European Arachnology 2008 (W. Nentwig, M. Entling & C. Kropf eds.), pp. 129–146.
 ISSN 1660-9972
(Proceedings of the 24th European Congress of Arachnology, Bern, 25–29 August 2008).

Influence of scrub encroachment and rank vegetation development on the epigeic spider fauna (Arachnida: Araneae) of dry meadows in the "Untere Lobau" (National Park Donau-Auen, Vienna, Austria).

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Abstract

The effect of scrub invasion and rank vegetation on epigeic (= ground-living) spiders in dry meadows in the National Park Donau-Auen in Vienna (Austria) was investigated. The dry meadows are xeric alluvial biotopes located on gravel ground and characterised by flower-rich vegetation. The study was carried out at 50 randomly selected plots in the area of "Untere Lobau" in the southeast of Vienna. Epigeic spiders were sampled by means of pitfall traps during three periods lasting two weeks each (29 April to 13 May, 25 June to 9 July and 6 to 20 September 1999). At each plot scrub coverage was measured within a radius of 8 m around the plot centre and vegetation density (pasture yield) was measured using a disc pasture meter as developed by Bransby & Tainton (1977). The principal threat to the dry meadows comes from encroachment of scrub and the development of rank vegetation that may result from fertiliser application (nutrient-rich inundations) and/or lack of grazing. Since scrub encroachment changes the physical structure in grassland it might also affect different spider species in various ways. Thus, we tested the effect of scrub invasion and the increase of rank vegetation on seven sets of spider species according to their habitat affinities: dry grassland specialist, forest specialist, forest generalist, "forest steppe", grassland specialist, grassland generalist and ruderal generalist spiders. We used binary logistic regression to model the distribution of spider species using the presence or absence of spiders in each study site as the dependent variable, and environmental parameters (scrub cover, vegetation density) as the independent variables. Forest specialist species, forest generalist species and "forest steppe" species showed a significant positive linear relationship with scrub cover, whereas dry grassland species showed a significant negative linear relationship. Ruderal generalist species significantly decreased with increase of vegetation density. A bell-shaped relationship between vegetation density and grassland species indicated an optimum of species occurrence at 15 cm grass sward height. In contrast, forest specialist species showed an U-shaped relationship along the vegetation density gradient indicating high probability of occurrence at sites of very low, as well as very high vegetation density. We expect that the results of this study can be useful for further monitoring or management projects in the National Park Donau-Auen.

Key words: scrub invasion, scrub cover, vegetation density, floodplains, Danube

INTRODUCTION

The National Park Donau-Auen east of Vienna was established in 1996 and is acknowledged as a protected area (IUCN Category II National Park) by the International Union for Conservation of Nature and Natural Resources (IUCN). At present, the total area of National Park amounts to 9300 ha of which 15% are categorised as grasslands (Internet: http://www.donauauen.at). Particular landscape elements include the so called "Heissländen", i.e. xeric alluvial biotopes characterised by gravel ground and dry grassland vegetation (Margl 1973; Schratt-Ehrendorfer 2000a). From a conservation viewpoint, the most valuable vegetation type of the dry grasslands in the "Untere Lobau" is the plant association "Teucrio botrys-Andropogonetum ischaemi" (see Schratt-Ehrendorfer 2000b). Recently, the dry meadows have become threatened by encroachment of scrub and the development of rank vegetation (Schratt-Ehrendorfer 2000b). Long-term habitat change in the area is the result of a vegetation succession since the regulation of the Danube River in the second half of the 19th century (~1860) (Schratt-Ehrendorfer 2000a, b). Today, the forthcoming possibility of water enhancement in the "Untere Lobau", an alluvial area along the Danube downstream of Vienna, with nutrient-rich water from the main channel of the Danube must be considered a major threat to these habitats of high conservation value (Schratt-Ehrendorfer 2000b).

The effects of scrub invasion and increase in rank vegetation on the spider fauna was investigated in the framework of a LIFE-Project at several "Heissländen" of the "Untere Lobau" (Rotter 2006) that is situated in the western part of the National Park Donau-Auen. Since scrub encroachment and rank vegetation development change the physical structure in grasslands they might also affect different spider species in various ways. As Gajdoš & Toft (2000: p. 95) pointed out: "Structural characteristics of the vegetation are generally thought to be the most important factor for habitat selection of spiders and thus for determining the composition of spider fauna".

Thus, we tested the effects of scrub cover and vegetation density on different subsets of spider species according to their habitat affinities: dry grassland specialist, forest specialist (including interior forest edge), forest generalist, "forest steppe", grassland specialist, grassland generalist and ruderal generalist species. We aimed (i) to determine the responses of different spider groups to scrub cover and vegetation density (height of grass sward) and (ii) to recommend management targets for the valuable dry meadows that might be appropriate to maintain spiders of high conservation value in the National Park Donau-Auen.

MATERIAL AND METHODS

Study area and study sites

The study area is a rectangle (2500 x 500m) extending from 48°09'21"N, 16°31'45"E (lower left coordinate) to 48°10'00"N, 16°34'30"E (upper right coordinate). Based on a map of the city of Vienna (municipal authority MA 41, 1998) 50 study sites were selected that were distributed in nine different "Heissländen" (see Rotter 2006).

Each study site represents a grid cell of 20 x 20 m. Using aerial photographs (colour infrared images; ÖBIG 1991) only grid cells were selected which (i) showed a significant proportion (maximum 90%) of grassland, (ii) did not overlap with roads or buildings and (iii) were accessible by land.

Environmental parameters

Scrub cover was determined within a radius of 8 m around the centre of each study site. Therefore, in the first step the exact position, height and diameter of all shrubs and trees (including tree crowns) in each study site was determined using a compass and a tapeline. In a second step a graphical representation of the data was made and the percentage of scrub cover in relation to total ground size was calculated. For details see

Rotter (2006). Original data are given in Appendix 1.

The most abundant scrubs in the study area were (in order of presence): common hawthorn (*Crataegus monogyna),* common privet (*Ligustrum vulgare),* common dogwood (*Cornus sanguinea),* rose species *(Rosa sp.),* European cornel (*Cornus mas*), European barberry (*Berberis vulgaris*), white poplar (*Populus alba*), European black pine (*Pinus nigra*) and field elm (*Ulmus minor*) (Rotter 2006).

Vegetation density (i.e. grass fuel load, grass sward height, plant biomass) in the study sites was measured twice (April and August) with a disc pasture meter as developed by Bransby & Tainton (1977). The disc pasture meter is a simple inexpensive instrument which has been demonstrated to be useful for making rapid yield estimates of standing grass (Brainsby & al. 1977; Trollope & Potgieter 1986) or for quantitatively describing standing biomass in grassland ecosystems (Dörgeloh 2002). A round disc of 20 cm diameter and 100 g of weight was released from 50 cm height along a wooden stick. Twenty measures were taken randomly in each 20 x 20 m sampling quadrat. For statistical analysis the mean value was used.

