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CHANGES IN THE SPIDER (ARANEAE) FAUNA ALONG A HEATHLAND-MARSH TRANSECT IN DENMARK

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Abstract

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Pitfall traps were operated through a full year in nine habitats along a 200 m transect covering a variety of heathland and wetland vegetation types (*Calluna, Erica, Empetrum, Molinia, Myrica, Salix, Carex, Phragmites*). Principal Component Analysis and similarity indices distinguished two groups of spider communities, a heathland and a marsh community. Surprisingly, the fauna of the *Molinia* meadow belonged to the heathland type, in spite of higher habitat similarity with marshes. Neither vegetation structure, soil moisture or proximity in the habitat mosaic could explain the pattern of spider species composition.

Introduction

The factors that determine the species composition of spider communities are poorly understood. As with other groups of animals, physical and chemical factors of the environment influence the occurrence of each species (Nørgaard, 1951; Foelix, 1996). Duffey (1962, 1966) argued that the spatial structure of the vegetation was an important factor, especially for vegetation-living web-spinning spiders. This view was extended by Curtis, Bignal (1980) to include the surface or near-surface-living spider communities recorded by pitfall trapping.

In a previous study (Gajdoš, Toft, 2000) we analysed the changes that had occurred over a span of 20 years in the ground-living spider fauna in a habitat mosaic of several types of heathland and poor meadow in North-western Jutland, Denmark. We found a surprising similarity in faunistic composition between vegetation types that were quite

T a b l e 1. Characterisation of the habitats of the transect studied (cf. Fig. 1). +: coverage <5%. Moss: cover of soil surface between higher vegetation; Ca- *Calluna vulgaris,* Cp- *Carex paniculata,* Df- *Deschampsia flexuosa,* Dp- *Deschampsia palustris,* En- *Empetrum nigrum,* Et- *Erica tetralix,* Ja- *Juncus articulatus,* Mc- *Molinia coerulea,* Mg- *Myrica gale,* Pa- *Phragmites australis,* Sr- *Salix repens,* Sc- *Salix cinerea.*

Traps	**Vegetation type**	**Soil**	**Life form**	**Vegetation coverage §**
1-2.	Mixed Calluna / Empetrum heath	High / dry	Dwarf shrub	Cv 50%, En 30%, Et 15%, Ja +, Sr +, moss 100%
3-4.	Erica tetralix heath	Low / wet	Dwarf shrub	Et 90%, Mc +, lichens +, moss 60%
5-6.	Empetrum heath	High / dry	Dwarf shrub	En 70%, Df 10%, Sr 10%, Et 5%, Mc +, moss 40%
7-8.	Molinia meadow	Low / wet	Meadow	Mc 90%, Et 10%, En 5%, Sr +, moss +, lichens +
9-10.	Myrica gale/ Molinia swamp	Low / very wet	Shrub (ca. 0.6 m)	Mc 50%, Mg 40%, Carex +, Salix +, Pa +, moss +
11-12.	Empetrum heath	High / dry	Dwarf shrub	En 60%, Df 40%, Et 5%, lichens +, moss 60%
13-14.	Salix marsh	Low / wet	Shrub (ca. 2 m)	Sc 100%; litter 50%, Cp 20%, Pa 10%, Mc +, Dp +, moss +
15-16.	Carex marsh	Low / wet	Tussocks	Cp 85%, Dp +, Pa +
17-18.	Phragmites marsh	Low / wet	Meadow	Pa 100%

distinct with respect to both soil water content and vegetation structure. Although changes over time within each habitat type were also minute, they were larger than the differences between habitats. These findings seemed to contradict a clear relationship between vegetation structure and spider community composition. An alternative hypothesis that the close proximity of the habitats was responsible for the similarity in species composition could not be ruled out.

In the present study we extended the transect used earlier into a neighbouring marsh area. The marsh also had a variety of habitat types intermingled. We wanted to see if the uniformity of the fauna extended to the marsh habitats, since they were only slightly more humid than the wet heathland habitats but included a wider variety of vegetation structure. Further, the extended transect included juxtaposition of dry heathland and wet marshland and thus the possibility of testing the proximity hypothesis.

