

KETTLE HOLES IN THE AGRARIAN LANDSCAPE: ISOLATED AND ECOLOGICAL UNIQUE HABITATS FOR CARABID BEETLES (COL.: CARABIDAE) AND SPIDERS (ARACH.: ARANEAE)

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ABSTRACT

Kettle holes are small depressional wetlands and because of the high variability of site factors they are potential hotspots of biodiversity in the monotone arable land. We investigated eight kettle holes and two agrarian reference biotopes for carabid beetles and spiders. The animals were captured with pitfall traps from May to August 2005, along with surveys of the soil and vegetation. We asked whether each kettle hole has specific ecological properties which match with characteristic carabid beetle and spider coenoses and whether they represent isolated biotopes. Differences in the composition of ecological and functional groups of carabid beetles and spiders between the plots were tested with an ANOVA. The impact of the soil variables and vegetation structure on the distribution of species was analyzed with a Redundancy Analysis. The assemblage similarities between the kettle hole plots were calculated by the Wainstein-Index. Ecological groups and habitat preferences of carabid beetles had maximal expressions in seven different kettle holes whereas most of the ecological characteristics of the spiders had maximal expression in only two kettle holes. High assemblage similarity values of carabid beetle coenoses were observed only in a few cases whereas very similar spider coenoses were found between nearly all of the kettle holes. For carabid beetles, kettle holes represent much more isolated habitats than that for spiders. We concluded that kettle holes have specific ecological qualities which match with different ecological properties of carabid beetles and spiders and that isolation effects affect carabid beetles more than spiders.

Keywords: agrarian landscape, ecological group, habitat preference, landscape ecology, migration, wetland

INTRODUCTION

Kettle holes in the agrarian landscape are like a negative print of islands in the ocean – they represent wet islands within the predominantly dry arable land surrounding them. From the scientific point of view, kettle holes are glacially created small standing water bodies

(≤ 1 ha), which act as depressional wetlands and mostly undergo a wet-dry cycle. They are spread widely in the agrarian and woody landscapes of young moraine regions in Northern Europe (Bosiacka & Pienkowski 2012; Gerke *et al.*, 2010; Kalettka *et al.*, 2001; Kalettka & Rudat, 2006; Waldon, 2012) and Northern America (Euliss *et al.*, 2008; Gleason *et al.*, 2011).

Kettle holes are characterized by a high variability of site factors, and therefore are potential hotspots of structural and biological diversity. The vegetation and fauna of kettle holes is often much more diversified compared to the biota of the surrounding monotone arable land. However, over the last 60 years many kettle holes have become subject to intensive agricultural land use practices and active removal, which has caused severe pollution, structural degradation and decrease of biodiversity. But, many kettle holes are still important biotopes, that contribute to biodiversity in the agrarian landscape (Lischeid & Kalettka, 2012; Niedringhaus & Zander, 1998; Pätzig *et al.*, 2012; Waldon, 2012; Pienkowski, 2000).

Whereas the topography, genesis and use of kettle holes in Northeast Germany have been investigated over a long time (Kalettka, 1996; Kalettka *et al.*, 2001), awareness of the ecological value of kettle holes and other small water bodies has only recently been increasing (Boix *et al.*, 2012). Kettle holes have been studied and characterized in terms of hydrogeomorphological properties (Gerke *et al.*, 2010; Kalettka & Rudat, 2006; Schindler 1996), limnology (Greulich & Schneeweiss, 1996; Haacke *et al.*, 1996; Lischeid & Kalettka, 2012; Kleeberg *et al.*, 2015), macrophytes (Luthardt & Dreger, 1996; Pätzig *et al.*, 2012; Waldon, 2012), amphibians (Greulich & Schneeweiss, 1996; Schneeweiss, 1996; Berger *et al.*, 2010), and conservation and management (Frielinghaus, 1996; Kalettka, 1996; Berger *et al.*, 2010). DeMeester *et al.* (2005) recommend the study of ponds and pools as model systems for ecology, evolutionary biology and conservation biology because of their great variability in types, and abiotic gradients. This allows for study of the relations between their characteristics in biodiversity, assemblage composition, food webs and ecological gradients. Because of their small size they are often severely threatened by human activities such as agricultural management and thus may serve as an early warning system for long-term ecological changes. Scheffer *et al.* (2006) state that in contrast to the often argued point that due to isolation shallow lakes and ponds are not rich in species, small water bodies often contain species-rich communities of specific groups of organisms, e.g., submerged plants and invertebrates. The authors suggest that the connection of isolated habitat fragments may sometimes lead to a loss of species diversity and thus decrease rather than enhance landscape-level biodiversity.

For kettle holes, there are only a few studies on invertebrate fauna (Niedringhaus & Zander, 1998; Kleeberg & Schmidt, 1999; Brose, 2001, 2003a,b). However, because of their species richness and diverse ecological requirements, invertebrate fauna is well suited to characterize the ecological singularities of the kettle holes compared to the circumjacent arable fields. However, besides the papers of Brose (2001, 2003a, b), there are no systematic field studies published on carabid beetles and spiders of kettle holes in Germany. Kleeberg & Schmidt (1999) and Schmidt (2005) provide brief species lists of carabid beetles collected from kettle holes in the federal countries of Brandenburg and Mecklenburg-Vorpommern.

Our study intends to extend the knowledge about the invertebrate fauna of kettle holes and to describe them as unique wet spots in the agrarian landscape. The objective of our investigation is to highlight differences in species composition and the composition of ecological and functional groups of carabid beetle and spider assemblages of the kettle holes, and to investigate the differences between kettle holes of different hydrogeomorphological types and agrarian reference habitats. Furthermore, we wanted to find evidence that there is

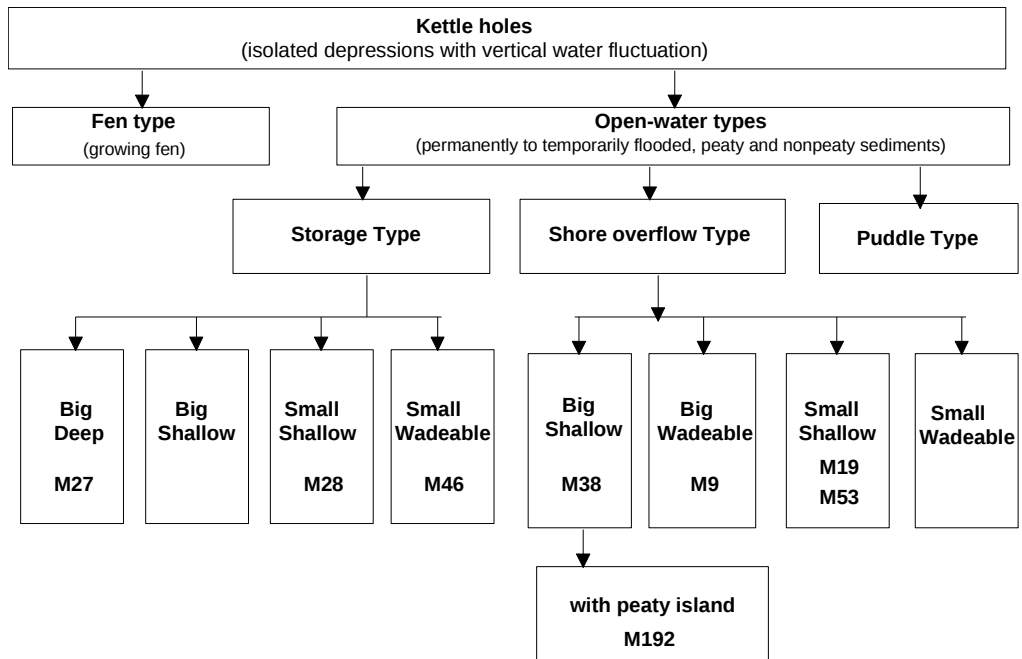
an isolation effect for the carabid beetle and spider assemblages between the kettle holes, and that this isolation effect impacts the two animal groups differently. We will discuss whether differences in the migration mode of carabid beetles and spiders lead to isolation effects. Our hypotheses are that abiotic factors and the vegetation structure explain most of the variance of species composition at the kettle holes and the agrarian reference habitats. Furthermore, we assume that each kettle hole has a unique setting of site factors that bear specific carabid beetle and spider coenoses with specific ecological traits and habitat preferences. Finally and to a different extend kettle holes represent spatially isolated habitats for carabid beetle and spider assemblages.

MATERIALS AND METHODS

Hydrogeomorphic types of kettle holes

The kettle holes of northeast Brandenburg were typed by Kalettka & Rudat (2006). A total of 144 kettle holes exhibiting different hydrological and morphological variables were assigned to five different hydrogeomorphological (HGM) classes (Figure 1). Eight from these 144 kettle holes of different HGM types were selected for investigation in this study (see labels in Figure 1).

Fig. 1: The hydrogeomorphological types of kettle holes in Northeast Brandenburg (Kalettka & Rudat, 2006) with labels of the eight kettle holes investigated in this study



Study area

Our study was comprised eight selected kettle holes of different hydrogeomorphological types (Figure 1), and two agrarian reference biotopes (see Table A1 for description), situated south of the city of Müncheberg in the young moraine landscape of the northeastern plain of Germany. The soils of the area are predominantly sandy. The annual precipitation ranges between 357 and 793 mm*a⁻¹, and the average temperature is 8.8 °C. (Meteorological station

Müncheberg 1973-2002; Federal Ministry of Transport, Building and Urban Development, Deutscher Wetterdienst, 2011, unpublished data). The nomenclature of the examined kettle holes followed an internal catalogue (Kalettka, unpublished data) with the letter “M” designating the region of Müncheberg and a number specifying the location. As reference sites, we examined a barley field (MuA62) and a dry set-aside (MuS05) in the vicinity of the investigated kettle holes.

