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## The distribution of cave twilight-zone spiders depends on microclimatic features and trophic supply

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**Abstract.** Caves are not closed systems. Trophic dynamics in these habitats are driven by resource availability, and species that move between cave and outdoor environments may play a major role in resource availability. Spiders are among the most abundant invertebrates in caves; however, very few studies have tested factors hypothesized to affect the distribution of spiders among caves, and it is not known whether the trophic features of caves play a role in determining the occurrence, abundance, or breeding success of spiders. We assessed the distribution of the cave-dwelling orb-weaver spider *Meta menardi* in Italy, in a Mediterranean and in a Pre-alpine area during summer and winter. We analyzed the relationships between spider distribution and multiple cave features, describing both the abiotic and the biotic environment. Using visual encounter surveys, the detection probability of this species was high, indicating that this technique provides reliable information on spider distribution. In Mediterranean caves, spider presence was more likely in cold and wet caves with abundant dipterans. In Pre-alpine caves, spider presence was more likely in deep caves with abundant dipterans. Dipteran abundance was the variable best explaining spider distribution when pooling all sampled caves. This study shows that adults of *M. menardi* do not occur randomly among caves, but select caves with specific features. Prey availability and abiotic features are major determinants of habitat suitability for cave spiders. The strong relationship between spider distribution and prey availability suggests that the distribution of these spiders might be an indicator of the resources available in the twilight zones of caves.

*Additional key words:* biospeleology, Diptera, foraging, Limonia, Tetragnathidae

Cave habitats are generally characterized by a combination of darkness or low light, relatively stable temperature and humidity, and limited availability of trophic resources (Culver & Pipan 2009). Caves can be divided into three different zones according to the amount of light they receive: the entrance, twilight, and dark zones (Culver & Pipan 2009). The entrance zone holds the actual cave ingress and the immediately surrounding area; this zone is more exposed to climatic variations external to the cave environment than are the other two

zones. The twilight zone is located between the entrance and the dark zone; light intensity is low, and this zone is exposed to slight microclimatic fluctuations according to surface events. The dark zone is the area where no light is detectable. The boundaries of these zones are quite variable among caves, depending on cave morphology and entrance exposure.

In cave studies, it is important to realize that the underground habitat is not a closed system (Romero 2009, 2011), not only for abiotic components like chemicals, air, and water, but also for organic resources (Culver et al. 2004). Even the deepest hypogeous karsts may be influenced by the organic

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matter percolating from the surface, and other surface-related processes (Pipan et al. 2008; Stafford et al. 2008). There are also many organisms that move in and out caves, or that live in underground environments for a part of their life cycles (Romero 2009; Manenti & Ficetola 2013; Lunghi et al. 2014). Recently, Sket (2008) proposed a standardized nomenclature identifying four categories of cave-dwellers. Troglobionts are organisms adapted to cave life; these organisms usually spend all of their life cycle in caves, and cannot survive for a long period of time outside of a cave. The other three categories describe organisms that are not exclusive cave inhabitants: eutroglophiles, subtrogllophiles, and troglloxenes. Eutroglophiles are “essentially epigeous species” that are able to have permanent subterranean populations, and subtrogllophiles are “species inclined to perpetually inhabit a subterranean habitat” that remain associated with the epigeous environment for some biological function (Sket 2008). Troglloxenes are organisms that normally live outside caves, but can occasionally be found in subterranean habitats, where they do not reproduce and are often considered as strays (Vandel 1964; Sket 2008), although recent studies reveal that some troglloxenes exploit caves with special ecological features and interact actively with cave habitats (Lunghi et al. 2014). Cave communities primarily depend on the input of energy and nutrients from the surface, which mostly occurs through two mechanisms: passive transport (mostly by water and air), and the entering of organisms. Microfauna, microflora, guano, larvae, and eggs are the main source of energy and nutrients (Gers 1998; Fenolio et al. 2006). Depending on the transport mechanisms, these nutrients are often patchily distributed in caves and their location constitutes a main driver of the distribution and survival of other cave organisms.