Study area

The locality Tørvekjær is situated near Klitmøller, Thy (northwestern Jutland), Denmark, ca. 3.5 km from the North Sea. It is situated in a flat area between the coastal dunes and the lake Vester Vanned Sø. The habitats studied were situated along a transect (total length ca. 200 m) that sloped only slightly (ca. ½ m in total) from the sandy heath into the marsh. Sandy ridges (10-30 cm in height) perpendicular to the transect, deposited by the prevailing westerly winds, create an alternation of high-dry and low-wet habitats. Thus, the area forms a mosaic of quite different habitat types, each of small extent. All habitats are oligotrophic. A more detailed botanical characterisation is given in Table 1. The low-wet habitats, incl. the *Erica* heath, may be flooded during winter and early spring, resulting in reduced spider catches during these periods.

Material and methods

Pitfall traps were operated through a full year (May 1997 to May 1998), two traps at each site, buried 1-2 m apart. They consisted of a plastic flower pot creating the outer permanent hole, and a fitting plastic beaker (∅11 cm) as the removable catching unit. The traps were covered by a roof and contained a mixture of 3% formalin and ethylene glycol, with detergent added. They were emptied bi-weekly during the active season, and approximately monthly during winter.

The material was identified to species and the summed catches over the year for every trap were the units analysed. First, they were subjected to a Principal Component Analysis (PCA) using the CANOCO program version 2.1 (ter Braak, 1987, Jongman et al., 1987). All species caught were included in the analysis, which was performed on log-transformed numbers. Second, two similarity indices for pairwise comparisons were used (cf. Southwood, 1966): the Sørensen quotient of similarity QS=2j/(a+b), where a and b are the number of species in the two samples, and j the number of species common to both samples; and the percentage of similarity $\%S=E_i \min(p_{ia},p_{ib})$, which sums the lowest values for the proportional abundances (p) of each species (i) in the two samples (a,b). The Sørensen index is qualitative because it considers species presence or absence only, whereas the percentage similarity index is quantitative because it takes the numerical representation of the species into account.

Results

A total of 135 species were identified among 5641 individuals. The full list of species and the total numbers collected at each of the nine habitats, are given in Appendix 1. There was no relationship between the number of individuals and the number of species recorded from the habitats (see summary rows at the end of Appendix 1). However, the number of species per individual caught was significantly higher in the wetland habitats than in the heathland habitats (incl. *Molinia* site) (P=0.038, t-test).

Principal Component analysis

The pairs of traps from each habitat are clearly grouped in pairs also in the Principal Component (PC) plot (Fig. 1), indicating a generally greater similarity within than between pairs. It is further seen that the heathland habitats (incl. the *Molinia* meadow) form one group, and the marsh habitats another, along the first PC-axis. The marsh habitats seem to stretch out along the second PC-axis. However, no clear gradients in ground water content or vegetation structure can be discerned in the pattern revealed. The same is true when the

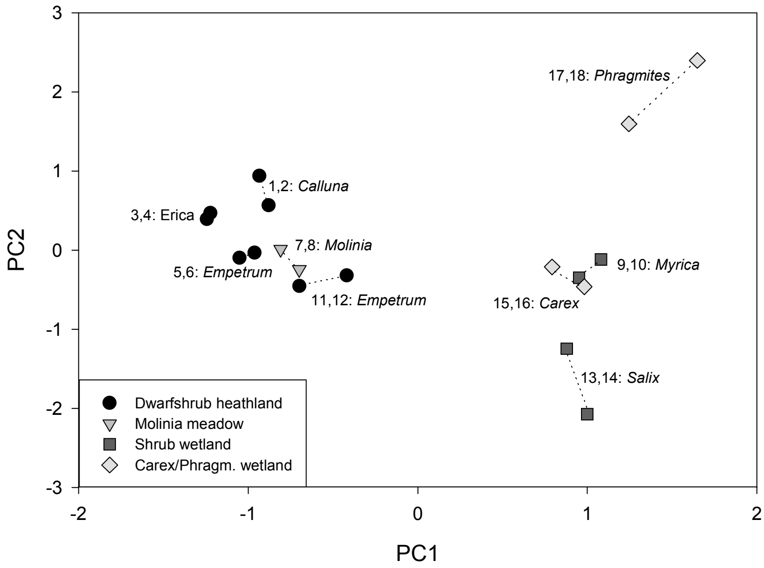

Fig. 1. Site plot of the Principal Component Analysis. Each symbol represents the total catch of a trap through a year. Dotted lines connect pairs of traps. Trap numbers and habitat type indicated.

heathland habitats are considered: wet and dry habitats, and dwarf shrubs and grass meadow mingle with no interpretable pattern.

