



## Do cave orb spiders show unique behavioural adaptations to subterranean life? A review of the evidence

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### Abstract

Interest for subterranean biology has risen sharply in recent years due to the simplicity of the cave environment. However, most studies have focussed on morphology with few studies looking at behaviour. The cave orb spiders show some unique behavioural adaptations compared to other orb spiders, including rudimentary orb webs, off-web foraging and a complex life cycle with a surface phase. Here, we compare these behavioural adaptations in the European *Meta menardi* and *Meta bourmeti* to similar behaviours in surface-dwelling orb spiders. We find that current data suggest (1) an extreme reduction in the number of frame threads, (2) evidence of capturing non-flying prey, but not necessarily evidence for off-web foraging and (3) dispersal through a surface-dwelling life stage, but with data lacking on the role of ballooning and their return to caves. We conclude that *Meta* spiders have potential as model organisms for studies on behavioural adaptations and flexibility.

### Keywords

behavioural flexibility, cave spiders, dispersal, orb web geometry, prey capture, Tetragnathidae.

## 1. Introduction

Subterranean habitats are some of the least studied terrestrial ecosystems and we have little current knowledge on the natural history and behaviour of the majority of organisms found in them. However, interest has grown in recent years and cave ecosystems are now generally recognised as natural ecological and evolutionary laboratories due to the isolation of their organisms, the fewer and more simple biotic interactions due to low species richness and abundance and the number of similar morphological adaptations found in a range of organisms (Poulson & White, 1969; Pipan & Culver, 2013; Mammola, 2018). Cave ecosystems are characterised by stable environmental conditions, low light levels and as a consequence usually no primary production and they are as a result generally nutrients poor (Culver & Pipan, 2009). Caves though are not homogenous in their ecology, but can be divided into three zones. The entrance zone is generally defined as the area immediately near the entrance which is reached by direct sunlight and is characterised by being relatively nutrient rich due to the number of epigean animals that accidentally enter the cave. The twilight zone is characterised by very low light levels and a much lower abundance of organisms. Finally, the dark zone starts where light can no longer be detected by the human eye and stretches until the end of the cave. This is usually the largest and most nutrient poor zone, but it is also where the largest number of cave adapted species can be found. Following the traditional speleological terms (Sket, 2008), organisms with adaptations, in almost all cases this refers to morphological adaptations, to caves and other subterranean habitats are classified as troglomorphs. All troglomorphs are also troglobionts, which are organisms that are obligatorily associated with subterranean habitats for all life stages. In contrast, troglaphiles usually spend some time outside them, while troglaxenes are visitors to the subterranean habitat, but spend most of their life outside.

Unsurprisingly, spiders are generally well represented in caves given their exaptations to subterranean life including, for most families, low reliance on vision and low metabolism allowing them to survive months without feeding (Foelix, 2011). There are more than 1000 species of troglobiont spiders and at least an equal number of troglaphile spiders belonging to 48 families out of 47 000 described species of spiders in 113 families (Mammola & Isaia, 2017). In Europe, 195 troglobiont and 291 troglaphile species are currently recognised in 22 families (Mammola et al., 2017a). The most species

rich families are Linyphiidae with 222 subterranean species (including the almost exclusively troglobiont genera *Centromerus* and *Troglohyphantes*), Dysderidae with 56 species and the predominantly subterranean Nesticidae with 50 species (Mammola et al., 2017a).

Surprisingly, given the scarcity of flying insects, orb spiders in the family Tetragnathidae (genera *Meta* and *Metellina*) are common in European caves, although all are troglaphiles and mainly limited to the twilight zone (Mammola & Isaia, 2014). Orb webs are two-dimensional highly organised structures consisting of radii running from the central hub to the frame and overlaid by the capture spiral that are adapted to intercept and retain flying insects (Eberhard, 1990b). Thus, the orb web can be viewed as a physical record of the spider's foraging behaviour, which together with the ease of getting spiders to construct orb webs in the laboratory and the highly quantifiable nature of the web have made orb spiders and their webs model organisms for the study of a wide range of different behaviours (Zschokke & Herberstein, 2005; Hesselberg, 2015). Orb spiders show a remarkable behavioural flexibility and modify their web-building and foraging behaviour in response to a wide range of internal and external factors including micro-climatic conditions (Vollrath et al., 1997; Liao et al., 2009; Turner et al., 2011; Wu et al., 2013), prey capture experience (Pasquet et al., 1994; Heiling & Herberstein, 1999; Blamires, 2010), leg loss (Vollrath, 1987; Pasquet et al., 2011) and spatial constraints in the micro-habitat (Krink & Vollrath, 2000; Barrantes & Eberhard, 2012; Harmer et al., 2012; Hesselberg, 2013). Despite their relatively simple and small brains, they show impressive cognitive abilities (Hesselberg, 2015; Japyassu & Laland, 2017) including spatial learning of prey impacts (Nakata, 2013), alertness to web damage and faster repairs in windy conditions (Tew et al., 2015), simple numerosity (Rodríguez et al., 2015), and memories of previous web-building behaviour (Eberhard, 1988) and prey capture (Rodríguez & Gamboa, 2000; Rodríguez et al., 2013).

We know almost nothing about the behaviour of any cave spider (Mammola & Isaia, 2017), but the cave orb spiders have been alleged to possess a number of unique behavioural adaptations to subterranean life not found in terrestrial orb spiders. Here, we review the evidence for adaptive modifications of the standard orb web and for unusual foraging as well as the highly interesting life cycle and dispersal behaviour and contrast it to closely related epigeal tetragnathid spiders. Our aim is to highlight the research potential of studying the behaviour of these large, conspicuous and relatively abundant, but overlooked, troglaphiles.