Capture design and species identification

The carabid beetles and ground dwelling spiders were captured in pitfall traps (Barber, 1931). At each plot, five traps with an upper diameter of 6.5 cm were arranged in a straight line at a distance of 5m from each other. The killing and preserving fluid consisted of Ethanol (70 %) and acetic acid (90 %) at a proportion of 7:1 with water added to 1 L.

From April 28th to August 31st 2005, the traps were operated and changed every fortnight. The contents of the traps were carried to the laboratory, transferred to 70 % ethanol, and stored at 4 °C until ready for examination. For each single trap, the animals were identified to the species level. At the barley field the traps could not be operated between July 06th and July 20th and between August 17th and August 31st due to harvesting and ploughing.

The carabid beetles were identified by Heidi Riedel based on Müller-Motzfeld (2004) and the spiders by Ralph Platen based on Heimer & Nentwig, (1991); Roberts (1985, 1987, 1995); and Wiehle (1956, 1960). Specimen copies are deposited at the collection of the Institute of Land Use Systems at the Leibniz Centre of Agricultural Landscape Research (ZALF). The ecological data for carabid beetles were drawn from the catalogue of the Gesellschaft für angewandte Carabidologie (GAC 2009, modified); Larsson (1939) and Lindroth (1992a, b), and for the spiders the data were drawn from Platen *et al.* (1991, 1999, modified). The nomenclature follows Köhler & Klausnitzer (2014) for carabid beetles and Platnick (2013) for spiders. *Bembidion mannerheimii* C.R. Sahlberg and *Bembidion neresheimeri* J. Müller were not distinguished.

Soil analyses

On June 29th and October 06th 2005, soil cores were collected with a 100 cm³ volume cylinder at each plot. The soil acidity was measured based on the pH at 22 °C, by mixing 10g of soil with a suspension of 0.01 N CaCl₂ and then homogenized with a mechanical shaker for 30 min. The soil texture was determined with a set of soil sieves with mesh widths of 0.63, 0.2 and 0.063 mm after drying 100g of the soil at 105 °C for 24 h. Each soil fraction was weighed separately. The loss of ignition was determined by burning up to 5g of dry soil in a porcelain cup at 450 °C for 24 h. The remaining inorganic material was weighed and calculated as the percentage of the initial weight. Afterwards, the percentage of organic material was calculated. The water volume was determined by drying the soil within a 100 cm³ core cylinder for 24 h at 105 °C (all of the methods were according to Schlichting *et al.*, 1995).

Vegetation surveys

Vegetation surveys were performed according to the Braun-Blanquet estimation scale (Dierschke, 1994) twice at each plot, on May 30th and July 26th, 2005 and on five areas of 5 m² with a distance of 1 m apart from the pitfall traps. Along with the cover values of the plant species, the vegetation structure - vegetation height, herb and grass cover and the percentage of bare ground were visually estimated. The environmental variables at each plot are summarized in Table A1 in the appendix.

Classification and analyses of ecological data

The carabid beetle and arachnid species caught were characterized by ecological and functional traits. The ecological traits characterize the species' preferences towards abiotic factors, i.e. humidity, light exposure, and temperature in the field. These traits are summarized in the ecological group (EG). The data for carabid beetles were drawn from Barndt *et al.* (1991) and for arachnids from Platen *et al.* (1991). The functional traits were assigned to different functional groups: The habitat preferences (HP) for carabid beetles were based on the catalogue of the GAC (2009) with regard to the north-eastern lowland of Germany. The corresponding habitat preferences for arachnids were based on Platen *et al.* (1991, modified) (Tables A3 and A4). The wing morphology (WM) and hibernation modes (HM) for carabid beetles were taken from Larsson (1939) and Lindroth (1992). The individual body mass of the carabid beetle species was calculated with the formula of Jarosik (1989) and divided into five body mass classes (BMC). For spiders the individual body masses were calculated by the formula of Henschel *et al.* (2006), which were also divided into five body mass classes (Tables A3 and A4).

Statistical analyses

Before the statistical analyses, the individuals of each species were summed up for each trap for the entire investigation period. The impact of the environmental variables on the species composition was analyzed by a Redundancy Analysis (RDA) (Braak & Smilauer, 2002). Kettle hole M192 was not included in the analysis for carabid beetles, because too few animals were caught. The characteristic hydrogeomorphological features, area, average water depth and slope inclination that were essential for the assignment to the different classes were first included in the analyses but were removed because no significant impact on the species composition was found. Before the analyses, the species data were Hellinger transformed (Legendre & Gallagher, 2001). The following environmental variables were included in the RDA: water volume, four soil fractions, pH, the portion of organic material, the height and total coverage of the vegetation and the proportion of bare ground. Differences in the ArcSinSqrt- transformed percentage number of individuals of ecological and functional groups of the carabid beetle and spider coenoses between the kettle hole and the reference plots were calculated by a one-way ANOVA. Subsequently, the significance was determined by a Duncan-Test ($p \leq 0.05$) for pairwise comparison (Sokal & Rohlf, 2012). The transformed data were tested to normal distribution by the Kruskal-Wallis Test and for homoscedasticity by the Levene-Test. The assemblage similarity was calculated by the Wainstein-Index (Mühlenberg, 1993).

The computer programs that were used were the Web-App Biometrie Andersson-Info Anderßon & Anderßon (2015), CANOCO Vers. 4.5 (Braak & Smilauer, 2002) and SPSS Vs. 19 (IBM Corp., Armonk, NY, USA).

RESULTS

General

In total, 11,136 individuals out of 114 carabid beetle species and 119 species of spiders from 17,216 individuals were caught (Table 1). For lists of the species with detailed information on the ecology see Tables A2 and A3.

The highest number of carabid beetle species was found at kettle hole M46. The highest number of individuals occurred at the set-aside MuS05 was nearly 2,000 individuals. Only 5 % of this number of individuals was caught at the peaty kettle hole M192. At this site, also the lowest number of species also occurred which was five times lower than in M46.

Table 1: Numbers of species and individuals carabid beetles and spiders at the plots investigated. For the explanation of the abbreviations of the plots see chapter 2.1.

SE= Standard error. Dark grey shaded cells indicate the highest numbers, whereas light grey shaded cells represent the lowest numbers.

Carabidae	M9	SE	M19	SE	M27	SE	M28	SE	M38	SE
Spec.	64	2.43	53	1.63	56	2.38	67	1.12	47	3.07
Ind.	1,773	38.33	678	22.88	1,123	29.30	610	14.26	495	13.27
Spiders	M9	SE	M19	SE	M27	SE	M28	SE	M38	SE
Spec.	54	1.63	45	1.63	47	1.94	65	2.14	44	1.57
Ind.	1,897	21.69	1,254	37.40	1,909	63.95	2,221	51.83	1,236	37.76
Carabidae	M46	SE	M53	SE	M192	SE	MuS05	SE	MuA62	SE
Spec.	71	2.28	58	1.28	14	1.79	46	1.72	35	0.74
Ind.	1,938	35.38	856	8.48	100	4.18	1,968	54.58	1,595	11.60
Spiders	M46	SE	M53	SE	M192	SE	MuS05	SE	MuA62	SE
Spec.	46	1.47	55	1.40	44	2.85	40	1.67	28	1.77
Ind.	2,614	106.47	1,963	22.77	997	25.00	2,291	64.83	834	24.07

For spiders, the highest number of species occurred at M53 and the lowest number at the barley-field MuA62. This is where the lowest number of individuals also appeared which was nearly two times lower than at M53. The number of individuals was three times lower than at M46 (Table 1).

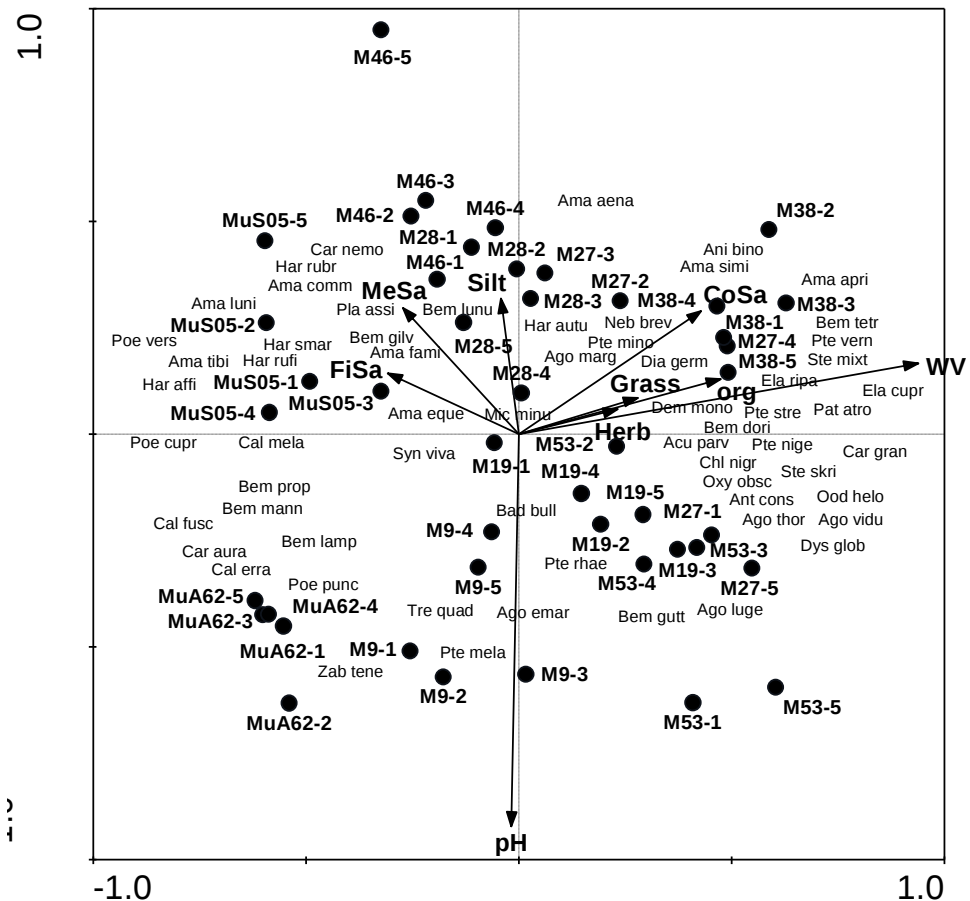
The impact of environmental variables on species composition of carabid beetle and spider assemblages

