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Original article

Niche partitioning in orbweaving spiders *Meta menardi* and *Metellina merianae* (Tetragnathidae)

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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 epigean 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 epigean/hypogean ecotone.

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 epigean 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 epigean/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 epigean 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 trogloxene and a dozen of troglophile (for both definitions see Vandel, 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).