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Original article

Niche partitioning in orbweaving spiders *Meta menardi* and *Metellina merianae* (Tetragnathidae)Tone Novak^{a,*}, Tina Tkavc^b, Matjaž Kuntner^{c,d}, Amy E. Arnett^e, Saška Lipovšek Delakorda^a, Matjaž Perc^f, Franc Janžekovič^a^a Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, SI-2000 Maribor, Slovenia^b Prušnikova ulica 18, SI-2000 Maribor, Slovenia^c Institute of Biology, Scientific Research Centre of the Slovenian Academy of Sciences and Arts, Novi trg 2, SI-1001 Ljubljana, Slovenia^d Department of Entomology, National Museum of Natural History, NHB-105, Smithsonian Institution, P.O. Box 37012, Washington DC 20013-7012, USA^e Center for Biodiversity, Unity College, 90 Quaker Hill Road, Unity, ME 04915, USA^f Department of Physics, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, SI-2000 Maribor, Slovenia

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ABSTRACT

Hypogean habitats are relatively simple exhibiting low diversity, low production and relative constancy of environmental factors, and are therefore appropriate for studying species coexistence *in situ*. We investigated the coexistence of two closely related, similarly sized orb-weaving spider species, *Meta menardi* and *Metellina merianae*, living syntopically in a Slovenian cave. We studied the annual dynamics of both species within a mixed population, and the impact of the ambient temperature, relative humidity, airflow and illumination, and compared their trophic niches to legacy data on prey of both species from 55 caves in Slovenia. We predicted a large overlap in their spatial niches and substantial differences in their temporal and trophic niches. We found that their spatial niches overlap greatly with few exceptions, mostly on the dates of notable meteorological changes in the cave but that their temporal niches differ significantly with r-strategy resembling epigeal annual dynamic in *M. merianae* and a steady low abundance course in *M. menardi* within the cave. We also found that different predatory strategies significantly segregate their trophic niches: *M. merianae* uses a typical orb-weaving hunting strategy, while *M. menardi* combines web hunting with off-web hunting. Our findings suggest that both the diverse dynamics and trophic niches enable the coexistence of *M. menardi* and *M. merianae* despite their similar spatial niches, and that *M. menardi*, in particular, is optimally adapted to the epigeal/hypogean ecotone.

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1. Introduction

Spider coexistence has been well studied with particular reference to differences in habitat and microhabitat preferences (Romero and Vasconcellos-Neto, 2005), predator-controlled coexistence (Spiller and Schoener, 1998), interspecific predation (Uetz, 1977; Elgar, 1992; Heuts and Brunt, 2001; Balfour et al., 2003; Wise, 2006) and kleptoparasitism (Agnarsson, 2003). Interspecific competition in spiders has been demonstrated in relatively simple habitats, such as litter, estuaries, wetlands and agricultural ecosystems (Uetz, 1979; Marshall and Rypstra, 1999). However, despite some evidence of competition for space and prey (Spiller, 1984a,b), interspecific competition in web building spiders has

remained difficult to demonstrate (Schaefer, 1978; Connell, 1980; Wise, 1981, 1993; Horton and Wise, 1983).

In the dynamics of multispecies systems, measuring interspecific relations is difficult due to many different interactions (Wootton and Emmerson, 2005). In some cases, observational information *in situ* may be more practical than performing a simulated experiment (Yodzis and Innes, 1992; Moore et al., 1993; Wootton and Emmerson, 2005). Simple epigeal ecosystems exhibit a moderate gradient of habitat structure in comparison to the complex ones because of the structural simplicity of their vegetation (Marshall and Rypstra, 1999). However, hypogean habitats such as caves and artificial tunnels, are simpler yet due to low diversity, low production, and relative constancy of environmental factors (Culver, 2005), and thus seem very suitable for investigating species coexistence *in situ*.

Some species of orbweaving spiders in the genera *Meta* and *Metellina* inhabit European caves syntopically. Similar in

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appearance, *Metellina* Chamberlin and Ivie, 1941 species have traditionally been listed in *Meta* C. L. Koch, 1836 (Simon, 1894; Roberts, 1995) and both indeed show phylogenetic proximity (Kuntner and Alvarez-Padilla, 2006; Kuntner et al., 2008; Alvarez-Padilla et al., 2009). Many *Meta* and *Metellina* species are troglophiles, inhabiting the epigeal/hypogean ecotone in temperate caves worldwide (Ribera, 2004; Culver, 2005). The European species *Meta menardi* (Latreille, 1804) and *Metellina merianae* (Scopoli, 1763) commonly inhabit European caves (Marusik and Koponen, 1992; Ribera and Juberthie, 1994) and man-made caverns where they often co-occur (Leruth, 1939; Tercafs, 1972; Bourne, 1976, 1977; Bourne and Robert, 1978; Novak and Kuštor, 1982; Eckert and Moritz, 1992; Smithers, 1996; Buhlmann, 2001). Both are medium sized species – adult *M. menardi* are about 1.5-times the mass of that of *M. merianae* – with comparable phenologies. Additionally, their life histories appear similar. For example, second instars of both species migrate out of caves, where the third instars of *M. menardi* disperse by ballooning (Smithers and Fox Smith, 1998; Smithers, 2005b). Its fourth instars return to subterranean habitats in the late summer and moult into fifth instars (Smithers, 2005b). Spatially, the two species appear quite different. For example, *M. merianae* inhabits mostly humid twilight epigeal habitats (Pennington, 1979; Eckert and Moritz, 1992; Smithers and Fox Smith, 1998; Smithers, 2005b) and shows no adaptations to the hypogean environments (Eckert and Moritz, 1992). *M. merianae* is reported to dwell closer to the entrance of caves, and *M. menardi* deeper inside. In caves hosting both species, *M. merianae* tends to prefer lower and *M. menardi* higher wall sites (Bourne, 1976, 1977). In a cave entrance section, representing the transition zone between surface and subsurface environments, there is a distinct gradient of several abiotic factors, especially light, temperature and humidity (Culver, 2005). There, both species often share the same microhabitats, which may result in a substantial niche overlap.

