

SPIDER BIODIVERSITY IN CONNECTION WITH THE VEGETATION STRUCTURE AND THE FOLIAGE ORIENTATION OF HEDGES

Frédéric Ysnel and Alain Canard: Laboratoire de Zoologie et d'Ecophysiologie,
UMR CNRS 6553, Université de Rennes I, Campus de Beaulieu, 35042 Rennes
Cedex, France

ABSTRACT. The relationship between the structure of spider communities and an index of hedge ecological quality (based on an analysis of vegetation architecture using vegetation diversity and foliage cover) was investigated. The comparison deals with six hedges each of low, medium and high ecological value. The species richness and species composition of dominant spiders was the same for hedges of different quality. Thus it is concluded that these two simple parameters cannot reflect the diversity of the hedge foliage. Indicating species of the differences between ecological quality of two hedges could be required among the groups of species absent from one type of hedge. However, the foliage orientation of the hedges may induce substitution of spider species; thus special attention must be paid to the foliage orientation when comparing the spider communities inhabiting the hedges.

Keywords: Foliage cover, foliage orientation, species richness

Shrubby and raised hedges constitute one of the major elements supporting faunistic diversity within rural landscapes. In western France in particular, studies undertaken on woody areas have shown the close associations between the vegetation architecture of the hedges and the diversity or density of the hedge-inhabiting fauna, especially birds, small mammals, reptiles and insects (Saint Girons 1994; Constant & Eybert 1995; Burel 1996). On a regional scale, classifications, based on vegetation, have been established to define the suitability of hedges for certain fauna, such as game birds (Brown & Aubineau 1989). To achieve the goals of hedgerow management (maintenance of biodiversity, wood production, amelioration of climatic effects and improvement of water quality), a special index of classification for the ecological value of the hedges was developed by Rozé (1995). This index was based on an analysis of the major architectural characteristics of hedges (vegetation diversity and percentage of foliage cover). Numerous workers have detailed the strong relationship between vegetation structure and the composition of spider communities; and it is often argued that this is the most important parameter involved in web site selection (Wise 1993). Consequently, it is expected that the diversity of spiders and the

species composition of the dominant spiders in hedge foliage can reflect the hedge ecological value when that value is defined by an index of quality integrating the vegetation architecture. The aim of this work was to investigate the relationship between the variation in the ecological index proposed by Rozé (1995) and the variation in the associated spider communities. A comparison of the spider communities inhabiting hedges of different ecological values is presented.

METHODS

Study area and index of hedge quality.—The area investigated was situated in an agricultural landscape of Brittany (western France) consisting of fallow-fields (24.5 ha) surrounded by raised hedges for which density reached 1700m/10 ha. The plot was in the district of Candé–La Brocherie at 1°2'W, 47°34' N. The evaluation method used to assess hedge quality took into account the floristic composition and structure of the hedges (Rozé 1995; Table 1). A high biological value was allotted to the hedges when they were established on a complex of ditches or slopes, when the foliage cover of the shrubby and arborescent layers was high, and when brambles and nettles were wanting. Additional points were allotted when species, which were not very

Table 1.—Card-data for the evaluation of the biological quality of one hedge. The number of points is indicated in parentheses.

1) Slope/Ditch complex	
ditch	(1)
slope	(1)
double hedge	(1)
ditch elevation (>1 m)	(2)
2) Trees	
percentage of re-covering	
<20%	(0)
20 < % < 50	(1)
>50%	(2)
spontaneous species (oak. . .)	(1)
not frequent species (alder, hornbeam. . .)	(1)
seedlings	(1)
3) Shrubs	
percentage of re-covering	
<20%	(0)
20 < % < 50	(1)
>50%	(2)
specific diversity 2–3 sp.	(1)
>4 sp.	(2)
original vegetation (spindle tree. . .)	(1)
4) Edge vegetation	
<i>Endymion non scripus</i> & <i>Anemone nemorsa</i>	(3)
<i>Umbilicus rupestris</i> & <i>Polypodium vulgare</i>	(2)
<i>Ruscus aculeatus</i> & <i>Rubis perenigra</i>	(2)
<i>Teucrium scorodonia</i> & <i>Stellaria holostea</i>	(1)
<i>Juncus effusus</i> + hydrophilous vegetation	(1)
<i>Rubus fruticosus</i> & <i>Dactylis glomerata</i>	(0)
<i>Pteridium aquilinum</i>	(0)
<i>Rubus fruticosus</i> & <i>Dactylis glomerata</i>	(0)
<i>Urtica dioica</i>	(-1)