To determine the impact of soil and vegetation structure variables on the species composition of the carabid beetle and spider assemblages at the kettle hole and reference plots, Redundancy Analyses (RDA) were performed (Figures 2 and 3; Table 2). The species data at all the kettle holes were included into the analyses but the results for the kettle hole M192 could not be displayed properly in the RDA-diagram for carabid beetles because of its extreme outlier position because only a hundred individuals out of 14 carabid beetle species were caught there. Except for the barley field MuA62, the carabid beetle assemblages of the single plots were very heterogeneous (Figure 2). This may be due to the position of the single traps of the plots which are sometimes greatly separated from each other. The water volume had the greatest impact (due to the length of the arrow) together with organic matter and vegetation (due to their close vicinity to the first axis) on the right hand side. The gradient of

the variable water volume points towards the wettest kettle hole M38, the extension in the opposite direction points to the driest plots MuS05 and MuA62 (for exact values: see Table A1). The gradients organic matter and the herb and grass coverages also point to the right, where most of the kettle plot pitfall traps are displayed. In addition, the gradient “coarse sand” also points to the right, which is due to the high portion of this soil fraction in M38 (Table A1).

Fig. 2: The impact of the environmental variables on the composition of the carabid beetle assemblages. An ordination diagram on the basis of a Redundancy Analysis (RDA).

Grass= cover grass layer, Herb= cover herb layer, CoSa= coarse sand, MeSa= medium sand, FiSa= fine sand, org= percentage organic matter, and WV= water volume. For a legend of the abbreviations in the plots: see Chapter 2.1. The numbers of single traps follow the name of the plots. For a legend of the abbreviations in the species: see Table A2. Horizontal axis: 1st, vertical axis: 2nd canonical axis. Species with a < 30 % variance explanation are not plotted in the figure.



The arrows of the remaining soil fractions point to the left, where the plots on mineral soil MuS05 and MuA62 are present.

Table 2: The variance explanation in the carabid beetle and spider species data by the environmental variables (relative numbers).

EnvVar= environmental variables, FiSa= fine sand, MeSa= medium sand, Herb= cover herb layer, Grass= cover grass layer, org= percentage organic matter, CoSa= coarse sand, WV= water volume, VarExpl= variance explanation, Total= total variance explanation by all of the environmental variables

Carabid beetles										
EnvVar	Silt	FiSa	MeSa	Herb	pH	Grass	org	CoSa	WV	Total
VarExpl	0.02	0.04	0.04	0.05	0.06	0.06	0.07	0.07	0.22	0.47
Spiders										
EnvVar	pH	Silt	Herb	org	FiSa	CoSa	MeSa	WV	Grass	Total
VarExpl	0.01	0.01	0.04	0.04	0.05	0.06	0.09	0.09	0.11	0.40

All of the environmental variables explain nearly one half of the variance in the species data, and the water volume contributes to nearly one half of the total variance explanation (Table 2).

The carabid beetle coenoses are well separated from each other, and arable field species are displayed near MuA62 (*Bembidion lampros* (Herbst), *B. properans* (Stephens), *Carabus auratus* Linné, and *Zabrus tenebrioides* (Goeze)), meadow and dry grassland species near MuS05 (*Poecilus versicolor* (Sturm), *Amara communis* (Panzer), *A. lunicollis* Schiödte, and *Harpalus affinis* (Schränk)), and wetland species near M38 (*Elaphrus cupreus* Müller, *Patrobis atrorufus* (Stroem), *Pterostichus vernalis* (Panzer), and *Stenolophus mixtus* (Herbst)). At the remaining kettle holes, except for M46, several species of wet, open habitats are plotted (*Agonum* spp., *Anthracus consputus* (Duftschmid)) which are characteristic of specific kettle holes (M9, M27, M28). For habitat preferences of the species: see Table A2).

For spiders, a RDA with the same constraints as the analysis for carabid beetles was performed (Figure 3). The spider assemblages at the plots appeared to be much more homogeneously distributed all over the plots than those of the carabid beetles (Figure 2) which may be based on the mostly near-by plotted single traps of the specific plots. Thus, apart from the very wet (M38 at the bottom, M192 to the right) kettle holes and the dry set-aside MuS05 at the top, the remaining plots are much more crowded together near the center of the ordination diagram, which indicates that the all-together similarity of the spider assemblages of all of the plots considered is greater than that of the carabid beetle assemblages (compare Figure 3 with Figure 2, and see chapter 3.4). For spiders the peaty kettle hole M192 was included in the RDA diagram which resulted in an “outcast” position of M192 due to its deviant assemblage and a subsequent “compression” of the remaining kettle hole plot positions.

occurrence (*Erigone* spp., *Oedothorax apicatus* (Blackwall)), whereas at the remaining plots the species are displayed close to the center and thus occur with similar quantities at the plots displayed. For habitat preferences of the species: see Table A3).

Ecological and functional groups

Differences in the composition of the carabid beetle and spider assemblages with regard to their ecological and functional groups were calculated by a one-way ANOVA. Whilst the carabid beetles had maximal values of the proportions of individuals of different ecological and functional groups in every kettle hole (except for M27), the correspondent numbers for spiders concentrated primarily in three kettle holes. Within a block of four kettle holes, no maximal and minimal values occurred (Table 3). The maximum and minimum values for the ecological groups and the habitat preferences do not always match well with the measured abiotic variables (Table A1).

Table 3: The composition of the carabid beetle assemblages were classified according to ecological and functional groups. The average percentage of individuals per trap and year (ArcSin SQRT transformed).

The letters a, b, c, d, e, f indicate statistically significant differences (Duncan-Test, $p < 0.05$). BMC= body mass class. For the abbreviations of the Roman numerals see Table A2

Parameters	M9	M19	M27	M28	M38	M46	M53	M192
hygrophilic	21.8 ^{a,b,c}	22.2 ^{a,b,c}	21.4 ^{a,b,c}	25.4 ^{a,b}	17.6 ^{b,c}	23.6 ^{a,b,c}	28.9 ^a	15.3 ^c
predominantly hygrophilic	13.2 ^{b,c}	13.4 ^{b,c}	8.4 ^c	16.1 ^b	25.2 ^a	14.1 ^{b,c}	9.7 ^{b,c}	0.0 ^d
xerophilic	10.1 ^d	10.9 ^d	13.9 ^{c,d}	16.1 ^c	32.7 ^a	21.9 ^b	9.1 ^d	2.4 ^e
eurytopic	35.8 ^{b,c}	43.4 ^a	30.6 ^{c,d}	24.7 ^{d,e}	22.7 ^e	41.7 ^{a,b}	41.7 ^c	5.4 ^f
arable fields	29.2 ^a	11.9 ^b	16.1 ^b	12.5 ^b	18.8 ^b	33.8 ^a	18.0 ^b	5.4 ^c
meadows and pastures	16.0 ^c	16.8 ^c	9.2 ^d	19.0 ^{b,c}	23.8 ^{a,b}	26.9 ^a	9.3 ^d	0.0 ^e
wet, open habitats	38.8 ^{a,b,c}	30.6 ^{b,c}	43.0 ^{a,b}	44.2 ^{a,b}	27.0 ^c	32.7 ^{a,b,c}	40.1 ^{a,b,c}	45.8 ^a
dry, open habitats	4.8 ^{e,f}	9.4 ^{c,d}	13.2 ^{b,c}	15.3 ^b	29.6 ^a	15.5 ^b	8.2 ^{d,e}	2.4 ^f
brachypterous	11.5 ^{a,b}	10.5 ^{a,b}	6.0 ^{b,c}	14.9 ^a	10.9 ^{a,b}	11.2 ^{a,b}	8.1 ^{a,b,c}	2.2 ^c
dimorphic	47.3 ^{a,b,c}	50.5 ^{a,b}	46.1 ^{a,b,c}	34.7 ^{c,d}	30.7 ^d	26.1 ^d	38.6 ^{b,c,d}	52.9 ^a
macropterous	40.2 ^{c,d}	36.8 ^d	43.2 ^{b,c,d}	51.3 ^{a,b,c}	54.3 ^{a,b}	61.2 ^a	49.8 ^{a,b,c,d}	36.7 ^d
spring breeders	33.2 ^a	23.3 ^b	23.7 ^b	17.9 ^b	22.6 ^b	33.4 ^a	20.7 ^b	4.4 ^c
autumn breeders	51.4 ^c	66.0 ^b	52.9 ^c	68.8 ^b	64.7 ^b	54.4 ^c	68.2 ^b	85.6 ^a
BMC I	30.8 ^{b,c}	46.7 ^a	40.4 ^{a,b}	37.7 ^{a,b}	25.3 ^c	25.9 ^c	38.7 ^{a,b}	14.6 ^d
BMC II	25.9 ^{c,d}	23.7 ^{c,d}	26.9 ^{b,c,d}	37.0 ^b	50.3 ^a	16.7 ^d	31.0 ^{b,c}	21.8 ^{c,d}
BMC III	29.5 ^b	21.6 ^{b,c}	27.6 ^{b,c}	23.5 ^{b,c}	15.5 ^c	53.8 ^a	27.7 ^{b,c}	60.5 ^a
BMC IV	31.8 ^a	21.0 ^{b,c}	21.8 ^b	14.1 ^d	15.5 ^{c,d}	13.0 ^d	18.2 ^{b,c,d}	2.3 ^e

For example, in one of the wettest kettle holes (M38), xerophilic carabid beetles and those that prefer dry open habitats have maximal numbers of individuals (Table 3). However, the number of individuals of carabid beetles that prefer wet, open habitats had minimal numbers.