Fig. 2 shows the species plot of the PCA; only species with 320 individuals are shown. Species to the left are the ones most characteristic of the heathland habitats (of which the most abundant are *Gnaphosa leporina*(L. KOCH), *Drassodes cupreus* (BLACKWALL)*, Peponocranium ludicrum* (O. P.-CAMBRIDGE), *Centromerita concinna* (THOTRELL)). The species to the right in the figure are those characteristic of marshes (the most numerous being *Haplodrassus moderatus* (KULCZYŃSKI)*, Zora spinimama* (SUNDEVALL)*, Pocadicnemis pumila* (BLACKWALL)*, Bathyphantes parvulus* (WESTRING)). Several very abundant species (e.g. *Euryopis flavomaculata* (C. L. KOCH)*, Pardosa pullata* (CLERCK)*, Agroeca proxima* (O. P.-CAMBRIDGE)*)* were distributed over the full range of habitats (they fall in the middle of the graphs).

Similarity analysis

All the possible pairwise similarity values for spider species composition are illustrated in Fig. 3. The patterns revealed confirm the results of the Principal Component Analysis. Thus, all heathland habitats are very similar to other heathlands, all wetland habitats to other wetlands, whereas the similarity between heathland and wetland habitats are much

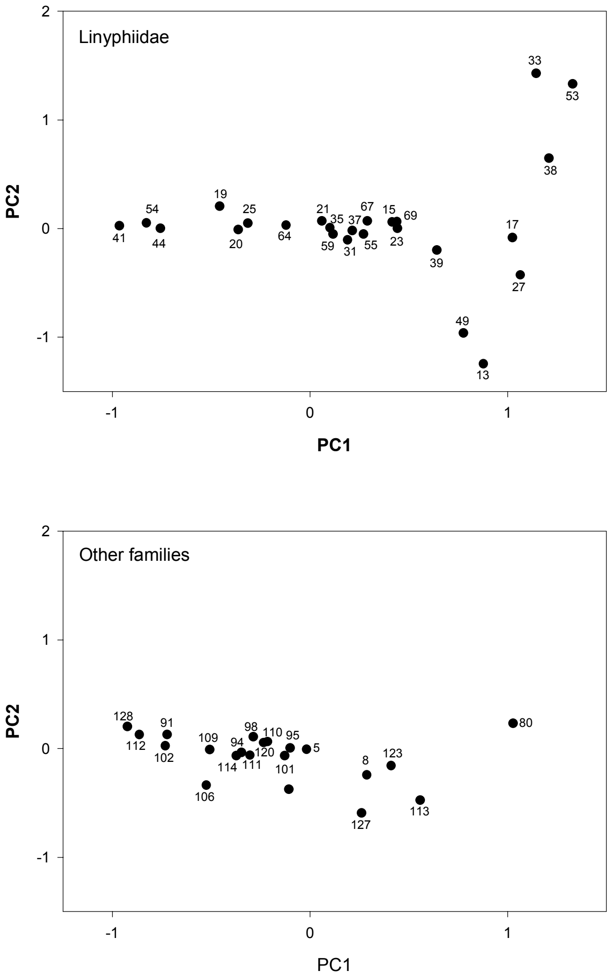

Fig. 2. Species plots of the Principal Component Analysis. Only species with 320 individual caught are illustrated. 5- *E. flavomaculata*, 7- *P. gibbum*, 8- *R. lividus*, 13- *A. scopigera*, 15- *B. gracilis*, 17- *B. parvulus*, 19- *C. bicolor*,20- *C. concina*, 21- *C. dilutus*, 23- *C. sylvaticus*, 25- *C. obsrurus*, 27- *D. bifrons*, 31- *G. rubens*, 33- *H. biturbeculatum*, 35- *L. ericaceus*, 37- *L. mengei*, 38- *L. tenuis*, 39- *L. zimmermani*, 41- *M. carpenteri*, 44- *M. rurestris*, 49- *M. viaria*, 53- *O. retusus*, 54- *P. ludicrum*, 55- *P. pumila*, 59- *S. abnormis*, 64- *T. pallens*, 67- *W. acuminata*, 69- *W. atrotibialis*, 80- *P. clercki*, 91- *A. pulverulenta*, 94- *P. nigriceps*, 95- *P. pullata*, 98- *T. terricola*, 101- *A. proxima*, 102- *S. gracilepis*, 106- *C. diversa*, 109- *D. cupreus*, 110- *D. pubescens*, 111- *D. pusillus*, 112- *G. leporina*, 113- *H. moderatus*, 114- *H. signifer*, 120- *Z. latreillei*, 123- *Z. spinimana*, 127- *O. trux*, 128- *X. cristatus*.