frequently distributed at a regional scale, were present. The range of hedge ecological quality values varied from 1–20 which provided a comparative index for the biological quality of each hedge. **Collection of spiders and data analysis.**—Our previous investigations into the spider communities inhabiting shrub layers in western France have demonstrated that there was no considerable variation between the species composition of the “spring community” and the “annual community” for successive years (Canard 1979; Canard 1984; Ysnel et. al. 1996). These results concerning the temporal stability of the spider commu-

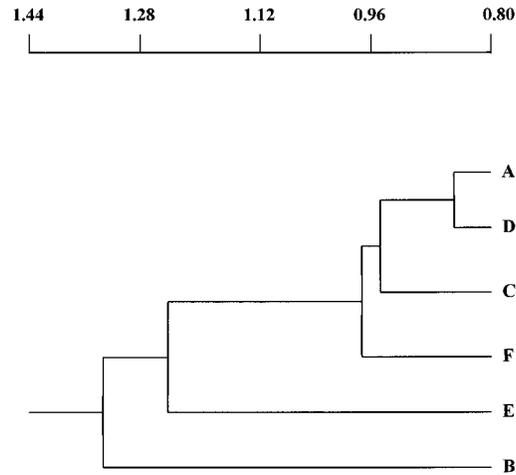


Figure 1.—Dendrogram of hedge similarity (UGPMA clustering method) concerning foliage spider communities.

nities justified our comparison here of different hedge communities during spring.

Six hedges (A–F) were selected according to their index of biological quality to provide two hedges in each of three categories: hedge A (index of 20) and B (19) to “high”; hedge C (11) and D (9.5) to “medium”; and hedge E and F (6.5) to “low.” All the selected hedges were situated in a complex of three contiguous fallow-fields. The foliage spiders were collected by six series of branch-beating during spring 1997 (March, April, May) using a beating tray of 0.7 m² and a walking stick. Two people collected the spiders, one person was beating while another one was collecting the spiders from the tray with the aid of a pooter. Spiders were sampled over a total of 75 m for each hedge, which was comprised of 15 samples, with each sample of 5 linear meters at each of three heights: low (ground level), medium (at 1 m) and high (at 2 m). For each 5 meter sample at a given height, five tablecloths were placed on the ground and three whacks per tray were given to help achieve an “equal beating effort” across all samples. Since the beating method collects spiders only during their diurnal activity period (McCaffrey et. al. 1984), the timing of beating was randomly distributed across all hedges and heights sampled. This method obviously undersampled nocturnal spiders. To estimate the potential influence of foliage orientation, sampling was carried out along 20 m

Table 2.—Foliage spider communities and ecological value of hedges (ind/m: mean number of individuals per linear meter; sp/m: mean number of species per linear meter; J': Shannon evenness index).

Hedge quality	Specific diversity		sp/m ±SD	ind/m ±SD	J'	Foliage orientation
High	hedge A	47	2 ± 0.56	14.3 ± 2.7	0.68	NE
	hedge B	35	1.5 ± 0.35	6.2 ± 2.1	0.87	W
	Total specific diversity:	53				
Medium	hedge C	34	2.1 ± 0.34	11.3 ± 3.4	0.84	E
	hedge D	41	2.1 ± 0.30	9.7 ± 1.9	0.81	SE
	Total specific diversity:	46				
Low	hedge E	44	1.8 ± 0.73	6.6 ± 2.7	0.81	N
	hedge F	30	1.3 ± 0.22	5.2 ± 2.4	0.79	W
	Total specific diversity:	51				

of each side of hedge D during September 1997.

The nomenclature of spiders used follows Platnick (1997). The juveniles of the following genera were considered to belong to only one species: *Agroeca* sp., *Episinus* sp., *Zora* sp., *Pirata* sp., *Evarcha* sp., *Micaria* sp., *Cheiracanthium* sp., *Zelotes* sp., *Zygiella* sp., *Tibellus* sp., *Xysticus* sp.