Both species, as most orb weavers, are sit-and-wait predators (Legrand and Morse, 2000), building similar planar orb-webs with an open hub (Levi, 1980; Kuntner, 2006). However, the webs of both species differ in size and proportion. While a *M. merianae* web is typically about twice the size of that of *M. menardi*, the mesh size (length of individual sticky spiral sections between adjacent radii) of *M. menardi* web is almost twice the size of that of *M. merianae*, being too large to ensnare small prey (Eckert and Moritz, 1992; Smithers, 1996, 2005a). Like *Meta japonica* (Yoshida and Shinkai, 1993, sub *M. menardi*; Tanikawa, 1993; Platnick, 2000–2009), *M. menardi* attaches the web radii directly to the rocks (Eckert and Moritz, 1992; Smithers, 1996). Associated foraging behaviour and prey capture for this species have been well documented (Pötzsch, 1966; Tercafs, 1972; Bourne and Robert, 1978; Smithers, 2005a). The differences in web structure between *M. menardi* and *M. merianae* and the potential prey their webs can physically ensnare suggests a low trophic niche overlap between the two species.

In caves in Slovenia, three main groups of potential prey to cave-dwelling *M. merianae* and *M. menardi* can be distinguished with respect to their abundance and mobility (Novak, unpublished data). First, individuals of about three dozen of troglone and a dozen of troglophile (for both definitions see Vandell, 1964; Sket, 2008; Culver and Pipan, 2009) prey species are present but sparse on the walls throughout the year. Second, a massive immigration of about two dozen overwintering species appears during the late fall; and, third, much less abundant individuals of about a dozen estivating species enter caves in the height of summer. Once placed, overwintering and estivating individuals do not displace, or displace rarely. Gradually, a quarter to a half of them disappear in fissures and man-inaccessible cave passages. Migratory individuals leave caves in spring and fall, respectively. To *M. merianae* and *M. menardi*, such prey dynamics provides only seasonally limited

access to food. Food resources for orb-weaving spiders within caves are thus generally limited.

Meta menardi and *M. merianae* are common and often syntopic in caves of central and northern Slovenia (Novak, 2005). Here, we investigate the overlap of their temporal, spatial and trophic niches in natural conditions within a cave with relatively abundant mixed populations. As a consequence of unequal presence of individuals of both species in all cave sections during the year (Novak, unpublished data) we hypothesized that 1) there is a significant segregation between their temporal niches within the cave. We also hypothesized that 2) specific physical characteristics are preferred by one or the other species in the outermost and innermost parts of the cave resulting in significant differences in their spatial niches, and that no such difference appears in the middle cave section where the environmental conditions should suit both species. Because *M. menardi* is reported to be a more generalist predator than *M. merianae* which captures mostly flying prey (Eckert and Moritz, 1992; Smithers, 1996, 2005a) we also hypothesized 3) a significant difference between their trophic niches expecting a larger prey list and lower ratio of flying vs. non-flying prey in *M. menardi*.

2. Material and methods

2.1. Study site

Field investigations were performed in the Pilanca cave in northern Slovenia (entrance at N46°24'57", E15°10'38", altitude 646 m; mapped in Novak, 2005), inhabited by a relatively dense mixed population of *M. menardi* and *M. merianae*. This 120 m long cave has a vertical ascent of 35 m, its entrance is 31.5 × 8.5 m. The cave's first hall measuring 76 × 35 × 8 m is followed by the second hall measuring 20 × 6 × 8 m, and a collapsed part. Further than 20 m inside the cave the temperature never drops below 0 °C. The light reaches the cave sections up to 100 m into the interior. The cave is the beginning of a large non-researched gallery causing cold summer outward and warm winter inward airflows. Such conditions render the cave much warmer compared to others in Slovenia, and, between 30–76 m, creates microhabitats with relatively narrow abiotic gradients for the majority of the year.

2.2. Data collection

Our investigations took place once a month, on average, from July 2004 to June 2005 up to 96 m inside the cave, in the middle of the day. The whole investigated area within the cave was partitioned into three sections: the outermost (0–30 m inside), the middle (30–60 m) and the innermost (>60 m inside) section. Specimens of both species occurred in apparently mixed populations on the lower wall and up to 3 m above the cave floor irrespective of the ceiling height (4–12 m), thus enabling data collecting within a unique gradient of environmental parameters along the cave. A small, separate group of 2–8 (sub)adult *M. menardi* within a 9 m high ceiling concavity at 60 m inside was inaccessible for measurements and thus not included in statistical procedures. Censuses and individual measurements were performed on each date of investigation. Using a hand lens, adults, subadults and juvenile stadia were determined and sexed except for the juveniles of less than 5 mm in length, based on specimen size and maturity (Pennington, 1979; Eckert and Moritz, 1992).