This may be because the portions of coarse and medium sand also had high values at M38 (Table A1). The most consistent results can be seen at M46. The sandy soil fractions and the grass cover had maximum values whereas the soil moisture is rather low. Coincidentally, the numbers of individuals of the arable field and grassland species were maximal. Due to the very low numbers of species and individuals at the peaty kettle hole M192, most of the values, except for the number of individuals of species preferring wet, open habitats were negligible (Table 3).

The results for spiders are more consistent (Table 4). In M9, where the lowest value of soil moisture was measured, the highest numbers of individuals of xerophilic and arable field species were present.

At M19, a kettle hole that is rather wet and has a large extent of grass coverage, the numbers of individuals of hygrophilic and grassland spiders and those that prefer wet, open habitats is maximal. At M192 ombrophilic and forest species were the maxima (Table 4). Most of the minimal values appeared in M192.

Table 4: The composition of the spider assemblages were classified according to ecological and functional groups. The average percentage of individuals per trap and year (ArcSin SQRT transformed).

The letters a, b, c, d indicate statistically significant differences (Duncan-Test, $p < 0.05$). BMC= body mass class. For the abbreviations of the Roman numerals see Table A3

Parameters	M9	M19	M27	M28	M38	M46	M53	M192
hygrophilic	65.6 ^{a,b,c}	69.5 ^a	61.9 ^{b,c,d}	60.4 ^{c,d,e}	56.0 ^{e,f}	57.9 ^{d,e,f}	67.5 ^{a,b}	52.9 ^f
xerophilic	17.8 ^a	13.2 ^b	9.1 ^c	8.0 ^c	8.9 ^c	13.0 ^b	13.4 ^b	7.5 ^c
ombrophilic	15.8 ^d	15.1 ^d	26.2 ^c	28.2 ^{b,c}	32.4 ^a	28.6 ^{b,c}	17.7 ^d	35.8 ^a
arable fields	19.6 ^a	13.8 ^{b,c}	11.2 ^{c,d}	9.5 ^{c,d}	11.2 ^{c,d}	11.6 ^{c,d}	16.4 ^{a,b}	7.2 ^d
meadows and pastures	55.3 ^b	62.6 ^a	56.6 ^b	56.1 ^b	49.5 ^c	52.7 ^{b,c}	56.1 ^b	17.5 ^d
wet, open habitats	57.5 ^{b,c}	63.8 ^a	58.3 ^{b,c}	58.0 ^{b,c}	52.8 ^{c,d}	54.5 ^{b,c,d}	59.9 ^{a,b}	50.7 ^d
forests	15.8 ^d	15.1 ^d	26.2 ^c	28.2 ^{b,c}	32.4 ^{a,b}	28.2 ^{b,c}	17.7 ^d	35.8 ^a
BMC I	8.6 ^d	13.3 ^{a,b}	9.4 ^d	11.6 ^{b,c,d}	14.5 ^{a,b}	12.5 ^{a,b,c}	9.7 ^{c,d}	15.4 ^a
BMC II	64.8 ^d	70.8 ^{a,b,c}	72.7 ^{a,b}	66.2 ^{c,d}	70.1 ^{a,b,c}	71.5 ^{a,b}	73.4 ^a	67.7 ^{b,c,d}
BMC III	19.5 ^a	12.6 ^b	12.1 ^b	18.9 ^a	11.8 ^b	12.0 ^b	11.7 ^b	6.7 ^c

Assemblage similarity

One method used to determine possible isolation effects is to calculate the assemblage similarity between the kettle hole plots. Here, the Wainstein-Index was used. For carabid beetles, nine kettle hole plots showed an assemblage similarity $>30\%$, where M9 and M53 exceed this value in four cases, each (Table 5). It is striking that the highest similarity value did not occur between plots M27 and M28 which are no greater than 100 m apart. The lowest similarity values were calculated for M192 and M38, two kettle holes that are both very wet, however at M192 only a few carabid species and low numbers of individuals were caught.

Table 5: The percentage assemblage similarity matrix (Wainstein-Indices) calculated for carabid beetles (left) and spiders for all the investigated plots. For the abbreviations of the plots see chapter 2.1. The maximal values are shaded dark grey while the minimal values are light grey.

	M9	M19	M27	M28	M38	M46	M53	M192	
M9		51.7	39.1	38.6	33.4	43.5	34.5	9.7	M9
M19	30.9		53.5	46.2	35.6	56.6	32.1	8.9	M19
M27	31.9	29.2		56.5	52.8	46.1	48.4	23.7	M27
M28	38.7	31.5	33.1		43.1	40.6	48.9	20.8	M28
M38	14.9	16.0	21.6	12.4		38.9	45.1	17.2	M38
M46	18.6	21.3	18.2	23.1	12.4		37.6	9.4	M46
M53	38.9	32.4	38.9	35.7	16.1	16.2		24.6	M53
M192	14.5	15.0	13.3	11.9	5.8	10.7	12.9		M192
	M9	M19	M27	M28	M38	M46	M53	M192	

For spiders, nearly all of the kettle hole plots (87.5 %), with the exception of the peaty kettle hole M192 show assemblage similarities above 30 % among themselves. The highest values range between 52 % and 57 %. The highest values appeared between M46 and M19 and between M27 and M28 which are within close proximity. The lowest values < 10 % of assemblage similarity appeared between M192 and the drier kettle holes M9, M19, and M46 (Table 5, Table A1).

Potential migration ability of carabid beetles

To explore differences in the potential migration ability of carabid beetles from kettle holes and the reference sites, we calculated the percentages of species and individuals with different wing morphology. In both groups of plots, only a few brachypterous species and individuals were found. The percentage of dimorphic species was approximately 5 % higher at the plots than in the kettle holes, but the number of individuals was twice as high in the latter group (Table 6).

Table 6: The absolute and percentage of carabid beetle species and individuals of different of wing morphology at the kettle hole and the reference plots.

N spec= number of species, N ind= number of individuals

Wing morphism	N spec	% spec	N ind	% ind
Kettle holes (N=8)				
brachypterous	3	2.5	80	1.1
dimorphic/polymorphic	29	24.2	2608	35.3
dimorphic/polymorphic with flight observations	3	2.5	439	5.9
monomorphic/ polymorphic macropterous	12	10.0	261	3.5
macropterous with flight observations	73	60.8	3993	54.1
Set aside/ arable field (N=2)				
brachypterous	4	7.0	733	20.6
dimorphic/polymorphic	18	31.6	694	19.5
dimorphic/polymorphic with flight observations	2	3.5	37	1.0
monomorphic/polymorphic macropterous	5	8.8	107	3.0
macropterous with flight observations	28	49.1	1992	55.9

However, nearly 60 % of the species occurring at the reference plots and approximately 70 % from the kettle hole plots exhibit macropterous wing morphologies, and for the predominantly portion, flight observations exist. This indicates that potential migration ability by flight both is very high between the kettle holes and the open land represented by the reference plots.

DISCUSSION

We found that carabid beetle assemblages are very specific to each of the investigated kettle holes. Even if the kettle holes are very close to each other, which was the case for M27 and M28, the carabid beetle assemblages differ to a considerable extent. In contrast, spider assemblages appear to be relatively consistent between the kettle hole plots. For carabid beetles, Hamel (1988, 1996) described the kettle holes as unique “individual” environments within the agrarian landscape. The conditions of individual kettle holes differ considerably in terms of hydrogeomorphological and other abiotic site factors, which may indicate that the differences found in the composition of the carabid beetle assemblages are caused by differences in the environmental variables. From the RDA, we determined that the water volume and the percentage of organic matter of the plot soil are two of the most important

differentiating factors between the kettle holes. Humidity is cited as being the most important factor for the composition of carabid beetle assemblages, e.g., Hengeveld (1979), Holopainen *et al.* (1995), and Dijk (1996). Indeed, Hengeveld (1979) attributed the patterns of distribution by some carabid beetle species within a field, including *Pterostichus melanarius* Illiger and *Pterostichus madidus* (Fabricius), to the corresponding patterns of soil moisture. The water volume explains 22 % of the variance in the carabid beetle species data. However, the numbers of individuals of hygrophilic species do not match the soil humidity at the kettle hole plots in any case, which may be because the water volume was measured only twice a year, once in August which does not occur within the period of maximal activity of carabid beetles. The extreme poorness of carabid beetle species and individuals that was observed in the peaty like kettle hole M192 was also reported by Barndt (2005) for a kettle hole moor in eastern Brandenburg.