## 2. Cave orb spiders

The largest family of orb spiders is Araneidae followed by Tetragnathidae and the cribellate Uloboridae (Foelix, 2011), but the only orb spider family with described representatives in the subterranean environment is Tetragnathidae. This is a large family with 987 species in 46 genera (Kallal & Hormiga, 2018). Currently, 7 cave-dwelling spiders are known in the genus *Meta* and two in *Metellina* (Table 1), although it is likely that there are subterranean species in other tetragnathid genera; for example, *Orsinome* has been reported in caves in Tasmania (Eberhard, 1992). The genus *Meta* currently has 23 species, but as it has been treated as the ‘waste-bin’ of the Metaine subfamily this is likely to change. In 2018 alone, 11 species were transferred from *Meta* to other genera (mainly *Metellina* and *Tetragnatha*) (Kallal & Hormiga, 2018; Marusik & Larsen, 2018). Given that Marusik & Larsen (2018) use a relatively large size as a criterion for including species in *Meta* (and in *Metellina*), many of the Asian species are likely incorrectly placed in *Meta* (Table 1). *Meta meruensis* for example most likely belongs in the genus *Leucauge* (Marusik & Larsen, 2018). In general, we know very little about the natural history of most *Meta* spiders and for many species, we have not even been able to determine if they are cave-dwellers or not (Table 1). Although most of the species with known habitats are subterranean, this appears not to be a key characteristic of the genus as *M. stridulans* is an endemic of Madeira, where it inhabits laurel forests (Crespo et al., 2014).

In this review, we will focus on the two species of *Meta* spiders that we know most about — the common European cave orb spiders *M. menardi* and *M. bourneti* — with a brief mention of *Metellina merianae*, which, together with *M. villersi* (Denis, 1955), is the only known *Metellina* regularly found in caves. *Meta bourneti* (Simon, 1922) (Figure 1) is a large spider (the male is 10–13 mm and the female 14–16 mm in total length) with a dark brown cephalothorax and a usually uniformly yellowish brown to black abdomen. It is classified as a troglophile and usually found in the twilight zone of caves, where it builds relatively small orb webs compared to closely related epigean tetragnathids. It is widely distributed in southern Europe and around the Mediterranean including northern Africa. It is also found in southern parts of the UK, where it is likely to be an introduced species (Mammola, 2017). *Meta menardi* Latreille, 1804 (Figure 1), also sometimes referred to as the European cave spider, is a large spider (the male is 10–12 mm and the female 12–15 mm in total length). It has a red-brown cephalothorax and a

**Table 1.**  
Overview of species in the genus *Meta*.

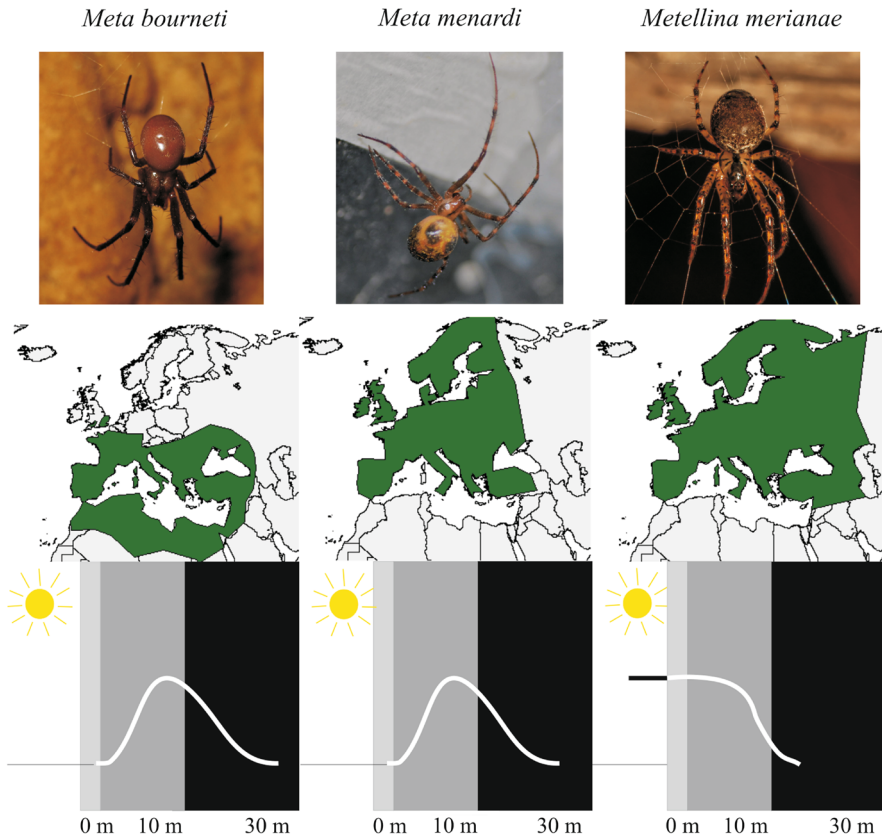
Species	Authority	Known distribution	Carapace width (mm)	Total length (mm)	Number of publications <sup>a</sup>	Habitat
<i>Meta abdominalis</i>	Patel & Reddy, 1992	India	1.2	3.8	1	Unknown
<i>M. birmanica</i>	Thorell, 1898	Myanmar			1	Unknown
<i>M. bourmeti</i>	Simon, 1922	Europe to Georgia, North Africa	6.0	14.5	24	CAVES
<i>M. dolloff<sup>b</sup></i>	Levi, 1980	USA	6.3	14.0	2	CAVES
<i>M. japonica</i>	Tanikawa, 1993	Japan	4.4	10.9	5	CAVES
<i>M. manchurica</i>	Marusik & Koponen, 1992	Russia, Korea		12.2	7	CAVES
<i>M. menardi</i>	(Latreille, 1804)	Europe to Turkey	6.0	16.0	124	CAVES
<i>M. meruensis<sup>c</sup></i>	Tullgren, 1910	East Africa		8.5	5	Unknown
<i>M. mixta</i>	O. Pickard-Cambridge, 1885	China			1	Unknown
<i>M. monogrammata</i>	Butler, 1876	Australia		13.0	1	Unknown
<i>M. montana</i>	Hogg, 1919	Indonesia	1.5	5.0	1	Unknown
<i>M. nebulosa<sup>d</sup></i>	Schenkel, 1936	China			1	Unknown
<i>M. nigradorsalis</i>	Tanikawa, 1994	China, Japan	1.8	5.8	4	CAVES
<i>M. obscura</i>	Kulczyński, 1899	The Canary Islands, Madeira	4.5	6.5	2	Unknown
<i>M. ovalis</i>	(Gertsch, 1933)	North America	4.5	13.7	19	CAVES
<i>M. qianshanensis</i>	Zhu & Zhu, 1983	China	2.0	12.3	4	Unknown
<i>M. rufolineata</i>	(Urquhart, 1889)	New Zealand		6.8	3	Unknown
<i>M. serrana</i>	Franganillo, 1930	Cuba			1	Unknown