Air temperature (*T*), relative air humidity (*H*), and airflow (*A*) were measured for each individual, approximately 1–2 cm away, using a handheld aspiration psychrometer (Ahorn FN A846, Germany). The airflow was determined by measuring the velocity of horizontal movements of fog or candle smoke (Novak et al., 2004).

Both techniques give the same results. Local wind directions within the Pilanca cave were strongly turbulent, which is similar to the Predjama cave system where local turbulences within the cave cause constant inward airflow in about one third of microhabitats, irrespective of wind directions, during its daily inversions (Novak et al., 1980). Generally, during the warm months, over the span of a day, the main, cooler cave wind-current flows outwards above the floor and weak warm air flows inwards below the ceiling. The outward air flow is most intensive in April (Fig. 2), but 32% of the air currents in investigated spider placements were inward, and about 15% of the wind directions differed for more than 90° in repeated measurements within a few minutes; therefore the measurements of the wind direction within the microhabitats settled were not used in the main study. Still, the air flow turbulences did not disturb spiders as some of them were found persisting in the same places for more than a half of the year. The light intensity (*I*) was determined using a light meter (Lunasix; Gossen, Germany) towards the most illuminated background, either the entrance or a wall or the ceiling.

During the investigation, only 28 prey items for both *M. merianae* and *M. menardi* were recorded in the cave; therefore to test for differences in diet we used unpublished data on prey species obtained during systematic ecological investigations in 55 cavities in Slovenia from 1977 to 2002 (Novak, 2005). These data were obtained by wall, ceiling and ground inspections, pitfall trapping and Berlese selection, and include the evidence of prey of feeding spiders. Besides, we determined the average fresh mass by weighing specimens of the prey species or estimating their mass. Both spider species were also tested for differences in abundance of cursorial vs. flying prey.

2.3. Data analysis

Statistical analysis was first performed using a comparative normalized spatio-temporal density map of the two species with corresponding temporal traces of average values (average across all measurements during the particular day) of *T*, *H* and *A*, whereby the normalization of the density map was performed with respect to the total population size of *M. menardi* and *M. merianae*, respectively. The variations of the ecological variables were also tested using Principal Component Analysis (PCA) represented by two Ecological Principal Components (EPCs). For this procedure, the percent data of *H* were *arc-sin* transformed to normalize distribution. We first tested each species separately for differences in the EPCs between the three cave sections, and then for the interspecific differences within each section. Differences between *M. menardi* and *M. merianae* in their ecological requirements according to EPCs were tested with LSD one-way ANOVAs separately per dates. Relative frequencies of the prey pool taxa were determined in accordance with taxon abundances in all the 55 cavities, and in the webs, respectively. The differences between the relative frequencies of potential prey species and the frequencies of preyed specimens in the webs of both species were tested using χ^2 tests separately for flying and non-flying taxa. The niches were compared using the Pianka niche overlap index (Pianka, 1973),

$$O_{jk} = O_{kj} = \frac{\sum_{i=1}^n E_{ij}E_{ik}}{\sqrt{\sum_{i=1}^n (E_{ij}^2) \sum_{i=1}^n (E_{ik}^2)}}$$

where O_{jk} = overlap of species *j* and *k*; *i* = the resource level; *n* = number of resource levels; E_{ij} = the proportion of the abundance of the species *j* in the level *i*, divided by the number of plots within the level *i*.

The mass selectivity of prey was tested comparing masses of prey caught vs. prey available in the cave. The program SPSS 17.0 was used in these procedures.

3. Results

Individuals and egg-sacs of one or both species were at least temporarily present in all three investigated sections of the cave. Adults and juveniles of both species lived syntopically in mixed communities up to 78 m into the interior, but their dynamics differed considerably (Fig. 1). The yearly ranges of the ecological parameters in microhabitats settled were very similar (*M. menardi*: *T* = 2.6–18.3°C, *H* = 39.5–100.0%, *A* = 0–30 cm s⁻¹ and *I* = 0–11.000 lx; *M. merianae*: *T* = 1.7–20.6 °C, *H* = 35.6–100.0%, *A* = 0–40 cm s⁻¹ and *I* = 0–11.000 lx). *M. merianae* did not extend more than 78 m into the interior, while *M. menardi* reached 91 m. The *M. menardi* abundance was relatively more stable through the year than *M. merianae* (Fig. 1); the abundances significantly differed between species in adults ($\chi^2 = 59.37$; *df* = 11; *p* < 0.001) and in juveniles ($\chi^2 = 513.24$; *df* = 11; *p* < 0.001). Over the year, juveniles represented two thirds of all specimens (67% in *M. menardi* and 66% in *M. merianae*). Fig. 2 shows relative frequencies of the two species within the three cave sections. The segregation of spatial niches between *M. menardi* and