Although very important for the ecology of cave fauna, the trophic resources that cave habitats provide are not easily documented. One way to detect food resources within caves is to focus on organisms that reside within and rely upon resources available in caves (Olsen 2011). Unfortunately, most of these organisms follow the patchy distribution of nutrients and are not abundant. Spiders are a remarkable exception, as they are often abundant in caves (Isaia et al. 2011). Spiders inhabit a wide range of habitats with differential resource availability, and show great diversity in behavioral and feeding ecology. Of the 44,540 species within the order Araneae (true spiders) (Platnick 2014), about 1000 species show typical troglomorphic features, and many more can

be found at cave entrances (subtrogllophiles) (Romero 2009). These top predators of underground environments can reach high abundance (Romero 2009). All spiders are carnivorous, the majority of them being considered as polyphagous (Isaia et al. 2011). Cave spiders prey on almost anything as big as they are, including slugs, worms, flying insects, and even small vertebrates (Romero 2009). Spiders of the twilight zone are among the first predators living within caves, intercepting organisms coming from the surface. Therefore, studying spiders of the twilight zone can provide useful insights on the food subsidy entering caves.

Cave orb-weaver spiders of the genus *Meta* are common members of the twilight-zone community. This genus has a nearly global distribution and includes several closely related species with similar ecological requirements, although many of them are poorly studied. The spider *Meta menardi* (LATREILLE 1804) is widespread in European subterranean systems (Tercafs 1972). Members of the genus *Meta* have complex life histories. Adults of *M. menardi* are photophobic and spend their life in a wide range of subterranean habitats (e.g., caves, underground artificial springs, mines, cellars), building their webs in the cave region extending from cave entrance to the recesses of the twilight zone and to the initial parts of the dark zone (Tercafs 1988; Smithers 2005a; Lunghi et al. 2014). In these habitats, females generally lay their egg cocoons in late summer, providing parental care. Contrary to adults, the spiderlings, which are usually born in late winter (Mammola & Isaia 2014), are positively phototaxic. In early spring spiderlings disperse outside caves, feeding and molting in the epigean habitat until mid-summer (Smithers & Fox Smith 1998). From late spring to early autumn, *M. menardi* are more easily detectable in the sectors close to the cave entrance, while during winter periods they are detectable in deep sectors (Manenti unpubl. data). A similar pattern has been described for its congener *M. ovalis* (GERTSCH 1933): adults in summer are more common around cave entrances, while in winter they are more common in the dark zones, although no direct evidence of a migration of the individuals has been detected (Rector 2009).

*Meta menardi* is considered well-adapted to the epigean/hypogean ecotone (Novak et al. 2010), thanks to its combined methods of hunting both with webs on cave ceilings, and without webs on cave walls (Tercafs 1972; Smithers 2005a). It feeds on a variety of invertebrates, including dipterans and chilopods (Smithers 2005a), and sometimes also on small vertebrates such as young salamanders

(Pastorelli et al. 2006). The distribution of spiders in the genus *Meta* in caves changes between hot and cold seasons (Smithers 2005b; Rector 2009), potentially due to air circulation and organisms entering caves (Culver & Pipan 2009).

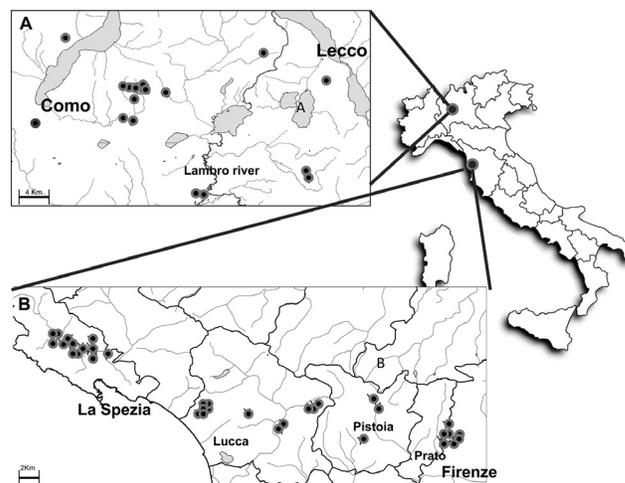
One of the less studied aspects of the life history of *M. menardi* is how spiders locate suitable caves, and whether these spiders occur randomly in underground environments, or whether they select cavities with specific environmental features. For instance, it is possible that deeper caves, which have stronger air circulation (Cigna 1968), may be more detectable by the spiders, but this hypothesis has not been tested yet. Excluding a community-wide study (Lunghi et al. 2014) and a study dealing with individual abundance in the sectors of three caves (Mammola & Isaia 2014), we are not aware of quantitative analyses assessing the relationships between *M. menardi* occurrence, cave features, and the availability of trophic resources across a large number of caves. The aim of this study was to identify the mechanisms behind the pattern of occurrence of twilight-zone spiders in caves. We assessed relationships between the distribution of *M. menardi* and multiple cave features, considering parameters describing both the climatic and morphological features of caves and the abundance of potential prey, to answer three specific questions: (1) do *M. menardi* occur randomly in caves?; (2) do their requirements change in different climatic regions?; and (3) is the occurrence of twilight-zone spiders affected by prey abundance?

