

Epigeic spiders of two Danish peat bogs

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Abstract

The epigeic spider communities of two Danish peat bogs were investigated. A total of 9447 individuals from 155 species were collected from April to October 2001. The vegetation was divided into five habitats based on dominant plant species. Habitat preferences were established on the basis of multivariate statistics and discussed in relation to earlier investigations. The fauna showed a high degree of originality and was dominated by habitat specialists, such as *Pirata uliginosus* (Thorell, 1856), *Antistea elegans* (Blackwall, 1841) and *Trochosa spinipalpis* (F. O. P.-Cambridge, 1895). The rare linyphiid *Diplocephalus dentatus* Tullgren, 1955 was recorded in high numbers in both bogs and is new to Denmark. Eigenvalues of a Redundancy Analysis (RDA) indicated that the cover of the five dominant plant species could explain approximately half of the variability in species distribution. Nevertheless, floristically similar vegetation zones proved to be highly different in spider species composition between the two bogs.

Key words: Ordination, RDA, habitat affinities, peat bogs, Denmark

INTRODUCTION

During the past few centuries, Danish peat bogs have been subjected to accelerated destruction, due to human activities such as drainage and peat cutting. Although most peat bogs are now protected from direct human modifications, general eutrophication from agriculture and burning of fossil fuels accelerates the invasion of more nutrient-demanding plant species (Hammer 1998).

Investigations of the spider faunas of foreign peat bogs by Casemir (1976), van Helsing (1976), Almquist (1984) and Kupryjanowicz et al. (1998) reveal the presence of several rare species not found in other habitats. Despite this, peat bogs have been given very little arachnological attention in Denmark. The few investigations that have been undertaken in Denmark (Nørgaard 1952, Nielsen & Toft 1989) have only dealt superficially with the distribution of individual species within the

bogs, and therefore the spider microhabitat preferences within peat bogs are poorly understood.

Detailed investigations on microhabitat preferences of spiders in other habitats have been performed by numerous authors using ordination techniques (Coulson & Butterfield 1986; Schultz 1995; Schultz & Plaisier 1996; Finch 1997; Merken 2002; Pommeresche 2002.). In addition, Snazell (1982), Rushton et al. (1987) and Downie et al. (1995) also consider the importance of selected environmental factors in determining the distribution of spider species. It is generally accepted that the plant composition and architecture is of vital importance for the web building spider species. However, its importance for the composition of epigeic communities is less well understood. Although the investigations mentioned above indicate a connection between plant and spider communities, Gajdoš and

Toft (2000a,b) found vegetation structure to be a poor indicator of epigeic spider assemblages in a heathland- marsh transect.

To date, conservation criteria in Denmark are based mainly on botanical data. However, the presence of a few indicator plant species does not necessarily indicate the presence of interesting or rare species of other organisms. Knowledge and evaluation of the spider species composition, for example, could therefore give more detailed information and thereby help in the evaluation of biotic communities.

The objectives of the present study were (1) to describe the epigeic spider faunas of two Danish peat bogs, (2) to determine the habitat preferences of individual species using ordination, (3) to investigate the effect of vegetation composition on the epigeic spider communities and (4) to give an evaluation of the spider assemblages using measures of diversity, habitat specificity and relative abundance of spider species indicative of habitat disturbance.

MATERIALS AND METHODS

Sites

For the investigation, two localities were chosen, Gjesing Mose and Sømosen, both situated in Løvenholm Forest on Northern Djursland, Jutland (56°26'N, 10°30'E). Today the forest consists mainly of beech (*Fagus*) and cultivated spruce (*Picea*). In the late 18th century, however, the area consisted mainly of heath and moorland with woodland comprising only a minor part of the area (Andersen 1984). Today, the situation is reversed, with the few remaining heaths and bogs being threatened by the invading forest. Furthermore, all bogs in the area have been exploited through peat cutting, changing large parts dramatically. However, the remaining parts of the peat bogs seem to have a relatively intact flora, (Hammer 1998), and therefore it might be expected that the spider fauna will be similar to that found in other peat bogs. Gjesing Mose and Sømosen are remainders of actively growing peat bogs and sampling has been confined

to the apparently least disturbed parts. The two bogs are separated by approximately 1800 meters of dry forest. Both localities have a distinct zonation of vegetation types and are distinguished as different patches according to plant species dominance. Thus, distinction was made between habitats dominated, at least partially, by heather (*Calluna vulgaris*), bell-heather (*Erica tetralix*), moorgrass (*Molinia caerulea*) on areas exposed to sun, cotton grasses (*Eriophorum* spp.) and finally moorgrass on areas shaded by birch forest (*Betula* sp.).

The *Calluna*-patches were quite different in the two bogs. In Gjesing Mose, the stand was composed almost exclusively by tall, senile plants, leaving an open structure and a layer of moss. In Sømosen, the stand was heavily grazed by deer, resulting in a more dry, dense but also low structure. The *Erica*-patches also differed substantially. In Gjesing Mose, *Erica* occurred in a large patch with senile *Calluna*-shrubs on bare, frequently flooded soil, whereas in Sømosen, the patch was approximately 15m² and surrounded by *Eriophorum* spp. and *Molinia*. The *Eriophorum*-habitat in Sømosen was a floating peat blanket, whereas in Gjesing Mose, the peat moss appeared to grow on the wet, organic peat soil. In Gjesing Mose, the *Molinia*-patch was situated on wet, boggy soil, never drying out during the summer. Peripheral trees shaded the area during parts of the day. In Sømosen, the *Molinia*-area was completely sun-exposed and was only wet in spring and early summer. It was frequently flooded in these periods as opposed to the *Molinia*-patch in Gjesing Mose.

Sampling

Spiders were caught by pitfall traps covered with roofs. For enhancement of the catch, each trap was supplied with a plastic barrier, approximately 60 cm in length, to guide the spiders to the trap. The traps consisted of two plastic cups, one inside the other, both with a diameter of approximately 8 cm, containing a 4% formaldehyde solution and a small

amount of detergent. Traps were emptied bi-weekly. Five traps were placed in each habitat in each bog, giving a total of 25 traps per locality. For each habitat type, traps placed in Gjering Mose were numbered 1-5, traps in Sømosen 6-10. The trapping period was from April 1 until the end of September 2001.

Only adult specimens were recorded and treated in this investigation. As the entire year was not covered, no inferences regarding phenology could be made. Thus, the catches of each trap were summed over the trapping period.

Pitfall traps are widely used since they give a large catch of many species with relatively little effort. However, the method can be criticised for several drawbacks. For a discussion of this issue, see Uetz and Unzicker (1976) and Topping and Sunderland (1992). Nevertheless, because other widely used sampling methods, such as sweep-net sampling or visual search, would be too inefficient in the vegetation types found in the study areas, pitfall sampling was chosen for this investigation.

