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Epigeic spider communities in inland dunes in the lowlands of Northern Germany

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Abstract
The spider communities of 13 open inland dunes which lie scattered in the lowlands of Northern Germany have been analysed by means of pitfall trapping. The spider communities of the sandy places clearly differ from the communities of the neighbouring habitats which are heathland, dry grassland or pine forest. But there is no uniform spider community in the *Spergulo-Corynephoretum* habitat which is unique to inland dunes. The concrete vegetation and environmental factors of the site and its surroundings determine the species composition. Vegetation cover (especially lichen, moss and herbs) and the kind of neighbouring habitat mainly influence the species composition of the inland dunes. The influence of the geographical location and of the climate (atlantic in the west, more subcontinental in the east of Northern Germany) on the spider communities is discussed.

Key words: Araneae, inland dunes, Northern Germany, ecology, environmental factors, vegetation cover, biogeography

INTRODUCTION

Inland dunes are rare habitats in the lowlands of Northern Germany. They are sparse in plants but contain a large number of specialised and rare spider species. The hithero available information about spiders in the inland dunes of Northern Germany is very poor and restricted to single locations (e.g. Lademann 1995; Finch 1997). Until now we have to rely on investigations from dune habitats in Southern Germany (e.g. Braun 1956; Leist 1994; Bauchhenß 1995). The comparability with dune habitats in the north is limited because the climate and soil conditions are different.

In this study, the spider communities of 13 open inland dunes in Northern Germany have been analysed and compared. The dunes differ in vegetation cover, neighbouring habitats, size and geographical location. The significance of these environmental features for the distribution of spider species is of special interest.

The following questions were asked in this study:
(i) - Is there a community of spider species which is characteristic of open inland dunes and unique to these habitats?
(ii) - In what way do the distinguishing features of the habitats influence the species composition?
(iii) - What role does the geographical location play?

MATERIAL AND METHODS

Investigation areas

The investigation areas lie scattered in the lowlands of Northern Germany: along the rivers Ems, Weser, Elbe and Oder and in the Lüneburg Heath (Fig. 1). The greatest distance be-

tween the western areas along the Ems and the eastern area along the Oder is about 500 km. The climate in the lowlands of Northern Germany changes from atlantic in the west to more subcontinental in the east: the annual precipitation sums are 700-750 mm along the Ems and 550-650 mm along the Elbe and Oder. The annual amplitudes of air temperature are greater in the east than in the west (Deutscher Wetterdienst 1965).

The inland dunes investigated differ in vegetation cover: some are sparsely covered with *Corynephorus canescens* and *Carex arenaria*, some are completely covered with lichen and some have more moss and herbs. They also differ in size: the smallest area is about 0.1 ha, the greatest about 13.6 ha. They are surrounded by different neighbouring habitats: by heathland, dry grassland or *Pinus sylvestris*-forest (more detailed descriptions of the sampling sites in Merkens 2000).

Spiders

The spiders were caught in pitfall traps. Four pitfall traps, each filled with 4% formalin solution, were installed in the sandy sites (*Spergulo-Corynephoretum*) in all investigation areas. Two pitfall traps were installed in the neighbouring habitats. In six investigation areas the pitfall traps were used for two years (October 1995 to November 1997) and in the other seven investigation areas they were used for 17 months (October 1995 to March 1997). To compare the areas the data were standardized (individual sums x 100/number of sampling days/number of pitfall traps).

Vegetation structure

The vegetation structure was documented by the measurements of the average cover of lichen, moss, grass, herbs, straw and total vegetation cover in an area of 1 m^2 around each pitfall trap. Five classes of vegetation cover were defined and separately assessed for the abovementioned vegetation types: 0 = 0% cover, 1 = 1-25% cover, 2 = 26-50% cover, 3 = 51-75% cover, 4 = 76-100% cover. The average cover was calculated on the basis of 100 estimates of 10 cm^2.

Statistical methods

The faunistic data were subjected to a detrended correspondence analysis (DCA). By means of this procedure locations with similar species composition, and species with similar distribution patterns come close in the ordination diagrams. The locations of pitfall traps are arranged in an order which represents the most effective ecological gradient of the species communities (Jongman et al. 1987).