## Methods

### Study area and surveys

To describe the relationship between the occurrence of *Meta menardi* and cave trophic resources, we investigated caves of two different climatic regions in different seasons. In December 2011 and January 2012, we investigated 30 caves (both natural and artificial) of the Pre-alpine region in Lombardy, between the districts of Lecco and Como (Fig. 1A). The presence/absence of *M. menardi* was also assessed in these caves between December 2012 and February 2013. During June 2012 we also investigated 53 caves in the Mediterranean region of Italy in the districts of La Spezia (20), Lucca (17), Pistoia (4), Prato (8), and Florence (4) (Fig. 1B).

Adults of *M. menardi* are large, flashy spiders (Roberts 2010), often highly visible in caves among other troglophilic invertebrates (Lunghi et al. 2014). Moreover, individual spiders do not seem to move very much and often stay in the same cave sectors



**Fig. 1.** Pre-alpine (A) and Mediterranean (B) study areas in northern Italy. Black circles indicate studied caves. Due to geographical proximity, some circles are superimposed.

(Rector 2009). Thus, we used visual encounter surveys (Crump & Scott 1994) for a qualitative assessment of the presence/absence of adults of *M. menardi* in caves, by sampling the whole caves or as deeply into the cave as allowed by our equipment. Analyses of detection probability (see below) confirmed that this approach provides reliable estimates of species occurrence. For each cave, we measured parameters related to biotic and abiotic features potentially important for spider occurrence and abundance. In particular, we recorded three variables describing micro-climate and the physical environment: air temperature ( $^{\circ}\text{C}$ ), relative humidity (%), and maximum light intensity (measured in lux). All three variables were measured at 6 m from the cave entrance. We selected this depth because several cave-dwelling organisms attain high abundance at this distance from the entrance, and more generally, the composition of cave communities is strongly related to cave features at this depth (Salvidio et al. 1994; Ficetola et al. 2012; Lunghi et al. 2014). These parameters were measured using a PCE-EM882 hygrometer and luxometer. The minimum light intensity recordable by the light-meter was 0.01 lux. We also recorded the width of the cave at 6 m from the entrance, and the maximum cave depth (m). For very deep caves, we used measurements of cave depth from surveys (Ficetola et al. 2012). At 6 m from the entrance, we also recorded the maximum wall heterogeneity (i.e., cleft richness: Camp & Jensen 2007) by placing a string of 1 m length in the most heterogeneous and fractured part of the sector and measuring the real

distance occurring between the two string extremities using a measuring tape. A shorter distance between the two extremities corresponds to higher wall heterogeneity, as clefts make the string path more curved. We measured heterogeneity on each side of the cave and averaged the two measurements. As a biotic factor, we recorded the number of dipterans of the species *Limonia nubeculosa* MEIGEN 1804 encountered along the same string. When unrolling the string along the wall surface we counted the number of dipterans occurring along the path. Again, we used the average of dipterans counted on the two cave sides. *Limonia nubeculosa* is a flying species very common in cave environments during both winter and summer. Cave dipterans can be important indicator of the resources available underground, as their main sources of food are other insects, carrion, guano, and allochthonous plant debris (Barnes et al. 2009).