In late October 2001, the cover of all plant species below 1m in height was analysed in a 1m² area surrounding each trap. Floristic data are shown in Appendix 2. The cover of *Eriophorum angustifolium* was included in the cover of *Sphagnum*, since it almost always occurred on *Sphagnum* and had very little covering effect in itself, its leaves pointing almost straight up. Consequently, some of the cover values exceed 100%.

For identification of the spiders, nomenclature and identification was based on Roberts (1987, 1995) and Heimer & Nentwig (1991).

DATA ANALYSIS

Diversity and similarity

Assuming that the species data conformed to the log-series distribution, diversity of the spider fauna from each habitat was calculated using the α -index:

$$\alpha = N(1-x),$$

where N is the total number of individuals, and x is estimated from

$$S/N = ((1-x)/x) * -\ln(1-x),$$

where S is the number of species in the sample. Compared to other diversity indices, the α -index has the advantage of being insensitive to differences in sample size between habitats (Magurran 1988).

To establish how different the fauna of the different habitat types were, similarity was calculated as percentage similarity:

$$\%S = \sum_{i=1}^S \min(P_i(a), P_i(b))$$

(Southwood & Henderson 2000) summing the lowest relative abundances of the i^{th} species in the two habitats (a,b) under comparison. Whereas most other diversity indices are qualitative, the percentage similarity is sensitive to the abundance of species as well. As a consequence, more emphasis is put on the dominant species, reducing noise from the rare species. Since this method compares abundance of each species in two traps or habitats, no transformation of the data was used.

Habitat specificity index

Since some environments are naturally species-poor and dominated by very few species, a measure of the quality of the spider fauna should therefore not be based on diversity and species richness alone, but also on an ecological evaluation of the species list itself. Therefore, a habitat specificity index HS modified after Toft et al. (1993) was calculated for the spider fauna of each habitat types at both localities: Each species is assigned a value of 1, 2, 3 or 4, depending on its habitat width. Habitat widths were estimated using the method of Hänggi et al. (1995), for some species modified by own experience from Northern Europe, and are shown in the species table in Appendix 1.

The index was calculated using the formula

$$HS = \frac{f(1) + 2f(2) + 3f(3) + 4f(4)}{f(1) + f(2) + f(3) + f(4)}$$

where $f(1)$ - $f(4)$ are the summed abundances of individual species with values of 1-4, respectively. The result is a value between 1 and 4, a high value indicating dominance of habitat specialists, whereas a value close to 1 is characteristic of a fauna comprised of habitat generalists. To enable comparison with earlier investigations, the index was calculated using untransformed data. The reason for including species abundance and not just presence/absence data in the index used here is the assumption that a disturbance might alter the relative abundances of specialist and generalist species without necessarily eradicating the specialists completely.

Hänggi (1987) proposed an index for quantifying the quality of the fauna. This index considers habitat specificity and the number of records in the region of the study site (Northern Switzerland). It disregards the abundance of individual species, leaving a strictly qualitative measure. Calculation of this index requires knowledge of species distribution on a regional or national scale, which is not yet available for Denmark. Furthermore, it might not be able to discriminate between localities with identical species lists but with different dominant species.

Expansive species

Růžička (1986) found a negative correlation between habitat stability and the relative abundance of so-called expansive species. The species were defined as efficient colonisers of areas that were recently exposed to anthropogenic disturbance. In this investigation, the definition includes frequent ballooning and some larger, highly mobile habitat generalists that disperse by running. The relevant species are marked with (E) in Appendix 1. The relative abundances of such species are calculated for each habitat, using $\log(x+1)$ -transformed data.

Ordination

To investigate spider affinities in relation to measured parameters (covers of dominant plant species), the data were analysed using ordination. Ordination is a group of multivariate methods, seeking to extract underlying structures from large groups of data. The result is a simplification of tendencies in the data set, hopefully facilitating interpretation of the results. A preliminary Detrended Correspondence Analysis (DCA) revealed an overall linear response to the variables used (plant species covers). Therefore the appropriate method was Redundancy Analysis, RDA, included in the program CANOCO 4.0 (ter Braak & Smilauer 1998).

The analysis works as follows, following Jongman et al. (1995): Each of the n traps is given an initial arbitrary score, x_i , above 0. Scores for each species are calculated by weighted summation of species abundance:

$$b_k = \sum_{i=1}^n y_{ki} x_i,$$

where y_{ki} is the abundance of species k in trap i . From these species scores, new trap scores are calculated using

$$x_i = \sum_{k=1}^S y_{ki} b_k.$$

In RDA, these site scores are then adjusted by linear regression to the measured parameters. The range of these fitted trap scores defines the first ordination axis. The remaining axes are extracted in a similar fashion but to avoid correlation with other axes, an orthogonalization procedure is used. The proportion of variance in species distribution explained by an axis is illustrated by its eigenvalue. An eigenvalue of 0.35 indicates that the axis, and the combination of spider-distributing factors it represents, explains 35% of the species distribution. Since the axes in RDA are produced from the combination of environmental variables and the species distribution in the traps, it also excludes any variation not attributable to the variation in the selected environmental

variables. Therefore, this type of analysis is called canonical or constrained ordination.

In the ordination procedure, no distinction was made between covers of a plant species in the *Betula*-*Molinia*-area and in the other habitat types. For example, it was not possible to distinguish an affinity for *Molinia* growing in association with *Betula*, from the affinity for sun-exposed *Molinia*. This distinction must be based on the species table (Appendix 1).

RESULTS

General characteristics of the fauna

The species list includes 155 species from 9447 adult individuals (Appendix 1). The catch in Gjesing Mose included 123 species, whereas Sømosen yielded 121 species. Most abundant in the traps were the cursorial lycosids such as the large *Trochosa terricola* Thorell, 1856 and *T. spinipalpis* (F. O. P.-Cambridge, 1895), the smaller hygrophilous *Pirata uliginosus* (Thorell, 1856) and *Pardosa sphagnicola* (Dahl, 1908), and the ubiquitous habitat generalists *Pardosa pullata* (Clerck, 1757) and *Pardosa prativaga* (L. Koch, 1870). The hygrophilous *Antistea elegans* (Blackwall, 1841) was also very abundant, mainly due to a large catch of males in September. Among the 79 species of linyphiids, *Diplocephalus dentatus* Tullgren, 1955 and *Walckenaeria alticeps* (Denis, 1952) were the most abundant, followed by *Oedothorax gibbosus* (Blackwall, 1841). More than half the *O. gibbosus* specimens were males, of which only three were of the *gibbosus* type.