The correlation between distribution patterns of species and the quality of environmental features was analysed by the Pearson correlation for continuously scaled features

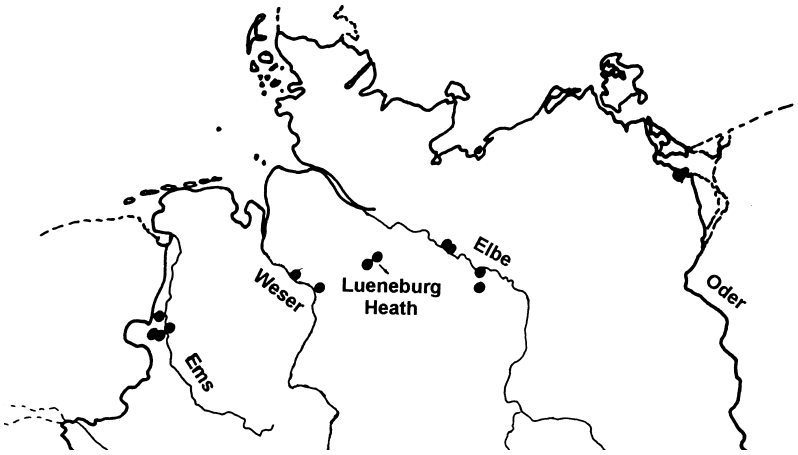

Fig. 1. Geographical location of the investigation sites in Northern Germany.

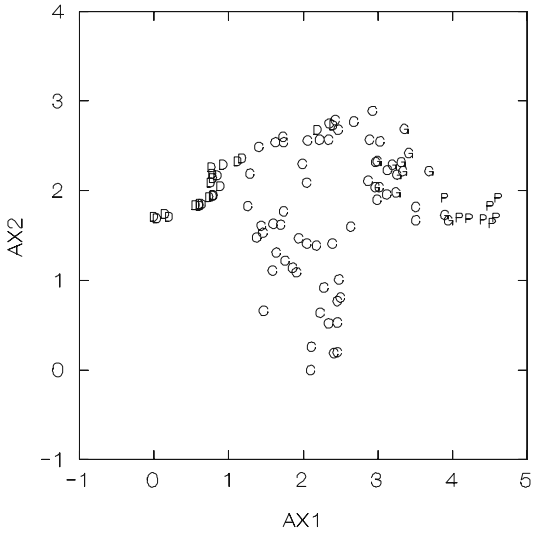

Fig. 2. Detrended correspondence analysis of the spider fauna of all sites: *Spergulo-Corynephoretum* (C), dry grassland (D), heathland (G), *Pinus sylvestris*-forests (P). Each symbol represents one trap.

(cover of the individual elements of the vegetation, habitat size) and by the Spearman rank correlation for ordinally scaled features (neighbouring habitats, geographical location; ordinal numbers were allocated to the different habitats and geographical locations: 1 = heathland, 2 = grassland, 3 = pine forest; 1 = Ems, 2 = Weser, 3 = Lüneburg Heath, 4 = Elbe, 5 = Oder). The correlation coefficients determine the degree of correlation between the abundance of species and the environmental features (Sachs 1978).

RESULTS

Altogether 35991 mature spiders from 286 species and 21 families were caught by pitfall traps. The Linyphiidae, Lycosidae, Gnaphosidae and Salticidae were the most frequent families in the sandy sites. In the investigation areas up to 46% of the species and up to 66% of the individuals were stenotopic species of sandy habitats. The stenotopy of the species has been estimated on the basis of the results of this study and is therefore regionally valid.

Is there a community of spider species which is characteristic of open inland dunes and unique for these habitats? The habitat types can clearly be distinguished along the first axis of the DCA ordination diagram (Fig. 2): heathland and forests on the right, open sand in the middle and grassland on the left. The spider community of the open inland dunes was generally separated from the communities of the neighbouring habitats. Along the second axis the site scores of the dunes show great variation, while the site scores of the surrounding habitats vary little. This means that there is no uniform spider community of the inland dunes. The species composition differs between the individual sites.