### Statistical analyses

A site is surely “occupied” if a member of a species is found at that site, but the lack of detection of a species during all sampling occasions does not necessarily indicate that the species is absent (MacKenzie 2006). Thus, presence/absence observations can lead to an underestimation of occupancy and might influence the results of statistical analyses, increasing the risk of data over-interpretation. We used PRESENCE 5.5 (Hines 2006) to estimate the reliability of the results of our visual encounter surveys. If  $\psi$  is the probability that a site is occupied and  $p[j]$  the probability of detecting the species in the  $j^{\text{th}}$  survey, given that it is present at the site, MacKenzie et al. (2002) use a probabilistic argument to describe the observed detection history for a site over a series of surveys.

We used a multiple season model for the caves observed in winters 2011–2012 and 2012–2013, to assess the probability of detection of *M. menardi*. We also evaluated the misdetection rate of visual encounter surveys, calculated as the percentage difference between the observed occupancy and the occupancy estimated by PRESENCE.

To evaluate the relationships between the distribution of spiders (presence/absence) and environmental variables, we first analyzed the two cave samples (Mediterranean in summer and Pre-alpine in winter) separately. Subsequently, the two datasets were merged in a global analysis. For analyses of the two separate datasets, we used generalized linear models assuming binomial error distributions to assess the relationships between the presence/absence of *M.*

*menardi* and the recorded variables. For the analysis of the combined dataset, we used generalized linear mixed models with binomial error distributions; to account for heterogeneity between the two study areas, sampling area and season were included as random factors in the models.

We used the small-sample-size corrected version of Akaike’s information criterion (AICc) to identify the models best describing spider distributions, and to assess the relative support of models considering different variables. AICc trades-off explanatory power versus number of predictors; parsimonious models explaining more variation have the lowest AICc values. We built models representing all the possible combinations of independent variables, and we considered the model with the lowest AICc as the “best AICc” model. As AICc may select overly complex models, we considered a complex model only if it had an AICc less than the AICc of all of its simpler nested models (Richards et al. 2011). We also calculated AICc weight  $w$ , as a measure of the relative support of each model (Burnham & Anderson 2002). To improve model interpretation, we also assessed the significance of variables composing the best model using a likelihood ratio test (Stephens et al. 2007); we used the proportion of explained deviance,  $D^2$ , to measure the amount of variation explained by the models.

If necessary, environmental variables were transformed prior to analyses using common logarithm (illumination, cave depth, and width) or square-root (dipteran abundance) transformations, to improve normality and reduce skewness. Analyses were performed using the packages *vegan*, *car*, *MuMIn*, and *lme4* in the R 3.0 environment (Oksanen et al. 2012; R Development Core Team 2012).

### Results

We found individuals of *Meta menardi* in 43.7% of the caves surveyed in the Mediterranean area and in 60% of caves in the Pre-alpine area. We found 1–50 individuals per cave (mean 7.8). PRESENCE analysis showed that the detection probability of the species was very high (detection probability=97% per survey), indicating the high reliability of our visual encounter surveys and a limited risk of false negatives in assessing spider occurrence (misdetection rate=0.37%). We did not detect specimens of the congeneric species *M. bourneti* SIMON 1922 in any of the studied caves.

In Mediterranean caves in summer, the occurrence of *M. menardi* was strongly related to both cave microclimatic features and the abundance of

dipterans. Caves hosting *M. menardi* had lower temperature, higher humidity, and higher abundance of dipterans than caves without the spider (Table 1; Fig. 2). The best AICc model, which explained 24% of the observed variation, suggests that spiders are associated with caves having high humidity and abundant dipterans (Table 2). Abundance of dipterans was the variable most likely to be important, as it was included in all tested models with AICc weight > 0.1 (Table 3). Temperature, cave morphological features, and illuminance were included in models with AICc scores slightly higher than the best model (Table 3).

In Pre-alpine caves in winter, those with *M. menardi* had higher humidity and greater abundance of dipterans than unoccupied caves, while temperature was similar (Table 1; Fig. 3) among *M. menardi*-occupied and unoccupied caves. The best AICc model (AICc weight = 0.303) suggests that *M. menardi* occurrence is positively associated with deep caves and a high abundance of dipterans; this model explained 65% of the observed variation. Occurrence of *M. menardi* was positively related to dipteran abundance, while the relationship between spider occurrence and depth was not significant (Table 1). Nonetheless, there was uncertainty in model selection. A model with slightly higher AICc

score (AICc = 21.4) was identical to the model developed for the Mediterranean caves, indicating an association of spiders with caves having high humidity and abundant dipterans. As for the Mediterranean caves, dipteran abundance was included in all tested models with high support (Table 3).