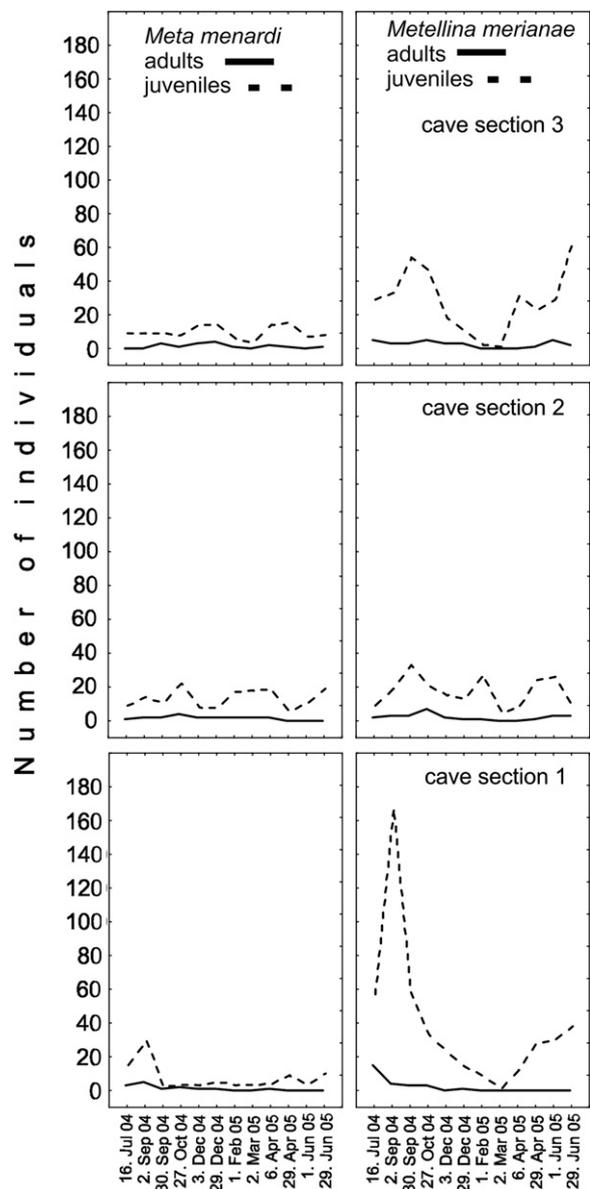


Fig. 1. Annual dynamics of *Meta menardi* and *Metellina merianae* in the Pilanca cave.

M. merianae occurs twice during a year. *M. merianae* was more abundant during the warm half of the year in the outermost cave segment with temperatures of over 12 °C, high humidity and low airflow, while *M. menardi* predominated in the middle cave section during the coldest quarter of the year with temperatures in the entrance section below 6 °C. Within the innermost section no fluctuation with respect to the species ratio was found.

The results obtained with the comparative density map were additionally strengthened via the PCA of the variations in *T*, *H*, *A* and *I*. The 1st and the 2nd EPCs together explained 70.4% of variation (Figs. 3 and 4). The 1st EPC represented the *A* and *H*; the correlation coefficients, *r*, between 1st EPC and *A* was 0.89, and between 1st EPC and *H* was -0.87. The 2nd EPC represented *T* and *I*, the *r*

between 2nd EPC and *T* was 0.76, and between 2nd EPC and *I* was 0.77. In each species considered separately by the three cave sections, on each date, there were significant differences at least in one EPC (Table 1). Such interspecific differences within separate sections occurred on five of 12 recording dates, in all three sections (Table 2). The Pianka niche overlap index for both PCs were $O_{PC1} = 0.891$ and $O_{PC2} = 0.863$.

In the 55 investigated caves, 109 potential prey taxa were determined, and 31 were confirmed as prey to both spiders (Table 3). Of the 31, *M. menardi* used 25 species as prey (22.9%; 7 flying vs. 18 non-flying ones) and *M. merianae* used 12 (11.0%; 7 vs. 5). Three of the prey species common to both spiders were flying, and three cursorial. *Meta menardi* unselectively preyed on species with a body