Sampling

Spiders were obtained by pitfall trapping. A single pitfall (glass jar of 5.1 cm opening diameter, 8 cm depth, filled with 80 ml ethylene glycol as preservative, covered with a transparent plastic roof) was exposed in the centre of each study site for three 14-day periods (29 April to 13 May, 25 June to 9 July and 6 to 20 September 1999). Adult spiders were determined to species level using the keys of Heimer & Nentwig (1991) and Nentwig & al. (2003). Nomenclature of spiders follows Platnick (2010).

Data analysis

Prior to the statistical analyses each spider species was classified according to its habitat affinities/preferences by using relevant information both from the literature (e.g. Buchar 1992; Reinke & Irmler 1994; Hänggi & al. 1995; Kreuels & Platen 1999; Bolaños 2003; Nentwig & al. 2003; Buchar & Růžička 2002; Entling & al. 2007) and from own databases. Species were classified into seven habitat categories as follows:

- dry grassland specialist species: xerothermophilic species that are bound to open dry and warm habitats (see Bauchhenss 1990).
- forest specialist species: species preferring shady forest interior conditions with stable cold humid microclimate, as well as interior forest edges (sensu Whitcomb & al. 1981).
- forest generalist species: widely distributed species that show a high frequency of occurrence in forests
- "forest steppe" species: species occurring in light and dry open forests with grassy understorey, like oak-hornbeam forests, (Pannonian) forest steppe and xerothermic forest edges
- grassland specialist species: species showing a preference for open habitats and an avoidance of forests
- grassland generalist species: widely distributed species that show a high frequency of occurrence in grasslands
- ruderal generalist species: widely distributed species that show a high frequency of occurrence in ruderal sites, fields and gardens; i.e. sites of agricultural disturbance

Binary logistic regression was used to model the distribution of spider species along the two environmental gradients: scrub cover and vegetation density. In the regression models for each category the presence/absence of each spider species was used as the dichotomous dependent variable and environmental parameters were used as the continuous independent variables. For the different categories the following numbers of cases were finally included in the analyses: dry grassland species (133 presence / 1017 absence), forest species (69 / 831), forest generalist species (62 / 738), forest steppe

Table 1. Spider species presence in the 50 study sites in the "Untere Lobau" (Vienna, Austria) and categorization of each species according to its habitat affinity.

Araneae	Category	Presence
Agroeca brunnea (Blackwall, 1833)	Forest specialist	2
Agroeca cuprea Menge, 1873	Dry grassland specialist	7
Agyneta ramosa Jackson, 1912	Forest specialist	2
Alopecosa cuneata (Clerck, 1757)	Grassland generalist	16
Alopecosa mariae (Dahl, 1908)	Dry grassland specialist	1
Alopecosa pulverulenta (Clerck, 1757)	Grassland generalist	6
Alopecosa trabalis (Clerck, 1757)	Dry grassland specialist	33
Arctosa figurata (Simon, 1876)	Dry grassland specialist	21
Arctosa lutetiana (Simon, 1876)	Grassland specialist	40
Argenna subnigra (O. P.-Cambridge, 1861)	Dry grassland specialist	2
Atypus piceus (Sulzer, 1776)	"Forest steppe"	19
Aulonia albimana (Walckenaer, 1805)	Grassland generalist	28
Centromerus sylvaticus (Blackwall, 1841)	Forest generalist	2
Ceratinella brevis (Wider, 1834)	Forest generalist	7
Ceratinella scabrosa (O. P.-Cambridge, 1871)	Forest specialist	1
Cheiracanthium campestre Lohmander, 1944	Dry grassland specialist	1
Clubiona comta C. L. Koch, 1839	Forest specialist	1
Clubiona diversa O. P.-Cambridge, 1862	Grassland specialist	1
Diplocephalus cristatus (Blackwall, 1833)	Ruderal generalist	1
Drassodes lapidosus (Walckenaer, 1802)	Grassland generalist	1
Drassodes pubescens (Thorell, 1856)	Grassland generalist	5
Drassodes villosus (Thorell, 1856)	"Forest steppe"	1
Drassyllus praeficus (L. Koch, 1866)	Dry grassland specialist	3
Drassyllus pusillus (C. L. Koch, 1833)	Grassland generalist	6
Dysdera hungarica Kulczyński, 1897	"Forest steppe"	3
Enoplognatha thoracica (Hahn, 1833)	Ruderal generalist	1
Episinus truncatus Latreille, 1809	"Forest steppe"	1
Erigone dentipalpis (Wider, 1834)	Ruderal generalist	1
Euryopis flavomaculata (C. L. Koch, 1836)	Forest specialist	6
Evarcha arcuata (Clerck, 1757)	Grassland specialist	3
Evarcha falcata (Clerck, 1757)	Forest generalist	1
Gnaphosa alpicola Simon, 1878	"Forest steppe"	5
Hahnia nava (Blackwall, 1841)	Grassland generalist	12
Hahnia ononidum Simon, 1875	Forest specialist	9
Hahnia pusilla C. L. Koch, 1841	Forest generalist	1
Haplodrassus signifer (C. L. Koch, 1839)	Grassland generalist	6
Haplodrassus silvestris (Blackwall, 1833)	Forest specialist	2
Harpactea rubicunda (C. L. Koch, 1838)	"Forest steppe"	3
Hypsosinga sanguinea (C. L. Koch, 1844)	Grassland specialist	1
Lasaeola prona (Menge, 1868)	Dry grassland specialist	3
Malthonica campestris (C. L. Koch, 1834)	Forest specialist	1
Meioneta affinis (Kulczyński, 1898)	Grassland specialist	5
Meioneta rurestris (C. L. Koch, 1836)	Ruderal generalist	7
Meioneta saxatilis (Blackwall, 1844)	Forest generalist	2
Micaria dives (Lucas, 1846)	Dry grassland specialist	1
Micaria formicaria (Sundevall, 1831)	Dry grassland specialist	2
Micaria fulgens (Walckenaer, 1802)	Dry grassland specialist	3
Micrargus subaequalis (Westring, 1851)	Grassland specialist	1