Among the more numerous species *Trochosa ruricola* (de Geer, 1778), *Xerolycosa nemoralis* (Westring, 1861), *Zelotes clivicola* (L. Koch, 1870) and *Diplocephalus dentatus* were found mainly in Gjesing Mose, whereas *Alopecosa pulverulenta* (Clerck, 1757), *Dicymbium tibiale* (Blackwall, 1836), *Microneta viaria* (Blackwall, 1841), *Pardosa lugubris* (Walckenaer, 1802) and *Pardosa sphagnicola* were the most abundant in Sømosen. *Walckenaeria dysderoides* (Wider, 1834), *Walckenaeria kochi* (O. P.-Cambridge, 1872), *Gongylidiellum*

murcidum Simon, 1884, *Lepthyphantes cristatus* (Menge, 1866) and *Scotina gracilipes* (Blackwall, 1859) were found exclusively in Gjesing Mose, whereas *Maro minutus* O. P.-Cambridge, 1906, *Aphileta misera* (O. P.-Cambridge, 1882) and *Araeoncus crassiceps* (Westring, 1861) were found only in Sømosen. Most of the large and mobile lycosids occurred in all habitats, but also the smaller linyphiids *Bathypantes gracilis* (Blackwall, 1841), *Dicymbium tibiale* and *Diplocephalus dentatus* were found in all habitat types.

Diversity

The *Calluna*-habitats had the highest species richness (Fig. 1). More than half of the total number of species was recorded for each locality. Most of the remaining sites had more or less similar species numbers, although *Erica* in Sømosen had somewhat fewer species. Nevertheless, for each locality, all habitat types contained about half of all species.

Calluna in Gjesing Mose had the highest diversity (Fig. 2). Apart from *Erica* in Sømosen and *Molinia* in Gjesing Mose, most other habitats had similar α -values, but *Erica* in Sømosen had a very low diversity. The low diversity was to be expected, due to the high records of *Antistea elegans*, *Pardosa pullata* and *Pirata uliginosus*, which constituted almost half of the total catch. *Molinia* in Gjesing also had a low α -diversity, since one third of the catch was *P. uliginosus*.

Similarity

The catches of the five defined habitat types differed substantially between localities (Table 1). The *Erica*-patches were only 32.2% identical. The remaining habitats had similarities around 50%, *Eriophorum* with the highest score of 57.9%. Between different habitat types within each locality, similarities were generally higher in Sømosen than in Gjesing Mose. This was probably caused by the smaller distances between patches in Sømosen, i.e. *Erica*, *Molinia* and *Eriophorum*-habitats in Sømosen

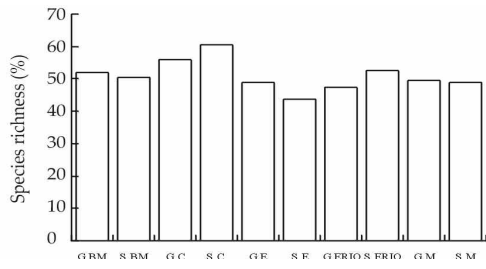


Fig. 1. Species richness of habitats as percentage of total species number for each locality. Abbreviations: G: Gjesing Mose, S: Sømosen, BM: Betula-Molinia, C: Calluna, E: Erica, Erio: Eriophorum and M: Molinia. Total species number: Gjesing Mose: 123, Sømosen 121.

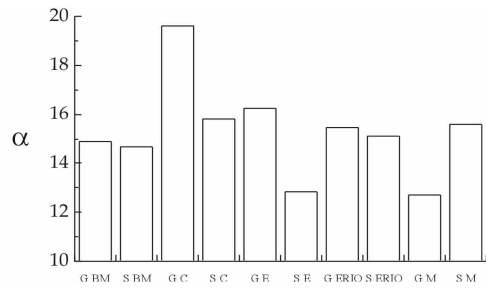


Fig. 2. α -index species diversity values for habitat types and localities. Abbreviations: G: Gjesing Mose, S: Sømosen, BM: Betula-Molinia, C: Calluna, E: Erica, Erio: Eriophorum and M: Molinia.

Table 1. Percentage similarity matrix of the spider faunas of the different habitat types. Between-locality similarities of same habitat types in bold. Between-locality similarities of same habitat types was often lower than similarity between different habitats at the same locality.

		Sømosen					Gjesing Mose				
		Betula-Molinia	Erica	Calluna	Eriophorum spp.	Molinia	Betula-Molinia	Erica	Calluna	Eriophorum spp.	Molinia
Sømosen	Betula-Molinia	-									
	Erica	44.4	-								
	Calluna	53	42.4	-							
	Eriophorum spp.	39.5	76.8	42.7	-						
	Molinia	64.1	59.6	49.2	49.2	-					
Gjesing Mose	Betula-Molinia	48.2	42.3	21.8	38	39	-				
	Erica	27.6	32.2	38.4	43.1	41.5	33.8	-			
	Calluna	46.6	36.3	45	31.8	53.1	40	49.7	-		
	Eriophorum spp.	43.6	56.3	35.7	57.9	56.2	41.7	44.4	45,8	-	
	Molinia	48,4	63,1	29,3	55,8	52,8	59,1	45,8	38,4	49,5	-

were adjacent. The highest similarity in Gjesing Mose was seen between *Molinia* and *Betula-Molinia*. The two habitats were separated by 60 meters of dry *Betula*-forest, so the similarity is probably caused by the structural similarity of the vegetation and not by proximity.

Habitat specificity

Generally, there was a high dominance of specialists. However, some differences were seen: a higher abundance of generalists was seen in both *Calluna*-areas and the *Erica*-habitat in Sømosen (Fig. 3). The two *Erica*-habitats had very different values of 2.5 and 3.2, respec-

tively. The *Erica*-habitat in Sømosen was situated next to a peat bog area with dominance of *Eriophorum* spp.. It mainly contained specialised wetland species, including the only specimens of the tyrphobiont *Aphileta misera*. In Gjesing Mose, the *Erica*-habitat was dominated by *Calluna*. The soil below the shrubs was bare and frequently flooded. Among the most abundant spiders there were generalists such as *Trochosa terricola*, *T. ruricola*, *Erigone atra* Blackwall, 1833 and *Pardosa prativaga*. The *Molinia*-habitat in Gjesing Mose also had a very specialised fauna, in contrast to the *Molinia*-habitat in Sømosen. The *Betula-Molinia*-patches both had a very specialised fauna, having HS-values > 3.

Expansive species

The proportion of individuals of expansive species out of all spiders collected reveals only small differences between habitats (Fig. 4). Generally, there was an extremely low abundance of disturbance indicators. The highest abundances were seen in the *Calluna-Eriophorum*- and *Erica*- patches in Gjesing Mose and *Molinia* in Sømosen. The abundances were almost identical in the remaining habitat

types.