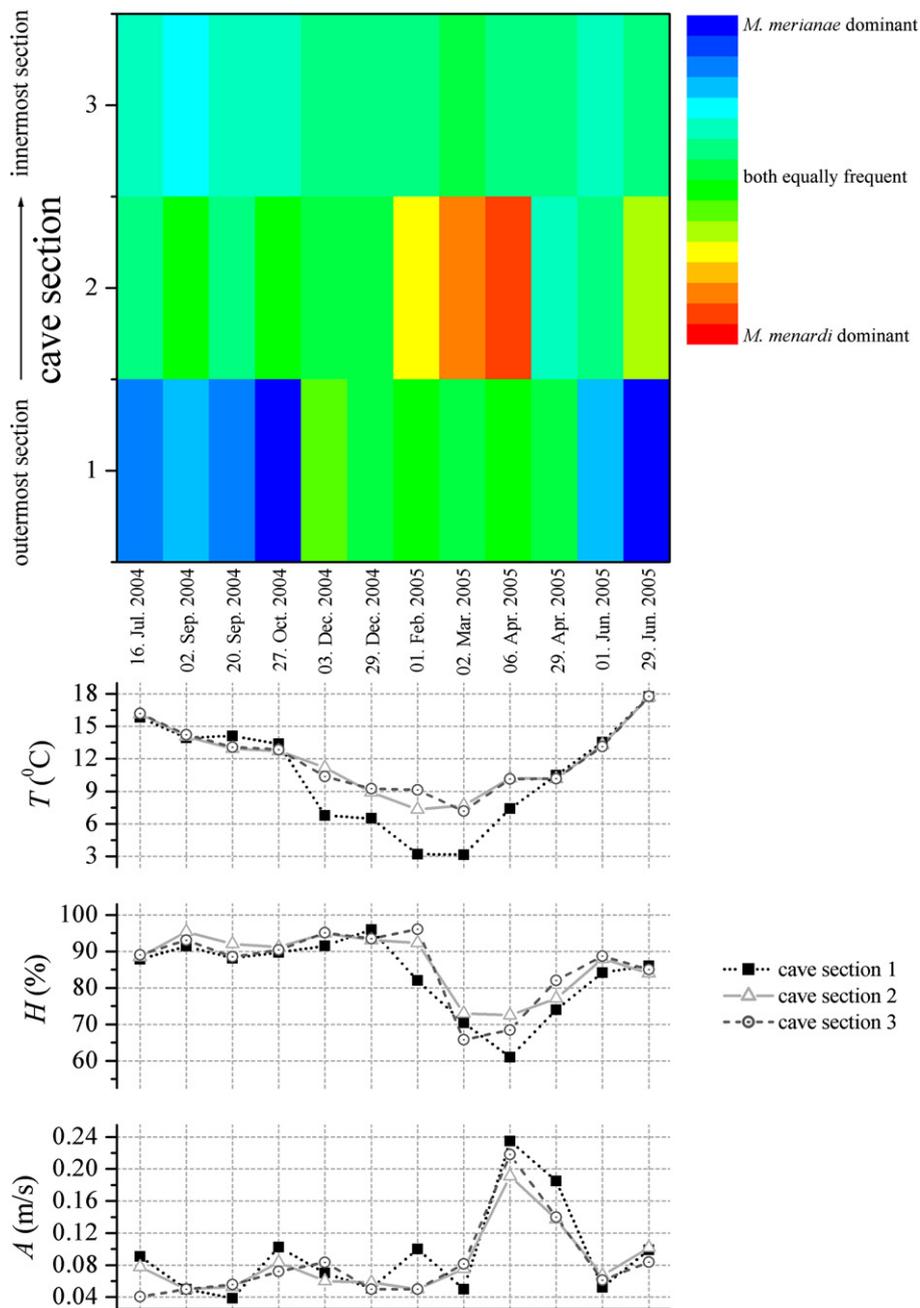


Fig. 2. Comparative normalized spatio-temporal density map of *Meta menardi* and *Metellina merianae* with corresponding temporal traces of *T*, *H* and *A*. Note that the dates depicted on the upper panel refer also to symbols depicted in subsequent temporal plots.

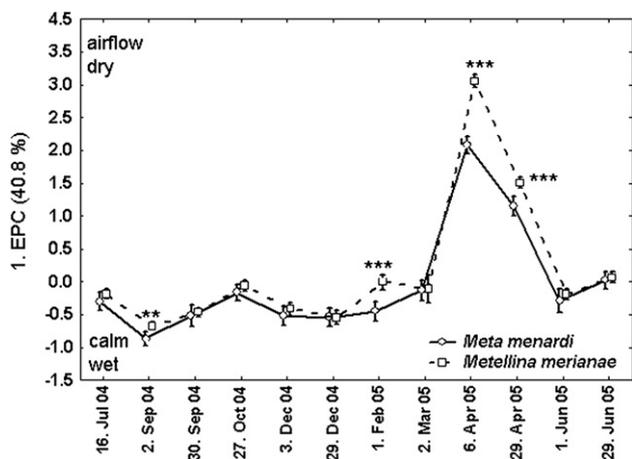


Fig. 3. Comparison between *Meta menardi* and *Metellina merianae* in their 1st ecological principal component. Significant differences between species are asterisked (mean \pm SE, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns non significant).

mass between 1–473 mg/individual, while *M. merianae* preyed on smaller and mid-sized species (1–88 mg/individual) (Fig. 5). *M. menardi* swiftly traced prey which had touched its web radii, up to about 25 centimetres away from the web on walls. Consequently, the Pianka niche overlap index was of middle value, $O_{ij} = 0.602$. In *M. menardi*, the frequencies of preyed species differed significantly from those recorded in caves ($\chi^2 = 61.50$; $df = 24$; $p = 0.001$), while there were no difference in *M. merianae* ($\chi^2 = 7.92$; $df = 11$; $p = 0.721$). There was no significant difference in frequencies of caught flying vs. cursorial prey between both spiders ($\chi^2 = 3.17$; $df = 1$; $p = 0.075$). No case of interspecific predation has been recorded between *M. menardi* and *M. merianae*. Three cases of cannibalism have been observed in *M. menardi*, females feeding on males. We detected no case of male–male contest.