Araneae	**Category**	**Presence**
Microneta viaria (Blackwall, 1841)	Forest specialist	1
Minyriolus pusillus (Wider, 1834)	Forest generalist	1
Myrmarachne formicaria (De Geer, 1778)	Grassland specialist	3
Neriene clathrata (Sundevall, 1830)	Forest generalist	1
Neriene radiata (Walckenaer, 1842)	Forest specialist	1
Ozyptila atomaria (Panzer, 1801)	Grassland specialist	4
Ozyptila claveata (Walckenaer, 1837)	Dry grassland specialist	5
Ozyptila praticola (C. L. Koch, 1837)	Forest generalist	2
Pachygnatha degeeri Sundevall, 1830	Ruderal generalist	1
Palliduphantes alutacius (Simon, 1884)	Forest specialist	4
Palliduphantes pallidus (O. P.-Cambridge, 1871)	Forest generalist	1
Panamomops affinis Miller & Kratochvíl, 1939	Forest specialist	5
Panamomops fagei Miller & Kratochvíl, 1939	Forest specialist	1
Panamomops mengei Simon, 1926	Forest specialist	2
Pardosa agrestis (Westring, 1862)	Ruderal generalist	1
Pardosa alacris (C. L. Koch, 1833)	Forest specialist	20
Pardosa bifasciata (C. L. Koch, 1834)	Dry grassland specialist	24
Pardosa hortensis (Thorell, 1872)	Grassland specialist	2
Pardosa riparia (C. L. Koch, 1833)	Grassland specialist	1
Pelecopsis mengei (Simon, 1884)	Grassland specialist	1
Pellenes nigrociliatus (Simon, 1875)	Dry grassland specialist	1
Phaeocedus braccatus (L. Koch, 1866)	Dry grassland specialist	2
Phlegra fasciata (Hahn, 1826)	Grassland specialist	1
Phrurolithus festivus (C. L. Koch, 1835)	Forest generalist	9
Pisaura mirabilis (Clerck, 1757)	Forest generalist	2
Sitticus penicillatus (Simon, 1875)	Dry grassland specialist	1
Steatoda phalerata (Panzer, 1801)	Dry grassland specialist	1
Tapinocyba insecta (L. Koch, 1869)	Forest specialist	4
Tenuiphantes zimmermanni (Bertkau, 1890)	Forest generalist	1
Thanatus formicinus (Clerck, 1757)	Grassland specialist	14
Titanoeca schineri L. Koch, 1872	"Forest steppe"	9
Trachyzelotes pedestris (C. L. Koch, 1837)	"Forest steppe"	7
Trichopterna cito (O. P.-Cambridge, 1872)	Dry grassland specialist	1
Trochosa terricola Thorell, 1856	Forest generalist	22
Walckenaeria atrotibialis (O. P.-Cambridge, 1878)	Forest generalist	4
Walckenaeria dysderoides (Wider, 1834)	Forest generalist	2
Walckenaeria furcillata (Menge, 1869)	Forest specialist	4
Xerolycosa miniata (C. L. Koch, 1834)	Grassland specialist	3
Xysticus bifasciatus C. L. Koch, 1837	Grassland specialist	5
Xysticus erraticus (Blackwall, 1834)	Grassland specialist	1
Xysticus kochi Thorell, 1872	Grassland generalist	8
Xysticus luctator L. Koch, 1870	"Forest steppe"	1
Xysticus ninnii Thorell, 1872	Dry grassland specialist	1
Xysticus robustus (Hahn, 1832)	Dry grassland specialist	2
Zelotes apricorum (L. Koch, 1876)	Forest specialist	3
Zelotes electus (C. L. Koch, 1839)	Dry grassland specialist	10
Zelotes gracilis (Canestrini, 1868)	Dry grassland specialist	1
Zelotes latreillei (Simon, 1878)	Grassland generalist	6
Zelotes longipes (Simon, 1878)	Dry grassland specialist	6
Zora spinimana (Sundevall, 1833)	Forest generalist	4

species (49 / 401), grassland species (106 / 744), grassland generalist species (94 / 406), ruderal generalist species (12 / 288).

For each of the seven spider data sets, a two step logistic regression method was used: In the first step each single continuous variable (scrub cover, vegetation density) was tested in relation to each dependent variable. In the second step a quadratic interaction term was added to the model to determine significant quadratic relationships between dependent and independent variables. For each model this interaction term was simply calculated as the square product of an existing single continuous variable (i.e., scrub cover*scrub cover; vegetation density*vegetation density). The predictive success of each logistic regression model was assessed by the percentage of correct/incorrect classifications of the dependent, and the model appropriateness for overall fit by Hosmer and Lemeshow Goodness-of-Fit tests.

Data were analyzed using the SPSS 11.5 statistical package for Windows (Norušis 2002).

RESULTS

Faunistics

In total 1083 adult individual spiders were caught during the three sampling periods in the 50 study sites (for original spider data see Appendix 2). We recorded 98 species from 21 spider families (Tab. 1). Highest species numbers were found in the familiy Linyphiidae (26), Gnaphosidae (19) and Lycosidae (14). Twelve spider species were recorded in at least ten study sites: *Arctosa lutetiana* (Simon, 1876): 40, *Alopecosa trabalis* (Clerck, 1757): 33, *Aulonia albimana* (Walckenaer, 1805): 28, *Pardosa bifasciata* (C. L. Koch, 1834): 24, *Trochosa terricola* Thorell, 1856: 22, *Arctosa figurata* (Simon, 1876): 21, *Pardosa alacris* (C. L. Koch, 1833): 20, *Atypus piceus* (Sulzer, 1776): 19, *Alopecosa cuneata* (Clerck, 1757): 16, *Thanatus formicinus* (Clerck, 1757): 14, *Hahnia nava* (Blackwall, 1841): 12 and *Zelotes electus* (C. L. Koch, 1839): 10 (Tab. 1).

Habitat categories

About one fourth of the spider fauna are dry grassland dependent species (N = 23) (Tab. 1). Forest specialist species (18), forest generalist species (16) and grassland specialist species (16) represents each about one sixth of the overall species richness. Approximately one tenth was identified as “forest steppe” species (9) or grassland generalist species (10), respectively. The smallest group among the overall species richness are the ruderal generalist species (6).

Rarity

Referring to the number of records in the databases of Hänggi & al. (1995) and Bolaños (2003) for Central Europe, Staudt (2008) for Germany and Buchar & Růžička (2002) for the Czech Republic, the following species must be considered as rare: the dry grassland specialists *Alopecosa mariae* (Dahl, 1908), *Lasaeola prona* (Menge, 1868), *Micaria dives* (Lucas, 1846), *Pellenes nigrociliatus* (Simon, 1875), *Phaeocedus braccatus* (L. Koch, 1866), *Sitticus penicillatus* (Simon, 1875) and *Zelotes gracilis* (Canestrini, 1868); the “forest steppe” spiders *Drassodes villosus* (Thorell, 1856), *Dysdera hungarica* Kulczyński, 1897, *Gnaphosa alpica* Simon, 1878 and *Titanoeca schineri* L. Koch, 1872; and the forest specialists *Malthonica campestris* (C. L. Koch, 1834), *Palliduphantes alutacius* (Simon, 1884) and *Panamomops fagei* Miller & Kratochvíl, 1939.

Logistic regression

Among the seven spider groups and the two environmental parameters tested in the regression models, four significant relationships were found along the scrub cover gradient and three significant relationships along the vegetation density gradient (Tab. 2, Figure 1a,b).

Dry grassland spiders showed a significant negative linear relationship with increasing scrub cover (Nagelkerke’s $R^2 = 0.016$; Hosmer and Lemeshow Goodness-of-Fit = 1.16, df = 8, P = 0.99; 88.4% correct classification) (Fig. 1a). In contrast, significant positive

Table 2. Logistic regression analyses of habitat variables influencing presence and absence of seven spider groups in the "Untere Lobau" (Vienna, Austria) as determined by pitfall trap samplings at 50 sites: logistic regression coefficients (ß), coefficients standard error (S.E. (ß)), the Wald test and statistical significances for logistic regression models; significant relationships (P < 0.05) are given in bold.