lower. It is also seen that the spider fauna of the Molinia meadow is highly similar to that of the heathlands, but much less so to that of the wetlands.

The faunistic identity between heathland and wetland communities, respectively, can be illustrated by comparing the similarity values (Fig. 3) with those obtained by comparing the catches from the two traps in each habitat. Over the nine habitats, the Sørensen QS varies between 66.6 and 75.9%, and the %S between 64.9 and 82.2%. Thus, the values for within-habitat similarity are only slightly smaller than for between-habitat (within habitat type) similarity.

Fig. 3 A and B show equal Sørensen QS within heathlands and wetlands but a relatively lower percentage similarity for the wetlands. The pattern of Fig. 3B is equivalent to the larger scatter of the wetland sites along the PC2 axis in Fig. 1. The different results of the similarity indices indicate, that the variation between the wetland sites is not due to difference in species content but to differences in the numerical representation of species.

Discussion

Our results do not confirm a strong relationship between habitat structure and species composition of epigeic spider communities; also we did not find spider communities to be strongly related to soil moisture of the habitats. Though there was a clear separation into two groups of spider communities, from heathlands and marshes respectively, we can identify no habitat characteristic that would have predicted the exact separation of sites. The main question was the assignment of the *Molinia* meadow. Both because of its vegetation and its soil humidity we would have expected its spider fauna to be more similar to that of the marsh habitats than to the heathlands. But we found a high similarity in species composition between the dwarf shrub heathlands, whether dry or humid, and the *Molinia* meadow.

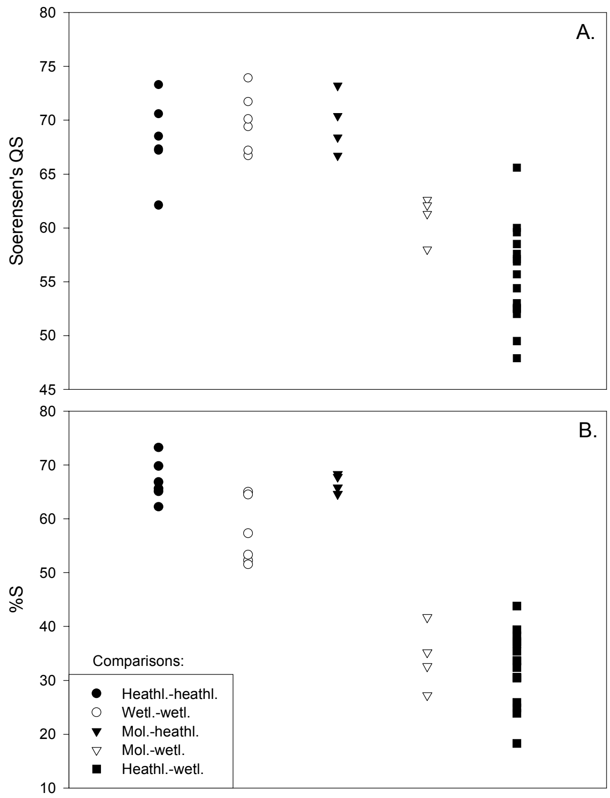

Fig. 3. Similarity indices for all pairwise comparisons of habitats (summed catches of two traps per habitat). A. Sørensen's Quotient of Similarity. B. Percentage of Similarity.