4. Discussion

4.1. Syntopic occurrence

Our prediction, that *M. menardi* and *M. merianae* would exhibit significant segregation between their temporal niches, was confirmed. The dynamics of adults did not differ much between the species, while changes in abundance in the juveniles were much

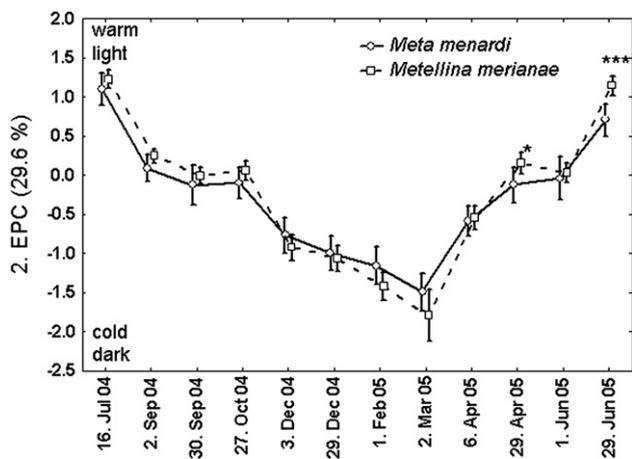


Fig. 4. Comparison between *Meta menardi* and *Metellina merianae* in their 2nd ecological principal component. Significant differences between species are asterisked (as in Fig. 3).

larger in *M. merianae*. Alternating their epigeal and hypogean ecophase, the cave populations of both species partly re-establish each year. They coexist in caves because they are adapted to the same type of environment and can utilize its resources (cf. Connell, 1980) in a fluctuating manner. Note that only the species' dynamics during their hypogean ecophase were investigated. In this sense, the observed abundance fluctuations of *M. merianae* with a peak in September–October resembles the course in r-strategic epigeal species (e.g. Quadros et al., 2009). On the other hand, the steady dynamics with a moderate December adult and a moderate September juvenile abundance peak in *M. menardi* reflects its possible ecological adaptation to the relatively prey-poor epigeal/hypogean ecotone habitat throughout the year. Thus, these species exploit cave resources differently throughout the year. Contrary to previous studies (Bourne, 1976, 1977; Bourne and Robert, 1978; Eckert and Moritz, 1992), we found more *M. merianae* than *M. menardi* in the cave. This can be explained by the relatively large entrance and the cave passage, both which favour the more epigeal *M. merianae*.

4.2. Autecology and spatial niche comparison

We predicted a significant difference between the spatial niches of both species in the outermost and innermost cave sections, and no difference in the middle section where the environmental conditions should suite both species. We, however, found no support for this hypothesis. In the outermost cave section, the predominance of *M. merianae* in the warm half of the year is the consequence of its conspicuous yearly abundance culmination in the late summer. A gradual predominance of *M. menardi* from February till April in the middle cave section coincided with a gradual decrease in abundance of *M. merianae* from September until March, most likely caused by a relatively high mortality of juveniles. This suggests that this species is poorly adapted to a low food supply during the winter in the cave. The retreat of *M. menardi*, avoiding sites with ice formations (Růžicka and Klimeš, 2005), from the outermost into this section was not observed. In the innermost section, the abundance fluctuations resulted in relative abundance evenness throughout the year.

Though both species show similar ranges with respect to the measured parameters, *M. menardi* is more stenoecious than *M. merianae*. As expected for its troglophilous character, *M. menardi* chose less windy and less dry (EPC1) habitats than *M. merianae* throughout the year, with a conspicuous difference during the cave spring drought. Except in two dates, there was no difference with respect to temperature and illumination (EPC2) between the two species. We found larger intraspecific differences in the EPCs of each species between the three cave sections, and relatively limited interspecific differences within a single section. This indicates that *M. menardi* and *M. merianae* co-exist in relatively wide ranges of the *T*, *H*, *A* and *I* yearly meteorological fluctuations within their microhabitats, thus creating their conspicuous spatial niche overlap. Significant differences occurred mostly during the months of notable meteorological changes in the cave, like in April (the lowest yearly *T* and highest *A*) and in June (the highest *T*). These differences are probably caused by the enlarged *T* and *A* ranges, while we have no explanation for such differences in September and December. A few meteorological comparative data are available only for *M. menardi*. With the exception of the highest late summer *T*, the species *T* ranges in the Pílanca cave were similar to those established experimentally (Szymczakowski, 1953: 2.5–15 °C; Dresco-Derouet, 1960: 5–14 °C) or *in situ* in other European caves (Negrea and Negrea, 1972: 10–16 °C; Bourne and Robert, 1978: 2–14 °C). The recorded *H* values are in general in agreement with previous experimental (Dresco-Derouet, 1960: 80–98%) and *in situ*

Table 1

Differences in the EPCs between the three cave regions in *Meta menardi* and *Metellina merianae* by dates.

Date/Species	EPC	16.7.04	2.9.04	30.9.04	27.10.04	3.12.04	29.12.04	1.2.05	2.3.05	6.4.05	29.4.05	1.6.05	29.6.05
<i>M. menardi</i>	EPC1	0.047	<0.001	0.002	0.903	0.006	0.346	<0.001	0.149	0.115	0.006	0.548	0.353
	EPC2	<0.001	0.001	<0.001	0.003	0.001	<0.001	0.018	<0.001	0.787	<0.001	0.004	<0.001
<i>M. merianae</i>	EPC1	<0.001	<0.001	<0.001	0.004	<0.001	0.797	<0.001	0.130	<0.001	<0.001	0.045	<0.001
	EPC2	<0.001	<0.001	<0.001	<0.001	<0.001	0.003	0.001	0.115	0.111	<0.001	<0.001	<0.001

Table 2

Differences between *Meta menardi* and *Metellina merianae* in the EPCs (One-way ANOVA) in the three cave regions.