Variable	β	SE	Wald	df	Signi-ficance	Odds ratio
Dry grassland spiders						
Scrub	-0.01	0.00	8.59	1	**0.003**	0.99
Scrub + Scrub^2	-0.02	0.00	0.03	1	0.872	1.00
Vegdens	-0.03	0.02	2.54	1	0.111	0.97
Vegdens + Vegdens^2	-0.01	0.01	2.95	1	0.086	0.99
Forest specialist spiders						
Scrub	0.03	0.00	35.23	1	**0.000**	1.03
Scrub + Scrub^2	0.00	0.00	2.15	1	0.142	1.00
Vegdens	0.06	0.03	4.73	1	**0.030**	1.06
Vegdens + Vegdens^2	0.01	0.01	4.42	1	**0.036**	1.01
Forest generalist spiders						
Scrub	0.02	0.01	12.67	1	**0.000**	1.02
Scrub + Scrub^2	0.00	0.00	0.33	1	0.565	1.00
Vegdens	0.03	0.03	4.30	1	0.354	1.03
Vegdens + Vegdens^2	0.01	0.01	1.11	1	0.293	1.01
"Forest steppe" spiders						
Scrub	0.02	0.01	10.58	1	**0.001**	1.02
Scrub + Scrub^2	0.00	0.00	0.52	1	0.470	1.03
Vegdens	-0.01	0.03	0.04	1	0.848	0.99
Vegdens + Vegdens^2	0.00	0.01	0.01	1	0.932	1.00
Grassland specialist spiders						
Scrub	-0.00	0.00	0.89	1	0.346	1.00
Scrub + Scrub^2	0.00	0.00	0.12	1	0.731	1.00
Vegdens	0.02	0.02	0.43	1	0.510	1.02
Vegdens + Vegdens^2	-0.01	0.01	4.31	1	**0.038**	0.99
Grassland generalist spiders						
Scrub	-0.01	0.01	3.61	1	0.058	0.99
Scrub + Scrub^2	0.00	0.00	0.52	1	0.472	1.00
Vegdens	-0.03	0.03	1.38	1	0.240	0.97
Vegdens + Vegdens^2	-0.00	0.01	0.06	1	0.803	1.00
Ruderal generalist spiders						
Scrub	-0.04	0.02	3.20	1	0.074	0.96
Scrub + Scrub^2	0.00	0.00	3.15	1	0.077	1.00
Vegdens	-0.23	0.08	7.44	1	**0.006**	0.80
Vegdens + Vegdens^2	0.00	0.02	0.00	1	0.979	1.00

relationships with increasing scrub cover were found in all three species groups that show an habitat affinity to forests: forest specialist spiders (Nagelkerke's $R^2 = 0.089$; Hosmer and Lemeshow Goodness-of-Fit = 9.99, df = 8, P = 0.26; 92.3% correct classification), forest generalist species (Nagelkerke's $R^2 = 0.035$; Hosmer and Lemeshow Goodness-of-Fit = 10.89, df = 8, P = 0.21; 92,3 % correct classification) and "forest steppe" spiders

(Nagelkerke's $R^2 = 0.045$; Hosmer and Lemeshow Goodness-of-Fit = 5.39, df = 8, P = 0.72; 89.1% correct classification) (Fig. 1a).

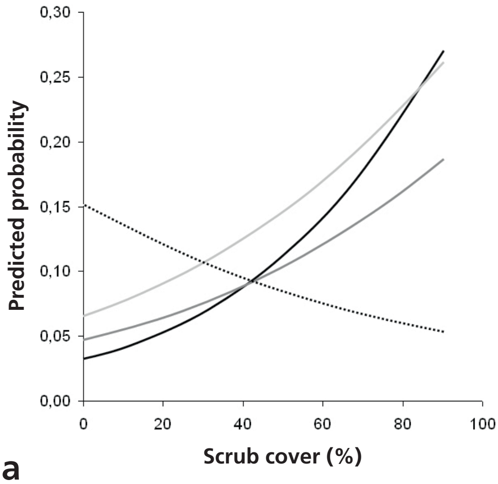
Along the vegetation density gradient there was also a significant positive linear relationship with forest spiders' presence. Moreover, this linear model was significantly improved when the quadratic interaction term was added to the model (Nagelkerke's $R^2 = 0.024$; Hosmer and Lemeshow Goodness-of-Fit = 10.57, df = 8, P = 0.23; 92.3% correct classification) (Fig. 1b). The resulting unimodal U-shaped curve indicated lowest probability of forest species presence at a site with approximately 12 cm grass sward, but increased probability of occurrence at sites of very low and very high amounts of vegetation density. In contrast, a significant unimodal bell-shaped relationship was found between vegetation density and grassland spiders (Nagelkerke's $R^2 = 0.011$; Hosmer and Lemeshow Goodness-of-Fit = 3.34, df = 8, P = 0.91; 87.5% correct classification) with an optimum of presence probability at about 15 cm grass sward (Fig. 1b). Vegetation density and ruderal generalist species showed a significant negative relationship indicating a preference of these species for low plant height and/or open ground (Fig. 1b). No significant relationships were found between grassland generalist species and the two environmental gradients which were tested.

In all significant relationships between dependent and independent variables, the models show a good fit (Hosmer and Lemeshow Goodness-of-Fit Test, $P > 0.05$) and high correct classification rates. However, low Nagelkerke's R^2 values and Odds ratio's of about 1.0 indicate only a weak predictive power of the models (Tab. 2).

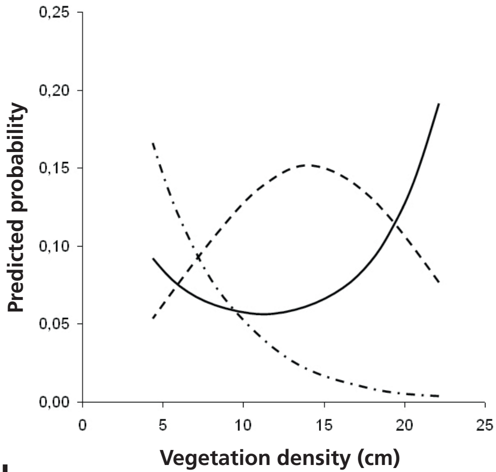
DISCUSSION

In biodiversity studies it is sometimes necessary to distinguish between species that are ecologically confined to a given habitat type and those that can survive in other habitat types as well. For example, Magura & al. (2001) investigated carabid beetle species richness in deciduous forest patches surrounded by an agricultural matrix. The authors distinguished between species of closed canopy deciduous forests (forest specialists) and widely distributed species (generalists). As expected, forest specialist species increased and generalist species decreased with increasing forest patch size. However, putting both categories together, the higher number of generalists masked the effect of forest specialists resulting in a negative relationship between carabid species richness and forest patch size. Without critically questioning such findings, one may be led to errant recommendations such as diminishing forest patches for the sake of enhancing species richness.