Clubiona sp., *Heliophanus* sp., *Leptyphantus* sp., *Ozyptila* sp., *Robertus* sp. and *Tetragnatha* sp. were counted as species where there were only juveniles in what was collected. In order to simplify the comparison of the spider communities, the “dominant species” refers to species represented by at least 4.5% of the total individuals collected in one hedge.

A cluster analysis was performed by NTSYS-PC program with the use of the UGPMMA method. The similarity matrices for community analyses were derived using the chi-squared distance by means of the following formula:

$$d_{ij} = \sqrt{\sum_k^p (x_{ki}/x_i - x_{kj})^2/x_k}$$

An ANOVA (multiway factor analysis) was also performed by STATGRAPHIC-PC program to test the differences between the hedges. This analysis considered variation from two factors: hedge quality and number of individual per species. The variables examined were first transformed in percentages for the anova analysis and the data from couple of hedges of low, medium or high value were pooled.

RESULTS

Species richness and index of density.—

A total of 72 genera and species was identified from the foliage of the six hedges studied (Appendix 1). The average species richness of the three categories of hedges remained virtually identical (Table 2), and a hedge of low ecological value could harbor a species richness greater than that in a hedge of high value.

Table 3.—Percentage of shared species between hedges (T = total number of species; s.s. = shared species).

	A-B	A-C	A-D	A-E	A-F	B-C	B-D	B-E	B-F
T	53	51	59	58	51	41	52	52	30
s.s.	24	27	29	25	21	22	26	22	20
%	45.2	53	49.1	43.1	41.2	53.7	50	42.3	66.7
	C-D	C-E	C-F	D-E	D-F	E-F			
T	46	43	40	58	50	48			
s.s.	25	27	23	28	24	23			
%	54.3	62.7	57.5	48.3	48	47.9			

Table 4.—Comparison between the spider communities inhabiting the two faces of the same hedge (relative abundance of species is given in parentheses; * = 1 individual).

Foliage orientation	W-NW	E-SE
Number of species	38	32
Total individuals	257	210
Dominant species	<i>Mangora acalypha</i> (13.2%) <i>Zilla diodia</i> (13.2%) <i>Anyphaena accentuata</i> (6.5%)	<i>Philodromus cespitum</i> (24.8%) <i>Nigma puella</i> (6.6%) <i>Heliophanus</i> sp. (8%)
Not common	<i>Clubiona brevipes</i> (2.7%) <i>Theridion mystaceum</i> (1.5%) <i>Theridion pallens</i> (1.5%) <i>Atea triguttata</i> (1.5%) <i>Hyptiotes paradoxus</i> (1.2%) <i>Meta segmentata</i> (0.7%) <i>Leptyphantus tenuis</i> (0.7%) <i>Araneus umbraticus</i> (*) <i>Microlinyphia pusilla</i> (*) <i>Synaema globosum</i> (*)	<i>Theridion tinctum</i> (1.4%) <i>Anelosimus</i> sp. (1.9%) <i>Bathyphantes gracilis</i> (*)

There is no significant differences between the average number of species collected by linear meter in hedges B, C, D and E. The average density of individuals collected fell considerably for the two hedges of low value and for one of the hedge of high ecological value (B). The difference in the mean number of spiders collected between the two hedges A and B (high value) was strongly related to the presence of numerous immatures of four species or genera (*Zygiella* sp., *Nigma puella* (Simon 1870), *Araneus diadematus* Clerck 1758, *Dictyna uncinata* Thorell 1856) in hedge A. This was confirmed by the low value of the Shannon evenness index for that spider assemblage.

Influence of foliage orientation.—The orientation of the foliage may influence the structure of the spider communities since the percentage of shared species is higher between two hedges of the same foliage orientation (hedges B and F, west orientation) than be-

tween two of the same ecological value (Table 3). This hypothesis is supported by the comparison of the spider communities sampled on the two faces of the same hedge (Table 4). We observed a substitution among the three dominant species and 12 of the species collected on this hedge were not common to both faces of the hedge investigated. Moreover, the UGPMA analysis separated the six spider communities into three clusters which were not congruent with the respective ecological value of the hedges (Fig. 1). This can also be related to the foliage orientation since the cluster analysis separated group of hedges (A,D, or C) sampled on their eastern face. Thus, variation in the relative abundance of individuals observed among the six communities could not be correlated with the ecological value of the hedges.