Considering the global sample, with sampling area as random factor, the best model included dipteran abundance, cave depth, and humidity. Spider presence was significantly more likely in deep and humid caves hosting more dipterans (Table 2).

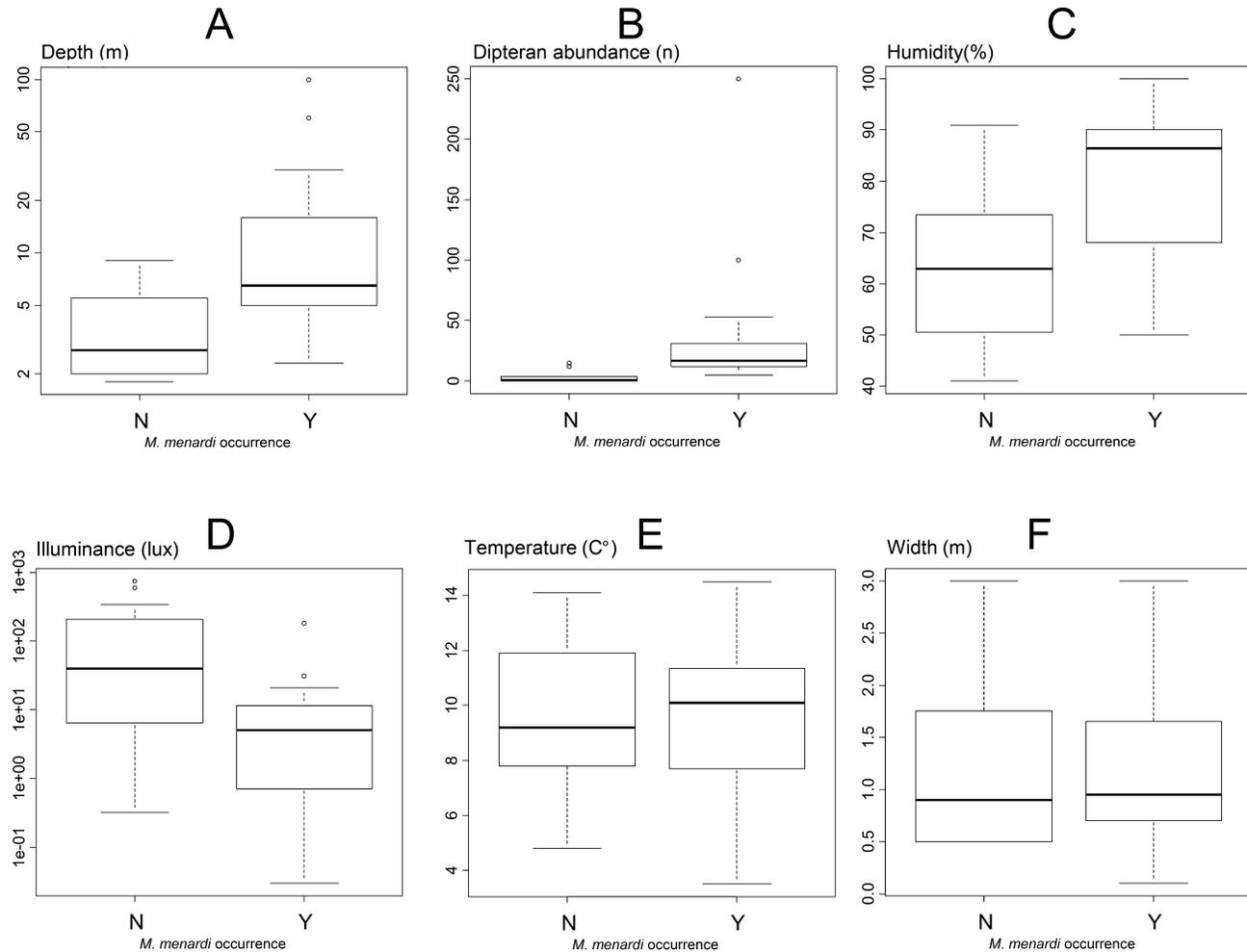
## Discussion

*Meta menardi* has a complex life cycle characterized by a phase in which spiderlings spread outside caves, and a phase some months later in which they search for caves (Mammola & Isaia 2014). Mechanisms allowing cave recognition and choice have not been studied yet, and it is difficult to know whether spiders choose caves randomly, or perform a selection on the basis of environmental cues other than the lack of light. Nonetheless, our results show that adults do not occur randomly among caves, but are associated with sites that have specific features. In particular, both cave climatic features and prey abundance affect the distribution of *M. menardi*. Habitat association models sometimes show low generality, as analyses performed on the same species, but in different areas/periods, may yield non-congruent results (Whittingham et al. 2003, 2007; Ficetola et al. 2009). In our study, distribution patterns of *M. menardi* in distinct areas and periods were consistent. The best model developed for the Mediterranean area included dipterans and humidity, and that model was identical to the second-best model developed for the Pre-alpine area. This suggests that our results are robust, and may show a good generality across the range of this species (Whittingham et al. 2007).