Vegetation architecture is one key environmental gradient for niche separation in spiders (see Wise 1993). Thus, by assigning the examined spiders from the "Untere Lobau" into habitat categories we focus on the vegetation structure (forest-grassland) and the species' habitat dependency (specialist-generalist). We distinguished between forest related species (forest specialists, forest generalists and "forest steppe" species) and open habitat related species (dry grassland specialists, grassland specialists, grassland generalists and ruderal generalists). This is a more detailed approach in comparison to classifications found in the literature. Classification of species according to their habitat affinities is common in spiders (e.g. Huhta 1971; Buchar 1992; Kreuels & Platen 1999; Buchar & Růžička 2002). Many authors roughly distinguish between forest species, open habitat species and generalists occurring in both habitat types. An improved classification is possible by considering both light and moisture (see Maurer & Hänggi 1990: p.19). For example, Matveinen-Huju (2004) classified boreal Finnish spiders according to their habitat affinities and distinguished between open habitats, semi-open habitats and shady habitats, on the one hand, and dry habitats, medium-moist habitats and moist habitats, on the other hand. A



a



b

Figs. 1a, b. Predicted probabilities of spider presence across the environmental parameters (a) scrub cover and (b) vegetation density as determined by binary logistic regression analysis; only significant relationships are plotted showing dry grassland specialist (dotted line), forest specialist (full black line), forest generalist (full dark grey line), "forest steppe" (full light gray line), grassland specialist (dashed line) and ruderal generalist spiders (dotted-dashed line) on the xeric alluvial grasslands ("Heissländen") in the "Untere Lobau", (Vienna, Austria). No significant relationships were found in grassland generalist spiders. For statistical details see Table 2.

similar approach was undertaken by Entling & al. (2007), based on a profound statistical analysis using data from 244 published spider communities involving 70 habitat types in order to derive niche properties of Central European spiders. Entling & al. (2007) distinguished between open habitats, semiopen habitats and forests, on the one hand, and dry habitats, mesic habitats and moist habitats, on the other hand, to classify the studied habitat types. There are several critical aspects to the assignment of species according to their habitat affinities. First, the accuracy of an assignment depends on the quality of the published data (Hänggi & al. 2005). Secondly, habitat tolerance of species varies with geographical location (see Duffey 2005 for a review). Third, inevitably, each assignment is – to a certain extent – arbitrary. Taking all these critical points into consideration, the final spider category list of the present study must be considered as the current state of an ongoing discussion process. Logistic regression models proved to be helpful to describe the distribution of different spider species groups along the scrub cover and the vegetation density gradient in the xeric alluvial grasslands in the "Untere Lobau". The logistic regression models for dry grassland specialist spiders showed a decreased probability of presence at a site as scrub cover increases. In contrast, forest specialist spiders, forest generalist spiders and "forest steppe" spiders significantly benefit from increasing scrub cover. Ruderal generalist spiders are negatively affected by increasing vegetation density indicating a preference for pioneer or disturbed habitats with bare open ground and less vegetation. Grassland specialist spiders show an optimum at about 14 cm vegetation density. In contrast, forest specialist spiders show lowest probability of occurrence at about 12 cm vegetation density indicating that forest spiders not only benefit from increasing vegetation density, but also from very low amounts of vegetation density. This effect may be due to the fact, that low vegetation density or even absence of any vegetation is either characteristic for open pioneer habitats or for very dense scrub cover conditions. In the latter case dense scrub cover or tree canopy may suppress or even eliminate grassy understorey through outshading. In the present study, all regression models show a good fit and a high correct classification rate. However, this does not mean that the models explain much of the variance in the dependent variables, only that they do so to a significant degree (Norušis 2005). In fact, all models show low values of predicted probabilities of spider presence, i.e. explain only a low degree of the variance, and must therefore be considered as poor predictors of spider species presence in the dry meadows of the "Untere Lobau".

Duelli & Obrist (2003) pointed out that conservation value differs between species. Evidently, a rare or threatened species has a higher conservation value than a common species, because it contributes more to regional or national biodiversity than an widely-distributed species. Consequently, dry grassland specialist species that depend on or are restricted to rare and threatened dry meadows are the primary conservation targets, notwithstanding the fact that rare species appear in other species category sets, too. We found the highest number of rare species (N=7) among the dry grassland specialists representing about 30% of all dry grassland specialist species. Highest percentage of rare species in one category, however, was found in the category of "forest steppe" spiders (44%), and the lowest amount among the forest specialists (16%). In the present study we define the rarity of a spider species in terms of its number of records in existing databases from Central Europe (Hänggi & al. 1995), Germany (Staudt 2008) and the Czech Republic (Buchar & Růžička 2002). However, number of citations in the checklist of the spiders of Hungary (Samu & Szinetár, 1999) indicate that these spiders might be also rare in Eastern Europe: the dry grassland spiders *Alopecosa mariae* (Dahl, 1908): 6 citations; *Lasaeola prona* (Menge, 1868): 2; *Micaria dives* (Lucas, 1846): 9; *Pellenes nigrociliatus* (Simon, 1875): 10; *Phaeocedus braccatus* (L. Koch, 1866): 7; *Sitticus penicillatus* (Simon, 1875): 2; *Zelotes gracilis* (Canestrini, 1868): 7; the "forest steppe" spiders: *Drassodes villosus* (Thorell, 1856): 2; *Dysdera hungarica* Kulczyński, 1897: 11; *Gnaphosa alpica* Simon, 1878: 2; *Titanoeca schineri* L. Koch, 1872: 16; and the forest specialists: *Malthonica campestris* (C. L. Koch, 1834): 12, *Palliduphantes alutacius* (Simon, 1884): 0, *Panamomops fagei* Miller & Kratochvíl, 1939: 1. Conservation of rare species is, of course, an important obligation of a National Park. We found that only dry grassland dependent species significantly suffer from scrub encroachment in the xeric alluvial grassland ecosystem studied, emphasising the need for counter measures. However, successful management of natural and semi-natural grasslands for biodiversity is a difficult task for conservationists and managers (Watkinson & Ormerod 2001). In order to halt succession and re-establish the open "savannah-like" character of the "Heissländen", scrub vegetation must be removed from time to time (Schratt-Ehrendorfer 2000a, b). This is enacted by the National Park management plans and done in so-called "natural areas with management measures" such as the "Untere Lobau" (Rotter 2006). Scrub encroachment and rank vegetation development is a process of plant succession that represents a continuum on the spatial scale as well as the temporal scale (Hurd & Fagan 1992; Dennis & al. 1998). On the one side, there are open xeric alluvial pioneer habitats (favouring opportunistic ruderal generalist spiders) and, on the other side, there are riverine forests representing the climax vegetation (favouring all sorts of forest-related spiders). Mallis & Hurd (2005) argue that spider community composition over time is, actually, not true succession, but rather repeated colonization by opportunistic species. Mrzljak & Wiegleb (2000) studied the colonization of former mining areas by spiders and found distinct spider assemblages in (i) vegetation free sites, (ii) sparsely vegetated short grass sites, and (iii) plant species rich, mature, short grass, as well as tall grass sites. Evidently, plant succession including scrub encroachment is accompanied by changing environmental conditions. Since spiders are sensitive to changes in vegetation habitat structure and, correspondingly, in microclimate (Uetz 1991; Duffey 1993), management measures affecting vegetation structure can have a huge impact on the spider community structure (Rushton & al. 1989; Gibson & al. 1992). Besides the type of management measure (e.g. grazing, mowing, scrub clearing) intensity of management (low, moderate, high) can affect spider assemblages in grasslands in different ways. In principal, it is difficult to make generalisations for management since each species has different habitat requirements. With regard to management intensity, Bell & al. (2001) argued that high intensity management in grasslands will favour species affiliated with open ground. This accords well with our finding that ruderal generalist spiders increase with decreasing vegetation density. Bell & al. (2001) recommend low-intensity management since it might be preferable for most species. Furthermore, management should be site-dependent (i.e. it is not appropriate for all spiders in the same way), extreme forms of management should be avoided and habitat management for spiders should be integrated into a holistic management plan to avoid conflicts among different conservation targets. Dale et al. (2000) stated that in land-use practice such guidelines, if based on ecological principles, provide useful practical rules of thumb for management decisions, for example, that managers should "preserve rare landscape elements and associated species", "retain large connected areas that contain critical habitats" or "implement land-use and management practices that are compatible with the natural potential of the area".