Specific composition of spider communities.—The ANOVA shows that there is a significant difference between the relative abundance of each species in the three types of hedges (source A: P-value < 0.05), but the relative abundance of a same species collected in the three type of hedges is not significantly different (source B; P-value > 0.05). Furthermore, there is no significant interaction amongst the two factors which strongly suggests the lack of relationship between hedge type and the structure of the spider community associated (Table 5). This has to be connected with the fact that 90% of the individuals col-

Table 5.—ANOVA analysis of three community categories (low, medium, and high).

Source	df	MS	F-ratio	P-value
Main effects				
A: species	72	53.2	12.95	0.000
B: hedge type	2	<0.01	0.00	1.000
Interactions AB	146	2.44	0.6	0.1
Residual	222	4.11		

Table 6.—Dominant species in each hedge with relative abundance (in percentage).

	A	B	C	D	E	F
<i>Zygiella</i> sp.	23	4.5	18	17.5	9.7	13
<i>Nigma puella</i>	16.6	9.3	14	15.6		22.5
<i>Philodromus</i> sp.	5.7	5.7		9	9.9	5.9
<i>Zilla diodia</i>	5	12	6.3	9.6	7.5	5
<i>Dictyna uncinata</i>	6		6.5	6		8.5
<i>Araniella opisthographa</i>		9.8			11	9
<i>Anyphaena accentuata</i>			4.5			
<i>Araneus diadematus</i>	9.4					
<i>Heliophanus</i> sp.		15				
<i>Paidiscura pallens</i>					11	

lected belonged to shared species (Appendix 1). Among the 10 dominant species collected in each hedge (Table 6), 5 are the dominant species in all hedges. The dominance of *A. diadematus* and of *Heliophanus* sp. has to be related to the numerous immatures collected in only one of the hedges of high ecological value. The same remark can be made concerning the dominance of *A. accentuata* (hedge C) and *P. pallens* (hedge E). Therefore, if we consider the representation of adult spiders, there were no dominant species which were characteristic of hedges of low, medium, or high ecological value. In addition, the analysis of species distribution according to functional groups did not reveal a significant difference in the representativeness of the various groups (Table 7). Very few species (Table 8) were collected on only one of the six hedges, and each was represented by only 1 or 2 individuals. Some species were absent from hedges of high value (e.g., *Lathys humilis* Blackwall 1855, *Araneus triguttatus* (Fabricius 1775) or, on the contrary, species were always absent from hedges of low value (e.g.,

Gibbaranea gibbosa (Walckenaer 1802), *Saitis barbipes* Simon 1868).

DISCUSSION

Very few comparative studies have been made on the spider communities of the hedgerow networks, and they are mainly based on the analysis of ground living spiders (Petto 1990; Bergthaler 1996). This first approach to investigating foliage spider communities shows that there were no direct relationships between spider biodiversity and an index that described hedge habitat quality based on the analysis of the vegetation architecture. Therefore, concerning the spiders inhabiting the foliage, easy field indicator parameters of hedge quality, as for instance spider species composition or relative abundance of species, are not useful.

By artificially modifying the density of the foliage of a big sage (*Artemisia tridentata*), Hatley & MacMahon (1980) demonstrated that spider species diversity and the number of guilds were positively correlated with indicators of shrub volume and foliage diversity. These variations were observed on spider communities which were colonizing a shrubby layer composed by only one vegetal species. We also found that the hedge type may influence the composition of spider assemblage in the foliage. But, in the present case, because the architecture of the foliage is too diverse, whatever the ecological value of the hedge is, the spider specific richness remains almost the same for hedges of high or low ecological value. Moreover, it can be argued that foliage orientation, which was not incorporated into the index of vegetation quality, induced substitution of spider species, further limiting again

Table 7.—Number of species according to hunting habits for the different group of hedges.

	Medi-			Total
	High value	an value	Low value	
Orb-web spiders	13	14	10	14
Frame-web spiders	11	11	13	16
Sheet-web spiders	9	6	9	16
Ambush hunters	11	8	9	12
Diurnal wanderers	12	10	10	16
Nocturnal wanderers	6	5	7	8

Table 8.—Single species in three categories of hedges (* Genus present in the two other types of hedges).