Physiological tolerance of abiotic factors such as humidity and temperature is quite variable in spiders (Bell et al. 2001; Mason et al. 2013). Generally, cave organisms have narrow physiological limits (Romero 2009). In Mediterranean areas humidity at the surface can be particularly low during summer, and this can affect hypogean environments. Wet caves may provide more suitable conditions for the physiological constraints of *M. menardi*. A study in Slovenian cave revealed that members of *M. menardi* prefer sectors with more stable microclimatic conditions, when compared to other troglophilous spiders (Novak et al. 2010). In Pre-alpine caves and considering the whole sample, the species

**Table 1.** Environmental features of caves with and without *Meta menardi*. All parameters except for cave depth were measured 6 m from the cave entrance. Values are means ± standard errors.

Area	Features	With	Without
		<i>M. menardi</i>	<i>M. menardi</i>
Mediterranean	Cave depth (m)	43.3 ± 11.1	57.4 ± 48.1
	Dipteran abundance ( <i>n</i> )	3.8 ± 1.8	0.25 ± 0.1
	Humidity (%)	83.5 ± 1.9	69.9 ± 2.8
	Maximum illuminance (lux)	7.8 ± 4.1	40.5 ± 7.9
	Temperature (°C)	21.8 ± 0.7	25.4 ± 0.7
Pre-alpine	Width (m)	1.7 ± 0.2	2.9 ± 0.4
	Cave depth (m)	17.7 ± 5.8	3.75 ± 0.6
	Dipteran abundance ( <i>n</i> )	36.6 ± 13.6	3.0 ± 1.4
	Humidity (%)	79.1 ± 3.6	63.1 ± 4.2
	Maximum illuminance (lux)	17.8 ± 10.3	160.3 ± 74.7
	Temperature (°C)	9.4 ± 0.7	9.6 ± 0.7
	Width (m)	1.1 ± 0.2	1.1 ± 0.1