Another factor that explains 6 % of the variance along the 2nd axis of the ordination diagram is the pH. Some authors have found that pH is an important but inconsistent factor between environments. Holopainen *et al.* (1995) found in their study of 16 arable fields that the pH is the least important factor separating carabid communities. Baguette (1987) suggested that pH may exert indirect effects on the degradation and availability of organic material in the soil, which, in turn, might affect prey availability for carabid beetles. However, in laboratory experiments, Paje & Mossakowski (1984) found that most carabid beetles preferred a pH consistent with that in their native environment. Concerning the mechanical soil properties, soil structure and particle size are directly related to the water capacity of soils. However, particle size has different impacts on the distribution of carabid assemblages, as seen in Figure 1. The arrows of fine particle sizes point in the direction of the non-kettle hole plots set-aside (Mus05) and barley field (MuA62). The factors of water volume and the percentage of organic matter are apparently more important in organic soils to determine carabid beetle assemblages. Particle size appears to be a great more determining factor in mineral soils and all fractions together explain ca. 20 % of the variance in the species data.

The distribution of the maximal proportions of numbers of individuals for carabid beetles demonstrate that each of the kettle holes have different ecological properties which meet different ecological requirements of the species. Thus, almost each of the kettle holes contains a ecologically different carabid beetle coenosis. In contrast, most of the different requirements of the spiders comply with the ecological characteristics of only three kettle holes. Within a block of four (five) kettle holes the spider assemblages are rather unspecific. In contrast to the carabid beetles, the ecological composition of the spider assemblages better fits with the environmental variables measured in the kettle holes. The RDA results reveal that 15 % of the variance in the spider species data are explained by the coverage of the grass layer which is consistent with the results of Bell *et al.* (2001) and Rypstra *et al.* (1999) who found that the vegetation structure was an essential factor in the distribution of spiders in the environment. Dense vegetation fulfils the spiders' requirements for web building and overwintering places. In comparison, water volume was only 9 % of the variance explanation and organic matter was 4 %. The directions and lengths of the environmental arrows in Figure 2 are mostly consistent with the abiotic and biotic factors measured at the kettle hole plots.

As many of the found carabid species by us are potentially capable of flying (Table 6), we predict that the carabid beetle fauna are more homogenously spread over the kettle holes than observed. However, Duelli *et al.* (1990); Joyce *et al.* (1999); Mader *et al.* (1990); Thomas & Marshall (1999); and Thomas *et al.* (1998, 2002, 2003) could show (using directional pitfall traps placed at the edges of hedgerows and other barriers between fields) that even winged

carabid beetles migrate between these environments by walking rather than by flying. Matalin (1994, 2003) determined the flight ability of 69 carabid beetle species caught in the south-western plain of the river Prut, Moldova Region, on the basis of biometrical data such as wing area and the development of flight muscles. From these measurements, he calculated an index of potential mobility (IPM), which ranges from zero (no potential for flight) and 1.0 (fully capable of flight). Roughly half of the species we caught in both, the kettle holes and the reference plots were macropterous. In comparison with Matalin's data, the IPM of our dimorphic species ranged from 0.002 to 0.53, from 0.25 to 0.83 in polymorphic macropterous species, and from 0.53 to 1.00 in monomorphic macropterous species (nine out of 10 species of all of the three wing morphological types). Kotze & O'Hara (2003) stated that dimorphic carabid species may survive better in environments with high dynamics, such as riverbanks than monomorphic macropterous and brachypterous species the former are able to disperse better between suitable habitats whilst the latter are capable to survive within newly colonized habitats. Bonn & Helling (1997) and Bonn (2000) found a high flight activity at the banks of the Elbe River in spring, when the river was inundated. They concluded that the beetles were in the process of colonizing new emerging habitats as the water level retreated. Boer (1977, 1990); Wallin (1985, 1987a,b) and Desender (1989) found a correlation between dispersal, habitat selection and reproduction in field inhabiting carabid beetles. Dyck and Baguette (2005) differentiate routine (random) from special movement (dispersal) and they stated that dispersal is a by-product of routine movements and predicted that dispersal would be hindered by habitat fragmentation and thus leads to increasingly isolated populations. We assume, that though many of the carabid beetles found in the kettle holes are capable of flight they would rather stay in a suitable environmental than take the risk to immigrate by flight which would require a high cost of energy. Furthermore, the risk is high of starving or being caught by predators on their airborne way. Blem (1980) stressed out that especially for small insects, dispersal by flight is relatively expensive, because the cost of locomotion is an inverse function of the body weight (Tucker, 1970). Tucker (1970) stressed out that locomotion by flight is more effective in dispersal than walking but he did not present an example with direct comparison of the costs of transport of these two modes of dispersal used by the same species. Desender (2000) could show that there is a seasonal pattern of light muscle development. He figured out that in most of the species studied there is a trade-off between dispersal and reproduction (oogenesis-flight syndrome). Ripe ovaries have a negative relation with functional flight musculature and vice versa. Tietze (1963) found a reduction of flight muscles in some morphological macropterous species. Geipel & Kegel (1989) investigated three extremely isolated roadside strips in Berlin to carabid beetles and found very few (< 4 %) of macropterous individuals with fully developed flight muscles. In contrast, approximately 85 % of the 454 individuals with weakly developed flight muscles had ripe ovaries and testes, respectively and thus were at the peak of their reproduction period. They found no evidence of an "oogenesis-flight syndrome" and concluded that even in highly isolated habitats macropterous or dimorphic carabid beetles chose to reproduce in their isolated habitats rather than prepare to emigrate by flight through the development of their flight muscles.

In contrast to carabid beetles, many spider species disperse by ballooning, e.g., Linyphiidae as adults and as juveniles, and nearly all other families at least as juveniles (Johnson, 1969; Dingle, 1978, 1980; Bonte *et al.*, 2003; Thomas & Jepson, 1997; Bell *et al.*, 2005). Spiders do not urgently need to compensate the loss of protein because some of them, e.g. *Erigone atra* Blackwall 1833 may survive hunger for more than a year (Bell *et al.*, 2005). For spiders, the loss of energy may be less than for carabid beetles which need to fill up their energy reserves by external sources, e.g., by hunting prey which means additional energy

consumption. From 119 species observed in this study, for 48 (40.3 %) ballooning data were recorded by Bell *et al.* (2005), and among those is included many of the most frequently caught, e.g., the species of the genus *Oedothorax* and most of the wolf spider species. However, it is unclear whether these species actually are moving frequently between the kettle holes by ballooning.

We conclude that both, the specific environmental properties in each of the kettle holes and the different modes of migration, lead to the different composition of carabid beetle and spider assemblages in the kettle holes. The carabid beetle assemblages are more specific for each of the kettle holes, whereas the spider assemblages are more similar between the kettle holes. Further studies may reveal whether the carabid beetle and spider populations primarily reproduce within the kettle holes, where they spend much of their lives, and how much migration activity occurs between different kettle holes and adjacent wetland populations. Genetic studies are necessary to determine the amount of gene flow between the populations, and to address the question of how much isolation each type of population experiences.

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APPENDIX

Table A1: The environmental variables determined at the plots investigated. All of the units are presented as percent except where otherwise indicated and for the pH.

PercOrg= Percentage of organic matter, WV= Water volume, CoSa= Coarse sand, MeSa= Medium sand, FiSa= Fine sand, CovHerb= Cover Herb layer, CovGrass= Cover Grass layer . n.v.=no value available.

Plots	Hydrogeomorphology					Soil					Vegetation			
	Catchment Area	Kettle hole Area	Shore Slope	Hydroperiod	Max. depth	pH	PercOrg	WV	CoSa	MeSa	FiSa	Silt	CovHerb	CovGrass
	[ha]	[ha]	[%]		[m]		[%]	[%]	[%]	[%]	[%]	[%]	[%]	[%]
M9	10.02	0.22	15.8	episodic	1.02	6.2	26.0	32.6	29.0	36.4	25.6	9.0	18.8	66.8
M19	2.22	0.10	23.2	semipermanent	1.66	5.3	21.2	67.1	19.8	39.2	28.8	12.2	35.5	62.5
M27	11.05	1.05	28.6	semipermanent	4.24	4.9	26.0	66.7	19.6	28.4	35.3	16.8	76.1	22.4
M28	1.06	0.09	22.7	periodic	1.80	4.2	18.8	44.4	18.1	30.1	24.3	24.9	13.5	79.1
M38	1.40	0.4	19.5	periodic	1.91	4.5	42.0	86.0	39.1	37.9	27.4	13.0	13.8	90.0
M46	n.v.	n.v.	26.2	episodic	1.14	4.1	13.5	39.0	23.1	51.3	39.1	37.0	6.1	90.5
M53	n.v.	n.v.	n.v.	n.v.	n.v.	6.2	23.2	56.3	15.9	36.0	32.3	12.1	30.8	87.9
M192	4.82	2.00	25.4	permanent	1.37	3.4	77.2	86.6	15.7	27.0	20.9	36.4	8.7	1.6
MuS05	-		-	-	-	5.1	11.2	12.2	13.8	37.4	31.6	17.2	65.4	23.4
MuA62	-		-	-	-	6.0	3.6	12.9	9.9	38.8	37.2	14.0	0.0	68.8

Table A2: A list of carabid beetle species including the short cuts used in Fig. 1, the total number of individuals caught in the trapping period and details on biology, ecological and functional groups.