Ordination

Due to the dissimilarities between localities seen in Table 1, the results from the two bogs were analysed separately. The ordination biplots of species, traps and environmental variables are shown in Figs. 5AB, 6AB.

Gjesing Mose

The eigenvalues of the four extracted RDA-axes were 0.213, 0.125, 0.073, and 0.043, respectively, indicating that approximately 45% of the variation in species distribution can be explained by the selected variables. The displayed first two axes account for approximately 65% of the explained variance. Interpretation from the diagram alone might therefore be inaccurate. A Monte Carlo permutation test showed significance ($F=3.275$, $P=0.005$) of the species distribution related to all axes. Since it always has the highest eigenvalue, the first axis generally also has the highest correlation coefficients. It was positively correlated with *Calluna* and *Erica*, and negatively correlated with both *Molinia* and *Eriophorum vaginatum*. It therefore mostly repre-

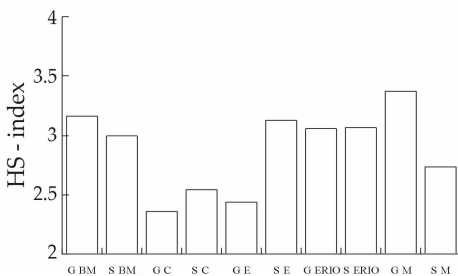


Fig. 3. Habitat specificity-index of the spider fauna of the different habitats, arranged pairwise. The index yields values from 1-4. High values indicate dominance of specialist species, low values indicate dominance of opportunists. Abbreviations: G: Gjesing Mose, S: Sømosen, BM: Betula-Molinia, C: Calluna, E: Erica, Erio: Eriophorum and M: Molinia.

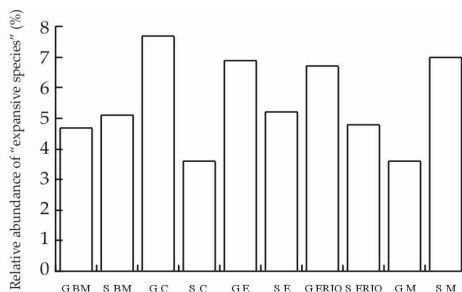


Fig. 4. Percentage of "expansive species" of all spider individuals for all habitats. Generally, there was an extremely low presence of disturbance indicators. Abbreviations: G: Gjesing Mose, S: Sømosen, BM: Betula-Molinia, C: Calluna, E: Erica, Erio: Eriophorum and M: Molinia.

sents a gradient from dense *Molinia* and *E. vaginatum* on wet soil to the more open, sun-exposed vegetation on drier ground. Spider species arranged along this gradient were the hygrophilous *Trochosa spinipalpis* and *Pirata uliginosus* at the moist end and the heathland species *Xerolycosa nemoralis* and *Haplodrassus signifer* (C.L. Koch, 1839) at the dry end.

The second axis represented 12.5% of the variation in species distribution, but is harder to interpret, as it was only weakly correlated with the measured variables. However, it separated the *Eriophorum*-traps (Fig. 5B). The traps Erio1, Erio2 and *Calluna* 3 and 5 were all placed 2-5 meters from the birch woodland. In species terms, the second axis stretched from hygrobionts such as *Pardosa sphagnicola*, *Pirata piscatorius* (Clerck, 1757) and *Bathypantes gracilis* to *Microneta viaria* and *Euryopis flavomaculata* (C.L. Koch, 1836), being woodland- and helophilous species, respectively. It is therefore likely that the second axis illustrates proximity to the surrounding dry birch forest and not a microclimatic, spider-distributing factor. The third axis explained only 7.3% of the species distribution, but is much more easily interpreted due to the very high correlations with the permanently wet *E. angustifolium* and *Sphagnum*-vegetation, indicating a moisture gradient. The axis probably also illustrates the degree of disturbance, since the *Sphagnum*-habitat was frequently flooded, especially during spring and autumn. In conclusion, vegetation density seemed to be the single-most important factor in determining the distribution of spider species in Gjesing Mose.

Sømosen

Slightly higher eigenvalues of 0.213, 0.204, 0.04, and 0.021, respectively, were seen for the ordination of the Sømosen data. Summing these values, 48% of the variation in species distribution was explained by the four axes, 82% thereof by the first two axes (Figs. 6AB). Therefore, more interpretation is possible from Fig. 6A than from Fig. 5A. A Monte Carlo test

showed significance of all axes in explaining the species distribution ($F=3.119$, $P=0.005$).

The first axis mainly illustrates a moisture gradient (Figs. 6AB). This is indicated by the dominance of hygrobionts such as *Oedothorax gibbosus* and *Pardosa sphagnicola* at one end, and *Haplodrassus signifer* and *Zelotes* spp. at the other end. The second axis represents the gradient from dense *Molinia*-vegetation with the skotophilous *Microneta viaria* to the open *Calluna*- and *Eriophorum*-sites with the moisture generalists but helophilous *Pardosa prativaga* and *P. pullata*. The vector for cover of *Calluna* is oriented at an intermediate angle with the first two axes. This indicates that the *Calluna*-vegetation is both open and dry. Figure 6b shows three distinct groups of traps: the *Molinia* and *Betula-Molinia* traps represent a dense, moderately wet environment, the isolated dry, short and open *Calluna*-traps and the wet and sun-exposed areas of *Eriophorum* and *Erica*. As for Gjesing Mose, the diagram does not account for all the explained variation. Thus, *Sphagnum* and *E. angustifolium* have strong correlations with the inferior axes 3 and 4, and therefore are not as closely connected to *E. vaginatum* and *Erica* as could be inferred from Fig. 6AB alone. Overall, moisture and vegetation density appeared to be the best indicators of spider communities in Sømosen.

Habitat affinities

Generally, few species showed similar affinities at both localities.