Evidently, in the "Heissländen" of the National Park Donau-Auen, as a rule of thumb, scrub invasion on xeric alluvial grassland should be removed wherever possible in order to enlarge and improve the habitats for dry grassland spiders (Rotter 2006; Schratt-Ehrendorfer 2002b). However, the complete removal of all scrubs in the area will have the effect of reducing structural diversity and potential loss of habitat for some valuable forest specialist and "forest steppe" spiders. We expect that a large part of the dry grassland dependent species might not only benefit from scrub clearings, but also from moderate grazing or mowing; especially the set of true xerothermophilic spiders that require high temperature and high solar radiation (Bauchhenss 1990). To prevent biodiversity decline in grasslands Rosén & Bakker (2005) concluded that scrub clearings are the most important action in the short perspective, but in a longer perspective, grazing is needed. Since grazing impacts the spatial pattern of scrubs (Seifan & Kadmon 2006) it might indirectly also affect spider species diversity (Rusthon 1988). Even high intensity management measures might be applicable in selected sites in order to create pioneer habitats that could develop into valuable grassland sites favouring xerothermophilic spiders during the process of plant succession. However, for each management action it is necessary to consider the level of impact, the timing and the species involved (Dennis & al. 1998). As Watkinson & Ormerod (2001) pointed out: "too much grazing may often lead to land degradation and the loss of biodiversity, while too little grazing may lead to succession from grassland to woodland".

In conclusion, we recommend the following rule of thumb for measures countering scrub invasion and high vegetation density in the xeric alluvial dry grasslands of the "Untere Lobau": (i) elimination/clearing of scrub of more than 30% cover, (ii) enhancement of the proportion of open scrub free areas and connection of the dry meadows in the total "Heissländen" area, (iii) maintenance of a vegetation density (grass sward) lower than 15 cm through grazing or low-moderate grazing/mowing. Notwithstanding the fact that we are not able to predict epigeic spider occurrences with a sufficient degree of precision, we believe that the results of this study can be useful for further monitoring or management projects in the National Park Donau-Auen.

ACKNOWLEDGEMENTS
Financial support for this study was provided by the Project "LIFE 98 NAT/A/005422". We thank the Nationalpark Donau-Auen GmbH and Wolfgang Reckendorfer for their good coordination work. Valuable research assistance in the field work was provided by Stefan Rotter. We are also grateful to John Plant for checking the English.

REFERENCES

Bauchhenss, E. 1990. Mitteleuropäische Xerotherm-Standorte und ihre epigäische Spinnenfauna: eine autökologische Betrachtung. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)* 31/32: 153–162.

Bell, J.R., Wheater, C.P. & Cullen, W.R. 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. *Journal of Zoology* 255: 377–387.

Bolaños, A. 2003. Spider assemblages and habitat bindings in Central Europe. Verlag Agrarökologie, Bern-Hannover.

Bransby, D.I. & Tainton, N.M. 1977. The disc pasture meter: Possible applications in grazing management. *Proceedings of the Grassland Society of Southern Africa* 12: 115–118.

Bransby, D.I., Matches, A.G. & Krause G.F. 1977. Disc meter for rapid estimation of herbage yield in grazing trials. *Agronomy Journal* 69: 107–113.

Buchar, J. 1992. Kommentierte Artenliste der Spinnen Böhmens (Araneida). *Acta Universitatis Carolinae, Biologica* 36 [1992]: 384–428.

Buchar, J. & Růžička, V. 2002. Catalogue of spiders of the Czech Republic. Peres, Praha.

Dale, V.H., Brown, S., Haeuber, R.A., Hobbs, N.T., Huntly, N., Naiman, R.J., Riebsame, W.E., Turner, M.G. & Valone, T.J. 2000. Ecological principles and guidelines for managing the use of land. *Ecological Applications* 10: 639–670.

Dennis, P., Young, M.R. & Gordon, I.J. 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* 23: 253–264.

Dörgeloh, W.G. 2002. Calibrating a disc pasture meter to estimate above-ground standing biomass in Mixed Bushveld, South Africa. *African Journal of Ecology* 40: 100–102.

Duelli, P. & Obrist, M.K. 2003. Biodiversity indicators: the choice of values and measures. *Agriculture, Ecosystems and Environment* 98: 87–98.

Duffey, E. 1993. A review of the factors influencing the distribution of spiders with reference to Britain. *Memoirs of the Queensland Museum* 33: 497–502.

Duffey, E. 2005. Regional variation of habitat tolerance by some European spiders (Araneae): a review. *Arachnologische Mitteilungen* 29: 25–34.

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R. & Nentwig, W. 2007. Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography* 16: 440–448, + Supplement.

Gajdoš, P. & Toft, S. 2000. A twenty-year comparison of epigeic spider communities (Araneae) of Danish coastal heath habitats. *Journal of Arachnology* 28: 90–96.

Gibson, C.W.D., Hambler, C. & Brown, V.K. 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. *Journal of Applied Ecology* 29: 132–142.

Hänggi, A., Stöckli, E. & Nentwig, W. 1995. Lebensräume mitteleuropäischer Spinnen. *Miscellanea Faunistica Helvetiae* 4: 1–460.

Heimer, S. & Nentwig, W. 1991. Spinnen Mitteleuropas. Ein Bestimmungsbuch. Paul Parey Berlin und Hamburg.

Huhta, V. 1971). Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. *Annales Zoologici Fennici* 9: 42–48.

Hurd, L.E. & Fagan, W.F. 1992. Cursorial spiders and succession: age or habitat structure? *Oecologia* 92: 215–221.

Kreuels, M. & Platen, R. 1999. Rote Liste der gefährdeten Webspinnen (Arachnida: Araneae) in Nordrhein-Westfalen mit Checkliste und Angaben zur Ökologie der Arten. *LÖBF-Schriftenreihe* 17: 449–504.

