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ORIGINAL PAPER

Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows

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Abstract Regular mowing of grassland is often necessary for plant conservation, but uncut vegetation is needed by many arthropods for overwintering. This may lead to conflicting management strategies for plant and arthropod conservation. Rotational fallows are a possible solution. They provide a spatio-temporal mosaic of mown and unmown areas that may combine benefits to both plants and arthropods. We tested if rotational fallows enhance spider overwintering in fen meadows. Rotational fallows consisted of three adjoining strips 10 m wide and 35–50 m long. Each year, one of these strips was left unmown (fallow) in an alternating manner so that each strip was mown two out of three years. Spiders were sampled during spring with emergence traps in nine pairs of currently unmown fallow strips and completely mown reference plots. Fallows significantly enhanced orb-weavers (Araneidae), sac spiders (Clubionidae) and ground spiders (Gnaphosidae). However, only 4.7% of the total variation in community composition was attributable to fallows. Community variation was larger between landscapes (34.5%) and sites (38.2%). Also β diversity was much higher between landscapes (45 species) and sites (22 species) than between fallows and mown reference plots (10 species). We conclude that the first priority for spider conservation is to preserve as many fen meadows in different landscapes as possible. Locally, rotational fallows enhance overwintering of the above-mentioned spider families, which are sensitive to mowing in other grassland types as well. Thus, rotational fallows would probably foster spider conservation in a wide range of situations. However, stronger effects can be expected from larger and/or older fallow areas.

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Introduction

Fen meadows are habitats of outstanding conservation value, because they feature a diverse and specialised flora and fauna, including many endangered species. Since the beginning of the 20th century, fen meadows in Central Europe have declined dramatically, mainly due to intensification of land use (van Diggelen et al. 2006). Many of the remaining fen meadows are legally protected. *Molinia* meadows and calcareous fens belong to natural habitat types of community interest listed in Annex I of the EU Habitats Directive (92/43/EEC of 21 May 1992). In Switzerland, approximately 90% of fens and other wetlands have been destroyed by human activity in the last 150 years (Grünig 1994). Despite their decline, fens still contribute substantially to biodiversity of plants and invertebrates in Switzerland. Moreover, many wetland species are classified as rare and endangered—for instance almost 50% of the plant species occurring in fens and other wetlands are recorded in the current Red List (Moser et al. 2002).

The preservation of fen meadows depends on appropriate management such as late-season mowing or extensive grazing, since abandonment leads to changes in vegetation composition (Billeter et al. 2003) and a decrease of plant species diversity (Diemer et al. 2001; Jensen and Meyer 2001). Traditionally, non-manured fen meadows of the Swiss Plateau were often divided into small lots, which were mown by different farmers once a year between September and November to provide litter (straw-like plant material) for livestock husbandry. This management favoured a habitat mosaic, which offered ecological niches for many arthropod and plant species but it is not profitable for farmers with regard to today's agricultural practice and economic conditions. Currently, mowing mostly occurs on large scale and simultaneously in early September and is subsidised by direct payments to agriculture (Bundesrat 1998).

Since arthropods form a large part of the overall species richness in grassland ecosystems and fulfil important roles as herbivores, predators, pollinators and prey for vertebrates, they are increasingly considered in management for nature conservation. However, large-scale mowing can contribute to a decrease of arthropod density and diversity in fen meadows as well as in other grassland ecosystems. Particularly immobile arthropod species and development stages (eggs, larvae, pupae) may be injured or killed and removed with the litter (Gerstmeier and Lang 1996). Furthermore, important refuges and suitable habitats for overwintering get lost when older stalks and tussocks are removed by late season mowing (Neumann and Krüger 1991). In the absence of litter arthropods may be more strongly exposed to harsh weather conditions, predators and flooding.