This was to be expected, because of the differences in moisture and sun exposure between the corresponding habitat types in the two bogs. The dissimilarity between the two *Erica*-patches is documented in Table 1. It demonstrates that the microclimatic conditions indicated by the presence of *Erica* were far from being the same across localities. Therefore *Erica* was excluded as a distinct habitat type. The following species could be labelled as characteristic species for the different habitat types:

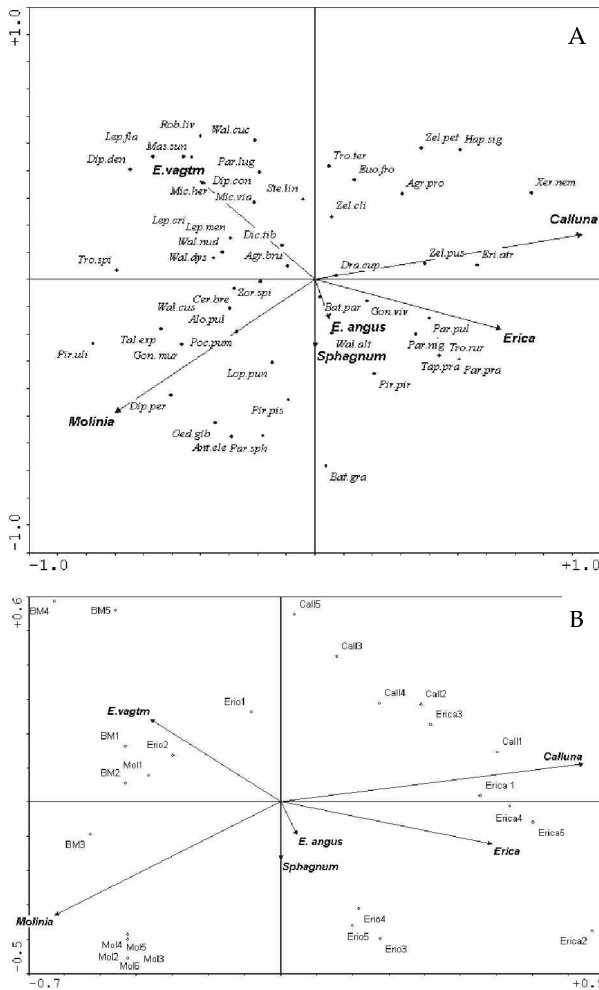


Fig. 5. (A) RDA biplot of spider species and cover of dominant plant species from Gjesing Mose. The horizontal axis illustrates the most important combination of spider-distributing environmental variables. It indicates the gradient from wet and dense *Molinia*-vegetation with hygrophilous species such as *Trochosa spinipalpis* and *Pirata uliginosus*, to drier *Calluna*- and *Erica*-patches with *Xerolycosa nemoralis* and *Haplodrassus signifer*. **(B)** RDA biplot of traps and cover of dominant plant species from Gjesing Mose. Closely located traps had similar catches. Arrows indicate cover of individual plant species. Call: *Calluna*-trap, other species codes, see Appendix 1.

Betula-Molinia:

Lepthyphantes cristatus, *Lepthyphantes flavipes* (Blackwall, 1854), *Tallusia experta* (O. P.-Cambridge, 1871) and *Walckenaeria cucullata* (C.L. Koch, 1836).

Calluna:

Xerolycosa nemoralis, *Zelotes clivicola*, *Drassyllus praeficus* (L. Koch, 1866), *Centromerita concinna* (Thorell, 1875), *Haplodrassus signifer*, *Drassyllus pusillus* (C.L. Koch, 1833) and *Z. petrensis* (C.L. Koch, 1839).

Eriophorum:

Dolomedes fimbriatus (Clerck, 1757), *Maro minutus*, *Pirata piscatorius* and *Phrurolithus festinus* (C.L. Koch, 1835).

Molinia:

Pocadicnemis pumila (Blackwall, 1841), *Walckenaeria cuspidata* Blackwall, 1833, *Walckenaeria nudipalpis* (Westring, 1851) and *Zora spinimana* (Sundevall, 1833).

Moist vegetation of all types:

Antistea elegans, *Diplocephalus permixtus* (O. P.-Cambridge, 1871), *Lepthyphantes menzei* (Kulczynski, 1887), *Lophomma punctatum* (Blackwall, 1841), *Micrargus herbigradus* (Blackwall, 1854), *Oedothorax gibbosus*, *Pirata uliginosus*, *Pardosa sphagnicola* and *Walckenaeria dysderoides*.

Sunexposed habitat types, wet and dry:

Pachygnatha degeeri Sundevall, 1830, *Pardosa*

Walckenaeria incisa (O. P.-Cambridge, 1871) has only recently been recorded from Denmark in small numbers from a forest locality (O. Gudik-Sørensen pers.comm.). Other rarities include the ant-associated and therefore presumably underrecorded *Evansia merens* O. P.-Cambridge, 1900 and the thermophilous *Micaria fulgens* (Walckenaer, 1802). *Aphileta misera* was sparsely recorded, despite the fact that van Helsdingen (1976) classifies it as an obligate typhobiont. In investigations by Kupryjanowicz et al. (1998) it is also reported as rare.

Results from bogs in other countries reveal a few specialised species that are absent in this investigation. The most prominent species is the common *Pirata hygrophilus* which has been found in several similar investigations (Casemir 1976; van Helsdingen 1976; Almquist 1984; Kupryjanowicz et al. 1998; Svaton & Pridavka 2000). According to Nørgaard (1952) it is found exclusively in shaded *Sphagnum*-areas. This is supported by results in Kupryjanowicz et al. (1998). Since the *Betula-Molinia*-patch in Gjesing Mose contained just this type of habitat, its absence is surprising.

Ordination

The ordination results had only moderate eigenvalues. Approximately 50% of the variability in spider species distribution in this study could be explained by the covers of dominant plant species. Downie et al. (1995) found even lower eigenvalues (28% explained) in an ordination based on slope, vegetation density and soil depth. Gajdoš and Toft (2000a,b) found a poor connection between vegetation structure and spider assemblages. Generally, higher eigenvalues are found in unconstrained ordination, which considers all variation in the species data. Thus, an unconstrained ordination done by Snazell (1982) could account for 85% of the species variation, and Curtis and Bignal (1980) found eigenvalues explaining almost 75%.

This suggests that the abiotic factors measured in the investigations mentioned above or

the composition of the vegetation can only partly explain the patterns in spider assemblages that are so clearly demonstrated in unconstrained ordination. In this investigation, the fact that within-locality similarities were greater than between-locality similarities between floristically similar habitat types indicates an influence from the neighbouring habitat patches. This is likely to have reduced the correlations between spider and plant species, thereby leading to too low an estimate of the effect of vegetation on the spider assemblages. Furthermore, an accurate measurement of plant architecture, as performed by Curtis and Bignal (1980), and of the abiotic factors would have been likely to produce higher eigenvalues. Therefore, plant composition and architecture probably still remain the primary factors, even on the scale used in this study.

Habitat affinities

Pirata uliginosus is sometimes described as less hygrophilous than other species of *Pirata* (Heimer & Nentwig 1991; Roberts 1995). This view is not supported by this investigation. *P. uliginosus* had its highest abundance in permanently wet, boggy areas, which agrees more with Casemir (1976) and van Helsdingen (1976), who classified it as sphagnophilous. In this study, *P. piscatorius* was confined to *Sphagnum*, but *P. piraticus* (Clerck, 1757) was the *Pirata* species found in the least moist conditions.