In what way do the habitat variables and surroundings influence the species composition? The results of the correspondence analysis of the sandy sites are shown in Fig. 3. There is a gradient of vegetation cover along the first axis: the sparsely covered and open sites are positioned on the left, the more overgrown sites on the right. As for the neighbouring habitats there is a gradient on the second axis: the sites with neighbouring grassland are separate from the sites which are neighbour to a forest. As for the size of the area and the geographical location the distribution of the sites in the diagram is irregular (data not shown).

On the basis of the calculated correlation coefficients between the abundance of several species and the environmental features it is possible to distinguish three species groups (Table 1):

(i) - The spider species of the first group correlate positively with the cover of lichen (and grass). This species group is composed heterogeneously. Some of the species are exclusively found at the sites which are covered with lichen (e.g. *Alopecosa schmidti*, *Drassyllus praeficus*), others clearly prefer this variant (e.g. *Typhochrestus digitatus*, *Aelurillus v-insignitus*). Some species are stenotopic of the sandy habitat, but show no preference for any of the variants of the plant community (e.g. *Zelotes longipes*, *Hypsosinga albovittata*). Some species are pioneers which are able to cope with a wide ecological amplitude and have an efficient spreading strategy (e.g. *Erigone atra*, *Araeoncus*

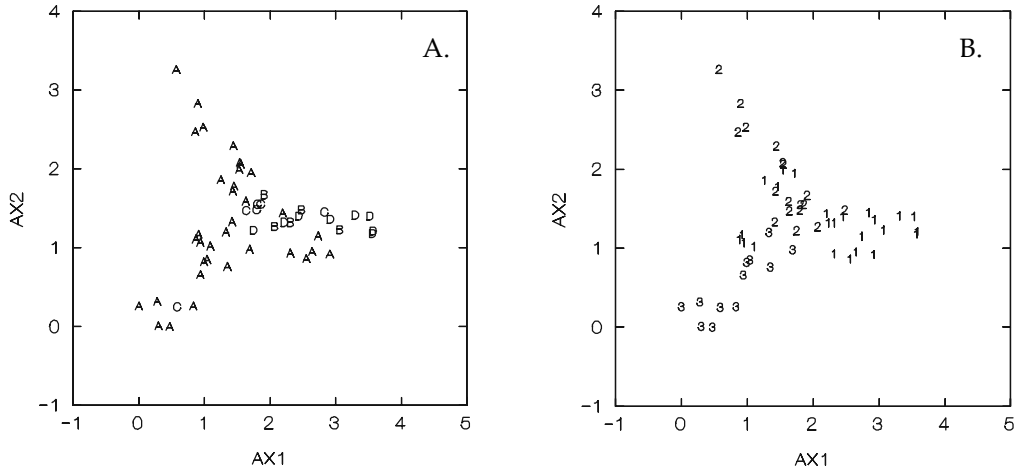

Fig. 3. Detrended correspondence analysis of the spider fauna of the *Spergulo-Corynephoretum* sites. Each symbol represents one trap. **(A)** Symbols are applied to the average cover of lichen and moss: A: average cover of both lichen and moss ≤ 0.5; B: average cover of moss > 0.5, of lichen < 0.5; C: average cover of lichen > 0.5, of moss < 0.5; D: average cover of both lichen and moss > 0.5. **(B)** Symbols are applied to the neighbouring habitats: 1: neighbouring heathland, 2: neighbouring grassland, 3: neighbouring *Pinus sylvestris*-forest.

humilis). Most of the species have a middle position in the ordination diagram (Fig. 4).

(ii) - The species of the second group correlate significantly and positively with the cover of moss and herbs. Most of these species are typical of heathland but were also found regularly in the sandy sites (e.g. *Trochosa terricola, Agroeca lusatica, Centromerita concinna*). Some species are stenotopic of the sandy habitat (e.g. *Zelotes petrensis*, *Alopecosa fabrilis*). All species of this group are positioned on the right side of the ordination diagram (Fig. 4).

(iii) - Four species of the third group correlate negatively with the vegetation cover: *Oedothorax apicatus*, *Arctosa perita, Archaeodictyna ammophila* and *Yllenus arenarius* are restricted to the initial stage of the *Spergulo-Corynephoretum* and live in the open sand. These species are positioned on the left side of the ordination diagram (Fig. 4).