Rotational management of whole grasslands and the establishment of rotating short-term fallows are recommended to counteract the adverse effects of large scale simultaneous mowing on arthropods (e.g. Morris and Rispin 1994; Morris 2000; Cattin et al. 2003). We studied rotational fallows in fen meadows. Each year in autumn, one of three adjoining strips was left unmown (fallow) in an alternating manner so that each strip was mown two out of three years. Here we focus on the importance of the fallows strips as refuges and overwintering habitats for spiders. Spiders are abundant and diverse in wetlands, and a large proportion of the Central European spider fauna depends on moist open habitats (Hänggi et al. 1995; Entling et al. 2007). Furthermore, many wetland spiders are sensitive to mowing (Decler 1990; Cattin et al. 2003; Schmidt et al. 2005). Especially during

winter, spiders may depend on the shelter given by hollow stalks of dead vegetation (Pühringer 1979; Neumann and Krüger 1991).

The aim of the present study was to compare species composition, species richness and abundance of overwintering spiders in both fallow strips of rotational fallows and annually mown reference plots.

Materials and methods

Study design

The study was carried out in nine fen meadows in northern Switzerland, which belonged to the plant communities *Molinion*, *Caricion davallianae* and *Magnocaricion* (Ellenberg 1996). Three meadows each were located in the landscapes of Greifensee, Schmerikon and Reusstal (Fig. 1). The sites at Greifensee and Schmerikon are lakeshore marshes, while those in Reusstal are situated in a river valley. One experimental plot with a rotational fallow was implemented in each of the nine meadows in autumn 2002. An experimental plot consisted of three adjoining strips 10 m wide and 35–50 m in length. In a rotational manner, one of these strips was spared from mowing each year (Fig. 2). Ten to fifty metres from each rotational fallow, a reference plot of the same size was chosen which continued to be mown completely every year. The meadows were mown annually in September and the litter was removed within a few weeks after mowing.

Spider sampling

Spiders were sampled with six randomly placed emergence traps (surface eclectors) in the unmown fallow strip and in the corresponding reference plot of each experimental site (Fig. 2). Thus, 108 emergence traps were employed in total (6 traps \times 2 plots \times 3 sites \times 3 landscapes). Emergence traps consisted of a 0.5 m \times 0.5 m metal frame, which was buried 5 cm in the ground and covered by a pyramidal, light-coloured gauze tent. A trapping device

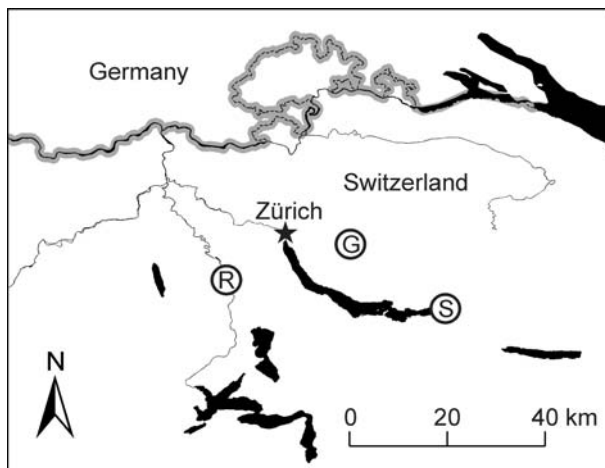


Fig. 1 Situation of the three study landscapes Greifensee (G), Schmerikon (S) and Reusstal (R) in northern Switzerland