The linyphiids *Maro minutus*, *Aphileta misera* and *Araeoncus crassiceps* were absent from Gjesing Mose. They are obligate typhobionts, and their apparent absence in Gjesing Mose may be caused by the nature of the two peat areas: The *Eriophorum*-habitat in Sømosen was a floating peat moss zone, whereas in Gjesing Mose, the peat appeared to be growing on the wet, organic soil. The floating moss to some extent rises and falls with the water level, whereas it is more exposed to flooding in Gjesing Mose. It is possible that these species do not tolerate a waterlogged or flooded peat moss layer.

Diversity and species richness

Interpretation from the diversity values alone is difficult. Uniform habitat patches were expected to have intermediate or low diversities, but this was not invariably true. The high diversity of the spider catch in the *Calluna*-patch in Gjesing Mose could be caused by the diverse structure of the old plant individuals, as well as by the proximity of other vegetation types. However, the diversity seen in the relatively small patch of *Erica* in Sømosen did not seem to have been enhanced by marginal effects, as it might have been expected. Generally, diversity seemed to be independent of vegetation structure or patch size.

Quality of the fauna

Toft et al (1993) calculated the habitat specificity index for the spider faunas of a heathland area with *Corynophorus*- and *Calluna*-heath and an associated *Sphagnum* bog. Since the index used by Toft et al. ranges from 1 to 5, the HS-values from this investigation must be multiplied by 1.25 for direct comparison. It is then revealed that even the lowest value found in the *Calluna*-habitat in Gjesing Mose is higher than the *Calluna*-habitat investigated by Toft et al. The highest value, found in the *Molinia*-habitat in Gjesing Mose, also exceeds the value found in the sandy *Corynophorus*-locality and the associated *Sphagnum*-bog. Especially the dry *Corynophorus*-heathland would be expected to have about the highest possible value due to its extreme microclimate, but almost half of the habitats in this study had more specialised faunas, even though their conditions seem less extraordinary. Generally the HS-values found in this study are substantially higher than those reported by Toft et al. (1993) and considerably higher than those found in grass- and marshland areas and cereal fields (Nielsen & Toft 1989). Therefore, a specialised fauna seems not only to indicate an extraordinary combination of physical microclimatic factors, but also to be a product of other factors, such as lack of disturbance, habi-

tat age and the characteristics of the surrounding areas. A fauna this specialised is vulnerable and of high conservation interest and only stresses the need for conservation of peat bogs.

The relative abundance of expansive species hardly differed between habitat types. The largest values were seen in the habitat patches that were frequently flooded. Růžička (1986) compiled values from a wide variety of habitats, ranging from nature reserves to highly disturbed agricultural areas. All values found in this investigation are well below the level of 45%, which effectively separated nature reserves from more disturbed habitats. These findings corroborate the conclusion based on the habitat specificity calculations, indicating that the two bogs contain original and valuable climax spider communities of great conservation value.

However, it must be considered that both bogs have been subjected to modifications, and even though the patches investigated have been left to natural succession in recent years, the disturbance might still have resulted in a distortion of the spider fauna. It would therefore be interesting to compare with investigations from more pristine localities.

Different indicators of nature quality

In this investigation it was clear that diversity, species richness, the number of expansive species and the HS-index will produce different results when used as measures of the quality of the fauna. The diversity measure would clearly point to the senile *Calluna*-patch in Gjesing Mose as the most valuable, whereas the species richness largely failed to discriminate between the habitat types.

It is also clear that the dominance of expansive species as an indicator of disturbance might not always help to determine the degree of naturalness or nature quality on small scales. The index of habitat specificity probably performs best when selecting biotopes for conservation based on spider communities. It

gives emphasis to those species that have narrower habitat demands and consequently are more sensitive to habitat modifications.

CONCLUSIONS

In general, habitat affinities were rarely clear-cut. Most numerous species tended to occur in more than one of the defined habitat types. Nevertheless, overall plant composition seemed to be a good indicator of spider communities, at least within localities.

The high dominance of specialists shows that the spider species composition is generally predictable. Therefore, the species list itself does not indicate anything that could not be inferred from floristic data. In other words, many of the species are more or less as rare and valuable as the peat bogs. Therefore, if spiders are to be used as indicators in peat bogs, it has been shown here necessary to perform an evaluation of the fauna based on relative abundance of individual species. It is then possible to distinguish between localities that might otherwise appear identical based on floristic data.