Some species significantly prefer sandy sites which are surrounded by heathland (e.g. *Typhochrestus digitatus*, *Agroeca lusatica*, *Drassyllus pusillus*; data not shown). Most of them are typically living in heathland or prefer places with an advanced stage of succession within the inland dunes.

The size of the habitat was of no importance to most of the species in this study. The individual numbers of two species (*Xysticus kochi*, *Dictyna major*) correlated significantly and positively with the size of the habitat.

What role does the geographical location play? Some of the stenotopic spider species occur exclusively or predominantly at eastern or western localities, respectively (Table 2): 12 species were mainly found along the rivers Elbe and Oder in the east, 8 species were mainly found along the Ems in the west. In the west several species were found regularly in dune habitats which otherwise typically occur in heathland or forest or which are common pioneer species. In the east these species live in their typical habitats but do not find their way into the sandy sites.

DISCUSSION

The spider communities of inland dunes in the lowlands of Northern Germany can generally be distinguished from the spider communities of the neighbouring habitats. One cannot, however, speak of a uniform species community which is characteristic and unique to open

Table 1. Correlations between abundance of individuals and vegetation cover. Significant correlation coefficients are indicated. Limits of significance: P = 0.05: r = 0.273 (x); P = 0.01: r = 0.354 (xx); P = 0.001: r = 0.443 (xxx).

Species	Total veg. cover	Cover of lichen	Cover of grass	Cover of herbs	Cover of moss
Haplodrassus signifer	0.550 (xxx)	0.524 (xxx)	0.310 (x)	.	.
Araeoncus humilis	0.570 (xxx)	0.835 (xxx)	0.644 (xxx)	.	.
Alopecosa schmidti	0.590 (xxx)	0.879 (xxx)	0.413 (xx)	.	.
Drassyllus praeficus	0.567 (xxx)	0.801 (xxx)	0.555 (xxx)	.	.
Thanatus arenarius	0.496 (xxx)	0.682 (xxx)	0.728 (xxx)	.	.
Xysticus striatipes	0.588 (xxx)	0.836 (xxx)	0.642 (xxx)	.	.
Zelotes longipes	0.510 (xxx)	0.584 (xxx)	.	.	.
Trichopterna cito	0.495 (xxx)	0.543 (xxx)	0.388 (xx)	.	.
Zelotes electus	0.362 (xx)	0.610 (xxx)	.	.	.
Pardosa monticola	0.423 (xx)	0.322 (x)	0.506 (xxx)	.	.
Hypsosinga albovittata	0.284 (x)	0.504 (xxx)	.	.	.
Erigone atra	0.394 (xx)	0.644 (xxx)	.	.	.
Bathyphantes gracilis	.	0.446 (xxx)	.	.	.
Typhochrestus digitatus	0.694 (xxx)	0.513 (xxx)	.	.	0.442 (xx)
Aelurillus v-insignitus	0.684 (xxx)	0.738 (xxx)	.	.	0.302 (x)
Centromerita concinna	0.391 (xx)	.	.	0.617 (xxx)	0.422 (xx)
Centromerus sylvaticus	0.417 (xx)	.	.	0.464 (xxx)	0.304 (x)
Tapinocyba praecox	0.374 (xx)	.	.	0.340 (x)	0.323 (x)
Alopecosa barbipes	0.315 (x)	.	.	0.379 (xx)	.
Walckenaeria monoceros	0.341 (x)	0.439 (xx)	.	0.539 (xxx)	.
Trochosa terricola	0.339 (x)	.	.	0.458 (xxx)	0.355 (xx)
Drassyllus pusillus	.	.	.	0.425 (xx)	0.312 (x)
Hahnia nava	.	.	.	0.376 (xx)	0.429 (xx)
Agroeca lusatica	.	.	.	0.516 (xxx)	.
Zelotes petrensis	.	.	.	0.543 (xxx)	.
Micaria silesiaca	.	.	.	0.373 (xx)	.
Alopecosa fabrilis	.	.	.	.	0.546 (xxx)
Phrurolithus festivus	.	.	.	0.311 (x)	.
Agelena labyrinthica	.	.	.	0.275 (x)	.
Xysticus kochi	.	.	0.321 (x)	.	.
Oedothorax apicatus	.	.	.	.	-0.293 (-x)
Arctosa perita	-0.386 (-xx)	-0.43 (-xx)	.	.	-0.327 (-x)
Archaeodictyna ammophila	-0.306 (-x)	.	.	.	.
Yllenus arenarius	-0.294 (-x)	.	.	.	.