We also found a high similarity between high and low heathland sites, that are strikingly different in soil moisture content.

Although ground humidity did not seem to influence the fauna of the heathland habitats, there was a clear distinction between heathland and marsh fauna. Since the vegetation was higher in the marsh than in any of the heath habitats, vegetation structure may be of influence here. However, the habitats available were so different with respect to vegetation structure (grassy vs. shrubby vegetation), vegetation height or degree of flooding, that a clear pattern was not to be expected.

An influence of neighbouring habitats in levelling out differences in spider species composition of the haitats is a possibility in a small-grained habitat mosaic, and may possibly explain some of the similarity between the habitats. However, the effect is certainly not so pervasive as to explain the detailed patterns. Thus, the *Molinia* meadow was neighboured by dry heathland on one side and very wet *Myrica* swamp (which even had *Molinia* as the dominant plant species (Table 1)) on the other, yet its fauna was clearly of the heathland type. Also, the trap 11-12 *Empetrum* site had marshes on all sides, and its fauna was of the heathland type.

In conclusion, the results distinguish two spider communities, related to heathlands and wetlands, respectively. However, the assignment to habitats is not based on habitat structure or soil humidity in any obvious way.

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Appendix 1. Total catches during one year (May 1997 – May 1998) in nine habitats along a heathland – marsh transect at Tørvekjær, Thy, Denmark (2 pitfall traps per habitat).

Species	**Study habitats (trap numbers)**									**Total**
	1,2	**3,4**	**5,6**	**7,8**	**9,10**	**11,12**	**13,14**	**15,16**	**17,18**	
Ero cambridgei KULC.	1							4		**4**
Ero furcata (VILL.)				1	1		1	4	3	**10**
Crustulina sticta (O. P.-C.)		1					1	1		**2**
Episinus angulatus (BL.)							1			**1**
Euryopis flavomaculata (C. L. K.)	3	2		1		10	2	7	2	**27**
Paidiscura pallens (BL.)									1	**1**
Pholcomma gibbum (WEST.)	3	3	7	17	4	9	18	5		**66**
Robertus lividus (BL.)	2	1	2	3	20	15	7	8	3	**61**
Theridion bimaculatum (L.)	1							1	2	**4**
Theridion tinctum (WALC.)			1							**1**
Agyneta conigera (O. P.-C.)		1		1	7		9	1		**19**
Agyneta subtilis (O. P.-C.)	3									**3**
Allomengea scopigera (GRUBE)					2			2	12	**16**
Allomengea vidua (L. K.)									1	**1**
Aphileta misera (O. P.-C.)								1		**1**
Bathyphantes gracilis (BL.)	1	2	2	1	7	1	3	5	4	**26**
Bathyphantes nigrinus (WEST.)					1		3			**4**
Bathyphantes parvulus (WEST.)				1	5		83	40	47	**176**
Bolyphantes luteolus (BL.)									1	**1**
Centromerita bicolor (BL.)	8	4	2	4			2	2	1	**23**
Centromerita concinna (TH.)	74	115	73	144	33	167	9	18	3	**636**
Centromerus dilutus (O. P.-C.)	10	11	10	14	13	10	14	22	17	**121**
Centromerus prudens (O. P.-C.)	1									**1**
Centromerus sylvaticus (BL.)	3	2	5	6	10	17	28	60	90	**221**
Ceratinella brevipes (WEST.)								1	1	**2**
Cnephalocotes obscurus (BL.)	10		3			6	1	2	1	**23**
Dicymbium brevisetosum LOCK.				1						**1**
Dismodicus bifrons (BL.)					1		22	1	5	**29**
Entelecara congenera (O. P.-C.)									1	**1**
Erigone atra (BL.)		1		1		3	1			**6**
Floronia bucculenta (CL.)					5		1	1	1	**8**
Gonatium rubens (BL.)	9	1	11	7	6	6	32	16	10	**98**
Gongylidiellum vivum (O. P.-C.)		1					1	1	1	**4**
Hypomma bituberculatum (WIDER)				1	2				26	**29**
Kaestneria pullata (O. P.-C.)	1									**1**
Lepthyphantes ericaeus (BL.)	17	2	14	30	20	15	17	17	17	**149**
Lepthyphantes flavipes (BL.)	1		1			1				**3**
Lepthyphantes mengei KULC.	20	11	13	13	30	10	81	88	39	**305**
Lepthyphantes tenuis (BL.)					2		4	1	18	**25**
Lepthyphantes zimmermanni BERT.			3		10	2	6	2	4	**27**
Linyphia triangularis (CL.)									1	**1**
Macrargus carpenteri (O. P.-C.)	1	6	13	3		6				**29**
Macrargus rufus (WIDER)		1								**1**
Meioneta beata (O. P.-C.)		1	3	6						**10**
Meioneta rurestris (C. L. K.)	1	6	2	6	1	6				**22**
Meioneta saxatilis (BL.)							2	3		**5**
Micrargus herbigradus (BL.)				2	1	2	4	5	1	**15**
Microlinyphia impigra (O. P.-C.)									3	**3**
Microlinyphia pusilla (SUND.)				1				1		**2**
Microneta viaria (BL.)						2	20		2	**24**
Minyriolus pusillus (WIDER)	2		1						1	**4**