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Species	Code	Niche width	GBM	SBM	GC	SC	G Erica	S Erica	G Erio	S Erio	GM	SM	Σ
Mimetidae													
<i>Ero furcata</i> (Villers)	Ero.fur	2							1				1
Theridiidae													
<i>Anelosimus vittatus</i> (C.L. Koch)	Ane.vit	2				1							1
<i>Episinus angulatus</i> (Bl.)	Epi.ang	4			4	1	3	1			1		10
<i>Euryopis flavomaculata</i> (C.L.Koch)	Eur.fla	2			4	4			3				11
<i>Robertus lividus</i> (Bl.)	Rob.liv	1	17	4	6	3		4	14			7	55
Linyphiidae													
<i>Ceratinella brevis</i> (Wider)	Cer.bre	1	5	1	2	2	1		1		6		18
<i>Ceratinella brevipes</i> (Westr.)	Cer.brp	4							1				1
<i>Walckenaeria acuminata</i> Bl.	Wal.acu	1		2		1						1	4
<i>Walckenaeria alticeps</i> (Denis)	Wal.alt	2	54	21	33	33	52	9	25	12	44	27	310
<i>Walckenaeria antica</i> (Wider) (E)	Wal.ant	2			1	1	3						5
<i>Walckenaeria atrotibialis</i> (O.P.-C.)	Wal.atr	2		2				4	1			5	12
<i>Walckenaeria cucullata</i> (C.L.Koch)	Wal.cuc	1	9	4	8						2	1	24
<i>Walckenaeria cuspidata</i> Bl.	Wal.cus	3	9	5		2	4	4		2	11	3	40
<i>Walckenaeria dysderoides</i> (Wider)	Wal.dys	2	13		1		1		9		6		30
<i>Walckenaeria incisa</i> (O.P.-C.)	Wal.inc	2	1						1				2
<i>Walckenaeria kochi</i> (O.P.-C.)	Wal.koc	3					1				6		7
<i>Walckenaeria nudipalpis</i> (Westr.)	Wal.nud	3	9	3	3	2	4	1		2	6	2	32
<i>Walckenaeria unicornis</i> O.P.-C.	Wal.uni	3			1						2		3
<i>Diacymbium brevisetosum</i> Locket (E)	Dic.nig	2	4	4									8
<i>Diacymbium tibiale</i> (Bl.)	Dic.tib	2	6	15	2	18	1	3	2	2		7	56
<i>Gnathonarium dentatum</i> (Wider)	Gna.den	3							4				4
<i>Dismodicus elevatus</i> (C.L.Koch)	Dis.ele	3									3	1	4
<i>Metopobactrus prominulus</i> (O.P.-C.)	Met.pro	4		1						2			3
<i>Gonatium rubellum</i> (Bl.)	Gon.rbl	4										1	1
<i>Gonatium rubens</i> (Bl.)	Gon.rub	2		2							4		6
<i>Maso sundevalli</i> (Westr.)	Mas.sun	1	16	2	1	1			1				21
<i>Pocadicnemis pumila</i> (Bl.)	Poc.pum	1	2	7	4	1	1	11	2	3	9	20	60
<i>Oedothorax agrestis</i> (Bl.) (E)	Oed.agr	3										1	1
<i>Oedothorax fuscus</i> (Bl.) (E)	Oed.fus	3	1					1		1			3
<i>Oedothorax gibbosus</i> (Bl.)	Oed.gib	3	6	8	2		2	13	10	29	38	10	118
<i>Oedothorax retusus</i> (Westr.)	Oed.ret	3								1			1
<i>Silometopus elegans</i> (O.P.-C.)	Sil.ele	4								1			1
<i>Cnephallocotes obscurus</i> (Bl.) (E)	Cne.obs	3		1		1	1				2		5
<i>Evansia merens</i> O.P.-C.	Eva.mer	4			2	2				1			5
<i>Tiso vagans</i> (Bl.) (E)	Tis.vag	2				2							2
<i>Minyriolus pusillus</i> (Wider)	Min.pus	2										1	1
<i>Tapinocyba pallens</i> (O.P.-C.)	Tap.pal	2	1	2	3				2		2	3	13
<i>Tapinocyba praecox</i> (O.P.-C.) (E)	Tap.pra	3				2	23		3		1	1	30
<i>Thyreostenicus biovatus</i> (O.P.-C.)	Thy.bio	2		3						1			4
<i>Thyreostenicus parasiticus</i> (Westr.)	Thy.par	2	1									2	3
<i>Lophomma punctatum</i> (Bl.)	Lop.pun	3	1	12				5	8	14	3	1	44
<i>Gongtylidiellum murcidum</i> Simon	Gon. mur	4	2		1						8		11
<i>Gongtylidiellum vivum</i> (O.P.-C.)	Gon.viv	2	4										

Species	Code	Niche width	GBM	SBM	GC	SC	G Erica	S Erica	G Erio	S Erio	GM	SM	Σ
<i>Diplocephalus permixtus</i> (O.P.-C.)	Dip.per	3	1					2	4	3	11		21
<i>Diplocephalus picinus</i> (Bl.)	Dip.pic	2		12		2			1				15
<i>Araeoncus crassiceps</i> (Westr.)	Ara.cra	4								6			6
<i>Typhochrestus digitatus</i> (O.P.-C.)	Typ.dig	4			1								1
<i>Erigone atra</i> (Bl.) (E)	Eri.atr	1	2	1	1		48		4	7	2		65
<i>Drepanotylus uncatus</i> (O.P.-C.) (E)	Dre.unc	3								1	4		5
<i>Aphileta misera</i> (O.P.-C.)	Aph.mis	4						5		1			6
<i>Agynera conigera</i> (O.P.-C.)	Agy.con	2							1				1
<i>Agynera ramosa</i> Jackson	Agy.ram	4		1								5	6
<i>Meioneta rurestris</i> (C. L. Koch) (E)	Mei.rur	2				1							1
<i>Microneta viaria</i> (Bl.)	Mic.via	2	6	51	4	4				1		21	87
<i>Maro minutus</i> O.P.-C.	Mar.min	3		1				1		11			13
<i>Centromerus dilutus</i> (O.P.-C.)	Cen.dil	2			1								1
<i>Centromerus incilium</i> (L. Koch)	Cen.inc	3		1	1				1			1	4
<i>Centromerus sylvaticus</i> (Bl.) (E)	Cen.syl	1					1						1
<i>Tallusia experta</i> (O.P.-C.)	Tal.exp	3	11		1		1			1	8	4	26
<i>Centromerita concinna</i> (Thorell)	Cen.con	2		1	2	15	4			3		1	26
<i>Saariaea abnormis</i> (Bl.)	Saa.abn	1							1			1	2
<i>Macrargus rufus</i> (Wider)	Mac.ruf	2	6	5	1					1	2	1	16
<i>Bathypantes approximatus</i> (O.P.-C.)	Bat.app	3	3							1	3		7
<i>Bathypantes gracilis</i> (Bl.) (E)	Bat.gra	1	1	9	3	1	5	15	11	32	12	12	101
<i>Bathypantes nigrinus</i> (Westr.)	Bat.nig	2	1	1									2
<i>Bathypantes parvulus</i> (Westr.)	Bat.par	3	2	1	1			1	11		1	20	37
<i>Diplostyla concolor</i> (Wider)	Dip.con	2	11	6	12	3	1		1	1	2	5	42
<i>Stemonyphantes lineatus</i> (L.)	Ste.lin	2	2	1	2	3	1	1		2	1		13
<i>Bolyphantes alticeps</i> (Sund.)	Bol.alt	1	1										1
<i>Lepthyphantes cristatus</i> (Menge)	Lep.cri	2	11										11
<i>Lepthyphantes ericaeus</i> (Bl.)	Lep.eri	2	1										1
<i>Lepthyphantes flavipes</i> (Bl.)	Lep fla	3	43	11	2	1		3	5	1	1	6	73
<i>Lepthyphantes mengei</i> Kulczynski (E)	Lep.men	2	6		4	1	1	1	1		6	6	26
<i>Lepthyphantes tenuis</i> (Bl.) (E)	Lep.ten	1	1					1	2				4
<i>Lepthyphantes zimmermanni</i> Bertkau	Lep.zim	2	2										2
<i>Linyphia hortensis</i> Sund. (E)	Lin.hor	4		1									1
<i>Linyphia triangularis</i> (Cl.) (E)	Lin.tri	1					1						1
<i>Neriene clathrata</i> (Sund.)	Ner.cla	2	6	4	2							4	16
<i>Microlinyphia pusilla</i> (Sund.) (E)	Mic.pus	2			1					1			2
Araneidae													
<i>Cercidia prominens</i> (Westr.)	Cer.pro	2				1						1	2
Tetragnathidae													
<i>Pachygnatha clercki</i> Sund.	Pac.cle	2	2										2
<i>Pachygnatha degeeri</i> Sund. (E)	Pac.deg	2				15	2	1			2	2	22
<i>Pachygnatha listeri</i> Sund.	Pac.lis	4	15	2	1	3		1	2	1		1	26
<i>Metellina mengei</i> (Bl.)	Met.men	4	3		1						1		5
Lycosidae													
<i>Alopecosa barbipes</i> (Sund.)	Alo.bar	4					1						1
<i>Alopecosa cuneata</i> (Cl.)	Alo.cun	3					1	4			2		7
<i>Alopecosa inquilina</i> (Cl.)	Alo.inq	4								1			1
<i>Alopecosa pulverulenta</i> (Cl.) (E)	Alo.pul	2		32	6	57		14		10	12	35	166
<i>Arctosa leopardus</i> (Sund.)	Arc.leo	4					5	1		1	1		8
<i>Pardosa lugubris</i> (Walck.)	Par.lug	4	7	223	35	318	3	40	34	21	18	59	758
<i>Pardosa monticola</i> (Cl.)	Par.mon	4							1				1
<i>Pardosa nigriceps</i> (Thorell)	Par.nig	4			5	52	9	7	1	5	8		87
<i>Pardosa palustris</i> (L.)	Par.pal	2					1						1
<i>Pardosa pratigaga</i> (L.Koch)	Par.pra	2	5	11	22	85	94	63	16	62	56	50	464
<i>Pardosa pullata</i> (Cl.)	Par.pul	2	1	5	35	456	49	103	23	126	39	28	865
<i>Pardosa sphagnicola</i> (Dahl)	Par.sph	4	8	36	6	5	11	53	26	105	60	14	324
<i>Xerolycosa nemoralis</i> (Westr.)	Xer.nem	4			34	8	22			1	1		66