inland dunes. The concrete vegetation and environmental factors of the site and its surroundings determine the species composition of the spider community. Vegetation cover and kind of the neighbouring habitat have been documented as the most distinguishing features. The composition of the spider community seems to follow the stage of succession of the plant community: some of the species are restricted to the initial stage of open sand and sparse vegetation cover, some species prefer a dense cover of lichen, others are restricted to a dense cover of moss and to immigrated herbs which indicate an advanced stage of succession.

The atlantic climate in the west of the lowlands seems to accelerate the succession of the inland dunes and to reduce the extreme character of the habitat. Along the Ems several common species of other habitat types were found regularly in the dunes. In the east these species stay in their typical habitats, probably because the sandy sites in the east are drier and hotter than those in the west.

Concerning the spiders, the inland dunes of the lowlands of Northern Germany are intermediate between the coastal dunes along the North Sea and the Baltic Sea on the one hand, and the inland dunes in the east of Germany on

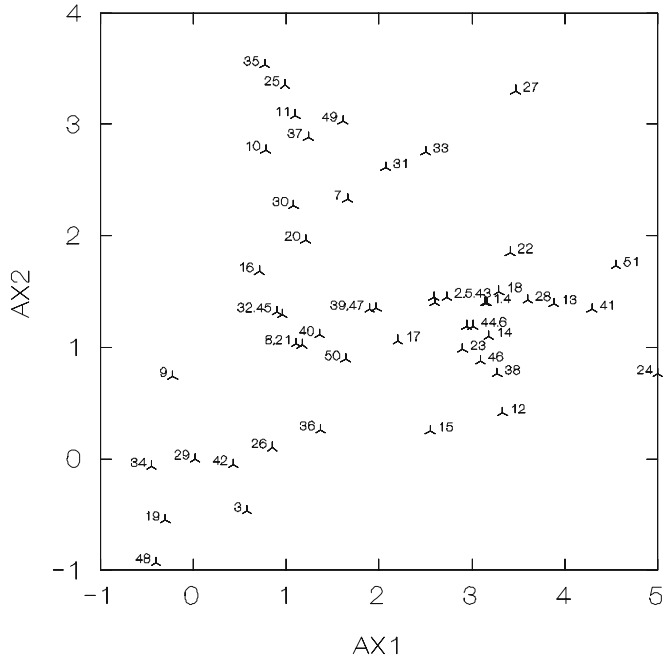

Fig. 4. Correspondence analysis of the spider fauna of the *Spergulo-Corynephoretum* sites. Ordination of species scores along the first and second axis of DCA. Numbering of the species:
1*Acartauchenius scurrilis*, 2*Aelurillus v-insignitus*, 3*Agelena labyrinthica*, 4*Agroeca lusatica*, 5*Alopecosa barbipes*, 6*Alopecosa fabrilis*, 7*Alopecosa schmidti*, 8*Araeoncus humilis*, 9 *Archaeodictyna ammophila*, 10*Arctosa perita*, 11*Bathyphantes gracilis*, 12*Berlandina cinerea*, 13*Centromerita concinna*, 14*Centromerus sylvaticus*, 15*Cheiracanthium virescens*, 16*Dictyna major*, 17*Drassyllus praeficus*, 18*Drassyllus pusillus*, 19*Enoplognatha serratosignata*, 20*Erigone atra*, 21*Erigone dentipalpis*, 22*Hahnia nava*, 23*Haplodrassus signifer*, 24*Haplodrassus silvestris*, 25*Hypsosinga albovittata*, 26*Lepthyphantes tenuis*, 27*Micaria fulgens*, 28*Micaria silesiaca*, 29*Oedothorax apicatus*, 30*Pachygnatha degeeri*, 31*Pardosa monticola*, 32*Pelecopsis parallela*, 33*Phrurolithus festivus*, 34*Porrhomma microphthalmum*, 35*Sitticus distinguendus*, 36*Sitticus saltator*, 37*Steatoda albomaculata*, 38*Tapinocyba praecox*, 39*Thanatus arenarius*, 40*Trichopterna cito*, 41*Trochosa terricola*, 42*Troxochrus scabriculus*, 43*Typhochrestus digitatus*, 44*Walckenaeria monoceros*, 45*Xysticus kochi*, 46*Xysticus sabulosus*, 47*Xysticus striatipes*, 48*Yllenus arenarius*, 49*Zelotes electus*, 50*Zelotes longipes*, 51*Zelotes petrensis*