Appendix 1.

Species	Study habitats (trap numbers)									Total
	1,2	**3,4**	**5,6**	**7,8**	**9,10**	**11,12**	**13,14**	**15,16**	**17,18**	
Oedothorax apicatus (Bl.)		1	1							**2**
Oedothorax gibbosus (Bl.)					5		3	2	7	**17**
Oedothorax gibbosus tuberosus (Bl.)					1			1		**2**
Oedothorax retusus (West.)					1			2	16	**19**
Peponocranium ludicrum (O. P.-C.)	19	12	38	26	1	25				**121**
Pocadicnemis pumila (Bl.)	12		7	23	10	18	46	50	29	**195**
Poeciloneta globosa (Wider)	1		3	1			2	2		**9**
Porrhomma pallidum Jack.							1		1	**2**
Porrhomma pygmaeum (Bl.)					1					**1**
Saaristoa abnormis (Bl.)	2	6	1	3	7	1	4	3	2	**29**
Saaristoa firma (O. P.-C.)							2		5	**7**
Silometopus elegans (O. P.-C.)						1	1	8	2	**12**
Stemonyphantes lineatus (L.)			1					1		**2**
Tallusia experta (O. P.-C.)					6	1		7	1	**15**
Tapinocyba pallens (O. P.-C.)	3	5	7	2		4	3	8	3	**35**
Tapinocyba praecox (O. P.-C.)	3					1	1			**5**
Tapinopa longidens (Wider)	1		4	2			2		1	**10**
Walckenaeria acuminata Bl.	1		1	4	4	6	4		7	**27**
Walckenaeria antica (Wider)	1		10	5		2			1	**19**
Walckenaeria atrotibialis (O. P.-C.)	8			2		1	13	12	7	**43**
Walckenaeria corniculans (C. L. K.)				1						**1**
Walckenaeria cucullata (C. L. K.)	1						1			**2**
Walckenaeria cuspidata (Bl.)			1	1	2	2	3		2	**11**
Walckenaeria dysderoides (Wider)	2	1				8	2	3	2	**18**
Walckenaeria kochi (O. P.-C.)						3	2	3	5	**13**
Walckenaeria monoceros (Wider)	1		5	4						**10**
Walckenaeria nudipalpis (West.)	1		1	2	3		4	2	4	**17**
Walckenaeria obtusa (O. P.-C.)				1	1		4	1		**7**
Walckenaeria unicornis (O. P.-C.)	1				2	3	1		4	**11**
Metellina segmentata (Cl.)	1						1		1	**3**
Pachygnatha clercki Sund.	1				37		7	11	29	**85**
Pachygnatha degeeri Sund.		1				1				**2**
Tetragnatha extensa (L.)								1		**1**
Tetragnatha pinicola L. K.	1									**1**
Araneus diadematus Cl.							1			**1**
Araneus quadratus Cl.		1								**1**
Cercidia prominens (West.)					1					**1**
Hypsosinga sanguinea (C. L. K.)		1		1					1	**3**
Larinioides cornutus (Cl.)							2			**2**
Neoscona adianta (Walc.)	1									**1**
Alopecosa accentuata	1	6	1							**8**
Alopecosa pulverulenta (Cl.)	20	26	24	18	1	5	1	1	1	**97**
Pardosa amentata (Cl.)					1					**1**
Pardosa monticola (Cl.)		2		3		1		2		**8**
Pardosa nigriceps	44	64	50	36	7	86	22	6	4	**319**
Pardosa pullata (Cl.)	25	74	44	154	26	59	54	34	31	**501**
Trochosa ruricola (De Geer)			2			1	3			**6**
Trochosa spinipalpis (O. P.-C.)							1			**1**
Trochosa terricola (Th.)	24	18	12	19	4	31	4	6	7	**125**
Antistea elegans (Bl.)	1									**1**
Hahnia nava (Bl.)	6	3		2						**11**
Agroeca proxima (O. P.-C.)	5	10	18	16	7	16	12	6	6	**96**