EG= ecological group: h= hygrophilic, (h)= moderately hygrophilic, x= xerophilic, (x)= moderately xerophilic, eu= eurytopic, hf= hygrophilic in forests, h(f)= hygrophilic in open sites and forests, (h)f= moderately hygrophilic and in forests, (h)(f)= moderately hygrophilic and predominantly in forests, (x)f= moderately xerophilic and in forests, (x)(f)= moderately xerophilic and predominantly in forests; HP= habitat preference: af= arable fields; fa= fallows; wet, open habitats (as summarized in Fig. 2): ba= banks, mo= moors, re= reeds; meadows and pastures (as summarized in Fig. 2): wm= wet meadows, pa= pastures; dry, open habitats (as summarized in Fig. 2): dg= dry grassland; forests (as summarized in Fig. 2): wf= wet forests, mf= moist forests, mdf= moderately dry forests; WM= wing morphs: br= brachypterous, di=dimorphic, di*= dimorphic with flight observations, ma= macropterous, ma*= macropterous with flight observations, HM= hibernation mode: Spr= spring breeders, (Spr)= predominantly spring breeders, Aut= autumn breeders, (Aut)= predominantly autumn breeders, Irr= Irregular hibernation mode, BMC= body mass class: I= < 5mg, II= 5-9.9 mg, III= 10-29.9 mg, IV= 30-100 mg; V= >100 mg. For the abbreviations for the plots: see Chapter 2.1.

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	EG	HP	WM	HM	BMC
<i>Abax parallelepipedus</i>	Aba para									1		(h) f	mf	br	Irr	IV
<i>Acupalpus exiguus</i>	Acu exig	5	3	2	18	1		11				h	wm	ma*	Spr	I
<i>Acupalpus flavicollis</i>	Acu flav			3	1	1	1					h	re	ma*	Spr	I
<i>Acupalpus parvulus</i>	Acu parv		7	3	10		1	13				h	re	ma*	Spr	I
<i>Agonum emarginatum</i>	Ago emar	22	2					1				h	re	di	Spr	II
<i>Agonum fuliginosum</i>	Ago fuli	2			1							h (f)	wf	di	(Spr)	I
<i>Agonum lugens</i>	Ago luge	62	18	26	28	1		19				h (f)	re	ma*	(Spr)	II
<i>Agonum marginatum</i>	Ago marg			1			1					h	ba	ma*	Spr	III
<i>Agonum sexpunctatum</i>	Ago sexp	3			1							(h)	wm	ma	Spr	II
<i>Agonum thoreyi</i>	Ago thor	23	4	8	10	3		19	3	1		h	re	ma*	(Spr)	II
<i>Agonum viduum</i>	Ago vidu	35	18	5	4	6		10				h	re	ma*	Spr	II
<i>Amara aenea</i>	Ama aene	5	8	55	28	123	72	15	1	344	11	(x)	dg	ma*	Spr	II
<i>Amara apricaria</i>	Ama apri		1			19	1			1		(x)	af	ma*	(Aut)	II
<i>Amara aulica</i>	Ama auli		1									(x)	fa	ma*	Aut	III
<i>Amara bifrons</i>	Ama bifr		1		1		3					x	fa	ma*	Aut	I
<i>Amara communis</i>	Ama comm					1	9			23	1	(h)(f)	pa	ma*	(Spr)	II
<i>Amara consularis</i>	Ama cons						2					(x)	af	ma*	(Aut)	II

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	EG	HP	WM	HM	BMC
<i>Amara equestris</i>	Ama eque									3		x	dg	ma	Aut	III
<i>Amara eurynota</i>	Ama eury					2	1					x	fa	ma*	Spr	III
<i>Amara familiaris</i>	Ama fami			2	1					7		(x)(f)	af	ma*	Spr	I
<i>Amara lunicollis</i>	Ama luni			2	8		40			54	16	(h)	pa	ma*	Spr	II
<i>Amara ovata</i>	Ama ovat						1		1			(h)	fa	ma*	(Spr)	II
<i>Amara similata</i>	Ama simi	2	1		6	67	10	2		1		eu	af	ma*	Spr	II
<i>Amara spreta</i>	Ama spre					1				4		x	af	ma*	Spr	II
<i>Amara tibialis</i>	Ama tibi						1			9	2	x	dg	ma*	Spr	I
<i>Anchomenus dorsalis</i>	Anc dors				1			1			5	(x)	af	ma*	Spr	I
<i>Anisodactylus binotatus</i>	Ani bino	25	9	85	11	18	79	5		4	1	(h)(f)	wm	ma*	Spr	III
<i>Anthracus consputus</i>	Ant cons		2	2	1			5				h	re	ma*	Spr	I
<i>Asaphidion flavipes</i>	Asa flav										1	eu	af	ma*	Spr	I
<i>Badister bullatus</i>	Bad bull	9			1		2	1				(x)(f)	mdf	ma*	Spr	I
<i>Badister dilatatus</i>	Bad dila							1				h	mo	ma*	Spr	I
<i>Badister dorsiger</i>	Bad dors				1							h	re	di	Spr	I
<i>Badister peltatus</i>	Bad pelt							1				h	re	ma*	Spr	I
<i>Badister sodalis</i>	Bad soda	2		1	8			5				h(f)	wf	br	Spr	I
<i>Badister unipustulatus</i>	Bad unip	2			5			10				h(f)	re	ma*	Spr	II
<i>Bembidion articulatum</i>	Bem arti	1		1				2			1	h	re	ma*	Spr	I
<i>Bembidion doris</i>	Bem dori	2	1	4	2	1	2	5				h	re	ma*	Spr	I
<i>Bembidion femoratum</i>	Bem femo								1			eu	af	di*	(Spr)	I
<i>Bembidion gilvipes</i>	Bem gilv	7	2		4		16			2		h	wm	di	Spr	I
<i>Bembidion guttula</i>	Bem gutt	40	17	2	3	7	10	41		5		h	re	di	Spr	I
<i>Bembidion lampros</i>	Bem lamp	1				6	4			17	42	(x)(f)	af	di	Spr	I
<i>Bembidion lunulatum</i>	Bem lunu						3					h	wm	ma*	Spr	I
<i>Bembidion mannerheimi</i>	Bem mann	27	4	1	6	2	40	3	1	10	68	h(f)	wf	br	Spr	I

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	EG	HP	WM	HM	BMC
<i>Bembidion properans</i>	Bem prop	2				1	3			3	33	(x)	af	di	(Spr)	I
<i>Bembidion quadrimaculatum</i>	Bem quad				1							(x)	af	ma*	Spr	I
<i>Bembidion tetracolum</i>	Bem tetr	1				21		1				eu	af	di	Spr	I
<i>Bembidion varium</i>	Bem vari	1		2	4		1	4				h	ba	ma*	Spr	I
<i>Blethisa multipunctata</i>	Ble mult	1			1			1				h	re	ma*	Spr	III
<i>Bradycellus csikii</i>	Bra csik					4						(x)	fa	di	(Aut)	I
<i>Calathus erratus</i>	Cal erra	2		4	1		1	1		11	42	x	dg	di	(Aut)	III
<i>Calathus fuscipes</i>	Cal fusc	2	2		3		1			195	168	(x)(f)	fa	di	(Aut)	III
<i>Calathus melanocephalus</i>	Cal mela	2	5				9			9	12	(x)	fa	di	(Aut)	II
<i>Carabus auratus</i>	Car aura	33	20	12	22	20	34	15		214	435	(x)	af	br	Spr	V
<i>Carabus granulatus</i>	Car gran	96	17	63	10	20	15	15	1		2	h(f)	wf	di	Spr	IV
<i>Carabus nemoralis</i>	Car nemo		1				6			5		(h)(f)	mf	br	(Spr)	V
<i>Carabus violaceus violaceus</i>	Car viol					1						(x)f	mdf	br	(Aut)	V
<i>Chlaenius nigricornis</i>	Chl nigr			8	1			4				h	wm	ma*	Spr	III
<i>Chlaenius tristis</i>	Chl tris					2	1					h	re	ma*	Spr	III
<i>Clivina fossor</i>	Cli foss	58	30	21	15	2	106	2		29	1	eu	af	di*	Spr	I
<i>Demetrias monostigma</i>	Dem mono	1				2						h	re	di	Spr	I
<i>Diachromus germanus</i>	Dia germ			1		5						h	wm	ma	(Spr)	III
<i>Dicheirotichus rufithorax</i>	Dic rufi	1										(x)	fa	ma*	Spr	I
<i>Dyschirius globosus</i>	Dys glob	36	193	36	19	3	21	95		8		h (f)	wf	di	Spr	I
<i>Elaphrus cupreus</i>	Ela cupr	1	3	17	5	21	1	29				h (f)	wf	ma*	Spr	II
<i>Elaphrus riparius</i>	Ela ripa	1	1		1	10		4				h	ba	ma*	Spr	I
<i>Harpalus affinis</i>	Har affi	2	1	1		1	119	8		28	67	(x)	af	ma*	Spr	III
<i>Harpalus autumnalis</i>	Har autu			1								x	dg	di	(Spr)	II
<i>Harpalus distinguendus</i>	Har dist	2			2		3					(x)	af	ma*	(Spr)	III