Table 1.  
(Continued.)

Species	Authority	Known distribution	Carapace width (mm)	Total length (mm)	Number of publications <sup>a</sup>	Habitat
<i>M. shenae</i>	Zhu et al., 2003	China			1	Unknown
<i>M. simlaensis</i>	Tikader, 1982	India	3.2	9.4	1	Unknown
<i>M. stridulans</i>	Wunderlich, 1987	Madeira	3.9	11.0	1	Laurel Forest
<i>M. trivittata</i>	Keyserling, 1887	Australia	1.8	5.4	1	Unknown
<i>M. turbatrix</i>	Keyserling, 1887	Australia	2.4	6.4	1	Unknown
<i>Metellina merianae</i>	Scopoli, 1763	Europe and the Middle East	2.4	9.0	48	CAVES
<i>Metellina villiersi</i>	Denis, 1955	Guinea		8.0	1	CAVES

Taxonomic status and distribution come from the World Spider Catalog (2019). Information on habitat and morphology (adult female size is indicated by total length and cephalothorax width in the table) comes from a range of papers cited in World Spider Catalog (2019):

- <sup>a</sup> Information on number of publications is the combined number of taxonomic publications listed in World Spider Catalog (2018) and publications on ISI Web of Science (species names searched in topics across all databases as of September 2017).
- <sup>b</sup> Only *Meta* spider that is on the IUCN red list as ‘Vulnerable’ (but added in 1996 so needs updating).
- <sup>c</sup> This species is likely to belong in *Leucauge* (Marusik & Larsen, 2018).
- <sup>d</sup> This species has apparently been described from juveniles alone (Schenkel, 1936).



**Figure 1.** Distribution of the European cave spiders (2nd row: known distributions taken from the World Spider Catalogue (2018) and from Araneae – Spiders of Europe (Nentwig et al., 2018)) and cave location preference (3rd row: the entrance zone is the first few metres inside the cave (light grey), the twilight zone (dark grey) stretches 10–15 m, depending on cave structure, before the dark zone starts (black)). 1st column: *Meta bournetii* Simon, 1922. Photo with permission from Didier Petot. 2nd column: *Meta menardi* Latreille, 1804. Photo with permission from Thomas Hesselberg. 3rd column: *Metellina merianae* Scopoli, 1763. Photo with permission from Richard McMellon.

yellow abdomen with darker stripes or large spots. Similarly, to *M. bournetii*, *M. menardi* is a troglophile that is predominantly found in the twilight zone of caves, although it is also recorded from other dark places including mines, cellars, manholes and in crevices and boulder fields (Růžicka et al., 2013). It is considered common across Europe including Scandinavia up to near the Arctic circle and as far east as Turkey. *Metellina merianae* Scopoli, 1763 (Figure 1) is a medium sized spider (the male is 7–8 mm and the female

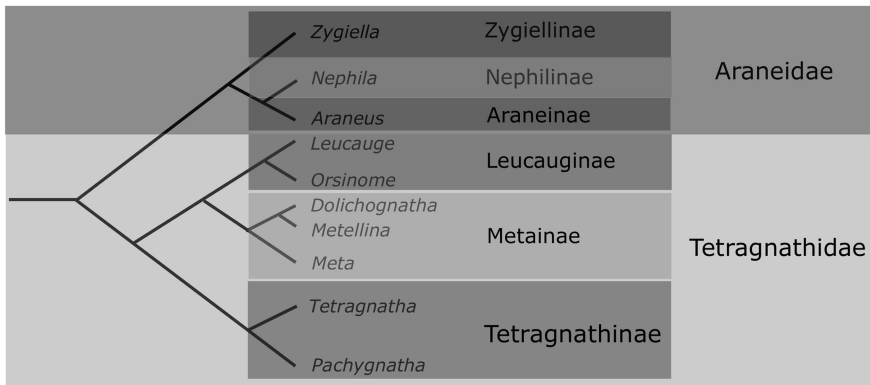
6–10 mm in total length) with a yellow-green cephalothorax and a green-brown abdomen overlaid with a darker chequer pattern. It is found in the entrance zone and the first part of the twilight zone in caves and other dark places, but unlike the two *Meta* species, it can also be found in terrestrial habitats including damp and shady woodland areas. There is no evidence of any behavioural adaptations to subterranean habitats in this species. It is common and widespread in Europe extending as far east as Caucasus and Iran.