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Species	Study habitats (trap numbers)									Total
	1,2	**3,4**	**5,6**	**7,8**	**9,10**	**11,12**	**13,14**	**15,16**	**17,18**	
Scotina gracilipes (BL.)	4	10	8	11		15	1		1	**50**
Cheiracanthium erraticum (WALC.)	1			1	1				1	**4**
Cheiracanthium virescens (SUND.)	2	4	1						1	**8**
Clubiona comta C. L. K.							1			**1**
Clubiona diversa O. P.-C.		2	3	8		4	2	1		**20**
Clubiona neglecta O. P.-C.						3				**3**
Clubiona stagnatilis KULC.					2		9	2	3	**16**
Drassodes cupreus (BL.)	10	41	49	30	1	31	5	5	4	**176**
Drassodes pubescens (TH.)	3	2	7	2	2	5	3	2	2	**28**
Drassyllus pusillus (C. L. K.)	5	3	3	2	1	6	3	2	1	**26**
Gnaphosa leporina (L. K.)	79	213	85	86	2	53				**518**
Haplodrassus moderatus (KULC.)				3	5	10	29	3	4	**54**
Haplodrassus signifer (C. L. K.)	17	18	11	18	2	45	9	6	2	**128**
Micaria aenea TH.	3									**3**
Micaria pulicaria (SUND.)							1			**1**
Zelotes apricorum (L. K.)	1					1				**2**
Zelotes clivicola (L. K.)									1	**1**
Zelotes electus (C. L. K.)	1							1		**2**
Zelotes latreillei (SIMON)	11	7	11	6	1	11	5	7	4	**63**
Zelotes longipes (L. K.)	4	4	2		1	1	1		1	**14**
Zelotes subterraneus (C. L. K.)	1					1				**2**
Zora spinimana (Sund.)	2	2	3	4	8	14	41	15	16	**105**
? *Philodromus aureolus* (CL.)							1			**1**
Thanatus striatus C. L. K.				1		1				**2**
Tibellus maritimus (MENGE)					2				1	**3**
Ozyptila trux (BL.)	1		3	2	3	2	8	4		**23**
Xysticus cristatus (CL.)	9	7	5	3		4				**28**
Xysticus erraticus (BL.)		2				3				**5**
Xysticus kochi TH.					2		1	1		**4**
Aelurillus v-insignitus (CL.)			1							**1**
Bianor aurocinctus (OHLE.)								1	1	**2**
Euophrys frontalis (WALC.)	2	1	3	2						**8**
Heliophanus flavipes HAHN	1									**1**
Total individuals	**529**	**735**	**605**	**804**	**349**	**793**	**713**	**557**	**556**	**5641**
Total no. of species	**67**	**49**	**53**	**59**	**56**	**58**	**73**	**65**	**72**	**135**