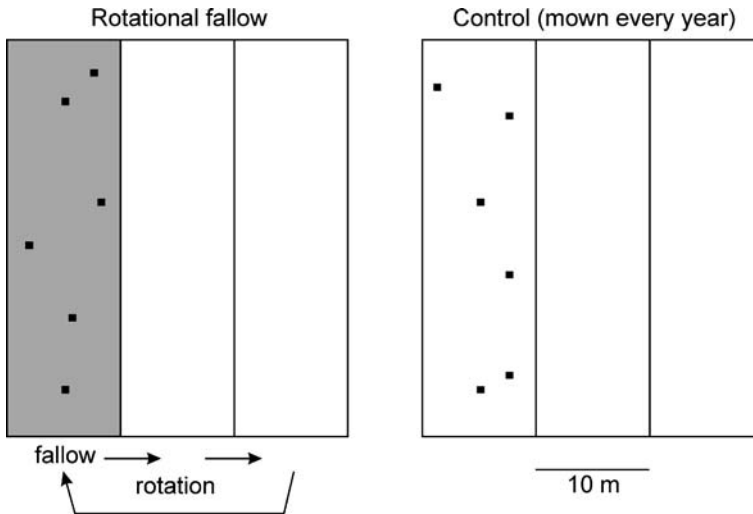


Fig. 2 Sketch of one rotational fallow with corresponding reference plot. Black squares mark the randomly placed emergence traps

filled with 2% formalin in water plus some detergent was installed at the tip of the gauze tent. Within each emergence trap a pitfall trap (plastic cup of 7 cm diameter) was buried in the ground. Pitfall traps were filled to one-third with a 3:1 mixture of water and ethylene glycol as preservative. Sampling started immediately after snowmelt in early March 2005 and lasted until mid of June 2005, when plant biomass after the traps completely. Since the traps were left at the same place for over 3 months, a majority of the spiders active in the enclosed area should have been caught. Traps were emptied fortnightly and invertebrates stored in 70% ethanol before sorting and identification. Immature spiders were determined to family and adults to species level. The nomenclature follows Platnick (2008).

Data analysis

Data from six emergence traps per experimental plot were combined for analysis, converted to abundances (individuals per 1 m²) and log-transformed. Species richness, overall abundance, and abundance of families and species were compared between fallow strips and annually mown reference plots with t-tests for matched pairs, or with corresponding non-parametric tests when assumptions for t-test were violated (exact, two-tailed significance levels from Wilcoxon Tests; SPSS Inc. 2004). The amount of community variation attributable to the fallow treatment was compared to the variation between sites and between landscapes. This was done in a series of (partial) ordinations (redundancy analysis, RDA) on log-transformed spider abundances using the programme CANOCO (ter Braak and Smilauer 2002). In each of these analyses, the significance of the studied factor was tested with Monte-Carlo Permutations on ‘canonical axes together’ ($k = 9999$ permutations). First, the amount of community variation between the three study landscapes was determined with a simple RDA with landscapes coded as dummy variables. The fallow and the control in each meadow were combined into whole-plots and permuted together, to achieve the correct level of replication ($n = 9$ sites). Then the contribution of sites to community variation was determined in a partial RDA after accounting for the variation between landscapes. Fallow and control plots were permuted freely across sites but only

within each landscape, to account for the nestedness of the sites within the three landscapes. Finally, the influence of rotational fallows on spider communities was determined after accounting for the variation between landscapes and sites in another partial RDA. Thereby, the nine sites were defined as whole-plots, within which the paired fallow and reference plots were permuted. Additive partitioning of species richness was conducted to quantify the contributions of alpha and beta diversity to total diversity over the whole range of spatial scales (Veech et al. 2002; Gering et al. 2003). We calculated average species richness on the level of plots, sites and landscapes, and the total number of species found in the study. The differences between the average richness at two adjacent levels represent β diversity for the respective lower level. For example, the average number of species per landscape minus the average number of species per site is β_S , the number of species attributable to variation between sites. Averages \pm SE are given in text and figures.

Results

Overall, 2114 spiders were sampled, representing an average abundance of 78 spiders per 1 m². Thereof, 1357 individuals were adult, belonging to 15 families and 98 species. Abundances of several spider families were higher in rotational fallows than in mown reference plots (Fig. 3). Orb-weavers (Araneidae; $t = 2.8$, $P = 0.024$), sac spiders (Clubionidae; $t = 2.6$, $P = 0.032$) and ground spiders (Gnaphosidae; $t = 4.2$, $P = 0.003$) were significantly enhanced by the fallows. Jumping spiders (Salticidae) showed a trend towards higher densities in the fallows ($t = 1.9$, $P = 0.089$). The remaining families did not show significant differences between rotational fallows and mown reference plots. No significant differences between fallows and reference plots were observed for overall species richness (22.2 ± 2.8 vs. 19.8 ± 3.0 ; $t = 1.3$; $P = 0.23$) or abundance (75 ± 13 m⁻² vs. 82 ± 21 m⁻²; $t = 0.07$; $P = 0.95$).