Magura, T., Ködöböcz, V. & Tóthmérész, B. 2001. Effects of habitat fragmentation on carabids in forest patches. *Journal of Biogeography* 28: 129–138.

Mallis, R.E. & Hurd, L.E. 2005. Diversity among ground-dwelling spider assemblages: habitat generalists and specialists. *Journal of Arachnology* 33: 101–109.

Margl, H. 1973. Pflanzengesellschaften und ihre standortgebundene Verbreitung in teilweise abgedämmten Donauauen (Untere Lobau). *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 113: 5–52.

Matveinen-Huju, K. 2004. Habitat affinities of 228 boreal Finnish spiders: a literature review. *Entomologica Fennica* 15: 149–192.

Maurer, R. & Hänggi, A. 1990. Katalog der schweizerischen Spinnen. *Documenta faunistica Helvetiae* 12: 1–33, + plus Katalog und Karten.

Mrzljak, J. & Wiegleb, G. 2000. Spider colonization of former brown coal mining areas–time or structure dependent? *Landscape and Urban Planning* 51: 131–146.

Nentwig, W., Hänggi, A., Kropf, C. & Blick, T. 2003. Spinnen Mitteleuropas / Central European Spiders. An internet identification key. Version vom 8. Dezember 2003. Internet: http//www.araneae.unibe.ch.

Norušis, M. 2002. SPSS 11.0 Guide to Data Analysis. Prentice-Hall, Upper Saddle River, NJ.

Norušis, M. 2005. SPSS 13.0 Advanced Statistical Procedures Companion. Prentice Hall. Upper Saddle River, NJ.

Platnick, N.I. 2010. The world spider catalog, version 11.0. American Museum of Natural History, Internet: http://research.amnh.org/entomology/spiders/catalog/index.html.

Reinke, H.-D. & Irmler, U. 1994. Die Spinnenfauna (Araneae) Schleswig-Holsteins am Boden und in der bodennahen Vegetation. *Faunistisch-Ökologische Mitteilungen* Supplement 17: 1–148.

Rosén, E. & Bakker, J.P. 2005. Effects of agri-environment schemes on scrub clearance, livestock grazing and plant diversity in a low-intensity farming system on Öland, Sweden. *Basic and Applied Ecology* 6: 195–204.

Rotter, D. 2006. Einfluss der Verbuschung auf Artengemeinschaften auf Heissländen in der Unteren Lobau. *Wissenschaftliche Reihe Nationalpark Donau-Auen* 22: 1–33.

Rushton, S.P. 1988. The effects of scrub management regimes on the spider fauna of chalk grassland, Castor Hanglands National Nature Reserve, Cambridgeshire, UK. *Biological Conservation* 46: 169–182.

Rushton, S.P., Luff, M.L. & Eyre, M.D. 1989. Effects of pasture improvement and management on the ground beetle and spider communities of upland grasslands. *Journal of Applied Ecology* 26: 489–503.

Samu, F. & Szinetár, C. 1999. Bibliographic check list of the Hungarian spider fauna. *Bulletin of the British Arachnological Society* 11: 161–184.

Schratt-Ehrendorfer, L. 2000a. Historischer und aktueller Zustand von Trockenstandorten (= Heissländen) in den Donauauen bei Wien (Lobau). *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich* 137: 127–135.

Schratt-Ehrendorfer, L. 2000b. Entwicklungstendenzen von Vegetationseinheiten an Sonderstandorten der Donauauen bei Wien (Untere Lobau). *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich* 137, 137–146.

Seifan, M. & Kadmon, R. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a mediterranean scrub community. *Basic and Applied Ecology* 7, 496–506.

Staudt, A. 2008. Nachweiskarten der Spinnentiere Deutschlands (Arachnida: Araneae, Opiliones, Pseudoscorpiones). Internet: http://www.spiderling.de/arages/index.htm.

Trollope, W.S.W. & Potgieter, A.L.F. 1986. Estimating grass fuel loads with the disc pasture meter in the Kruger National Park. *Journal of the Grassland Society of Southern Africa* 3: 148–152.

Uetz, G.W. 1991. Habitat structure and spider foraging. – In: Bell, S.S., McCoy, E.D. & Mushinsky, H.R. (ed.), Habitat Structure, pp. 325–348, Chapman and Hall, London.

Watkinson, A.R. & Ormerod, S.J. 2001. Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology* 38, 233–237.

Whitcomb, R.F, Robbins, C.S, Lynch, F.S, Whitcomb, B.L, Klimkiewicz, M.K. & Bystrak, D. 1981). Effects of forest fragmentations on avifauna of the eastern deciduous forest. In: Burgess, R.L. & Sharpe, D.M. (eds.), Forest island dynamics in man-dominated landscapes, pp. 125–205, Springer-Verlag, New York.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge (UK).

Appendix 1. Study sites and environmental parameters. 50 study sites are distributed in nine „Heissländen" (see Rotter 2006): "Dürrham" (DH 01-08), "Grabsteinhaufen" (GH 01-04), "Großer Rohrwörth" (GR 01-07), "Krowatenboden" (KB 01-03), "Kreuzgrund" (KG 01-13), "Küniglhäufl" (KH 01), "Lausgrund" (LG 01-11), "Sandhaufen" (SH 01-02), "Zainetau" (ZA 01).

Site	Scrub cover (%)	Vegetation density (cm)
DH01	28.60	10.60
DH02	0.59	6.90
DH03	2.79	6.35
DH04	30.05	21.63
DH05	88.59	20.35
DH06	21.54	15.28
DH07	32.51	8.40
DH08	31.34	9.33
GH01	12.29	4.43
GH02	24.02	12.03
GH03	12.63	14.38
GH04	58.89	16.00
GR01	7.95	13.40
GR02	0.00	7.83
GR03	8.62	9.55
GR04	26.90	22.13
GR05	66.88	17.75
GR06	9.04	10.43
GR07	19.41	15.40
KB01	12.20	8.05
KB02	90.33	11.98
KB03	62.48	10.68
KG01	3.12	5.45
KG02	77.06	9.18
KG03	8.76	8.63
KG04	9.42	8.50
KG05	22.16	17.03
KG06	15.98	18.80
KG07	6.19	7.90
KG08	60.68	19.28
KG09	48.52	20.33
KG10	5.66	11.90
KG11	6.91	13.93
KG12	15.19	14.88
KG13	65.08	15.20
KH01	12.70	9.50
LG01	15.25	14.85
LG02	52.40	17.50
LG03	4.68	15.43
LG04	7.72	13.20
LG05	11.72	12.05
LG06	39.73	10.48
LG07	1.81	15.13
LG08	38.50	19.40
LG09	3.00	7.50
LG10	36.75	17.65
LG11	69.13	13.18
SH01	28.56	15.63
SH02	16.71	18.35
ZA01	2.05	15.65

Appendix 2. Presence of spider species in the 50 study sites. Abbreviations: 01-08: "Dürrham" (DH 01-08); 09-12: "Grabsteinhaufen" (GH 01-04); 13-19:"Großer Rohrwörth" (GR 01-07); 20-22: "Krowatenboden" (KB 01-03); 23-35: "Kreuzgrund" (KG 01-13); 36: "Küniglhäufl" (KH 01); 37-47: "Lausgrund" (LG 01-11); 48-49: "Sandhaufen" (SH 01-02); 50: "Zainetau" (ZA 01).