Interestingly, although there is a large overlap in the distribution of all three species (Figure 1), none of them are sympatric on the micro-scale. Instead they show a significant degree of niche separation. *Meta menardi* and *Meta bournetii* are never found in the same cave (Mammola & Isaia, 2014). *M. bournetii* has a relatively wide tolerance of microclimatic conditions, whereas *M. menardi* has a relatively narrow range preferring cooler caves with high humidity and in the favourable habitats *M. menardi* apparently outcompetes *M. bournetii* (Mammola & Isaia, 2014). On the other hand, *Meta menardi* are found to co-occur with *Metellina merianae* with limited spatial niche separation, although *M. merianae* is usually found closer to the cave entrance than *M. menardi* (Novak et al., 2010). Instead the two species show a significant temporal niche separation with the number of juveniles of *M. merianae* showing large peaks at the end of the summer, whereas juvenile abundance of *M. menardi* is more evenly distributed with minor peaks in winter and spring (Novak et al., 2010). Throughout the rest of this review we compare aspects of the behaviour of *Meta* cave spiders with those of terrestrial tetragnathids; especially with the closely related *Metellina* (Alvarez-Padilla & Hormiga, 2011; Kallal & Hormiga, 2018; see Figure 2).

### 3. The orb web: behavioural adaptation or flexibility?

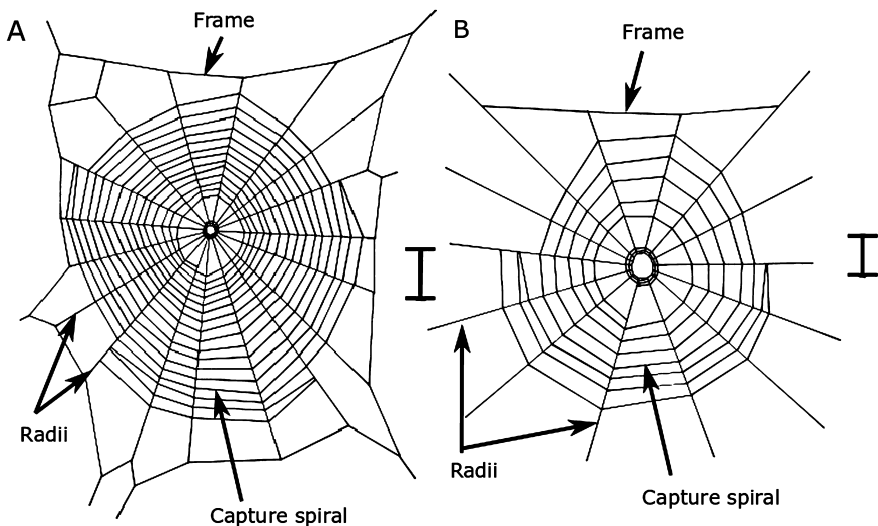
The orb web is one of the most conspicuous and geometrically ordered structures in nature. As mentioned in the introduction, the archetypical orb web consists of a central hub from which radii radiate outwards towards the frame and upon which the capture spiral is overlain (Figure 3A). This general structure is conserved across all the major orb-spider families, but with variation in the detailed geometry and in the material properties of the different silk types used (Vollrath & Selden, 2007; Sensenig et al., 2010). There are, however, minor differences among the families (Foelix, 2011). Tetragnathid webs, in contrast to araneid webs, tend not to have any threads in





**Figure 2.** Simplified phylogenetic tree of orb web spiders in the family Araneidae and Tetragnathidae highlighting subfamilies and genera of interest for the discussions presented in this paper. Adapted from the maximum likelihood analysis (Figure 1) of Kallal & Hormiga (2018).

the centre of their hubs and tend to be more horizontally inclined with the woodland species *Metellina menzei*, for example, having webs that varied in inclination with horizontal from 5 to 85° (Tew & Hesselberg, 2018). The



**Figure 3.** Schematic drawing of orb webs based on measurements of typical webs (Simonsen & Hesselberg, data not shown). Arrows points to frame threads, radii and the capture spiral. The vertical scale bars at the righthand side of each web is 20 mm in length. (A) *Metellina menzei* web; (B) *Meta menardi* web.

differences are not immediately apparent from a casual glance, but webs of *Meta menardi* and *M. bourneti* differ from the typical orb web in that they have very few frame threads (Figure 3B). The web is also smaller and less complex with fewer radii and capture spiral turns, which have led some authors to conclude that the web is rudimentary in nature and does not play any role in prey capture (Eckert & Moritz, 1992; Smithers, 1996). This has been refuted by Fritzen & Kaponen (2011), who observed a *M. menardi* catching a mosquito that flew into its web. In the Japanese cave spider *Meta japonica*, prey was also caught when intercepted by the web in similar manner to epigean orb spiders (Yoshida & Shinkai, 1993). A comparative quantitative study (Simonsen & Hesselberg, data not shown) on the web geometry of *M. menardi* and epigean tetragnathids demonstrated that while *M. menardi* webs have fewer radii (mean  $\pm$  SE:  $14.9 \pm 3.1$ ,  $N = 23$ ) than *Metellina mengei* (mean  $\pm$  SE:  $18.6 \pm 2.9$ ,  $N = 29$ ) (Figure 3), their webs have almost the same number of radii as the webs of another common northern European epigean tetragnathid; *Tetragnatha montana* (mean  $\pm$  SE:  $15.9 \pm 2.3$ ,  $N = 37$ ). *M. menardi* webs did have fewer capture spiral turns (mean  $\pm$  SE:  $6.1 \pm 2.0$ ,  $N = 23$ ) than both *M. mengei* (mean  $\pm$  SE:  $15.0 \pm 3.6$ ,  $N = 29$ ) and *T. montana* webs (mean  $\pm$  SE:  $14.0 \pm 3.1$ ,  $N = 38$ ). This is, however, in contrast to the Asian cave orb spider *Meta japonica*, which built larger webs but with a similar number of radii (mean  $\pm$  SE: Number of radii:  $17.0 \pm 4.3$ ,  $N = 47$  and number of capture spirals:  $14.6 \pm 5.3$ ,  $N = 42$ ) (Yoshida & Shinkai, 1993).