	Hedge quality		
	High	Medium	Low
Diurnal	<i>Salticus scenicus</i> <i>Pirata</i> sp.	<i>Bianor aurocinctus</i> <i>Pardosa hortensis</i>	<i>Alopecosa accentuata</i>
Nocturnal	<i>Micaria</i> sp.	<i>Agroeca</i> sp.	<i>Clubiona terrestris</i> *
Frame web	<i>Robertus arundineti</i> * <i>Robertus lividus</i> * <i>Philodromus dispar</i> *		<i>Theridion impressum</i> * <i>Theridion tinctum</i> * <i>Episinus</i> sp.
Ambush-hunters	<i>Ozyptila praticola</i> * <i>Tibellus</i> sp.		
Sheet-weavers	<i>Agyneta affinis</i> <i>Agyneta subtilis</i> <i>Pelecopsis parallela</i> <i>Walckenaeria acuminata</i>	<i>Agyneta rurestris</i> <i>Microlinyphia pusilla</i>	<i>Ceratinella brevipes</i> <i>Collinsia submissa</i> <i>Leptyphantus ericaeus</i> <i>Oedothorax fuscus</i> <i>Panamonops sulcifrons</i>

the ability of the index to reflect changes in spider diversity. This study also demonstrates that one hedge has to be carefully sampled on its two faces in order to identify the whole spider species inhabiting the foliage.

As density and specific diversity of spiders do not correspond to the general vegetal quality of hedges, are there any indicating species which show the habitat quality? The dominant species did not vary among hedges of different quality, which supports our former observations on the relatively stable composition of dominant species colonizing the shrubby layers within the same macroclimatic sector (Ysnel et al. 1996). However, the indicator species for the ecological quality of the hedges could be identified, not among the dominant species, but on the contrary, by considering the single species collected in one hedge. However, these species were poorly represented in the samplings and their absence from hedges of other quality could be sampling artifact or could be related to the foliage orientation of the hedge investigated. Some species are missing from the category of hedges with a high or low ecological value. These species, then, are likely to be more independent of the orientation of the hedges and their absence could be connected to the structure of the vegetation. Further investigations in other hedges of different ecological value are required to clarify these indicators. Concerning the maintenance of spider biodiversi-

ty, we must notice that the presence of hedge groups of different index on one area will lead to bigger specific diversity than the presence of only one edge group of high index.

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Appendix 1.—Total list of species with number of individuals collected in all the hedges.

Biological value of hedges	High		Medium		Low	
	A	B	C	D	E	F
Diurnal wanderers						
<i>Alopecosa accentuata</i> (Latreille 1817)					1	
<i>Anyphaena accentuata</i> (Walckenaer 1802)	33	11	35	20	5	5
<i>Ballus biimpressus</i> (Doleschall 1852)	14	13	4	7	7	1
<i>Bianor aurocinctus</i> (Ohlert 1865)				2		
<i>Ero aphana</i> (Walckenaer 1802)	6		8	5	1	1
<i>Evarcha</i> sp.		1			2	
<i>Heliophanus cupreus</i> (Walckenaer 1802)		13				1
<i>Heliophanus</i> sp.	19	61	2	15	4	13
<i>Macaroeis nidicolens</i> (Walckenaer 1802)	3	1	13	8	3	1
<i>Pardosa hortensis</i> (Thorell 1872)				1		
<i>Pardosa</i> sp.	1				1	
<i>Pirata</i> sp.	2					
<i>Pisaura mirabilis</i> (Clerck 1758)			1	1	1	
<i>Saitis barbipes</i> Simon 1868	2	1		3		
<i>Salticus scenicus</i> (Clerck 1758)		1				
<i>Zora</i> sp.	1			1		
Nocturnal wanderers						
<i>Agroeca</i> sp.				1		
<i>Cheiracanthium</i> sp.	3	1		3		1
<i>Clubiona brevipes</i> (Blackwall 1841)		6				5
<i>Clubiona compta</i> Koch C.L. 1839		5		1	13	
<i>Clubiona terrestris</i> Westring 1851					1	
<i>Clubiona</i> sp.	28	19	39	21	26	7
<i>Micaria</i> sp.	1					
<i>Zelotes</i> sp.	1	5	1			2
Frame-web spiders						
<i>Anelosimus vittatus</i> (Koch C.L. 1836)	14	3	17	7	20	4
<i>Dictyna uncinata</i> Thorell 1856	63	12	51	38	6	30
<i>Episinus</i> sp.					1	
<i>Lathys humilis</i> Blackwall 1855			25	1	6	
<i>Nigma puella</i> (Simon 1870)	172	39	108	98	5	80
<i>Paidiscura pallens</i> (Blackwall 1834)	9	5	12	21	52	12

Appendix 1.—Continued.