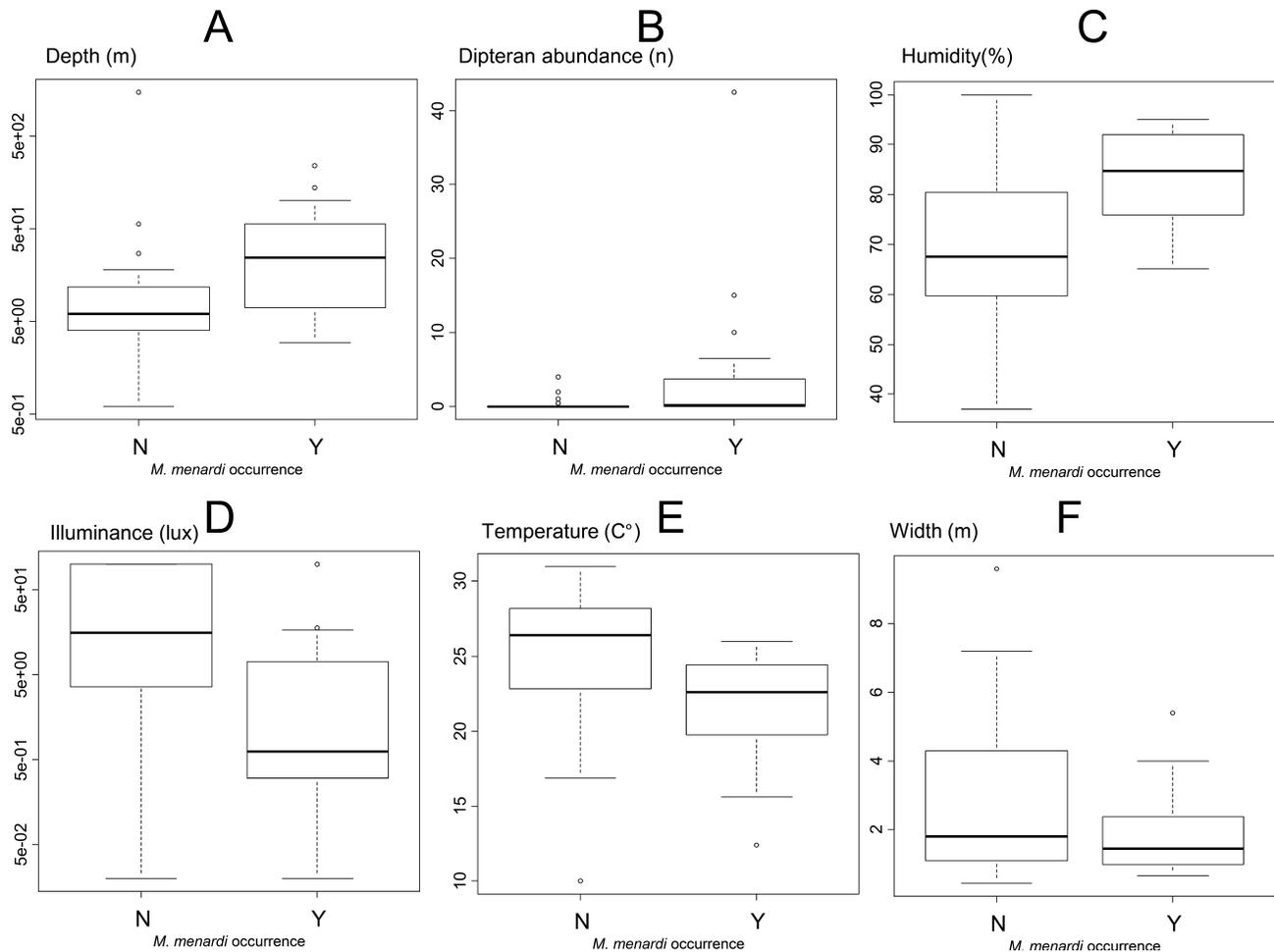
**Fig. 2.** Box-and-whisker plots showing relationships between the measured environmental variables and *Meta menardi* occurrence in Mediterranean caves. N indicates *M. menardi* absence; Y indicates *M. menardi* presence. **A.** Cave maximum depth (log-scale). **B.** Dipteran abundance. **C.** Humidity. **D.** Cave maximum illuminance (log-scale). **E.** Temperature. **F.** Cave width. Cave wall heterogeneity is not shown.

**Table 2.** Generalized linear mixed models describing the relationship between the occurrence of *Meta menardi* and the environmental variables included in the best models, which were selected on the basis of AICc scores.

Independent variable	<i>B</i>	$\chi^2_1$	<i>P</i>
Mediterranean caves			
Dipteran abundance	1.08	5.40	0.02
Humidity	0.06	7.52	<0.01
Pre-alpine caves			
Dipteran abundance	1.17	14.08	<0.001
Cave depth	3.89	2.93	0.09
Pooled sample			
Dipteran abundance	1.60	105.62	<0.0001
Humidity	0.72	8.06	<0.01
Cave depth	0.03	5.702	0.02

was associated with caves having a higher maximum depth, which are more likely to maintain constant environmental features (Culver & Pipan 2009). These caves could also be more easily detectable by juveniles of *M. menardi* in autumn, as during external seasonal changes, deeper caves have stronger air circulation (Cigna 1968) that could favor cave location by the spiders.