Thus, while the overall web geometry of *Meta* is probably not an adaptation to the subterranean habitat, the omission of frame threads is highly unusual. The terrestrial tetragnathids, *M. mengei* and *T. montana* had an almost 1:1 ratio between the number of frame threads and the number of radii, while *M. menardi* and *M. japonica* in contrast had ratios of 1:10 and 1:15, respectively (Yoshida & Shinkai, 1993; Simonsen and Hesselberg, data not shown). Most radii attach directly to the cave wall or ceiling, rather than to frame threads with the web then attaching to the substrate with a few long anchor threads as is usually the case in orb spiders (Zschokke, 2000; Foelix, 2011; Hesselberg, 2013). As discussed in the next section, this might be an adaptation to capture walking prey using the radii as trip wires to alert the spider of passing prey. However, most *Meta* webs are built across small crevices in the cave wall or ceiling with the capture spiral rarely being far from the substrate, so it is possible that spiders face spatial constraints

when constructing their webs. Orb spiders generally adjust to spatial constraints in the laboratory by changing the shape of their webs and reduce the spacing between spiral turns, but otherwise keep the web structure intact (Ades, 1986; Vollrath et al., 1997; Krink & Vollrath, 2000). However, the araneid *Eustala illicita* sometimes appeared to attach radii directly to the frame wall when building webs in narrow, elongated vertical frames in the laboratory (Hesselberg, 2013). Similarly, the tetragnathid *Leucauge argyra* was observed to occasionally attach radii directly to small-diameter cylindrical tubes (Barrantes & Eberhard, 2012). It is therefore possible that *Meta* spiders are just showing extreme behavioural flexibility to spatial constraints rather than showing specific adaptations to the cave environment. This is supported by observations that when *M. menardi* did build frame threads, these were constructed in the parts of the web that was furthest away from the cave wall (D. Simonsen, Pers. Obs.); potentially suggesting that the frame building behaviour occurs when *M. menardi* are released from the spatial constraints of the small crevice. None of the epigean spiders tested in the laboratory, however, showed the extreme reduction in frame threads seen in *Meta* spiders, so it remains most likely that this is an adaptation rather than behavioural flexibility. Manipulative laboratory experiments of *Meta* building in environments of varying spatial complexity, following the guidelines given by Zschokke & Herberstein (2005), are needed to conclusively answer this question. Such experiments might also shed light on the web-building behaviour of *Meta*, which has not been described so far. Given that both araneid and tetragnathid orb spiders construct their frame threads at the same time as they construct the radii (Eberhard, 1990a; Zschokke & Vollrath, 1995; Foelix, 2011), it would be interesting to see how *Meta* spiders have adapted the otherwise stereotypic building sequence to eliminate frame thread construction. They could also reveal what potential factors are involved when *Meta* spiders do build frame threads, particularly whether this behaviour is influenced by the environment.

#### 4. Foraging behaviour

The main function of the orb web is to intercept and retain flying insects (Eberhard, 1990b). To do so, the impact energy is dissipated through deformations of primarily the radii and in most cases through aerodynamic damping on the whole vibrating web (Lin et al., 1995; Sensenig et al., 2012;

Zaera et al., 2014), while the glue droplets on the capture spiral and its remarkable extensibility, retain the prey in the web long enough for the spider to run out and catch it (Nentwig, 1982; Swanson et al., 2007; Sahni et al., 2010). During prey interceptions, the spider relies on vibrational information relayed through the radii to give it information on prey location and prey size (Klärner & Barth, 1982), before rushing out from the hub (or via a signal thread from its retreat) towards the prey (Hesselberg & Vollrath, 2006; Turner et al., 2011). Depending on the size and defensive capabilities of the prey, the spider either directly bites the prey (small, harmless prey) or first wraps the prey in additional silk before approaching for the bite (larger, potentially dangerous prey) (Robinson et al., 1969; Hénaut et al., 2001, 2014). Similar, behavioural flexibility was shown by the Japanese cave spider *Meta japonica* in response to dipterans and ants being thrown into the web (Yoshida & Shinkai, 1993). It has though been claimed that *Meta* orb webs are rudimentary and do not play a role in prey capture and that spiders instead engage in off-web foraging to capture prey such as snails and myriapods, which crawl on the cave wall (Eckert & Moritz, 1992; Smithers, 1996).

The *Meta* orb web, however, clearly can function as a trap as the Japanese cave orb spider example above shows (see also Fritzén & Koponen, 2011). Studies of the prey actually consumed by spiders find that while dipterans (especially mosquitoes, gnats and crane flies), as in other orb spiders, is a major prey type (accounting for between 7 and 39% of all prey), between 36 and 69% of prey does not fly including snails, arachnids and myriapods (Table 2). This value may be even higher as some of the prey classified as flying in Table 2, spend more time resting or walking on the cave wall than flying (L. Knight, pers. obs.). It is unlikely that prey would fall from the cave ceiling into the web in such numbers, so the *Meta* spiders must engage in unusual foraging behaviour. However, we have been unable to find any published recordings or observations of actual off-web hunting, or of spiders with prey not on an orb web. This is of course not evidence that the behaviour does not take place. It could be rare and short in duration, and as *M. menardi* has been found to be more active at night (Mammola & Isaia, 2018), off-web foraging might take place at times when cave biologists are unlikely to be there to observe it. If it does take place, it would constitute a very interesting departure from normal foraging behaviour in orb spiders as the standard prey capture behaviour described above would not work outside

**Table 2.**Prey consumption of the cave orb spider *Meta menardi*.

Prey	Smithers (2005a) <sup>a</sup>	Novak et al. (2010) <sup>b</sup>	C. Terrell-Nield (unpubl) <sup>c</sup>
Location	Mine, UK	Caves, Slovenia	Caves, UK
Flying			
Diptera <sup>a</sup>	7%	30%	39%
Caddisflies	16%	0%	10%
Hymenopterans	0%	0%	0%
Lepidoptera	2%	0%	15%
Other <sup>b</sup>	6%	1%	0%
Total flying	31%	31%	64%
Non-flying			
Slugs and snails	19%	0%	1%
Myriapods <sup>c</sup>	36%	11%	20%
Isoptera	0%	5%	2%
Arachnids <sup>d</sup>	7%	43%	5%
Beetles	7%	10%	8%
Total non-flying	69%	69%	36%

Diptera mainly includes fungus gnats and mosquitoes; other flying prey includes lacewings, crickets and unidentified remains; Myriapods mainly includes millipedes; and Arachnids mainly includes spiders and harvestmen.

