow dunes, due to the concentration effect of wind collecting small animals and debris. Duffey (1968) noted that although the linyphiids made up 56.4% of the dune grassland spider fauna, the species found were widespread on grasslands elsewhere, except in northern extremes. However, there appears to be a common model for some genera of surface active linyphiids: *Oedothorax apicatus* (Blackwall) and *O. fuscus* are co-dominant on the beach and in embryo dunes along with *Erigone* species, particularly *E. atra* (Blackwall) (Duffey, 1968; Almquist, 1973a,b). Typically, both sexes in the *Oedothorax* and *Erigone* males do not build webs, and females can also kill without the aid of a web (Alderweireldt, 1994). This allows individuals to wander, avoiding physical disturbance to webs from drifting sand. Three remaining species, *Lepthyphantes tenuis, L. flavipes* (Blackwall) and *Bathyphantes gracilis* (Blackwall) are common to all zones. *L. tenuis* and *B. gracilis* never construct a web above bare soil without anchoring it to vegetation (Alderweireldt, 1994), and *L. flavipes* is normally found in the upper strata of vegetation, suggesting similar web site selection (Leclerc, 1991). *L. tenuis* may only spend an average of two days in the same web (Samu *et al.*, 1996) and physical perturbation has a major effect on the movement of *L. flavipes*, where the effect of high disturbance causes the spider to desert its web (Leclerc, 1991). Although these species are widely distributed in sand dunes, they tend to be found at higher densities in the mixed and grassland areas and are probably not as suited as *Erigone* and *Oedothorax* species to the frontal dunes.

The lycosids *Trochosa terricola* Thorell, *Pardosa pullata* (Clerck) and *P. nigriceps* (Thorell) require a dense grassland sward where the cover and structure of the vegetation are important habitat discriminators (Van der Aart, 1973). *Arctosa perita* shows a strong association with the frontal dunes, being positively correlated with bare ground, whilst *Xerolycosa miniata* (C. L. Koch) was negatively associated with this variable and its distribution was closely associated with dune slacks (see Bell & Haughton, 1995 for more detail). *Scotina gracilipes* occurred across much of the dune system and was not specific to any one zone or sensitive to any one variable but of note was the activity of males which increased considerably during late August (Bell & Haughton, 1995). *Zelotes latreillei* is a good example of a species which, although widespread in Britain and Europe is normally confined to chalk and coastal areas. Bell (1994), investigating the autecology of *Z. latreillei*, found negative correlations with bare ground, vertical structure and vegetation height, and a positive correlation with the number of plant species. Clearly, the habitat requirements of this species is a sward-rich, compact thatch of low vegetation where the bare ground is partly covered with moss, debris or other vegetation. Although stones and large dead matter were not quantified in this study, it is thought that these could be important for the placement of the nipple-shaped egg sac of *Z. latreillei*. This study has demonstrated a zonation for dune spiders which is probably influenced by the structure and diversity of the vegetation. Further work may identify the role of other factors, including microclimate.

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