The abundance of dipterans was a major predictor of spider occurrence, with consistent effects in both the Mediterranean and the Pre-alpine areas. The importance of dipterans is probably related to their role as prey items. Spiders are common predators in terrestrial ecosystems, and many of them, including the orb-weaving spiders, have been the subject of ecological studies mainly dealing with



**Fig. 3.** Box-and-whisker plots showing relationships between the measured environmental variables and *Meta menardi* occurrence in Pre-alpine caves. N indicates *M. menardi* absence; Y indicates *M. menardi* presence. **A.** Cave maximum depth. **B.** Dipteran abundance. **C.** Humidity. **D.** Cave maximum illuminance. **E.** Temperature. **F.** Cave width. Cave wall heterogeneity is not shown.

foraging ecology (Craig et al. 1996; Brown et al. 2003; Edwards & Edwards 2006; Knutson et al. 2010). Studies dealing with orb-weaver spider ecology have mostly considered epigeal habitats, and have focused on parameters such as web structure, prey availability, and relationships between spider occurrence and environmental characters such as light and temperature. However, the relationship between spider occurrence and prey availability has not been fully explored, especially considering spiders inhabiting the twilight zone. These rely for their survival upon prey entering caves. This zone, situated just beyond the entrance, offers an environment buffered from the variability of the outside environment, while still receiving some light. Despite being connected to the external environments, the darkness of the entrance zone acts as a barrier to many invertebrates (Smithers 2005a), thus in the twilight zone there is a substantial decrease in the amount of

potential prey compared to the surface. *Meta menardi* shows adaptation to cave life in its foraging behavior: in addition to using the orb-weaving foraging strategy for catching flying prey typical of surface dwelling members of its family, members of the species have the capability of capturing terrestrial arthropods, such as millipedes and crickets, along cave walls (Smithers 2005a). This capability may represent a shift between a sit-and-wait strategy toward a more wide-ranging foraging strategy that can be more efficient in the darkness, as shown in other predators in underground environments (Marenti et al. 2013). The combination of hunting both with webs and on cave walls allows *M. menardi* to consume a wide range of prey, including both flying and terrestrial animals (Smithers 2005a).

Interactions among terrestrial invertebrates are known to play a major role in the control of cave community structure (Schneider et al. 2011). As

**Table 3.** Scores (AICc) and weights (w) for the best and other candidate models to explain the occurrence of *Meta menardi* in Mediterranean and Pre-alpine caves. Models with an AICc difference <7 from the best model are shown. We considered a complex model only if its score was less than the scores of all of its simpler nested models (Richards et al. 2011).

Area	Rank	Model	AICc	w
Mediterranean	1	Dipterans, humidity	63.9	0.193
	2	Dipterans, temperature	64.7	0.134
	3	Cave width, cave depth, dipterans	64.9	0.122
	4	Dipterans, illuminance, cave depth	64.9	0.118
	5	Cave width, cave depth, wall heterogeneity	66	0.068
	6	Dipterans, illuminance, cave depth	66.3	0.059
	7	Cave depth, illuminance, wall heterogeneity, temperature	66.3	0.059
	8	Dipterans, illuminance	67	0.042
	9	Dipterans, cave depth	67.3	0.036
	10	Cave depth, wall heterogeneity	67.8	0.027
	11	Wall heterogeneity, humidity	68.4	0.021
	12	Illuminance, wall heterogeneity, temperature	69.1	0.014
	13	Dipterans	69.2	0.013
	14	Wall heterogeneity, temperature	70.4	0.007
Pre-alpine	1	Dipterans, cave depth	21.02	0.303
	2	Dipterans, humidity	21.04	0.302
	3	Dipterans	21.05	0.300

such, the study of features affecting the distribution of top predators (like spiders) in cave systems can yield important insights into the trophic structure of caves. Caves are generally resource-deprived habitats compared to other environments; the occurrence of orb-weaving spiders in caves depends on prey supply. Spiders inhabiting cave twilight zone habitats can serve as indicators of the general trophic content of caves and the magnitude of the supply of autochthonous resources.

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