Variation of spider communities was mostly attributable to differences between landscapes and between sites within landscapes (Table 1). Nevertheless, community composition was

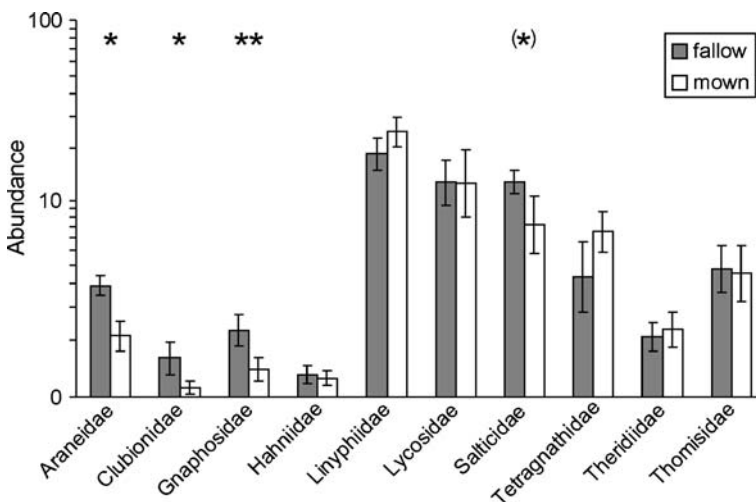


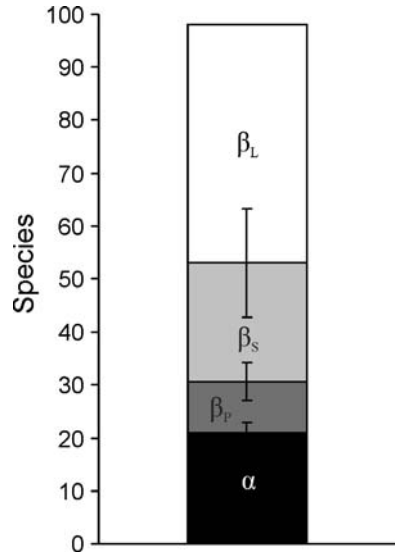
Fig. 3 Abundance (m⁻²) of spider families in rotational fallows (grey) compared to mown reference plots (white). Asterisks denote significance according to t-tests for matched pairs on log-transformed abundances (** $P < 0.01$; * $P < 0.05$; (*) $P < 0.10$)

Table 1 Amount of community variation attributable to differences between the three study landscapes, between the three sites within each landscape, and between the rotational fallow and reference plot within each site (RDA)

	% explained variation	<i>n</i>	<i>F</i>	<i>P</i>
Landscapes	34.5	9	4.0	0.005
Sites	38.2	18	2.1	<0.001
Plots (fallows vs. mown)	4.7	18	1.7	0.013

n is the number of exchangeable units used in the permutation test

Fig. 4 Hierarchical additive partitioning of species richness into β diversity between landscapes (β_L), between sites within landscapes (β_S), and between plots within sites (β_P). The mean number of species per plot (rotational fallows and mown reference plots) is represented by α diversity



significantly different between rotational fallows and mown reference plots, accounting for 4.7% of the overall variation. The differences between landscapes and sites were so large that only few species occurred at all sites in considerable numbers (Appendix A). Correspondingly, only two spider species showed significant differences between fallows and reference plots. The jumping spider *Evarcha arcuata* (Salticidae) had higher abundances in fallows (1.6 ± 0.4 vs. 0.2 ± 0.2 ; $Z = -2.4$; $P = 0.016$), whereas *Erigone dentipalpis* (Linyphiidae) was less abundant in fallows than in mown reference plots (0.7 ± 0.5 vs. 3.0 ± 1.1 ; $Z = -2.1$; $P = 0.047$). In accordance with the community patterns, hierarchical partitioning of species diversity underscored the importance of variation between landscapes and sites for overall species richness (Fig. 4). β diversity between landscapes contributed 45 out of the 98 species in total. Within landscapes, β diversity between sites contributed another 22 species, and 10 species were due to β diversity between rotational fallows and mown reference plots within sites.