<sup>a</sup>Based on observations of prey in webs over a year (prey  $N = 67$ , note there is a mistake in the total number of prey and hence of the relative frequencies given in Table 1 of Smithers, 2005a).

<sup>b</sup>Based on observations of prey in webs from 1977 to 2002. Relative frequencies were reported, so to estimate percentage, the following number of prey (mean value of band) was assumed for each of the study's frequency bands: 1 = 1 prey, 2 = 6 prey, 3 = 20 prey, 4 = 40 prey and this was then expressed as a percentage (total prey  $N = 156$ ).

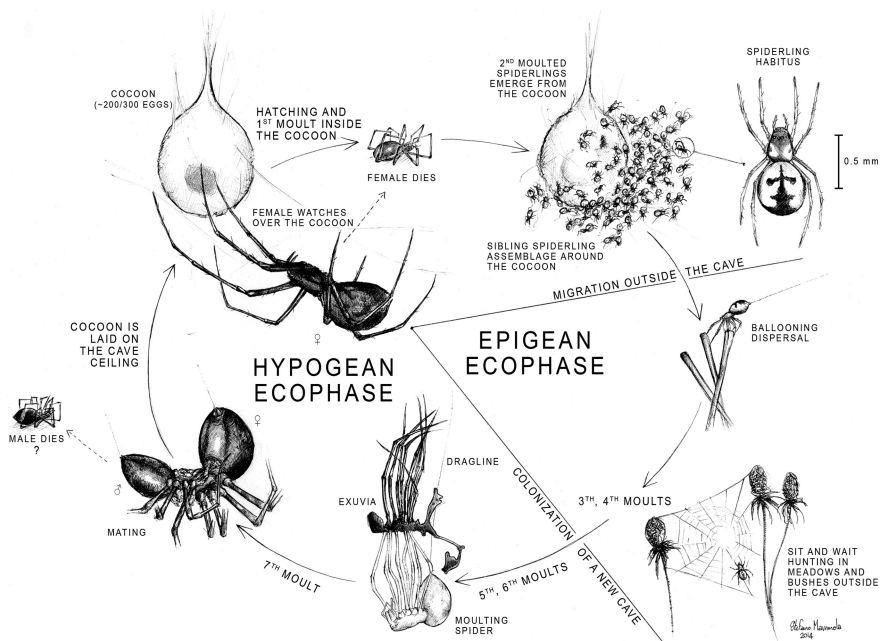
<sup>c</sup>Based on a combination of direct observations of prey in webs and analysis of prey remains dropped from the web and intercepted by nets placed underneath the web in autumn.

of a web. Instead *Meta* spiders would have to display the more ancestral stalking or sit-and-wait behaviour found in web-less spiders (Foelix, 2011). However, there are examples of tetragnathid species not building webs as adults including the aphid specialist *Pachygnatha degeeri* (Madsen et al., 2004; Harwood et al., 2005) and others in the same genus (Alvarez-Padilla & Hormiga, 2011), but nothing is known about their detailed prey capture behaviour. They are though often found wandering on the ground and are frequently captured in pitfall traps in agricultural land (Meek et al., 2002; Alvarez-Padilla & Hormiga, 2011), so presumably actively search for prey.

An alternative explanation to off-web foraging relates to the behavioural adaptations of the web itself as discussed in the previous section. The radii that directly attach to the cave wall could act as trip lines alerting the spider to passing prey that it can then rush out along the radii to attack. This would be similar to the foraging behaviour of some trapdoor spiders including *Nemesia meridionalis* (Family Nemesiidae) and *Idiosoma raphiduca* (Family Idiopodae) that construct signal or trip lines radiating out from the opening of their burrow (Buchli, 1969). When an invertebrate triggers one of the lines by touching it, the ensuing vibrations cause the spider to rush out of its burrow and seize the prey. A similar use of the radii as signal or trip lines may be a more likely explanation for prey capturing in *Meta* spiders than off-web foraging. It explains why no observations of the behaviour exist and partly explains the elimination of frame threads as their higher pre-stress may lower the vibrational transmission strength going along the radii to the hub through leaking, as is found with the higher pre-stressed non-sticky spirals in *Nephila* webs (Wirth & Barth, 1992; Landolfi & Barth, 1996; Mortimer et al., 2016). In addition, this prey capture strategy would also retain many of the normal orb spider prey capture behaviours (i.e. respond and reorient to vibrational information from radii and rush out along the radii towards the prey), although behavioural modifications to allow the spider to attack prey not caught up in a web are still required.