Araneae	Study sites
Atypidae	
Atypus piceus (Sulzer, 1776)	01, 10, 12, 15, 19, 21, 22, 23, 24, 27, 31, 35, 36, 37, 38, 42, 44, 45, 47
Dysderidae	
Dysdera hungarica Kulczyński, 1897	01, 21, 35
Harpactea rubicunda (C. L. Koch, 1838)	16, 23, 31
Theridiidae	
Enoplognatha thoracica (Hahn, 1833)	24
Episinus truncatus Latreille, 1809	26
Euryopis flavomaculata (C. L. Koch, 1836)	16, 22, 24, 31, 44, 48
Lasaeola prona (Menge, 1868)	02, 36, 43
Steatoda phalerata (Panzer, 1801)	09
Linyphiidae	
Agyneta ramosa Jackson, 1912	17, 32
Centromerus sylvaticus (Blackwall, 1841)	35, 37
Ceratinella brevis (Wider, 1834)	03, 04, 07, 11, 24, 31, 38
Ceratinella scabrosa (O. P.-Cambridge, 1871)	17
Diplocephalus cristatus (Blackwall, 1833)	29
Erigone dentipalpis (Wider, 1834)	29
Meioneta affinis (Kulczyński, 1898)	08, 10, 16, 23, 26
Meioneta rurestris (C. L. Koch, 1836)	03, 13, 18, 32, 36, 45, 49
Meioneta saxatilis (Blackwall, 1844)	15, 39
Micrargus subaequalis (Westring, 1851)	49
Microneta viaria (Blackwall, 1841)	38
Minyriolus pusillus (Wider, 1834)	26
Neriene clathrata (Sundevall, 1830)	23
Neriene radiata (Walckenaer, 1842)	04
Palliduphantes alutacius (Simon, 1884)	07, 16, 21, 31
Palliduphantes pallidus (O. P.-Cambridge, 1871)	18
Panamomops affinis Miller & Kratochvíl, 1939	05, 07, 20, 22, 44
Panamomops fagei Miller & Kratochvíl, 1939	38
Panamomops mengei Simon, 1926	23, 31
Pelecopsis mengei (Simon, 1884)	13
Tapinocyba insecta (L. Koch, 1869)	05, 12, 27, 30
Tenuiphantes zimmermanni (Bertkau, 1890)	26
Trichopterna cito (O. P.-Cambridge, 1872)	20
Walckenaeria atrotibialis (O. P.-Cambridge, 1878)	05, 07, 12, 16
Walckenaeria dysderoides (Wider, 1834)	07, 18
Walckenaeria furcillata (Menge, 1869)	01, 23, 32, 34
Tetragnathidae	
Pachygnatha degeeri Sundevall, 1830	02

Araneae	Study sites
Araneidae	
Hypsosinga sanguinea (C. L. Koch, 1844)	15
Lycosidae	
Alopecosa cuneata (Clerck, 1757)	02, 03, 13, 18, 19, 20, 21, 25, 26, 29, 32, 34, 43, 45, 48, 49
Alopecosa mariae (Dahl, 1908)	25
Alopecosa pulverulenta (Clerck, 1757)	04, 05, 07, 19, 37, 43
Alopecosa trabalis (Clerck, 1757)	01, 04, 05, 11, 12, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 25, 26, 27, 28, 29, 31, 32, 34, 35, 36, 39, 40, 41, 43, 44, 45, 47, 48
Arctosa figurata (Simon, 1876)	01, 10, 11, 13, 14, 18, 19, 20, 27, 28, 32, 33, 34, 37, 39, 40, 41, 42, 43, 46, 49
Arctosa lutetiana (Simon, 1876)	01, 04, 05, 06, 07, 08, 10, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 27, 28, 30, 31, 32, 34, 35, 36, 37, 38, 39, 41, 42, 43, 44, 46, 47, 48, 50
Aulonia albimana (Walckenaer, 1805)	01, 04, 05, 06, 07, 08, 10, 11, 12, 16, 17, 18, 19, 20, 22, 23, 24, 26, 28, 30, 35, 42, 43, 44, 45, 46, 48, 49
Pardosa agrestis (Westring, 1862)	09
Pardosa alacris (C. L. Koch, 1833)	02, 05, 06, 07, 08, 10, 11, 12, 15, 17, 19, 20, 22, 23, 24, 26, 35, 38, 47, 49
Pardosa bifasciata (C. L. Koch, 1834)	01, 02, 03, 06, 10, 11, 13, 14, 18, 19, 20, 25, 29, 32, 33, 34, 36, 38, 40, 41, 43, 46, 49, 50
Pardosa hortensis (Thorell, 1872)	08, 25
Pardosa riparia (C. L. Koch, 1833)	15
Trochosa terricola Thorell, 1856	04, 05, 07, 12, 17, 18, 19, 21, 22, 23, 26, 30, 31, 34, 37, 38, 42, 43, 44, 47, 49, 50
Xerolycosa miniata (C. L. Koch, 1834)	02, 03, 10
Pisauridae	
Pisaura mirabilis (Clerck, 1757)	07, 15
Zoridae	
Zora spinimana (Sundevall, 1833)	05, 07, 17, 26
Agelenidae	
Malthonica campestris (C. L. Koch, 1834)	44
Hahniidae	
Hahnia nava (Blackwall, 1841)	04, 07, 10, 18, 20, 23, 32, 34, 37, 41, 43, 49
Hahnia ononidum Simon, 1875	05, 06, 07, 08, 12, 16, 21, 22, 30
Hahnia pusilla C. L. Koch, 1841	17
Dictynidae	
Argenna subnigra (O. P.-Cambridge, 1861)	06, 45
Titanoecidae	
Titanoeca schineri L. Koch, 1872	07, 09, 16, 24, 26, 32, 37, 41, 45
Miturgidae	
Cheiracanthium campestre Lohmander, 1944	32
Liocranidae	
Agroeca brunnea (Blackwall, 1833)	05, 19
Agroeca cuprea Menge, 1873	07, 08, 19, 22, 27, 38, 50

Araneae	Study sites
Clubionidae	
Clubiona comta C. L. Koch, 1839	24
Clubiona diversa O. P.-Cambridge, 1862	11
Corinnidae	
Phrurolithus festivus (C. L. Koch, 1835)	07, 15, 17, 24, 32, 38, 46, 47, 49
Gnaphosidae	
Drassodes lapidosus (Walckenaer, 1802)	09
Drassodes pubescens (Thorell, 1856)	10, 12, 19, 25, 43
Drassodes villosus (Thorell, 1856)	01
Drassyllus praeficus (L. Koch, 1866)	04, 25, 46
Drassyllus pusillus (C. L. Koch, 1833)	13, 15, 28, 29, 37, 45
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