Dates/Region	EPC	16.7.04	2.9.04	30.9.04	27.10.04	3.12.04	29.12.04	1.2.05	2.3.05	6.4.05	29.4.05	1.6.05	29.6.05
I	EPC1	0.055	<0.001	0.726	0.259	0.084	0.445	0.965	0.394	0.039	0.547	0.316	0.218
	EPC2	0.412	0.275	0.461	0.983	0.427	0.240	0.284	0.602	0.196	0.196	0.646	0.003
II	EPC1	0.508	0.002	0.527	0.272	0.111	0.549	0.192	0.979	0.850	0.331	0.259	0.722
	EPC2	0.392	<0.001	0.977	0.813	0.047	0.264	0.122	0.090	0.007	0.035	0.806	0.511
III	EPC1	0.185	0.486	0.822	0.765	0.044	0.485	0.820	0.268	<0.001	0.028	0.585	0.551
	EPC2	0.440	0.270	0.094	0.097	0.025	0.270	0.732	0.222	0.748	<0.001	0.239	0.031

Table 3

Summary evidence of prey in webs of *Meta menardi* and *Metellina merianae* in 55 caves and artificial tunnels northern Slovenia (from Novak, 2005). The relative abundance scales: Cavities: 1 < 10 specimens, 2 11–100, 3 101–1,000, 4 1,001–10,000, 5 > 10,000. Webs: 1 single specimen, 2 2–10, 3 11–30, 4 > 30.

Prey	Approx. mean mass (mg/specimen)	Relative frequency in caves	Relative frequency in webs <i>M. menardi</i>	Relative frequency in webs <i>M. merianae</i>
<i>Oniscoidea</i>				
Oniscoidea undet.	15	1	2	1
<i>Trachelipus ratzeburgii</i> (Brandt 1833)	40	1	1	
<i>Araneae</i>				
<i>Liocranum rutilans</i> (Thorell 1875)	20	2	1	
<i>Meta menardi</i> ♂		115	5	2
<i>Nesticus cellulanus</i> (Clerck 1758)	18	3		2
<i>Opiliones</i>				
<i>Amilenus aurantiacus</i> (Simon 1881)	20	5	2	2
<i>Leiobunum rupestre</i> (Herbst 1799)	25	3	3	3
<i>Chilopoda</i>				
<i>Lithobius agilis</i> C. L. Koch 1847	25	2	1	
<i>Diplopoda</i>				
Diplopoda undet.	20	1	1	
<i>Glomeris</i> sp.		50	1	1
<i>Polydesmus complanatus</i> (Linnaeus 1761)	80	2	2	
<i>Polydesmus</i> spp.	80	1	1	
<i>Brachydesmus herzegowinensis</i> Verhoeff 1897	20	1		1
<i>Brachydesmus</i> spp.	20	1	2	
<i>Polyphematia moniliformis</i> (Latzel 1884)	40	2	1	
<i>Symphysophys serkoi</i> Strasser 1939	40	3	1	
<i>Ensifera</i>				
<i>Troglophilus neglectus</i> Krauss 1879	375	5	1	
<i>Troglophilus cavicola</i> (Kollar 1833)	473	5	1	
<i>Coleoptera</i>				
<i>Laemosthenus (Antisphodrus) schreibersii</i> (Küster 1846)	61	4	1	
<i>Catops</i> sp.	4	1	1	
<i>Choleva (Choleva) sturmi</i> Brisout 1863	5	2	2	
<i>Otiorhynchus (Troglophynchus) anophthalmus</i> (Schmidt 1854)	2	1	1	
<i>Lampyrus noctiluca</i> (Linnaeus 1767)	3	1	2	3
<i>Trichoptera</i>				
<i>Stenophylax permistus</i> McLachlan 1895	88	2		2
<i>Hymenoptera</i>				
Hymenoptera undet.	2	1		1
<i>Diphyus quadripunctorius</i> (Müller 1776)	50	2		1
<i>Diptera</i>				
Diptera undet.		5	1	3
Tipulidae undet.	10	1		1
<i>Limonia nubeculosa</i> Meigen 1804	5	5	3	4
Sciaridae undet.	1	2	3	3
<i>Calliphora vicina</i> Robineau-Desvoidy 1830	25	2	2	

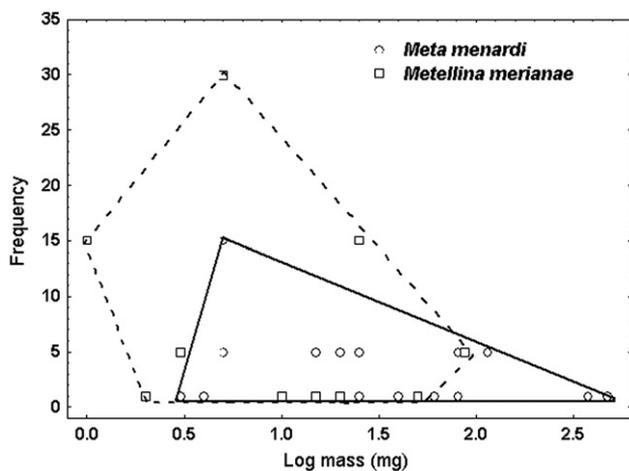


Fig. 5. Comparison between trophic niches of *Meta menardi* and *Metellina merianae* in their prey selection (minimal convex polygon). Log mass refers to the logarithmic value of the average prey species mass.