Discussion

Fallow strips contained different spider communities and higher abundances of Araneidae, Clubionidae and Gnaphosidae during spring, indicating improved conditions for spider

overwintering. However, the influence of the fallows was small compared to variation between landscapes and sites. Together, differences between landscapes and sites accounted for 73% of community variation, and 69% of total species diversity. This surprisingly high heterogeneity can be attributed to environmental, spatial and/or stochastic processes, the study of which was beyond the scope of the current investigation. Nevertheless, it underlines that conserving fen meadows in a wide range of geographic situations and with different site conditions is of primary importance for preserving spider diversity.

In spite of the overriding importance of heterogeneity between sites, a positive influence of fallows on the spider communities was found. Only the sheetweb-weaver *Erigone dentipalpis* (Linyphiidae) had significantly lower abundances in fallows than in mown reference areas. This ubiquitous spider of open habitats is of no particular conservation value (Bell et al. 2001). On the other hand, fallows enhanced the jumping spider *Evarcha arcuata* (Salticidae) and overall abundances of orb-weavers (Araneidae), sac spiders (Clubionidae) and ground spiders (Gnaphosidae). The same families are sensitive to mowing in other wetlands (Cattin et al. 2003; Schmidt et al. 2005), and indicate low levels of disturbance in agricultural habitats (Bell et al. 2001; Schmidt and Tschamtkke 2005). Mowing can be detrimental to spiders and insects also in mesic and dry grasslands (Pozzi and Borcard 2001; Stoner and Joern 2004; Thorbek and Bilde 2004). In particular, mowing reduces the vegetation structure needed by aerial web builders (e.g. Araneidae) and climbing spiders (e.g. Clubionidae). The reduced litter layer disfavours cursorial species (e.g. Gnaphosidae) (Bell et al. 2001). The benefit of rotational fallows observed in the current study is in accordance with these general patterns. Therefore, rotational fallows are a promising tool for enhancing these spider families also in mesic and dry grasslands. As we installed closed emergence traps in early spring, our findings represent the overwintering situation. It is possible that additional differences between fallows and mown areas appear during the vegetation period. For example, spider survival and/or reproduction may be higher in the more complex vegetation structure provided by the fallows during summer, when there is a mixture of dead vegetation and fresh growth. Intraguild interference between spiders and other predators may be reduced by the presence of litter in grassland vegetation (Langellotto and Denno 2004). In addition, spider communities in disturbed habitats comprise many immigrants (Rothenbücher and Schaefer 2006; Schmidt et al. 2008), which may be differently attracted to fallows compared to mown areas. A high importance of standing vegetation for spider overwintering has been reported from *Phragmites* reed beds (Pühringer 1979, Neumann and Krüger 1991). In a broader range of habitats, the majority of spiders overwintered close to the soil surface and in leaf litter (Schaefer 1976). Remarkably, the few species that overwintered on or in herbaceous vegetation include the families Araneidae and Clubionidae (Schaefer 1976), which were enhanced by rotational fallows in the current study. However, the prevalent overwintering of spiders in dead vegetation is probably specific to reed beds with their long periods of inundation. This may explain why the differences between fallows and mown reference areas in the current study were limited to only few spider families. Apparently, a one-year fallow period did not lead to enough litter accumulation to greatly enhance spider overwintering at the soil surface, except for Gnaphosidae.