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	EG	HP	WM	HM	BMC
<i>Harpalus flavescens</i>	Har flav						2					x	dg	ma	(Aut)	III
<i>Harpalus froelichii</i>	Har froe		1		1		1			1		x	dg	ma*	Spr	III
<i>Harpalus latus</i>	Har latu	3		1	4		57	1		3		(h)	pa	ma*	Irr	III
<i>Harpalus luteicornis</i>	Har lute		2	1	1		40			4		(x)	fa	ma	Spr	I
<i>Harpalus pumilus</i>	Har pumi											x	dg	di	(Spr)	I
<i>Harpalus rubripes</i>	Har rubr						1			6		x	fa	ma*	Irr	III
<i>Harpalus rufipes</i>	Har rufi	39	4	29	9	1	401	19	2	25	157	(x)	af	ma*	(Aut)	III
<i>Harpalus serripes</i>	Har serr						2					x	dg	ma*	Spr	III
<i>Harpalus servus</i>	Har serv		2		3		1			2		x	dg	ma	Spr	III
<i>Harpalus signaticornis</i>	Har sign			1		1	4	1		2	11	(x)	af	ma	Spr	I
<i>Harpalus smaragdinus</i>	Har smar	6	2	1	5		43	2		8	10	x	dg	ma*	(Aut)	III
<i>Harpalus tardus</i>	Har tard	1			2		2			2		(x)	fa	ma*	(Spr)	III
<i>Leistus ferrugineus</i>	Lei ferr	2			2							(x)(f)	mdf	br	Aut	I
<i>Leistus terminatus</i>	Lei term	2	3	3	2		1	5				h(f)	mo	di	Aut	I
<i>Limodromus assimilis</i>	Lim assi						3					h(f)	wf	ma*	Spr	III
<i>Loricera pilicornis</i>	Lor pili	33	11	22	15	4	12	24		8	37	(h)(f)	af	ma*	(Spr)	II
<i>Microlestes maurus</i>	Mic maur									2		(x)	fa	di	Spr	I
<i>Microlestes minutulus</i>	Mic minu		1		2						1	(x)	fa	ma*	Spr	I
<i>Nebria brevicollis</i>	Neb brev			4		4		1		1		(h)(f)	mf	ma*	(Aut)	III
<i>Notiophilus palustris</i>	Not palu	4		4		1	4				6	hf	wf	di	Spr	I
<i>Oodes helopioides</i>	Ood helo	137	23	41	55	21	8	81	7			h	re	ma*	Spr	II
<i>Oxypselaphus obscurus</i>	Oxy obsc	161	7	211	21	5	14	7				h(f)	wf	di	Irr	I
<i>Panagaeus cruxmajor</i>	Pan crux				1							h	re	ma	Spr	II
<i>Patrobus atrorufus</i>	Pat atro	4	3	43		29	2	7			1	h(f)	wf	di	(Aut)	II
<i>Poecilus cupreus</i>	Poe cupr	22	1	1			68	1		38	75	(h)	af	ma*	Spr	III
<i>Poecilus punctulatus</i>	Poe punc						3				85	(x)	af	ma	Spr	III

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	EG	HP	WM	HM	BMC
<i>Poecilus versicolor</i>	Poe vers	32	20	12	13		278	2		822	198	(h)	af	ma*	Spr	III
<i>Pterostichus diligens</i>	Pte dili	7	10	11	7	3	11	11	4			h	mo	di	(Spr)	I
<i>Pterostichus melanarius</i>	Pte mela	340	18	71	17		65	67		34	82	eu	pa	di	(Aut)	IV
<i>Pterostichus minor</i>	Pte mino	5	13	7	59	1	14	8	13			h(f)	mo	di	(Spr)	II
<i>Pterostichus niger</i>	Pte nige	59	49	39	11	16	24	6		4	3	(h)(f)	mf	di*	(Aut)	IV
<i>Pterostichus nigrata</i>	Pte nigr	237	43	76	37	3	165	112	33	5		h(f)	wf	ma*	(Spr)	III
<i>Pterostichus oblongopunctatus</i>	Pte oblo	36	4	16	3	3		22	25		1	(x)f	mdf	di	(Spr)	III
<i>Pterostichus rhaeticus</i>	Pte rhae	20		12	1		4	6				h	mo	ma	(Spr)	III
<i>Pterostichus strenuus</i>	Pte stre	13	14	24	9	2	17	28	1			(h)f	mf	di	Spr	I
<i>Pterostichus vernalis</i>	Pte vern	6	5	17	6	9	17	14	7	4		h	wm	di	Spr	I
<i>Stenolophus mixtus</i>	Ste mixt	6	28	47	55	15	16	49				h	re	ma*	Spr	I
<i>Stenolophus skrImshIrranus</i>	Ste skri		29	52	15	5	1	27				h	re	ma	Spr	I
<i>Stenolophus teutonus</i>	Ste teut	1	1	2	2		9					h	ba	ma	Spr	I
<i>Stomis pumicatus</i>	Sto pumi	3			1							h	wm	br	Spr	II
<i>Syntomus truncatellus</i>	Syn trun						1			1	1	(x)	fa	di	Spr	I
<i>Synuchus vivalis</i>	Syn viva	4			1		1	1		4		(x)(f)	fa	di	Aut	II
<i>Trechus obtusus</i>	Tre obtu	50	10	5	5		25	3		4	5	(h)(f)	fa	di	(Aut)	I
<i>Trechus quadristriatus</i>	Tre quad	23	2				1				2	(x)	af	ma*	(Aut)	I
<i>Trichocellus placidus</i>	Tri plac			1								h	re	ma	Spr	I
<i>Zabrus tenebrioides</i>	Zab tene							2			12	(x)	af	ma*	Aut	III

Table A3: A list of spider species including the short cuts used in Figs. 2, the total number of individuals caught in the trapping period and details on biology, ecological and functional groups.

EG= ecological group; h= hygrophilic, (h)= moderately hygrophilic, x= xerophilic, (x)= moderately xerophilic, eu= eurytopic, hf= hygrophilic and in forests, h(f)= hygrophilic in open sites and in forests, (h)f= moderately hygrophilic and in forests, (h)(f)= moderately hygrophilic and predominantly in forests (x)f= moderately xerophilic and in forests, (x)(f)= moderately xerophilic and predominantly in forests (summarized as ombrophilic in Table 4); HP= habitat preference: af= arable fields; fa= fallows ; wet, open habitats (as summarized in Fig. 3): ba= banks, mo= moors, re= reeds, woh= wet, open habitats; meadows and pastures (as summarized in Fig. 3): mea= meadows in general, wm= wet meadows, pa= pastures; dry, open habitats (as summarized in Fig. 3): Cah= Calluna heaths, dg= dry grassAutnd, doh= dry, open habitats; oha= open habitats; forests (as summarized in Fig. 3): wf= wet forests, mf= moist forests, mdf= moderately dry forests, mdfe= moderately dry forest edges, pif= pioneer forests, fo= forests in general; BMC= body mass class: I= < 1 mg, II= 1-4.9 mg, III= 5-9.9 mg, IV= 10-20 mg; V= >20 mg; Ball= Ballooning observed. For the abbreviations for the plots: see Chapter 2.1.

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	Ecol. Gr.	Pref. Hab.	BMC	Ball.
<i>Agroeca brunnea</i>	Agr brun	1			2							(f)	mdf	III	
<i>Agyneta affinis</i>	Agy affi										2	(x)	dg	I	
<i>Agyneta ramosa</i>	Agy ramo								1			h(f)	wf	I	
<i>Agyneta rurestris</i>	Agy rure							2		1	3	(x)	af	I	
<i>Allomengea scopigera</i>	All scop	6	1							1		h	mo	II	
<i>Allomengea vidua</i>	All vidu	3	1				1					h	wm	II	
<i>Alopecosa cuneata</i>	Alo cune	2	8	2	7	1	10	2	3	52	4	x	dg	III	
<i>Alopecosa pulverulenta</i>	Alo pulv	10	12	1	10	1	18	4		31	2	(h)	mea	III	x
<i>Alopecosa trabalis</i>	Alo trab	4				1			1	1		(x)(f)	mdf	V	
<i>Antistea elegans</i>	Ant eleg							1				h	mo	I	
<i>Araeoncus humilis</i>	Ara humi										4	(x)	af	I	x
<i>Araneus marmoreus</i>	Ara marm	1										(h)(f)	mdfe	IV	x
<i>Araneus quadratus</i>	Ara quad		1		1							h	wm	V	
<i>Arctosa leopardus</i>	Arc leop	5	9	43	20	93	11	44		1		h	wm	III	
<i>Arctosa lutetiana</i>	Arc lute							1				x	dg	III	
<i>Asagena phalerata</i>	Asa phal						1			1		x	dg	II	
<i>Baryphyma pratense</i>	Bar prat	20	3	3	1			6				h	re	I	
<i>Bathypantes approximatus</i>	Bat appr							1	1			h(f)	wf	I	x