studies (Bourne and Robert, 1978: 80–89%), but we found that individuals also withstand H values as low as 60% without moving from such places. We could also not confirm the distribution reports on lower placements in *M. merianae* against higher ones in *M. menardi* in caves (Bourne, 1976, 1977). Such distribution is rather cave specific, and could be the consequence of interspecific competition in suboptimal environmental conditions. In our study, the distribution was not precisely investigated. Such studies as well as a more detailed study of both the thermo- and hygro-preference of both species in natural and experimental conditions deserve further attention.

4.3. Foraging ecology and trophic niche comparison

We found support for the hypothesis that there is a significant difference between the trophic niches of both species with respect to the frequencies of preyed species vs. the prey pool in caves. However, we did not confirm significant differences in frequencies of caught flying vs. cursorial prey between the two spiders, although a trend was evident. The list of prey species recorded for *M. merianae* and *M. menardi* differ considerably (for *M. menardi* see also Tercafs, 1960; Bourne and Robert, 1978; Eckert and Moritz, 1992; Smithers, 2005a). Contrary to Smithers (2005a) and Bourne and Robert (1978), slugs and the butterflies *Triphosa dubitata* and *Scoliopteryx libatrix* have not been found as prey items of *M. menardi* in Slovenia. While the former is likely due to slug rarity in the investigated caves, the two butterfly species are frequent there (Novak and Kuštor, 1982; Novak, 2005). Such disparity of results could be due to undersampling, and suggests haphazard capture rates. The apparent absence of intraspecific cannibalism in *M. merianae* could be due to either of these two reasons, while the absence of interspecific predation (Heuts and Brunt, 2001) between *M. menardi* and *M. merianae*, is expected because web spiders in general are known to avoid contact with either conspecific or heterospecific webs (Wise, 1993), although a few cases had been reported (Smithers, 1996).

Although most spiders are opportunistic predators (Wise, 1993), the prey spectrum of any spider species never perfectly reflects all potential prey in their environment (Marshall and Rypstra, 1999). For example, larger epigeal species tend to prey on larger prey (Brown, 1981) which is also evident when comparing *M. merianae* and *M. menardi*. The functional relation between different web architecture, which is thought to be mostly genetically determined

(Eberhard, 1982; Kuntner et al., 2010, but, see Tso et al., 2007; Harmer and Herberstein, 2009), and the prey size, as well as partial foraging of *M. menardi* on walls (Eckert and Moritz, 1992; Smithers, 1996, 2005a), has been empirically confirmed to influence the efficacy of prey capture. Although experimental evidence suggests that orb webs with small mesh size may capture larger prey than those with larger webs (Blackledge and Zevenbergen, 2006), our data suggest that the pattern may be different in *Meta* and *Metellina*. Webs of *M. menardi* (smaller but with larger mesh size) allows the ensnarement of larger prey, while those of *M. merianae* (larger but with smaller mesh size) are more effective in capturing smaller individuals. These differences probably contribute to the diversification of their trophic niches. The ability of *M. menardi* to also trace prey on cave walls may additionally expand its prey list.

The combined way of hunting in webs and on walls by *M. menardi* (Tercafs, 1972; Wood, 2004; Smithers, 2005a) and *M. japonica* (Yoshida and Shinkai, 1993) has been proposed as an adaptation to the epigeal/hypogean ecotone. Large entrance sections, such as found in the Pilanca cave, enhance the movement frequency of epigeal flying prey species into the cave, and thus could favour the usual web hunting strategy of *M. merianae*. Deeper inside, caves are an appropriate residence of many troglone and troglophile species, with longer sedentary and short migration periods. For sit-and-wait spiders, they thus represent only an occasional prey item. On the contrary, the prey species crawling steadily on walls are available, in low abundances, throughout the year. In caves, the hunting strategy of *M. menardi* might be the most effective way of capturing prey in these habitats with limited resources. With the spider's ability to also capture occasional flying insects, such combined strategy likely represents an optimal foraging strategy to living in the energy-poor epigeal/hypogean ecotone zone.

5. Conclusions

M. menardi and *M. merianae* coexist in the entrance sections of the studied cave and can share its relatively abundant resources. However, *M. menardi* is a more stenoeconomic species in comparison with *M. merianae*. The annual abundances of both differ significantly with typical r-strategy epigeal dynamics in *M. merianae* and a steady low abundance in *M. menardi* within the cave. Their spatial niches are very similar; they are most diverse in the outermost and middle sections. The extended list of prey species and wider prey mass span in *M. menardi* indicate its broader trophic niche. The combined strategy of *M. menardi* (capturing both flying and cursorial prey, which is most likely energetically most rewarding) suggests that this spider is optimally adapted to living in the energy-poor epigeal/hypogean ecotone zone.

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