## 5. Life cycle, dispersal and population genetics

The cave orb spiders have a complex and unusual life cycle in that they have a mandatory hypogean and a mandatory epigean phase (Smithers, 2005b; Mammola & Isaia, 2014) (Figure 4). Cocoons are laid relatively close to the cave entrance, in locations experiencing moderate winds, to facilitate the dispersal phase and possibly to wind dry the cocoons to avoid excessive wetting (Mammola & Isaia, 2014; Chiavazzo et al., 2015). The cocoons have a characteristic tear drop shape with a length of about 30 mm and hang from the cave ceiling with a 20 mm long connecting thread (Figure 4). Each cocoon contains about 250 eggs (Eckert & Moritz, 1992). After several months, the spiderlings hatch and moult into the 2nd instar before emerging from the cocoon. The spiderlings look very different from the adults with a contrasting white and a dark pattern on the abdomen (Pennington, 1979) (Figure 5). They show positive phototaxis, but remain in tight clusters in the



**Figure 4.** The life-cycle of *Meta menardi* and *Meta bournetii*. From Mammola & Isaia (2014) with permission from Stefano Mammola.

cave entrance zone probably awaiting optimal epigean environmental conditions before dispersing from the cave (McIndoo, 1910; Smithers, 2005b). *M. menardi* spiderlings then spend 1 to 2 months outside, catching prey in orb webs alongside *M. merianae* and other terrestrial tetragnathids (Pennington, 1979), where they moult once or twice before returning to the cave as subadults. The exact timing of this varies, but in the temperate *M. menardi*, cocoons are usually laid in early summer, hatch in early autumn with the spiderlings leaving the subterranean habitat in early spring (Smithers, 2005b), before returning in the summer. Inside the cave, the subadults undergo a number of further moults before mating. The males probably die relatively soon after mating, although it is not known if they mate once or multiple times with different females. The female matures her eggs and constructs the cocoon, which she guards until her death 2–3 months later (Eckert & Moritz, 1992).

According to some studies, after leaving the subterranean habitat, *M. menardi* spiderlings disperse by ballooning (Smithers, 2005b; Novak et al., 2010; Mammola & Isaia, 2014), although this has not been directly observed.



**Figure 5.** 2nd instar spiderling of *Meta menardi*. Photo by Didier Petot.

However, juveniles of many species of spiders engage in ballooning to disperse away from siblings and to find new suitable habitats (Foelix, 2011). Ballooning involves the juveniles taking up a specialised tip-toe stance and releasing silk into the air using cues from ambient wind speed and atmospheric electric fields (Weyman, 1993; Morley & Robert, 2018). Once the silk thread is long enough, wind-induced drag will lift the spider up into the air and carry it significant distances. Spiders have been reported at an altitude of several kilometres and spiders have been found on islands hundreds of kilometres from the mainland (Bell et al., 2005). Ballooning spiders have no control over the direction or length of their dispersal and might land in unsuitable or lethal habitats (Bell et al., 2005). Ballooning is thus a particularly risky strategy for spiders with very narrow habitat requirements such as cave spiders. Given the scattered and relatively sparse occurrence of caves and other large suitable subterranean habitats, how do juvenile *Meta* spiders find their way back into caves? One solution might be that juveniles do not necessarily have to return to caves. *M. menardi* adults have reportedly been found in smaller crevices in scree, rocks and possibly hollow trees as well as a range of smaller man-made habitats (Penney & Ramsey, 1994; Smithers, 2005b; Fritzen & Kaponen, 2011; Růžička et al., 2013). Although



such smaller and potentially much more numerous micro-habitats may prove suitable for the development of juveniles into adults, it is unlikely they would allow for reproduction as this would require both a male and a female finding and co-inhabiting these small spaces. Thus natural selection is likely to act against juveniles settling in isolated small dark spaces. Another solution might be that juveniles randomly search for suitable habitats through a combination of walking and ballooning. Some researchers have speculated that the diurnal and seasonal air ventilation in larger caves may allow juveniles to detect the presence of caves (De Freitas et al., 1982; Lunghi et al., 2014), although it is difficult to imagine that this airflow would be detectable from any significant distance by small spiders moving on the ground or in vegetation. It remains a (remote) possibility that this air turnover might suck nearby ballooning spiders into caves, which could potentially be investigated with aerial traps near cave entrances. In any case random searching is likely to have a very low chance of success with a resultant abnormally high spiderling mortality and thus require a large production of juveniles. However, *Meta* spiders do not lay cocoons with more eggs than other orb spiders of comparable size. One study found that *M. menardi* cocoons have  $254 \pm 82$  eggs (Eckert & Moritz, 1992), while another reported between 300 and 400 eggs per cocoon (Smithers, 2005b). In comparison, one cocoon of *Argiope bruennichi* had 250 overwintering spiderlings (Bergthaler, 1995) while *Argiope aurantia* cocoons contain between 300 and 1400 eggs (Hieber, 1992). The most likely answer is therefore that only a small percentage of the juveniles disperse by ballooning with the majority remaining in the vicinity of their natal cave and returning to it after their terrestrial phase (possibly with some never leaving the cave in the first place). The evolution of the terrestrial phase could still be explained by the occasional successful ballooning and by the scarcity of suitable small prey items in the cave habitat (Smithers, 2005a, b). The lack of whole-scale ballooning is further supported by the fact that juveniles in webs have only ever been recorded in the immediate vicinity of suitable subterranean habitats (Fritzen & Kaponen, 2011), although this could perhaps be explained by sample bias. It is even possible that *M. bourneti* from Mediterranean karst environments do not balloon and possibly never leave the cave environment, as the very arid environment outside the caves is extremely hostile for the spiderlings (C. Ribera, personal communication).