Although rotational fallows were beneficial for spiders, a stronger influence could have been expected. The current scheme explained only 4.7% of community variation. For comparison, the difference between large reed beds that were annually mown or not over at least six years accounted for 41% of the total variation in spider communities (Schmidt et al. 2005). Thus, the benefit to spiders is likely to increase with age and area of the fallows (Ratschker and Roth 2000; van Buskirk and Willi 2004). Future studies on rotational fallows should also incorporate larger and more permanently undisturbed areas. Such

comparisons between several options would allow a more targeted conservation management. It is likely that a combination of annually mown areas, rotational fallows and permanently unmown sites provides the highest biodiversity (Benton et al. 2003).

In conclusion, the first priority for spider conservation is to preserve fen meadows in as many geographic and environmental situations as possible. Locally, rotational fallows are suitable to enhance overwintering of spider families that are sensitive to disturbance. The same spider families are sensitive to mowing also in other grassland types, so that rotational fallows would probably foster conservation in a wide range of situations. Stronger positive effects on spiders could be expected from larger and/or older fallow areas, which should be incorporated in meadow landscapes whenever this is compatible also with the conservation of other organisms.

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Appendix A Mean abundance of adult spiders in rotational fallow strips and mown reference plots, and number of individuals captured in each of the three study landscapes Greifensee (G), Schmerikon (S) and Reusstal (R)

Family	Species	Fallow	Reference	G	S	R
Araneidae	<i>Hyposinga pygmaea</i>	0.7 ± 0.3	0.9 ± 0.4	14	4	5
Gnaphosidae	<i>Drassyllus pusillus</i>	0.4 ± 0.2	0.1 ± 0.1	1		6
	<i>Zelotes latreillei</i>	0.1 ± 0.1	0.2 ± 0.1	4		1
Hahniidae	<i>Hahnia nava</i>	0.3 ± 0.2	0.1 ± 0.1			6
Linyphiidae	<i>Araeoncus humilis</i>	0.6 ± 0.3	2.3 ± 0.7	20	1	18
	<i>Ceratinella brevipes</i>	0.4 ± 0.2	0.1 ± 0.1	3	3	1
	<i>Nephalocotes obscurus</i>	0.9 ± 0.6	0.8 ± 0.6			23
	<i>Erigone atra</i>	0.1 ± 0.1	0.3 ± 0.2	4		2
	<i>Erigone dentipalpis</i>	0.7 ± 0.5	3.0 ± 1.1	19	1	31
	<i>Erigone jaegeri</i>	0.7 ± 0.7	0.7 ± 0.3	2	6	11
	<i>Gongylidiellum murcidum</i>	0.8 ± 0.6	0.2 ± 0.2	10	1	3
	<i>Mermessus trilobatus</i>	3.4 ± 0.7	3.9 ± 0.9	32	25	42
	<i>Panamomops sulcifrons</i>	0.4 ± 0.3	0.5 ± 0.4		1	11
	<i>Porrhomma</i> sp.	1.6 ± 0.5	1.1 ± 0.6	18		18
	<i>Tiso vagans</i>	1.0 ± 0.4	0.7 ± 0.6	1	22	
	<i>Troxochrus scabriculus</i>	1.3 ± 1.2	3.5 ± 3.2		4	61
	<i>Walckenaeria atrotribialis</i>	0.6 ± 0.3	0.1 ± 0.1		1	7
Lycosidae	<i>Alopecosa pulverulenta</i>	1.6 ± 1.2	0.5 ± 0.3	2		27
	<i>Arctosa leopardus</i>	0.4 ± 0.2	0.4 ± 0.2	11	1	
	<i>Pirata latitans</i>	1.3 ± 0.3	2.5 ± 1.7	30	11	9
	<i>Trochosa ruricola</i>	0.7 ± 0.3	0.5 ± 0.3	1	2	13
	<i>Trochosa terricola</i>	1.5 ± 0.6	1.0 ± 0.5	4	2	28
Salticidae	<i>Evarcha arcuata</i>	1.6 ± 0.4	0.2 ± 0.2	6	9	10
	<i>Heliophanus auratus</i>	4.1 ± 1.5	6.8 ± 2.8	22	43	83
	<i>Heliophanus flavipes</i>	0.9 ± 0.4	1.0 ± 0.5	19	3	4
	<i>Myrmarachne formicaria</i>	0.7 ± 0.5	0.4 ± 0.2	2		14
Tetragnathidae	<i>Pachygnatha clercki</i>	0.7 ± 0.5	0.6 ± 0.4	10		7
	<i>Pachygnatha degeeri</i>	7.0 ± 3.3	7.1 ± 2.1	9	41	140
Theridiidae	<i>Enoplognatha thoracica</i>	0.5 ± 0.2	0.4 ± 0.2	2	5	6