Biological value of hedges	High		Medium		Low	
	A	B	C	D	E	F
<i>Robertus arundineti</i> (Cambridge O.P. 1871)	2					
<i>Robertus lividus</i> (Blackwall 1836)	1					
<i>Robertus</i> sp.				3	1	
<i>Theridion impressum</i> Koch C.L. 1881					1	
<i>Theridion mystaceum</i> Koch L. 1870	25	1	11	6	9	14
<i>Theridion tinctum</i> (Walckenaer 1802)						2
<i>Theridion varians</i> Hahn 1831	7	2	21	1	7	3
<i>Theridion</i> sp.	50	20	102	16	51	26
Orb-weavers						
<i>Araneus diadematus</i> Clerck 1758	98	18	2	12	2	1
<i>Araneus sturmi</i> (Hahn 1831)	1	2	1	1	5	
<i>Araneus triguttatus</i> (Fabricius 1775)			1	4	3	
<i>Araniella opisthographa</i> (Kulczynski 1905)	28	41	30	22	56	32
<i>Argiope bruennichi</i> (Scopoli 1772)	3	2		1		
<i>Cyclosa conica</i> (Pallas 1772)	1			1		
<i>Gibbaranea bituberculata</i> (Walckenaer 1802)		3	7	24	5	1
<i>Gibbaranea gibbosa</i> (Walckenaer 1802)	1	1	2	4		
<i>Larinioides cornutus</i> (Clerck 1758)	2		5		1	
<i>Mangora acalypha</i> (Walckenaer 1802)	18	12	17	20	11	4
<i>Tetragnatha montana</i> Simon 1874		2		1		
<i>Tetragnatha</i> sp.	17	11	16	11	21	7
<i>Zilla diodia</i> (Walckenaer 1802)	52	50	49	60	37	17
<i>Zygiella</i> sp.	240	19	140	110	48	46
Sheet-weavers						
<i>Agyneta affinis</i> (Kulczynski 1898)		1				
<i>Agyneta rurestris</i> (Koch C.L. 1836)				2		
<i>Agyneta subtilis</i> (Cambridge O.P. 1863)	3					
<i>Bathypantes gracilis</i> (Blackwall 1841)	1			1		
<i>Ceratinella brevipes</i> (Westring 1851)					2	
<i>Collinsia submissa</i> (Koch L. 1879)						1
<i>Hypomma cornutum</i> (Blackwall 1833)	2				5	
<i>Lepthyphantes ericaeus</i> (Blackwall 1853)					1	
<i>Lepthyphantes tenuis</i> (Blackwall 1852)	8		1	2	1	
<i>Lepthyphantes</i> sp.	14	1	8	4	3	2
<i>Microlyniphia pusilla</i> (Sundevall 1830)				1		
<i>Oedothorax fuscus</i> (Blackwall 1834)					1	1
<i>Panamonops sulcifrons</i> (Wider 1834)					1	
<i>Pelecopsis parallela</i> (Wider 1834)	1	1				
<i>Porrhomma oblitum</i> (Cambridge O.P. 1870)	1		1		1	1
<i>Walckenaeria acuminata</i> (Blackwall 1833)	1					
Ambush-hunters						
<i>Diaea dorsata</i> (Fabricius 1777)			1		1	
<i>Misumenops tricuspidatus</i> (Fabricius 1775)	8	1	5	2	2	4
<i>Ozyptila praticola</i> (Koch C.L. 1837)	3					
<i>Ozyptila</i> sp.	1	1	12		4	1
<i>Philodromus cespitum</i> (Walckenaer 1802)	3	5	2	2		5
<i>Philodromus dispar</i> (Walckenaer 1802)	1					
<i>Philodromus rufus</i> (Walckenaer 1802)	1	1	1	2	6	
<i>Philodromus</i> sp.	60	24	29	57	49	21
<i>Synaema globosum</i> (Fabricius 1775)		1	4		1	
<i>Tibellus</i> sp.	1					
<i>Tmarus stellio</i> Simon 1875	2				1	
<i>Xysticus</i> sp.	6			3	1	2