It is clear that much more research is required into the dispersal phase of *Meta* spiders in order to evaluate any of the hypotheses mentioned above. However, as juveniles are far too small to carry tracking tags, it remains difficult to directly monitor their movements out of and back in to caves. More indirect methods such as population genetics studies might shed some light on the degree of dispersal (e.g., through gene flow; Slatkin, 1987) between spider populations in neighbouring caves and those further afield. Molecular markers have been used in many arthropod species, including spiders, to deduce effective population sizes and/or population structure (Moya et al., 2004; Vandergast et al., 2004; Flagel et al., 2014; Hjalmarsson et al., 2015; Sappington, 2018; Schwentner & Giribet, 2018). However, few studies have examined genetic differentiation among orb-weaving spiders (Lee et al., 2004; Kuntner & Agnarsson, 2011a,b). Troglobiont cave taxa usually occupy narrow distributions and usually exhibit poor dispersal abilities (Trontelj et al., 2009, Juan et al., 2010 and references therein), although the physical characteristics of subterranean habitats may condition the extent of gene flow (Rizzo et al., 2017). Troglophile and troglaxene species, in particular, should in theory exhibit higher levels of gene flow than troglobionts, albeit this is contingent on the ecological requirements and the geographic/climatic characteristics of each species (Caccone, 1985). Allele frequencies and DNA sequence differences among samples collected at different geographic scales are used to estimate gene flow levels to explain the observed patterns. Pairwise  $F_{ST}$  distances are typically used to quantify differentiation between sampled populations (Slatkin, 1987) along with descriptive population parameters such as haplotype ( $h$ ) and nucleotide ( $\pi$ ) diversity values, the latter defined as the average number of pairwise differences between DNA sequences (Nei & Li, 1979). The fast nucleotide substitution rate of mitochondrial DNA sequences and its maternal inheritance have made these markers particularly popular for these estimations, allowing detection of recent dispersal and vicariant events. Microsatellite DNA markers and, more recently, modern DNA sequencing technologies (next-generation sequencing) can provide genome-wide markers able to be used in phylogeography and population studies (Eaton & Ree, 2013). In particular, techniques able to scan a reduced representation of the genome, such as restriction-site-associated DNA sequencing (RADseq) (Miller et al., 2007), genotyping-by-sequencing (Elshire et al., 2011) along with several modifications of the two

original techniques are the most cost-effective approaches (Eaton & Ree, 2013; Andrews et al., 2016).

Different population structure patterns would be expected depending on the dispersal mechanisms. A dispersal predominantly by ballooning should render a homogenous genetic structure, even at considerable geographical distances, so that low  $F_{ST}$ , haplotype and nucleotide diversity values would be expected for both nuclear and mitochondrial markers. In contrast, a certain amount of population structure may be expected (very low differentiation within cave sites but higher between caves from different regions with isolation-by-distance) if most juveniles return to the natal caves or they essentially remain in their own caves for their entire life-cycle. A sex-biased dispersal model with sedentary females and dispersive males is common in orb spiders (Foellmer & Fairbairn, 2005; Kasumovic et al., 2007), but there is no evidence of males dispersing out of caves in *Meta* (Rector, 2009). However, such a behaviour could be detected by molecular ecology methods, as it would give contrasting patterns for mitochondrial and nuclear markers, with the former showing reduced gene flow compared to the latter (Miles et al., 2018).

## 6. Conclusion

The interest in using the subterranean environments and its inhabitants as model systems for studies in ecology and evolutionary biology has been growing in recent years (Culver & Pipan, 2009; Juan et al., 2010; Juan & Emerson, 2010; Trontelj et al., 2012; Pipan & Culver, 2013; Mammola, 2018). This is also true for spiders, where a large number of studies from Central and Southern European subterranean systems have been published (see, for example, Růžička et al., 2013; Manenti et al., 2015; Mammola et al., 2017a; Mammola & Isaia, 2017). As some of the largest and most conspicuous spiders in caves, *Meta* spiders have received considerable attention. However, almost all studies focus on ecology, biodiversity and biogeography, but as we have demonstrated in this review, there is a large untapped potential for using *Meta* as a model organism in behavioural studies as well. Although more quantitative research is needed especially on the non-European *Meta*, we found good evidence for cave orb spiders showing a number of specific behavioural adaptations to subterranean life. These include an unusual life-history, a somewhat modified orb web and potentially a novel prey capture

strategy involving both on- and off-web foraging. To fully explore the described behaviour, a truly interdisciplinary approach is needed that combines field studies in situ in subterranean habitats with molecular biological techniques and carefully controlled laboratory studies.

To determine the degree to which these behavioural adaptations are unique to cave spiders or alternatively are extensions of the natural behavioural flexibility of orb spiders, more comparative studies between the hypogean *Meta* spiders and closely related epigean species. A suitable candidate is *Metellina menzei* with recent studies shedding light on its mating behaviour (Prenter et al., 1994; Bridge et al., 2000), web structure and behavioural flexibility (Tew & Hesselberg, 2017, 2018), and foraging behaviour (Richards and Hesselberg, data not shown). Even more interesting would be comparisons between hypogean and epigean *Meta* spiders with at least one species, *Meta stridulans*, confirmed to be exclusively epigean as it inhabits the laurel forests of Madeira, Portugal, although almost nothing is currently known about its behaviour (Crespo et al., 2014). Obtaining a more detailed understanding of the behaviour and biology of *Meta* spiders may also shed light on the wider ecological relationship and dynamics of subterranean habitats, since they can potentially be considered an indicator species due to their relative abundance and role as top predators in the twilight zone. Although caves are to some extent shielded from the anthropogenic threats facing many terrestrial habitats, the subterranean habitat is intrinsically linked to what is happening aboveground. A recent study, for example, highlights the extinction risks facing cave spiders from global warming, which, with up to decades delay, also results in warmer subterranean temperatures (Mammola et al., 2017b). Similarly, pesticides, heavy metals and organic pollution can enter the subterranean environment through occasional troglodite visitors and underground streams (Wood et al., 2008; Medellín et al., 2017; Modrá et al., 2018). Epigean spiders are known to modify their behaviour and orb web geometry in response to pesticides (Samu & Vollrath, 1992; Benamú et al., 2013; Pasquet et al., 2016) and pesticide and heavy metal pollution can be determined from absorbed residues in spider silk (Samu et al., 1992; Xiao-Li et al., 2006; Tahir et al., 2018). Thus, it is an intriguing possibility that *Meta* webs and silks can be used as bioassays for assessing wider cave pollution levels.

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