Appendix A continued

Family	Species	Fallow	Reference	G	S	R
Thomisidae	<i>Ozyptila simplex</i>	1.3 ± 0.8	1.2 ± 0.7	3	1	29
	<i>Xysticus bifasciatus</i>	1.0 ± 0.5	0.7 ± 0.7	3	9	10
	<i>Xysticus cristatus</i>	0.1 ± 0.1	0.4 ± 0.1		2	4

Species occurring in less than five sites, with the number of individuals in rotations fallow strips versus mown reference plots in parentheses. Araneidae: *Cercidia prominens* (1/1); *Hypsosinga sanguinea* (1/0); *Mangora acalypha* (1/0); *Singa hamata* (2/0); Clubionidae: *Clubiona comta* (1/0); *C. phragmitis* (0/1); *C. reclusa* (2/0); *C. stagnatilis* (2/0); Corinnidae: *Phrurolithus festivus* (1/0); Dictynidae: *Dictyna uncinata* (1/0); *Lathys humilis* (0/1); Gnaphosidae: *Drassyllus lutetianus* (1/0); *Gnaphosa nigerrima* (1/0); *Micaria pulicaria* (4/1); *Zelotes subterraneus* (2/0); Hahniidae: *Antistea elegans* (1/1); *Tuberta maerens* (0/1); Linyphiidae: *Araeoneta crassiceps* (8/18); *Bathyphanes approximatus* (0/1); *Centromerus semiatra* (1/0); *Ceratinella brevis* (3/1); *C. scabrosa* (2/1); *Dicymbium nigrum* (1/0); *Diplostyla concolor* (0/1); *Glyphesis servulus* (2/0); *Gongyliellum latebricola* (0/3); *Hyllyphantes nigrinus* (6/0); *Meioneta rurestris* (1/6); *Oedotheorax gibbosus* (1/0); *O. retusus* (2/5); *Pelecopsis mengei* (1/0); *Satilatlas brittani* (4/2); Gen. sp. (0/1); *Tapinocyba insecta* (3/5); *Tapinocyba pallens* (1/2); *Tenuiphantes flavipes* (0/1); *T. tenuis* (4/0); *Troxochrus nasutus* (1/3); *Walckenaeria antica* (7/5); *W. dysderoides* (1/0); *W. vigilax* (4/3); Liocranidae: *Agroeca brunnea* (2/0); *Liocranoeca striata* (2/0); Lycosidae: *Arctosa lutetiana* (2/3); *Pardosa agrestis* (1/0); *P. amentata* (1/1); *P. lugubris* (16/38); *P. palustris* (6/11); *Pirata hygrophilus* (0/3); *P. tenuitarsis* (3/6); *Trochosa spinipalpis* (4/6); Pisauridae: *Pisaura mirabilis* (0/4); Salticidae: *Phlegra fasciata* (1/0); *Sitticus caricis* (1/0); *Talavera aperta* (4/4); Tetragnathidae: *Metellina mengei* (0/1); Theridiidae: *Enoplognatha caricis* (1/1); *Paidiscura pallens* (0/1); *Robertus neglectus* (0/2); *Steatoda triangulosa* (1/0); Thomisidae: *Ozyptila trux* (2/0); *Xysticus acerbus* (0/3); *X. audax* (1/0); *X. kempeleni* (0/2); *X. kochi* (0/2); *X. lineatus* (3/0)

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