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	Ecol. Gr.	Pref. Hab.	BMC	Ball.
<i>Bathyphantes gracilis</i>	Bat grac							1				(x)	af	I	x
<i>Bathyphantes nigrinus</i>	Bat nigr				1							hf	wf	I	x
<i>Bathyphantes parvulus</i>	Bat parv				2							(x)	fa	I	
<i>Centromerus dilutus</i>	Cen dilu				1							(h)f	mf	I	
<i>Ceratinella brevipes</i>	Cer brep	1		1	3			1	1	1		h	wm	I	
<i>Ceratinopsis stativa</i>	Cer stat						1					(h)	wm	I	
<i>Clubiona diversa</i>	Clu dive	1			1							h	wm	II	
<i>Clubiona flrrisia</i>	Clu fris	1										x	dg	II	
<i>Clubiona lutescens</i>	Clu lute				1	1						hf	wf	II	
<i>Clubiona phragmitis</i>	Clu phra	11	1	1	6	2	2	1	1			h	re	III	
<i>Clubiona reclusa</i>	Clu recl	3	2	1	5	3	2	3		1		(x)	fa	II	
<i>Clubiona stagnatilis</i>	Clu stag	4	3	3	1		7	3		1		h	re	III	x
<i>Clubiona terrestris</i>	Clu terr					1				1		(x)(f)	mdf	III	
<i>Clubiona trivialis</i>	Clu triv				2							(x)(f)	mdfe	II	
<i>Dicymbium nigrum brevisetosum</i>	Dic brev				1							(x)	pa	I	x
<i>Diplocephalus permixtus</i>	Dip perm					1						h(f)	wf	I	
<i>Diplostyla concolor</i>	Dip conc	2	1	4	26	2	4	4				(h)(f)	mf	I	x
<i>Dismodicus elevatus</i>	Dis elev					1						(x)f	mdf	I	
<i>Drassyllus lutetianus</i>	Drs lute	102	29	43	50	10	92	31	5	39	7	(h)	af	II	
<i>Drassyllus praeficus</i>	Drs prae			1	1							x	dg	II	
<i>Drassyllus pusillus</i>	Drs pusi			2	2					10	3	(x)	fa	II	
<i>Enoplognatha caricis</i>	Eno cari								1			h	re	II	x
<i>Enoplognatha oelandica</i>	Eno oela	1										x	dg	I	
<i>Enoplognatha thoracica</i>	Eno thor			1	1					1		(x)(f)	doh	II	x
<i>Erigone atra</i>	Eri atra	16	14	13	11	10	28	27	8	11	305	(h)	af	I	x
<i>Erigone dentipalpis</i>	Eri dent	2	3	1	11	1	5	2	1	3	121	(x)	af	I	x

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	Ecol. Gr.	Pref. Hab.	BMC	Ball.
<i>Erigone longipalpis</i>	Eri long										1	(x)	af	I	x
<i>Erigonella ignobilis</i>	Eri igno		1						1			h	mo	I	
<i>Euophrys frontalis</i>	Euo fron	1										(x)(f)	mdf	II	
<i>Euryopis flavomaculata</i>	Eur flav	1			9							(x)(f)	mdfe	II	
<i>Gnathonarium dentatum</i>	Gna dent	1	2		1	1		1				h	woh	I	x
<i>Gongylidiellum latebricola</i>	Gon late							1				(x)(f)	mdf	I	
<i>Gongylidiellum vivum</i>	Gon vivu								2			h	mo	I	x
<i>Haplodrassus signifer</i>	Hap signi						1			2		x	fa	III	
<i>Heliophanus auratus</i>	Hel aura			1								h	re	II	
<i>Hypomma bituberculatum</i>	Hyp bitu							3				h	re	I	x
<i>Hypomma fulvum</i>	Hyp fulv							1				h	re	I	
<i>Liocranoeca striata</i>	Lio stri						1					(h)f	mf	II	
<i>Marpissa radiata</i>	Mar radi	1										h	re	III	
<i>Micaria pulicaria</i>	Mic puli		1	1	1		1					(x)	fa	II	
<i>Microlinyphia pusilla</i>	Mic pusi									1		(x)	fa	II	
<i>Neottiura bimaculata</i>	Neo bima				1				1			(x)(f)	pif	I	
<i>Neriere clathrata</i>	Ner clat				7			1				(h)f	mf	II	x
<i>Notioscopus sarcinatus</i>	Not sarc								5			h	mo	I	
<i>Oedothorax apicatus</i>	Oed apic		10		8	4	6	7	5	1	66	(x)	af	I	x
<i>Oedothorax fuscus</i>	Oed fusc		5	5	6	11	2	4	1		1	h	wm	I	x
<i>Oedothorax gibbosus</i>	Oed gibb			1	2	1	1	3	7			h	mo	I	x
<i>Oedothorax retusus</i>	Oed retu	2	18	12	15	21	7	51	7		3	(h)	wm	I	x
<i>Ozyptila praticola</i>	Ozy prat					1						(x)f	mdf	I	
<i>Ozyptila trux</i>	Ozy trux	21	7	1	12	5	14	16	1	1	1	h(f)	wm	II	
<i>Pachygnatha clercki</i>	Pac cler	20	15	31	27	52	5	43		10		h	wm	II	x

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	Ecol. Gr.	Pref. Hab.	BMC	Ball.
<i>Pachygnatha degeeri</i>	Pac dege			1	2			2		51	7	(x)	af	I	x
<i>Pardosa agrestis</i>	Par agre	32	14	13	29	8	161	5	1	190	81	(x)	af	III	
<i>Pardosa amentata</i>	Par amen	83	39	282	249	121	163	149	13	6	5	(h)	wm	II	x
<i>Pardosa monticola</i>	Par mont				1							x	dg	II	x
<i>Pardosa paludicola</i>	Par pald	10	15	4	12	6	44	12	1		1	h	re	II	
<i>Pardosa palustris</i>	Par palu	1156	872	953	1056	562	1596	818	81	554	103	(x)	oha	III	x
<i>Pardosa prativaga</i>	Par prat	47	22	22	44	6	26	18	7	1136	70	h	wm	II	x
<i>Pardosa pullata</i>	Par pull	5	2	4	5	4	6	1	2	5		h	woh	II	x
<i>Pelecopsis parallela</i>	Pel para									2		(x)	dg	I	
<i>Phylloneta impressa</i>	Phy impr		1									(x)	fa	II	x
<i>PIrrata pIrraticus</i>	PIrr pIrra	38	12	18	46	14	72	54	4	1	1	h	mo	II	x
<i>PIrrata piscatorius</i>	PIrr pisc	3	1	8	9	3	2	10	11			h	mo	III	
<i>PIrrata tenuitarsis</i>	PIrr tenu	3		2	1			6	8			h	mo	II	
<i>PIrratula hygrophila</i>	PIrr hydr	164	88	361	449	252	173	560	330	16	1	h(f)	wf	II	
<i>PIrratula latitans</i>	PIrr lati	19	7	14	7	13	3	22	398		1	h	mo	II	
<i>Pisaura mIrrabilis</i>	Pis mIrra	3		1	1	1	5	1	1	3		(x)	fa	V	x
<i>Pocadicnemis juncea</i>	Poc junc			3	2		1	1	9			h	woh	I	
<i>Pocadicnemis pumila</i>	Poc pumi								1			(h)(f)	mf	I	
<i>Porrhomma pygmaeum</i>	Por pygm			1	1	1	1	1	1			h(f)	wf	I	x
<i>Robertus arundineti</i>	Rob arun							1	1	1		h(f)	mo	I	x
<i>Savignia frontata</i>	Sav fron		1									h	wm	I	x
<i>Tallusia experta</i>	Tal expe	3	2	1	3	1	4	1		1		(h)	pa	I	x
<i>Tapinocyba praecox</i>	Tap prae				2		1					x	dg	I	
<i>Tenuiphantes tenuis</i>	Ten tenu		1	1			1					(x)	pa	I	x
<i>Tetragnatha dearmata</i>	Tet dear		1	1		1						h(f)	wf	III	
<i>Thanatus striatus</i>	Tha stri	14					2	1				h	mo	II	

Species	Short cut	M9	M19	M27	M28	M38	M46	M53	M192	MuS05	MuA62	Ecol. Gr.	Pref. Hab.	BMC	Ball.
<i>Theridion varians</i>	The vari				1							(x)f	mdf	I	
<i>Tibellus oblongus</i>	Tib oblo						1					(x)	fa	III	
<i>Tiso vagans</i>	Tis vaga									1		(h)	wm	I	x
<i>Trochosa ruricola</i>	Tro ruri	13	6	29	17	11	107	19	16	59	1	(h)	fa	IV	x
<i>Trochosa spinipalpis</i>	Tro spin	1	1	6	2	1		1	36			h(f)	mo	IV	
<i>Trochosa terricola</i>	Tro terr				1							(h)(f)	fo	IV	x
<i>Troxochrus scabriculus</i>	Tro scab	1										(x)	doh	I	
<i>Walckenaeria antica</i>	Wal anti	1										(x)	fa	I	x
<i>Walckenaeria atrotibialis</i>	Wal atro	2							3			h(f)	wf	I	
<i>Walckenaeria cucullata</i>	Wal cuc									1		(x)f	mdf	I	
<i>Walckenaeria cuspidata</i>	Wal cusp		1		1							h(f)	wf	I	x
<i>Walckenaeria kochi</i>	Wal koch	1	1						11			h	mo	I	
<i>Walckenaeria monoceros</i>	Wal mono	1						1				(x)f	mdf	I	
<i>Walckenaeria nudipalpis</i>	Wal nudi	2	1		2		2	1				h	mo	I	x
<i>Walckenaeria obtusa</i>	Wal obtu					1						(x)f	mdf	II	
<i>Walckenaeria unicornis</i>	Wal unic							1	1			h	woh	I	
<i>Walckenaeria vigilax</i>	Wal vigi				1			2	3			h	mo	I	x
<i>Xerolycosa miniata</i>	Xer mini				1					18		x	dg	II	
<i>Xysticus audax</i>	Xys auda					1					1	x	Cah	II	
<i>Xysticus cristatus</i>	Xys cris	2		3	2	1	1	3		9		(x)	fa	II	x
<i>Xysticus kochi</i>	Xys koch	7	6	1	2		3	1		63	33	x	dg	II	x
<i>Xysticus ulmi</i>	Xys ulmi	35	7	4	8	2	12	6	1	3	3	h	woh	II	x
<i>Zelotes subterraneus</i>	Zel subt	1		1		1			2			(x)(f)	mdf	III	
<i>Zora spinimana</i>	Zor spin	7	6	3	8	1	7		2		3	(h)	fa	II	x