the other hand. There are species typically found in coastal dunes, e.g. *Philodromus fallax*, *Sitticus distinguendus*, *Haplodrassus dalmatensis*, *Erigone arctica* (Hänggi et al. 1995; Schultz & Finch 1996). In Northern Germany most of these species are restricted to the inland dunes in the west. Some specimens are also found in the investigation area along the Oder, which is not far from the Baltic Sea. On the other hand there are species with a clear centre of distribution in the east of Europe, e.g. *Yllenus arenarius*, *Alopecosa schmidti*, *Archaeodictyna ammophila*, *Berlandina cinerea* (Buchar 1975; Weiss & Marcu 1979; Prószynski 1978, 1986; Grimm 1985; Thaler & Buchar 1994). In the lowlands of Northern Germany they are found along the Oder and Elbe. Some of them reach their western distribution limits there.

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Table 2. Occurrence of several stenotopic and typical spider species in the inland dunes of five geographical regions. The regions are ordered from west to east. x: 1-3 individuals; xx: more than 3 individuals in the sandy sites.

Species	Ems	Weser	Lünebg.	Elbe	Oder
Species which are stenotopic or typical of sandy sites along the Elbe/Oder					
Alopecosa schmidti	.	.	.	xx	xx
Alopecosa trabalis	.	.	.	.	xx
Archaeodictyna ammophila	.	x	.	xx	xx
Argenna subnigra	.	.	.	xx	.
Berlandina cinerea	.	.	.	xx	.
Cheiracanthium gratum	.	.	.	.	xx
Drassyllus praeficus	.	.	.	xx	x
Enoplognatha serratosignata	.	.	.	xx	.
Hypsocephalus dahli	.	.	.	.	xx
Hypsosinga albovittata	.	.	x	xx	x
Micaria dives	x	.	.	.	xx
Ozyptila westringi	.	.	.	xx	.
Philodromus fallax	.	.	.	.	xx
Thanatus arenarius	.	.	.	xx	xx
Xysticus sabulosus	.	.	xx	xx	.
Xysticus striatipes	.	.	.	xx	.
Yllenus arenarius	.	xx	.	xx	.
Species which are stenotopic or typical of sandy sites along the Ems					
Ceratinopsis romana	xx	.	.	.	.
Erigone arctica	xx	.	.	.	.
Haplodrassus dalmatensis	xx	.	.	.	.
Micaria fulgens	xx	.	.	.	x
Micaria silesiaca	xx	.	.	.	.
Ostearius melanopygius	xx	.	.	.	.
Porrhomma montanum	xx	.	.	.	.
Sitticus distinguendus	xx	.	.	.	x
Zelotes petrensis	xx	.	.	.	.
Common species of heathland or forests, mainly in the sandy sites in the west of Northern Germany					
Drassodes cupreus	xx	.	x	.	x
Gnaphosa leporina	xx	.	x	.	.
Lepthyphantes pallidus	xx	.	.	x	.
Microneta viaria	xx	.	.	.	x
Pardosa lugubris	xx	x	.	x	x
Pardosa nigriceps	xx	.	.	.	.
Pirata hygrophilus	xx	.	.	.	.
Pisaura mirabilis	xx	.	.	.	.
Tapinocyba insecta	xx	.	.	.	.
Walckenaeria acuminata	xx	.	x	x	x
Walckenaeria cucullata	xx	.	.	x	.
Walckenaeria cuspidata	xx	.	.	.	x
Walckenaeria dysderoides	xx	.	x	x	.
Xerolycosa nemoralis	xx	.	.	x	.
Zora spinimana	xx	.	x	x	.

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