Species	Code	Niche width	GBM	SBM	GC	SC	G Erica	S Erica	G S Erio	S Erio	GM	SM	Σ
<i>Pirata piraticus</i> (Cl.) (E)	Pir.pir	3		2	2		2	2	14	4	4	3	33
<i>Pirata piscatorius</i> (Cl.)	Pir.pis	4		1		4		29	9	28	9	3	83
<i>Pirata uliginosus</i> (Thorell)	Pir.uli	4	272	75	9	29	10	127	17	98	477	77	1191
<i>Trochosa ruricola</i> (Degeer)	Tro.rur	2			1		33	1	2		22		59
<i>Trochosa spinipalpis</i> (F. O.P.-C.)	Tro.spi	4	171	112	29	43	31	42	29	29	165	34	685
<i>Trochosa terricola</i> Thorell (E)	Tro.ter	1	65	107	157	194	48	14	44	44	94	69	836
Pisauridae													
<i>Pisaura mirabilis</i> (Cl.) (E)	Pis.mir	2				3							3
<i>Dolomedes fimbriatus</i> (Cl.) (E)	Dol.fim	4		1		3		4	4	11		1	24
Argyronetidae													
<i>Argyroneta aquatica</i> (Cl.)	Arg.aqu	4										1	1
Hahniidae													
<i>Antistea elegans</i> (Bl.)	Ant.ele	4	87	29	11	41	61	129	206	205	235	31	1035
<i>Hahn timer helveola</i> Simon	Hah.hel	2				1				1			2
<i>Hahn timer montana</i> (Bl.)	Hah.mon	1					1						1
<i>Hahn timer pusilla</i> (Bl.)	Hah.pus	2	1	1									2
Agelenidae													
<i>Cicurina cicur</i> (Fabr.)	Cic.cic	1			2			1					3
<i>Cryphoea silvicola</i> (C.L. Koch)	Cry.sil	4	1										1
Dictynidae													
<i>Dictyna arundinacea</i> (L.)	Dic.aru	2							1				1
Liocranidae													
<i>Agroeca brunnea</i> (Bl.)	Agr.bru	2	12	9	13	3	6	3			6	8	60
<i>Agroeca proxima</i> (O. P.-C.)	Agr.pro	3	6		29	1	20		14	1	7	9	87
<i>Phrurolithus festivus</i> (C.L. Koch)	Phr.fes	2			4				4	10		2	20
<i>Scotina gracilipes</i> (Bl.)	Scog.ra	3					8						8
Clubionidae													
<i>Cheiracantium virescens</i> (Sund.)	Che.vir	4			3	1							4
<i>Clubiona frutetorum</i> (L. Koch)	Clu.fru	2										1	1
<i>Clubiona terrestris</i> (Westr.)	Clu.ter	2	1	1						1			3
Gnaphosidae													
<i>Drassodes cupreus</i> (Bl.)	Dra.cup	2	1	1	5	14	3	1		1	10		36
<i>Drassodes pubescens</i> (Thorell)	Dra.pub	2				2		1					3
<i>Haplodrassus signifer</i> (C. L. Koch)	Hap.sig	2	1		14	12	7		1				35
<i>Haplodrassus silvestris</i> (Bl.)	Hap.sil	4					1						1
<i>Micaria aenea</i> Thorell	Mic.aen	3				1					1		2
<i>Micaria fulgens</i> (Walck.)	Mic.ful	3			5	1	1	1					8
<i>Micaria pulicaria</i> (Sund.) (E)	Mic.pul	2			1	6	1		2	1	4		15
<i>Zelotes clivicola</i> (L. Koch)	Zel.cli	3	9		22	14	6	1	8	1	5	3	69
<i>Zelotes latreillei</i> (Simon)	Zel.lat	3			3	4	2	2	1	3			15
<i>Zelotes longipes</i> (L. Koch)	Zel.lon	4					1						1
<i>Zelotes petrensis</i> (C. L. Koch)	Zel.pet	4			15	4	1			2			22
<i>Zelotes subterraneus</i> (C.L. Koch)	Zel.sub	2	1	1	1	7	1		4				15
<i>Drassyllus praeficus</i> (L. Koch)	Zel.pra	4				10				1		1	12
<i>Drassyllus pusillus</i> (C.L. Koch) (E)	Zel.pus	2		4	5	26	7	5		7	4	1	59
Zoridae													
<i>Zora spinimana</i> (Sund.)	Zor.spi	1	3	12	7	6	1	1	3		7	10	50
Heteropodidae													
<i>Micrommata virescens</i> (Cl.)	Mic.vir	2		1									1
Philodromidae													
<i>Philodromus aureolus</i> (Cl.) (E)	Phi.aur	2								1			1
<i>Tibellus oblongus</i> (Walck.)	Tib.obl	2				1							1
Thomisidae													
<i>Xysticus bifasciatus</i> C.L. Koch	Xys.bif	4				1							1
<i>Xysticus cristatus</i> (Cl.) (E)	Xys.cri	2			2								2

